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PLATE I

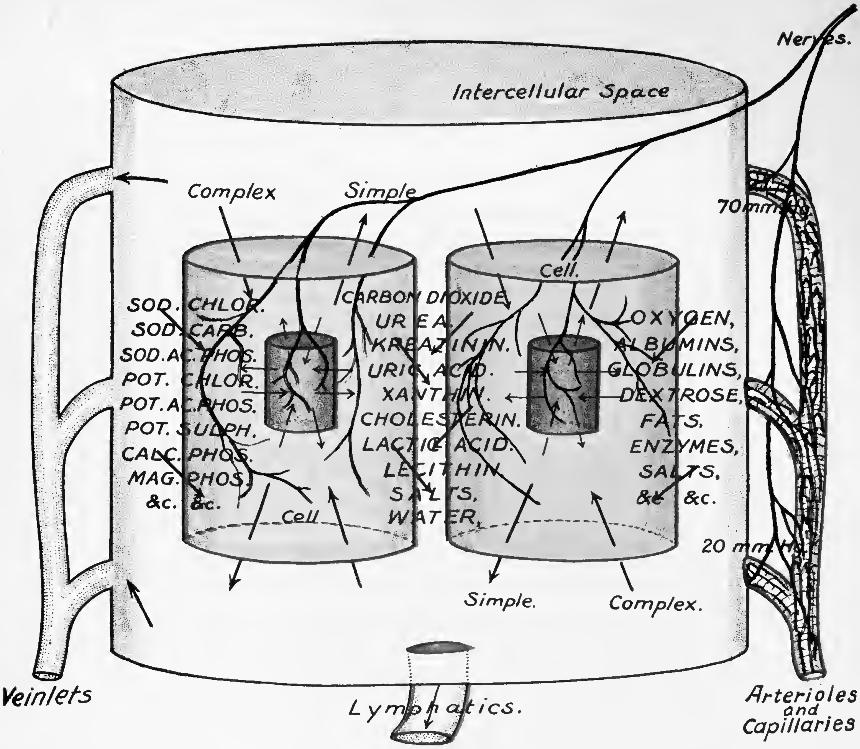

Diagram of Cell-metabolism.

The substances mentioned on the outer edges of the two cells are some of the materials of cell-anabolism, while those whose names are seen between the cells are katabolic products on their outward way into the circulation. The red lines show the locations of osmotic membranes.

A

TEXT-BOOK

OF

HUMAN PHYSIOLOGY

THEORETIC AND PRACTICAL

BY

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ILLUSTRATED WITH 300 ENGRAVINGS AND 9 PLATES

QUAE PROSUNT OMNIBUS

LEA & FEBIGER
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PREFACE.

This book was written primarily for medical and dental practitioners and students. It emphasizes, however, the mechanism of sense-organs, nerves, and muscles as the basis of the individual's efficiency; and it is the first text-book of medical physiology to recognize the more and more insistent demands of the mental process. For both of these reasons it is also especially adapted to the needs of students and teachers of physical education and of psychology.

The great indebtedness of the author to some of his colleagues and students in the preparation of the text and the illustrations is hereby gratefully acknowledged.

G. V. N. D.

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HUMAN PHYSIOLOGY.

CHAPTER I.

PROTOPLASM AND THE CELL.

The tissues of animals, including man, are made up of a substance which is variously termed protoplasm, bioplasm, and sometimes biogen. Protoplasm as found in the bodies of the more highly developed animals is variously changed ("differentiated") to adapt it to many special functions, so that, as may be seen, it is often hard to recognize the typical protoplasm in the many-colored tissues of a man: bone, muscle, epithelium, nerve, etc. The bodies of human beings, then, are made of highly differentiated sorts of protoplasm, each developed for some particular purpose in some special way. The functions of each can be understood, however, only when the fundamental general nature of all protoplasm has been learned. It is for this purpose that a chapter will be devoted to the composition, structure, and general functions of protoplasm.

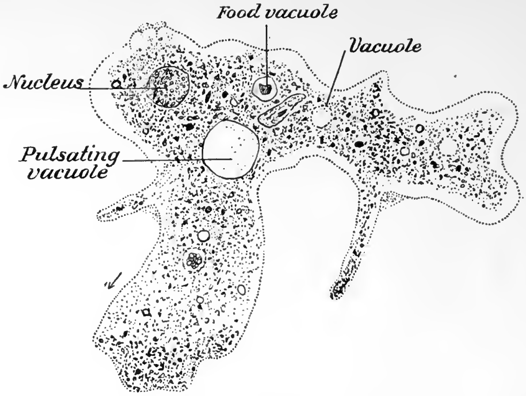
PROTOPLASMIC STRUCTURE.

The General Properties and Nature of Protoplasm.—As seen with the naked eye, or under a low degree of enlargement, undifferentiated protoplasm appears as a nearly transparent, usually colorless, viscid liquid. It is entirely insoluble in water. It is coagulated and killed by many agencies, *e. g.*, by about 50° C. of heat, by alcohol, strong acids, alkalies, and many other chemical substances; it is disorganized by powerful currents of electricity. Its specific gravity is about 1250; that is, protoplasm is about one-quarter heavier than water. Seen under the microscope, it reflects light nearly as actively as does oil. The most important characteristic of protoplasm physically is its colloidal fluidity, the consistence being such that it will flow freely and yet retain its proper shape, as determined by the sort of cell or animal which it composes. No property is more essential to living matter than this, for movement, the prime external attribute of all life, depends, of course, directly on the mobility of protoplasm, on the freedom of the motion of particle on particle.

Protoplasm is dependent on heat for its activity, which is greatest at a temperature of about 30° C. and decreases with lessening temperatures down to the freezing-point of water. When 0° C. is nearly reached, movements apparently cease altogether, although vital molecular movements doubtless continue. Certain forms of life, especially some spores and many kinds of bacteria, endure even the cold of liquid air and that of other still colder solidified gases, reviving uninjured when allowed to become warm again.

Such are some of the more important external characteristics of the physical basis of life, that is, of the quasi-undifferentiated protoplasm which composes many of the infusoria, etc. Differentiated protoplasm, comprising the tissues of animals of more complex structure, has many other colors, specific gravities, consistencies, and physical qualities, many of which are described by the science of histology.

FIG. 1



Ameba proteus. The nucleus, cytoplasm, metaplasm, "endoplasm," "ectoplasm," contractile vacuoles, food-vacuoles, other vacuoles, new and old, are easily made out. Oftentimes, besides, these formless masses of food debris are to be seen colored green, yellow, or red. × 60.

Hypotheses as to the Origin of Life.—About the origin of life, especially on this planet, there has always been much speculation, and we may well mention the four or five leading hypotheses, only one of which, however—the last—tends slowly to some degree of present confirmation: (1) One theory of the source of terrestial life may be read in the first chapter of Genesis. It is obvious that such an allegorical account of the matter, however picturesque, has little scientific interest in the light of evolutionary philosophy, for the account fails to state *how* the creation was performed, which in itself is the problem. (2) The theory of hylozoism, that the world itself is inherently alive and that the inorganic is consequently secondary to the organic, has much philosophical interest, but little present proof or importance as a scientific theory. (3) H. E. Richter, Lord Kelvin, and even the great Helmholtz, discussed the proposition that life is eternal and that its germs came to earth in meteors or in other ways from other planetary specks in the universe. This theory obviously but transfers the biological problem from this planet to some other. (4) For twenty centuries and more the theory of spontaneous generation was usually accepted, and Aristotle, founder of biology, shared the belief. This notion was simply that life originated continually from non-living matter. This was the natural and inevitable conviction in days when there were no microscopes, or none powerful enough to show the germs of animals. Today, without at all denying the possibility, past, present, or future, of the spontaneous origin of life from inorganic matter, we are almost satisfied to believe that every animal, as also every plant, at present originates in one way or another only from more or less similar living parents or parent. In other words, most biologists nowadays suppose that protoplasm (and by the term protoplasm we mean all living matter) springs only from germs and germplasm. (5) In 1866 Ernst Häckel suggested that from analogy it was proper to assume that life, or at least living forms, did begin to develop at some time or other in the earth's evolution from unorganized, nonliving matter. This is the supposition which at present receives the most attention from biologists as the probably true theory. Pflüger accepts this hypothesis, and has materially developed it by suggesting (1875) that in the vast chemical intermingling of the slowly cooling world there was early a union of the elements carbon, hydrogen, oxygen, nitrogen, and sulphur in a way which made possible the phenomena we called life in the new substance so produced. Pflüger, indeed, goes farther in hypothesis, and postulates that the combination characteristic of life in its last analysis is cyanogen (CN), the union of carbon and nitrogen. All the decomposition-products of protoplasm (for example, urea, creatin, guanin, uric acid) hold this cyanogen radicle or group, and this is good evidence that living protoplasm always contains it also, while it is likely that "dead protoplasm" does not. Cyanic acid, CNOH, Pflüger points out, is like protoplasm in many respects: it is fluid and transparent at low temperature, coagulating by heat; both break up into carbon dioxide and ammonia; and both produce urea by dissociation. "The similarity of the two substances is so great that I might describe cyanic acid as a semiliving molecule." Cyanogen and its compounds are formed only at incandescent heat, such as surely obtained on the earth in its early stages of cooling, and others of the components of protoplasm are made under a like condition. Perhaps a further quotation of Pflüger's words will best represent his ideas: "Thus," he says, "nothing is clearer than the possibility of the formation of cyanic compounds when the earth was entirely or partially in a state of incandescence or great heat. We see how extraordinarily all the facts of chemistry point to fire [see Heraclitus!] as the force that has produced the constituents of albumin by synthesis. Hence life was born from fire, and the chief conditions of its appearance are associated with a time when the earth was a glowing ball of fire. When we remember the incalculably long period in which the surface of the earth was cooling, we see that cyanogen, and the compounds that contained cyanogen, and carburetted hydrogen had sufficient time and opportunity to follow out to any extent their great tendency to the trasnposition and formation of polymeria (chains of atoms), and, with the coöperation of oxygen and afterward of water and salts, to evolve into the self-decomposable albumin, which is living matter." In unlimited time unlimited adaptation might, indeed, be rationally postulated. How great the number of millions of years involved in this particular part of evolution no man can accurately estimate. Now, as well as then, Pflüger, Häckel, and Verworn suppose it is cyanogen which introduces into living matter its "energetic internal motion," the essential of life, known in physiology as metabolism. (This process is defined below: see page 35.) There is nothing, however, in such a supposition to disprove the continued generation anew of protoplasm today. As will be seen when we discuss a special form of protoplasm, muscle, the *degree* of heat which may obtain in scattered molecules of a mass of living matter is unlimited. It may be high enough to allow of the production of new protoplasm from these molecules situated here and there in the living matter. The chemi-atomic action, oxidation, may be violent, and yet the relative mass of these molecules, although far too small to effect any considerable amount of living substance, may perhaps be large enough to generate anew a particle of protoplasm endowed with life.

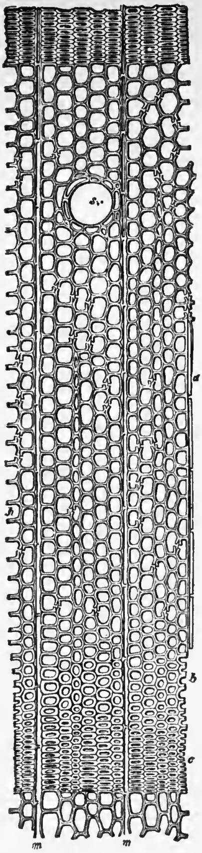
Other biological thinkers have supposed that there is a molecular union of some sort characteristic of the carbohydrate molecule also, since this seems to be present in every form of protoplasm, however small, as will be further seen below.

Such, in brief, are the most prominent theories as to the origin of life on the earth. A combination of the last two hypotheses discussed is certainly not unreasonable from any point of view.

Protoplasm not a Definite Chemical Substance.—It is necessary to have one idea in mind continually in studying the nature of protoplasm—namely, that it is a morphological substance rather than a definite chemical compound. To explain the meaning of this rather important statement, we may well consider what the word protoplasm does not mean. The term is not a physical notion. One does not think of protoplasm as a substance with an unchangeable set of physical properties or qualities, such as, for example, diamond or alcohol. Again, protoplasm is not a definite chemical substance. While it has, of course, some definite chemical composition at any one instant, still that composition is so enormously complex that no chemist can learn it. Its extreme lability or changefulness is a thing entirely characteristic of protoplasm, so much so that we cannot think of it as a chemical substance in the common usage of that term. Protoplasm, again, is not, strictly speaking, an anatomical substance, one with an absolutely definite structure like the femur or the kidney. It is not, finally, a physiological substance, one with a definite set of invariable functions like the eye or the stomachs of cattle. We learn to think of protoplasm as a certain general colloidal sort of living matter with certain characteristics and structure too complex to be easily defined.

Cells.—Animal bodies are made up of tissues. Tissues are divided into organs. Organs are composed of cells, which in turn have biological divisions. At the risk of impinging to some extent on histology, we must look (but briefly) at the parts which make up cells, as an introduction to the study of the composition and the properties of protoplasm. In 1665 (the famous year of the great London plague) Robert Hook, an English naturalist, discovered organic cells in vegetable tissues. He named them cells because the little "chambers" seemed to him, using the rude microscopes of the day (discovered only fifty years before), like hollow and empty cavities. A dozen years later, Malpighi, the Italian anatomist, recognized that these elements were masses of tissue, each with walls of its own, so that, after all, the animal cell is a chamber, although one largely filled with liquid.

Fig. 2



Radial section in the wood of a young spruce, to show the vegetable type of cell and also the circulatory mechanism of a plant. (U. S. Dept. of Agriculture, Farmers' Bulletin, No. 173.)

A living cell in general is made up of at least four or five parts, cytoplasm, nucleoplasm, or nucleus, the centrosome within the attraction sphere, and sometimes, if not always, a limiting membrane. The cytoplasm consists of a homogeneous, semifluid, and somewhat transparent mass (the enchylema), and, variously arranged within this, other perhaps more solid masses or lines or granules of a different nature. The nucleoplasm is composed of a nuclear sap, the enchylema, a linin network, various chromatic masses of nuclein, and a nucleolus. About all these, dividing it from the surrounding cytoplasm, is a nuclear membrane. The centrosome and the attraction-sphere containing it (concerned especially in reproduction) are apparently permanent organs of the cell; they are seen most often and most plainly at the time of the division of the cell. To some observers the centrosome appears as the center of activity of the cell.

That the cells of animals and plants have nuclei was discovered by Fontana in 1781. The nucleus of a cell is usually a rounded mass, but it may have other forms, as in vorticella (c-shaped) and the distributed granular form of certain rhizopods. It usually constitutes but a small part of the entire cell, but in this respect, also, the nucleus varies largely. In some sorts of leukocytes, for example, the nucleus largely fills the cell-wall. In one respect only is the nucleus constant—namely, in its presence in some place and form and size in every living cell. To this there is, for purposes of definition, no exception, for the erythrocytes (see page 263) are not called cells, but corpuscles, because they seem at present to have no nuclei. The *nuclear sap* is indistinguishable in its nature from the similar liquid of the cytoplasm. The *linin network* is an extremely delicate structure that does not stain with the ordinary dyes. C. Schneider maintains that the filaments of linin are continuous through

Fig. 3

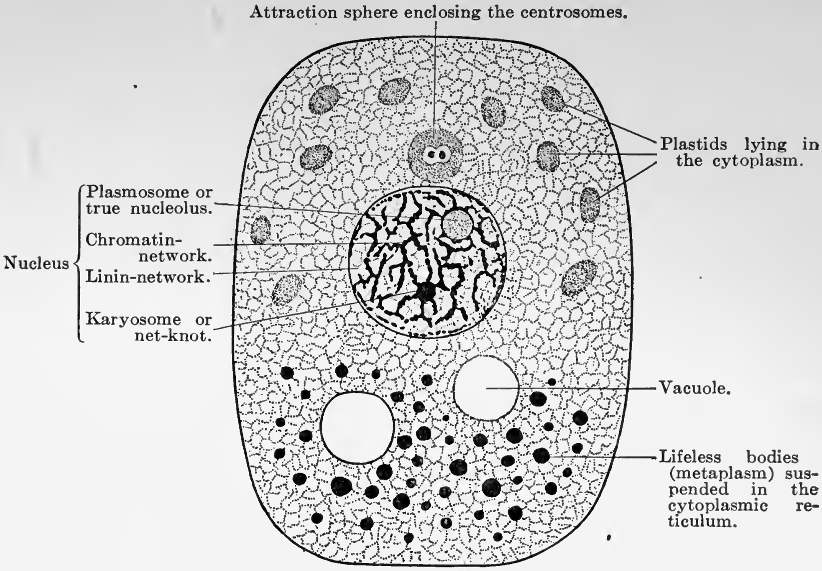
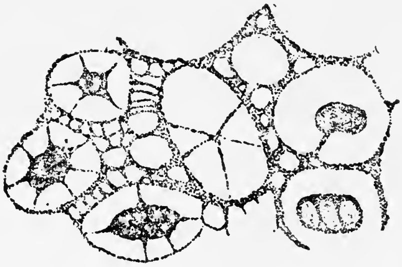


Diagram of a cell. (Wilson.)

Fig. 4



A bit of the nucleus of the infusorian Stylonichia. (Peytoureau.)

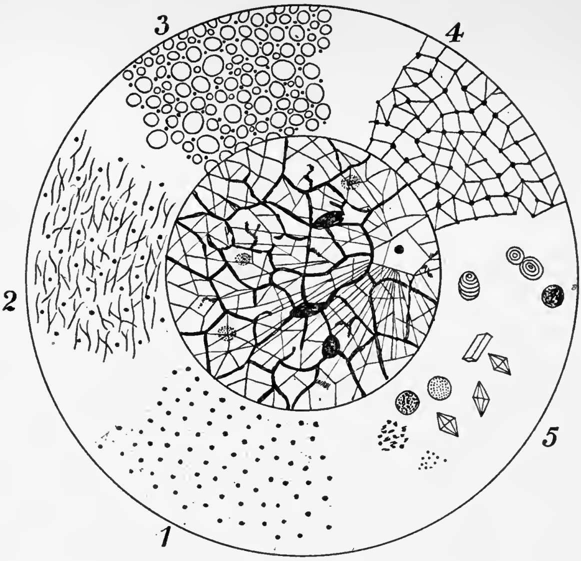
the nuclear membrane with the fibers in the cytoplasm, while Strasburger believes in its structural independence of the cytoplasm. The *masses of chromatin,* so conspicuous in many stained nuclei, are much more substantial than the linin network on which they are distributed. The exact relations of these two nuclear elements, the linin network and the chromatic masses, are still in doubt, but in one way or another they are surely structurally connected. By some competent observers, especially by certain neurologists, the chromatin bodies are considered to be chemically the most essential part of the nucleus. The *nucleolus* may be only one, or there may be many, sometimes bunched together into what seems a solid mass. These are situated in the nuclear sap, and are unconnected and unattached to either the linin network or to the chromatic granules. The *nuclear membrane,* dividing the nucleoplasm from the cytoplasm, is very delicate and perfectly transparent. Through it the important interchanges of the nucleus and the cytoplasm continually take place.

The *cytoplasm* constitutes much the larger mass of the majority of cells. In structure it appears to be much simpler than the nucleoplasm, having only two elements, a reticulum (or something similar in appearance) and a homogeneous transparent fluid pervading and surrounding it. Leydig and Schäfer suppose the more liquid portion to be the essential part, but many authorities so consider the network or reticulum. Some, of late, have maintained that the "reticulum" is artificial. A more reasonable supposition, however, is to recognize in both indispensable ingredients of the vital substance.

The Structure of Protoplasm.—This has been discussed by many biologists, but the results of their work are so various that their theories are of slight importance. The differences in what observers describe as seen under the high powers of the microscope depend more on mental differences than on anything else. This is a good illustration, as modern psychology has pointed out, that what one sees, or thinks he sees, depends to a considerable extent on the contents of his mind. The most likely supposition is that identified with the names of Kölliker, Künstler, and especially of Bütschli. The researches of Bütschli are classical, particularly those in which he has imitated with emulsions the movements of some varieties of protoplasm. On this supposition protoplasm, or at least cytoplasm, consists of a mass of minute spheres filled with transparent liquid, these being crowded together so closely that their liquid walls coalesce and form lines more or less straight and angular. It is only because of the optical conditions that the largest of these intersecting spherules appear to constitute a network. The spherules are freely movable and roll upon each other without breaking the continuity of the protoplasmic element which forms their walls. These exceedingly minute droplets of liquid (called chylema by Bütschli) are, according to this theory, the essential elements of protoplasm. Whether the fine fibrils and the minute granules which sometimes are to be found in the liquid between the droplets are incidental, or have some secondary function, is at present unknown. Such is the hypothesis as to the structure of bioplasm which is probably the most accepted today among biologists and cytologists. None the less, at the present stage in the development of human biological knowledge, the physical structure of protoplasm involves many doubts and mysteries.

Suppositions as to the Molecular Structure of Protoplasm.—There have been published one or two suppositions concerning the molecular or ultravisible structure of protoplasm which are worthy of repetition. They serve to fix the imagination, thus giving it a useful basis to start with, a condition much better than absolute vacuity. In lieu of the certain truth, a reasonable hypothesis is much better than nothing; "mere hypotheses" have often established their high value to science. C. Nägeli is the inventor of the micellar theory of the ultimate structure of protoplasm. It is a supposition merely, but a pertinent one. As atoms combine to form molecules, according to the atomic theory (long accepted, though never proved), so Nägeli imagines that in the case of living matter these molecules unite in groups to form still more complex units, which he names micellæ. Each micella is supposed to be made of hundreds or of thousands of molecules, although even then, large as the vital molecules surely are, they are too small to be seen with any instrument now known, or even with the ultraviolet rays. In protoplasm the micellæ unite to form

Fig. 5



Theories as to the physical structure of protoplasm. In the center is represented the structure of a nucleus: 1, the granular theory; 2, the filament theory; 3, the foam (or vacuole) theory; 4, the reticular theory; 5, some of the crystals, etc., found in bioplasm at various times. (H. K. Richardson.)

regularly arranged groups, in which the individual micellæ may consist of similar or of different chemical substances, and may vary largely in shape and in size. The micellæ may unite in clusters within the group, so that a group may consist of smaller groups, and these smaller groups seem to tend to form chains. These little lines or chains unite in a network, with large or small meshes, as the case may be. In these meshes is the water which gives to protoplasm its important nature as a colloid (on which many of the vital functions depend: see page 25). Nägeli discriminates three conditions in which the water of the colloidal protoplasm may exist in relation to the micellæ: the water of constitution or of crystallization, the water of adhesion, and capillary water. The first is as proper a part of the micellæ as is the water of a crystal; the water of adhesion is that held close to the micellæ by molecular attraction; the capillary water is that lymph filling up the meshes of the network outside the sphere of attraction of the micellæ. Other substances besides water may be firmly held to the micellæ, such as calcium salts, dyes, nitrogenous and carbohydrate substances previously dissolved. Growth is accounted for in this way.

On the other hand, W. B. Hardy has recently published a theory based on the nature and activity of the ions. (Ions are groups of atoms or dissociated parts of molecules which carry charges of electricity and so by their presence make a solution an electrolyte. All circulating animal and vegetal liquids are electrolytes, and these, being alkaline and pervading the tissues, make the latter electrolytes and alkaline also.) Hardy supposes that bioplasm is made up of groups of about ten thousand complex molecules. These groups (termed "particles") are held by electrical equilibrium in suspension in water. Protoplasm is thus a "hydrosol," and a hydrosol of the reversible type. Each particle or group of molecules, Hardy supposes, is surrounded by a double layer or zone of ions charged with electricity, the repulsion between the particles keeping up the normal fluidity of the protoplasm. When the difference of potential is changed the density of the hydrosol is altered in part by means of the chemical reactions between contiguous molecules, these reactions altering the electrical status of the ionic zones surrounding each particle. Thus we have coagulation and decoagulation. This theory also, though unsubstantiated, has no little interest in view of the importance in physiology of the doctrines of the osmosis and solution of salines.

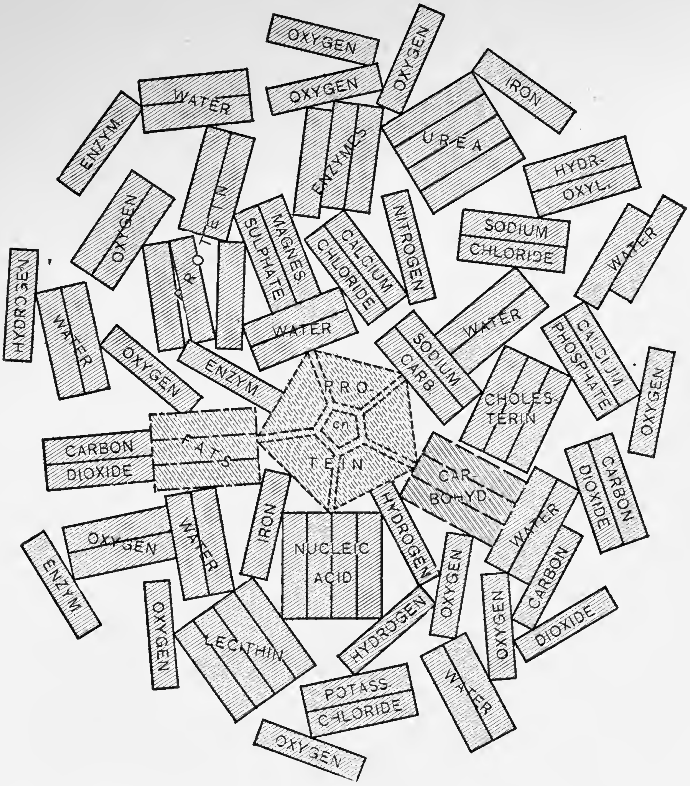
The Chemical Composition of Protoplasm.—If the physical structure and action of protoplasm are involved in many doubts and almost as many hypotheses, certainly its chemical composition is surrounded by more. Not but that we know the chemical "elements" entering into protoplasm, for these persist after its death and may be readily determined; nor yet but that some of the substances in protoplasm have been identified. It is the exact chemical arrangement of these elements and these complex substances, how they are combined and especially how they differ in the living and the dead, that baffle the skill, ingenuity, and deft technique of the biochemists. The last suggested problem is the most important—indeed, "dead protoplasm" is a contradiction in terms, and protoplasm when it has died, whatever that means, is no longer protoplasm but only a mass of matter hastening toward decomposition. We may be almost sure that it is then quite unlike, in its essentials of chemical structure, the composition of the same substance when alive. This problem of the analysis of protoplasm is, indeed, difficult, for when one applies any of the methods and reagents of analysis now known, the mass of protoplasm or biogen is forthwith no longer living but dead, and, therefore, changed in those very respects about which the chemist and the physiologist seek to learn. Here, again, is a field for shrewd hypothesis—a field that has been well cultivated, as almost any physiological chemistry will show. It begins to be obvious that by synthesis, rather than by analysis, the composition of protoplasm will be learned.

ELEMENTS.—Of the chemical "elements," numbering about eighty, there are a dozen which seem to be present without exception in all protoplasm, primal and differentiated. These twelve, a most important list, are *carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, chlorine, sodium, potassium, calcium, magnesium,* and *iron.* Besides these there are others less universally constant in biogen—namely, *silicon, fluorine, iodine, bromine, aluminum, manganese,* and *copper.*

COMPOUNDS.—So far in describing the chemical composition of protoplasm we have glanced mostly at the raw materials out of which protoplasm is evolved. It would be more satisfactory if, using these as building-stones, we could build in description all the details and marvellous structures which we know, from the numberless intricate functions which each particle of protoplasm includes. But this cannot as yet be done, and we must be content if we are told with some degree of certainty the principal features of the protoplasmic structure and the functional relations of these to each other and to the phenomena of life in general. (See chapters on Food and Nutrition.)

The most abundant compound present in primal or undifferentiated protoplasm, and in most of the animal tissues evolved therefrom, is *water.* Life is characterized principally by motion, and free and varied motion depends directly on the lability, the ease of movement, of the material. We know protoplasm as a liquid substance. The red-muscle flesh of the ox seems solid enough to the unaided eye, but carefully examined with a microscope or with reagents every component particle is seen to be a complicated cell filled with a thin fluid, lymph, which is at least 96 per cent. water. Even the bones are 12 or 15 per cent. water, and the tough and solid-looking ligaments connecting them, 77 per cent. Water is the universal solvent in nature, organic as well as inorganic. As Hoppe-Seyler says, "All organisms live in the water," for those which do not live literally under water have nearly all their organs composed of it and surrounded by it, and continue their being and functioning only through its means. "Organisms live not only in water, but in flowing water," the force of which statement will be fully realized later when the rapidity and ubiquity of the blood-lymph circulation is appreciated. Practically the same condition is brought about in undifferentiated protoplasm by its unceasing movements, through the growth and collapse of vacuoles (defined on page 48) by digestive currents through the animal, and in other comparable ways. The importance of water as a food and for other uses in the tissues is readily observed.

Fig. 6.



A protoplasmic particle. This highly diagrammatic illustration is intended to suggest the complexity and the instability of the unitary particle of protoplasm. At the center, perhaps, is protein with cyanogen (CN) as its core. Closely associated are a fat molecule or group and a carbohydrate molecule or group. Nearby are various anabolic materials and katabolic products often as complex as the fats, etc. Some of the groups about are partly disintegrated. Water and oxygen and carbon dioxide and salts are everywhere about and enzymes are not wanting.

The second important class of the constituents of protoplasm is included under the term *proteins*. These are the most abundant constituents of the nucleus and the cytoplasm. In the former they contain phosphorus, and are called nucleins. The cellular proteids, especially in the nucleus, according to the important theory advanced by Lilienfeld, Altman, and others, are all combinations in various proportions of one phosphorus-containing substance, *nucleic acid*, with several proteid-like bodies containing no phosphorus. According to Miescher this nucleic acid is a definite chemical body with the formula $C_{29}H_{49}N_9P_3O_{32}$, the phosphorus constituting as much as 14 per cent. of the substance. In combination with proteids this acid forms nucleins. The richer these nucleins are in nucleic acid the more acid they are, and the richer in phosphorus, the more important apparently is their biological role. For example: the important chromatin of the nuclei is a strongly acid substance rich in phosphorus; plastine, the basis of the substance of the nucleolus (Reinke), has less; linin, composing the linin network of the nucleus, still less; while in the nucleo-albumin of the cytoplasm the proportion of nucleic acid is small, the substance scarcely acid, and the quantity of phosphorus only 1 per cent., or even 0.5 per cent. Lecithin and cholesterin seem to be accessory and are not properly a part of the albuminous molecule (Delage). Biochemists seem to tend toward the supposition that nucleic acid is the basis of the proteid part of protoplasm, and the former is assuredly the predominant portion of the protoplasmic particle.

Chemical analysis yields various formulæ for different sorts of proteid. Bunge gives these four as typical, but calls attention to the divergence in the composition of proteid matter studied under the best of conditions.

Formula of the Proteid from

Hen's eggs	$C_{204}H_{322}N_{52}O_{66}S_2$
Horse's hemoglobin	$C_{680}H_{1098}N_{210}O_{241}S_2$
Dog's hemoglobin	$C_{726}H_{1171}N_{194}O_{214}S_3$
Gourd seed (globulin)	$C_{292}H_{481}N_{90}O_{83}S_2$

From such a list (and it might be extended almost indefinitely) it is obvious that, however much the idea "proteid" may mean, it does not identify any definite substance capable of being represented, as yet at least, by a numerical formula. As already has been noted, this fact may be due in small part to the impossibility of analyzing protein without first changing it materially. It is, however, due in much larger part and more importantly for the theory of biogen to a consideration of a different sort—namely, that *proteid has no constant composition to be numerically indicated.* We are not dealing here solely with mere chemical affinities between chemical elements of certain valencies and invariable reactions, such as those which take place, for example, when sulphuric acid and ethyl alcohol are heated together in a flask, producing ether:

$$(C_2H_5)OH + H_2SO_4 = (C_2H_5)SO_4H + H_2O$$
$$(C_2H_5)SO_4H + C_2H_5OH = (C_2H_5)_2O + H_2SO_4$$

The changes by which protoplasmic proteid is produced and changed and reproduced and changed again in plants and animals are practically based on this sort of interchange. There is present, however, in metabolic reactions a complexity which keeps many of the processes and their products from accurate description. It is this unimagined intricacy of chemical reaction and interaction in biogens which allows the occasional use of the expression "vital force" in its old sense. So numerous are the reagents and so numberless their reactions in certain organs, if not in every one, and in all protoplasm, that it seems almost as if there must be some unifying and controlling force, some principle behind and beneath them characteristic of life. If there is such a principle (and it is doubted by some), it would surely be as much inherent in the proteids of organisms as elsewhere. Perhaps, as Pflüger supposes, it would be there alone, or, as is more likely, in an atomic structure combined of proteids, lecithin, carbohydrates, the inorganic salts of several metals, etc., in one great ever-changing adaptable combination well meriting the title of the vital molecule. In no place, however, are conjectures more out of place than in text-books of science. We must hasten to declare, therefore, that about the actual composition and spatial arrangement of the molecule of proteid we know nothing—and we could certainly not know less about a hypothetical "vital molecule," built on a nucleoproteid as a basis. That air of pervading mystery for which the term "vital force" still stands is likely to continue until methods of chemical analysis new and more delicate by far than those in present use are devised and put in practice on living protoplasm—the enlightening science, not yet born, of real cytochemistry.

The definite chemistry of proteids has not advanced sufficiently to allow of any sort of agreement concerning them save that they contain carbon, hydrogen, oxygen, nitrogen, and sulphur, there being disagreement even as to the universal presence of phosphorus. The different proteids or albumins (we use the terms as synonymous) have not been identified with sufficient accuracy, so that a single classification is in use the world over. Compare in this respect the chemistry of the saccharides or of the glycerides with that of the proteids, and it is obvious how arbitrary any one classification of the latter must be. The following table is a common arrangement of the albuminous compounds as well as of the others which, so far as isolated, combine to make up protoplasm. It is unlikely that all of these are contained in every organism, however low, although functional representatives of them are probably so contained. These substances are technically known as the proximate principles of the animal body. The more promptly and permanently the names, relations, and functions of the substances in this table become familiar to the student, the easier and the more intelligible to him will be the essential composition and functions of animals.

As is seen in the following table, the proteids of the bodies of animals may be assumed to fall under six general classes: albumins, globulins, nucleoproteids, chromoproteids, glucoproteids, and enzymes (unorganized "ferments," which may not after all prove to be proteids). Into the chemical nature and differentiation of these, as into their varieties, it is not our province to go, for that is the domain of another science than physiology—namely, of biochemistry. All that we desire at present is to understand the structure and composition of protoplasm as the basis of vital phenomena.

CONSTITUENTS OF AN ANIMAL BODY.

- Water 65 per cent.
- Solids and gases
  - Organic. .
    - Proteins. .
      - Albumins . . . .
        - Serum albumin.
        - Myoalbumin.
      - Globulins . . . .
        - Myosin.
        - Serum globulin.
        - Myoglobulin.
        - Fibrinogen.
        - Globin.
        - Crystallin.
      - Nucleoproteid . . Nuclein.
      - Chromoproteids .
        - Hemoglobin.
        - Hemocyanin.
        - Hemoerythin.
        - Chlorocruorin.
        - Hematin.
      - Glucoproteids . . Mucin, etc.
    - Enzymes . . . .
      - Ptyalin, Amylopsin: Animal diastase
      - Pepsin.
      - Rennin.
      - Lipase.
      - Trypsin.
      - Erepsin.
      - Kinase.
      - Maltase.
      - Saccharose.
      - Lactase.
      - Emulsin.
      - Myrosin.
      - Oxidases.
      - Desamidase.
      - Tyrosinase.
      - Urease,
      - Thrombin, etc.
    - Albuminoids
      - Collagen: gelatin.
      - Elastin.
      - Keratin.
      - Neurokeratin.
    - Fats . . .
      - Olein.
      - Palmitin.
      - Stearin.
      - Lecithin, etc.
    - Carbohydrates
      - Glycose: dextrose.
      - Saccharose: lactose.
      - Amyloses: dextrin, glycogen.
      - Cholesterin.
      - Animal gum.
  - "Inorganic"
    - NaCl, Na_2CO_3, $NaHCO_3$, NaH_2PO_4, $NaSO_4$,
    - $CaHPO_4$, CaCl, $CaCO_3$, CaP_2O_8, $CaFl_2$,
    - KCl, K_2HPO_4, K_2SO_4, $MgPO_4$, $MgCl_2$,
    - NH_4Cl, SiO_2, HCl, Fe, Mn, O, CO_2,
    - H, N, NH_3, H_2S, CH_4.

The *cytoplasm* of a protoplasmic cell is, according to Delage, especially rich in nucleoproteids, in globulins, in lecithin, in cholesterin, in the chlorides and phosphates of potassium, sodium, calcium, and magnesium, and in iron. The first, the nucleoproteids, containing phosphorus, and relatively small in amount, make up the visible structures (fibrils, granules, etc.) of the cytoplasm; while the globulins, containing no phosphorus, form the amorphous liquid within and around these fibrils or granules. The *nucleoplasm* contains chromatin (which probably is lecithin and cholesterin in combination with a much larger proportion of nuclein), linin (plastine united with an albuminous substance) making up the finer network (see page 22), and a watery substance containing in solution various proteid bodies precipitable by acids and by alcohol. As to the other three classes of albumins, the chromoproteids, glucoproteids, and the enzymes, the first scarcely exist in primal or undifferentiated protoplasm, for they are little needed, respiration taking place without the intermediation of hemoglobin—for instance, one of the chromoproteids. Of the glucoproteids, the chief is mucin. The enzymes are numerous. Their functions are so various and they are so small in amount that little is known about their composition, while to describe their uses would be out of place here. We do not really know that they are proteids. It is sufficient at this point if it becomes clear that every organism probably contains as part of its substance these six classes of proteids, in some degree and proportion. In the present state of confusion concerning the relation of the proteids to organic function, it is a great satisfaction to be aware that the master chemists, such as Fischer, Bunge, Hoppe-Seyler, Hammarsten and Abderhalden, find as much difficulty in forming a correct idea of these matters in their minds as do those who look to their work and to their opinions for information. Here more than almost anywhere else is it plain that physiology is far from being as yet a science anywhere nearly "exact"—so continually does the "simple" prove infinitely complex.

One other general consideration concerning the proteids should be pointed out—namely, the possibility that changes much more extensive than has been supposed may normally take place in the chemical components of a cell. This may be one reason why constancy of analytic result has been found impossible—namely, that there is no "constancy" in the analyzed substances. The vital interactions in protoplasm are so complicated that it is almost impossible to say how far-reaching certain changes may be, how many new substances are formed, how often those which are present are changed back and forth in their qualitative as well as in their quantitative compositions. If proteids are changed to amino-acids and back again to proteids while passing quickly through the thin wall of the intestine it is difficult to estimate the making and the unmaking which a mass of protoplasm might occasion, given sufficient time and space.

The third sort of biogenic components or proximate principles we may consider are the *fats*. The fats as found in the bodies of animals occur in three pure forms, and as lecithin. These three are the triglycerides or ethers of oleic, palmitic, and stearic acids, which are a series of acids derived from monatomic alcohols by the process of oxidation. (Cholesterin is a monatomic alcohol, also, found in every cell: formula, $C_{26}H_{44}O$.) The first is a liquid at ordinary room temperature, while the others are solids, melting at 45° C. and 60° C., respectively. They thus would be more or less solid in the human body at a temperature of about 38° C., were they not held in solution by the olein, which solidifies only at five degrees below the centigrade zero. There are two ways in which these triglycerides and their compounds are parts of animals. They are deposited in masses in bone-marrow, under the skin, and elsewhere in the bodies of many animals. In minute quantity and in forms as yet hardly known they enter, it seems probable, into the composition of the (hypothetical) "vital" particle. Fat has not been found in the nuclei of cells. In the former case, as adipose tissue, the droplets of the triglycerides of palmitic, stearic, and oleic acids largely take the place of the cytoplasm of connective-tissue cells, distending the cell and crowding the nucleus and centrosomes so far to one side that they often are scarcely visible. This might be called the mechanical occurrence of the fats as proximate principles. The other case is more obscure, and, in fact, uncertain. It is, however, probable that fat in some form and amount enters into the composition of all protoplasm, the most likely form being the little-known substance lecithin. This is a very complex body discovered by Gobley and Diaconow, best classed as a fatty material, but made up of glycerin in combination with phosphoric acid, the three fatty acids more or less, and the cholin discovered by Strecker. Lecithin is most abundant in nerve-tissue, but seems to be a constituent of all cells. It is especially conspicuous apart from the nerves, in the blood corpuscles, muscles, bile, and milk. Of the function of lecithin in living matter we know little or nothing, but that it takes part with proteid and carbohydrate in the basal vital phenomena there is little doubt. Some have deemed it an important constituent of cell-walls, supposing that it determines more or less the osmoses in and out of the cell. Its formula is approximately $C_{44}H_{90}NPO_9$, which has interest at least as indicative of the elements entering into its composition.

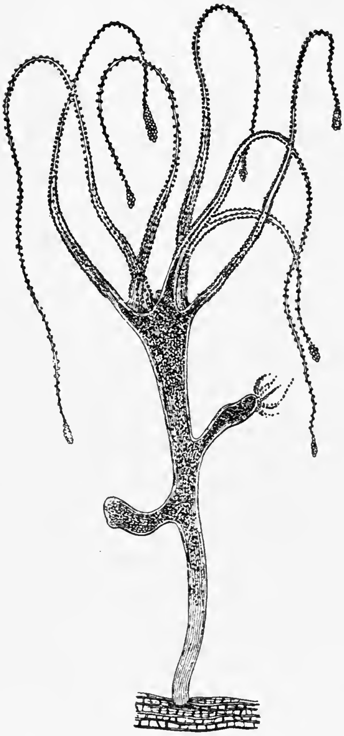
The *carbohydrates* are the fourth class of protoplasmic constituents we need discuss. They all contain hydrogen and oxygen in the proportion in which these elements constitute water (two to one), and carbon in varying amounts. Carbohydrates, like fats, exist in the nuclei of cells, if at all, only in minute amounts—too small to have been found. Our knowledge of the chemistry of the carbohydrates in its completeness is unlike that of the proteids, but their biochemistry is but little less vague than that of the proteids. Three classes of carbohydrates are represented conspicuously in the protoplasm of animals, the glycoses (monosaccharides), the saccharoses (disaccharides), and the amyloses (polysaccharides). The chief glycose of protoplasm is *dextrose,* which exists in animal bodies to the extent of 0.1 per cent., and often much more. Another name for dextrose is grape-sugar, but it must not be confused with dextrin, which is a polysaccharide, a cleavage-product of the hydration of starch. The formula of dextrose is $C_6H_{12}O_6$, and, as its name implies, it rotates the plane of polarized light, as seen in the polarimeter, toward the right. Dextrose is made in animal bodies from the hydrolysis of starch, of the disaccharides, from proteid, and by the hydration of glycogen, the form of starch found in animal protoplasm. Its important use is evidently to furnish motive energy to the organism, through its oxidation in the muscles and other organs. The most abundant saccharose or disaccharide found in animals is *lactose,* $C_{12}H_{22}O_{11}$. This has not been isolated from any tissue of the body save that of the mammary glands during lactation; it has been found in the amniotic fluid, and sometimes in the urine soon after parturition and after weaning. By hydrolysis it is split into dextrose and galactose. The epithelial protoplasm of the mammary glands makes lactose, probably from the dextrose of the blood. The important amylose or polysaccharide of protoplasm is *glycogen,* the animal homologue of vegetable starch. Its formula is $(C_6H_{10}O_5)n$, in which the n is probably six, making the probable formula of glycogen $(C_6H_{10}O_5)_6$, while that of vegetable starch is most likely $(C_6H_{10}O_5)_{20}$. This essential and interesting substance was discovered by Claude Bernard in 1857, and was called glycogen by him because he found it to be the immediate source of the tissue-sugar, dextrose. Glycogen is made from proteids, albuminoids, and carbohydrates in the food of the animal. It probably is a constituent of every living animal cell, as its homologue, starch, is of every vegetable cell. It may be glycogen, or some body very similar, which joins with the proteid and the "inorganic" salts to constitute the huge, labile, and changeful particle characteristic of life.

The last class of compounds which enter regularly into protoplasm are the *inorganic salts.* These are crystalloids, while the others, except water, are generally either fats or colloids known as "hydrosols." Reference to the systematic and summarizing table of proximate principles on page 30 will show just which of the inorganic salts are universal in protoplasm. Of these, the chlorides and phosphates of calcium, sodium, and potassium are doubtless the most important, and perhaps are the only ones universally present in bioplasm, undifferentiated or differentiated. Their source to the animal is obviously the food both of vegetable and animal origin, for all plants and all flesh contain these salts. One of the doubtful and difficult matters to decide in physiology at present concerns the extent of the usefulness of these "inorganic" salts (the name is obviously misleading) in animal protoplasm. Through physical chemistry the new movement in biophysics has developed rapidly of late, and A. P. Mathews, Loeb, Nägeli, and Hardy have opened fields involving ions and the theory of electrolytic dissociation which are likely to define wherein lies the great importance of these inorganic salts. Osmosis, hydrolysis, and coagulation are important processes in animal metabolism, yet they (and possibly muscular contraction and nervous conduction, etc.) may be wholly dependent on these salts for their accomplishment. It is on little differentiated protoplasm that many of these researches have been made, the sort that makes up the infusoria and other unicells and simpler multicells; and the investigations have shown conclusively that any considerable change in the inorganic salt content of these forms is disastrous to the animal. In the "high" forms of life the same fact is obvious in many ways. The most elaborate means are employed by the most highly developed animals to secure the uniformity of the composition of the tissues from time to time, and especially as regards the crystalloids or electrolytes of the circulating, but all-pervading fluids. Thus, whether ions are important in animal metabolism or not (and few today doubt their importance), salines can be proved to be so in many different respects and in every location within the bodies of living animals. Nothing has done more to render superfluous any doctrine of a "vital force" than the development of our knowledge concerning the importance of these simple chlorides, phosphates, carbonates, and sulphates of calcium, magnesium, sodium, and potassium. Just as surely nothing could do more to indicate the extreme complexity of vital reactions than the apparent need of including them as well as proteid and carbohydrate in our list of the components of the huge mass of molecules characterizing life.

PROTOPLASMIC FUNCTION.

The next part of the general physiology of protoplasm is naturally a description of its basal functions. We shall examine at present, then, in the merest outline only, those processes common to all protoplasm and try to learn what conditions and uses underlie its structural nature. We may conveniently, but somewhat arbitrarily, make four classes of the functions of protoplasm: (1) respiration, (2) nutrition, (3) irritability, and (4) reproduction and growth. Within these four types of organic activity may logically be included all the various processes characteristic of the tissues of animals.

Fig. 7

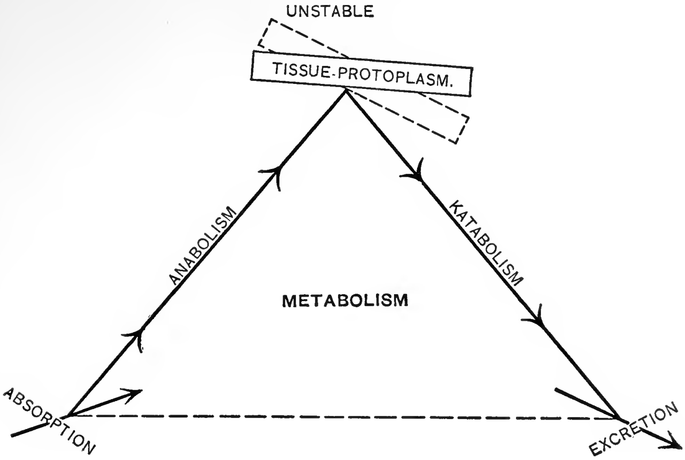


Hydra. A fresh-water species from France, the tentacles fully expanded. On the right side of the trunk is seen a budding daughter-hydra. (Dubois.)

Respiration.—Respiration is a function common to all that lives, to plants as well as to animals. It consists essentially of the taking in of oxygen and the throwing out of the products of the oxidation of the tissues, largely carbon dioxide and water. This function is one of the most fundamental of all vital processes, oxidation being the most universal of all the chemical changes in protoplasm. This union of oxygen with the tissues of animals and of plants furnishes the basis of the metabolism which is their life. Protoplasm respires inevitably and always. In the minute animals, especially those in the water, ameba, for example the change takes place directly between the protoplasm and the environment. In the higher animals, however, some mechanism is necessary for bringing the oxygen to the protoplasmic cells in the interior of the body. In all cases, whether in infusorium or in man, the basis of the process is an attraction of the living matter for oxygen. This attraction is apparently inherent in the protoplasm, and leads to the same general chemical changes which oxidation would lead to outside of an organism. Here as elsewhere it is only because of the unparalleled complexity of the chemical reactions that the process is not explainable in all its details. Of all the many interchanges between protoplasm and its environment, this interchange of oxygen and carbon dioxide is by far the most universal, and as a source of energy the most important.

Nutrition.—The nutrition of a mass of protoplasm is the sum of those chemical changes within it by which it is supplied with the means of liberating energy and of building tissue. These changes are almost infinitely complex; and are summarized under the name metabolism.

Fig. 8



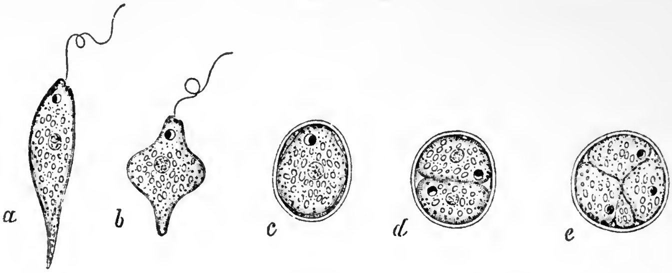
The nutrition triangle. Anabolism versus katabolism.

Metabolism has two phases: One of them, the upbuilding process, is called anabolism, from the Greek *ana*, up. The other phase is katabolism, or the downtearing of organic tissues, from the Greek *kata*, down. These words are of constant and ever-increasing use in physiology, for they indicate the chemism as the basis of the material life of all animals and plants.

Nutrition is divided into several parts—namely, digestion, absorption, assimilation, and excretion. In highly developed animals, and in many of the simpler, there are, besides these four, other nutritional processes, such as prehension, mastication, insalivation, deglutition, circulation, absorptive selection, urination, and defecation. The last two are strictly processes of nutrition only in a broad sense of the term. At the same time they are indispensable parts logically of the different processes of nutrition, and there are therefore treated in that connection. The most fundamental processes of all these are digestion, assimilation, and excretion.

Digestion is the organic function of preparing food for assimilation to the tissues or for the liberation of its energy in the tissues (these being the two uses of food). The important fact concerning this process is that digestion in its essentials is apparently the same in all animals, however simple or complex. Protoplasm is in the most general sense a particular sort of substance in all animals, and the foods of all animals have certain characters in common. The means, therefore, by which the food is changed into protoplasm would be naturally only one general process. Thus we find the digestive juices in a simple mollusk to be practically of the same composition as those of man. When an ameba (see page 49) surrounds a minute particle of food and secretes from its homogeneous substance a vacuole of liquid, this liquid digests the food-particle in all probability quite as a like fluid would digest a like food-particle in the human stomach.

Fig. 9



Euglena viridis, Ehr.: *a* and *b*, the freely active condition, *b* being one phase of its peculiar contortions; *c*, *d*, and *e*, encysted and dividing conditions. (Stein.)

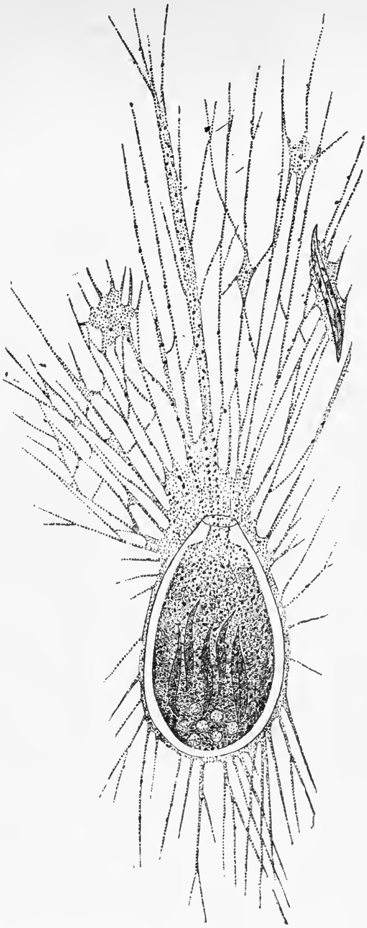
Assimilation is the process by which nutritive materials supplied as food, having been digested, are incorporated into the substance of the animal's protoplasm. Here the new materials may be katabolized and furnish energy (heat, power of movement, electricity, light, etc.), or they may become an addition to the protoplasm of the animal either to promote growth (as in early life) or merely to replace the tissue lost in the inevitable wear and tear of use. It is in this process of assimilation that is found the greatest difficulties in explaining the changes which have to be made before a food can become bioplasm. Little is actually known about the chemical changes by which the digested food materials are elaborated into tissue-protoplasm. The reason for this is obvious when it is considered that the building up is a molecular process, deep in the hidden tissues of the body, and that it immediately stops when analysis or direct observation is made possible. In other words, seemingly paradoxical, the anabolism of protoplasm occurs only in living matter, and the process cannot be observed, because in order to do so the matter must be killed.

Excretion.—Excretion is the third of the essential processes involved in nutrition. It is made necessary by the four circumstances that most food contains an indigestible element; that the parts of an organism select what they wish and reject the rest; that some digestible food escapes digestion, for one reason or another; and, most important of all theoretically, that the katabolism of the tissues produces much material not only lacking in any value to animals, but actually poisonous to them if retained. Thus we see that the removal of waste products is an indispensable process, not only practically but theoretically, for the products of katabolism are largely either poisonous in themselves or the natural food of harmful bacteria which in turn produce toxins that are often of a deadly nature.

Irritability.—Irritability is the term which is used to designate all the functions or vital manifestations of protoplasm not included in nutrition.

Irritability may be defined, perhaps too tersely, as the reactibility of protoplasm to stimulation, a definition indicative of the general meaning of the term. Indeed, as has already been indicated, irritability is not confined to animals or even to organisms, for gunpowder, as Thompson says, acts vigorously to the stimulation of a spark, and similar examples are, of course, numerous. Irritability is then the most general property of protoplasm. If respiration, nutrition, and reproduction are discussed under different heads, it is for convenience and because of their separate importance, rather than because these phenomena are outside the manifestations of irritability. Thus, respiration is a systematized reaction to the stimulation of an excess of carbon dioxide; nutrition, a reaction to a lack of oxygen and of food, and reproduction, a reaction to complex sexual strains and processes.

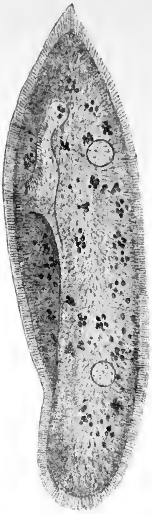
Fig. 10



Grovia oviformis feeding. (Dubois.)

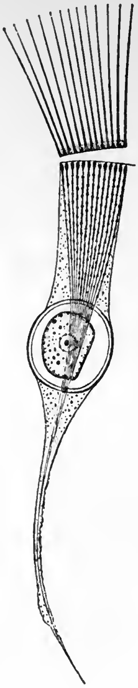
Movement.—Movement is the most conspicuous of the animal reactions to stimulation. If a speck in a distant landscape or in the field of a microscope moves, the presumption is almost instinctive that it is alive. So strong is the instinctive feeling in all animals that squirrels will sometimes run over a motionless figure as over a fallen log. Motion, though unsatisfactory to define either by common sense or by metaphysics, is a quality of protoplasm inherent in the matter of which it is made. Probably movement inheres as characteristic in the structure of the so-called biomolecule. The most important kinds of movement are produced by the active contraction of the protoplasm. These are three in number—namely, streaming, ciliary, and muscular. The first occurs in undifferentiated bioplasm and in the leukocytes, the second in cells which have evolved into a special sort of epithelium, and the last in highly specialized cells adapted to this one function of causing motion. All of these are obviously dependent on the fluidity of the living matter.

Fig. 11



Paramecium caudatum, Ehr. × 250. (Conn.)

Fig. 12



A cell of ciliated epithelium from a mollusk. (Engelmann.)

The streaming movements of protoplasm are of much interest, and in a sense are the type of which the other two are only variations. These movements may be seen in the ameba (Fig. 1), apparently only a speck of gelatinous liquid, comparatively at rest at first, somewhere on the slide of the microscope. Soon a slight bulging occurs at the edge of the cytoplasm, and this gradually increases and becomes a projection, extending outward as much as the former diameter of the cell, or even much farther. If the animal be bent on progression (for example, to escape from too bright a light), the whole body of protoplasm slowly streams, or flows, into this pseudopod, as it is called, the ameba, when this is done, having travelled its own diameter.

Often when one looks at the animal on the slide of a microscope there is no such progression in process, and several pseudopodia may be extended in several directions at the same time, all different in shape and size, save by accident, but all formed by this same peculiar streaming, rolling form of motion characteristic of the living substance. The striking impression which it gives is that the whole mass all through is equally alive and equally active and helpful in the general heaving and flowing movements of the pseudopodia slowly back and forth. Sometimes the movement is aimless, sometimes after food, but it seems almost as if the motion were inherent in the substance, pervading it thoroughly in every part. That is the so-called ameboid movement, difficult to describe, but fascinating and instructive when seen under the microscope. This is the basal, actively vital movement of the almost undifferentiated protoplasm, automatic and, in a sense, inseparable from the nature of the living substance save at special periods when certain animals may become encapsulated and rest. The physical principles on which these movements depend are in doubt, but the principle of surface-tension in liquids is probably the most important of them. Kühne, in 1864, showed that the extension of a pseudopod represents a decrease of the surface-tension at the point where it projects. He supposed this decrease to be caused by the absorption at that spot of some of the surrounding oxygen, the cohesion of the biomolecular atoms being lessened by the admission of these atoms of oxygen into the living molecule. The retraction of the pseudopod is accounted for by supposing that the absorption of the oxygen at that point causes an increase of surface-tension which retracts the pseudopod. Verworn's further supposition is that the mass of molecules thus more or less exhausted of their energy is restored to the vigor necessary for activity by metabolic interchange with the nucleus of the cell. Quincke showed, however, that oil drops in an alkaline liquid have an action similar, under certain conditions, to that of drops of living protoplasm. Bütschli's researches already mentioned are conclusive that some at least of the phenomena of protoplasm may be imitated with inorganic materials.

Fig. 13

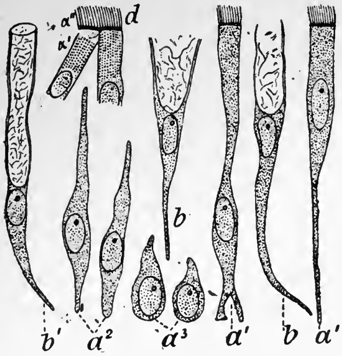
Diagram of a row of cilia to show the rhythmic nature of the contraction. (Verworn.)

The second class of movements in protoplasm due to its active contraction and passive relaxation consists of those called ciliary. A cilium is a thread-like projection from the protoplasm of certain cells, while a flagellum is an enlarged and somewhat elaborated cilium. Cilia appear to be present in nearly all animals above the very lowest, either on the surface of layers of ciliated epithelium (as in the bronchi and Fallopian tubes), or as flagella attached to the spermatazoa, or about such unicellular animals as paramecium. In the former case the function of the cilia is to move along light substances which adhere to them (for example, dust particles in case of the bronchi, ova in the Fallopian tubes). Flagella move the cell of which they are a part through its liquid environment, or else, as in hydra, move masses of liquid within the animal. The cilia are a somewhat differentiated part of the protoplasm proper, and in cases where a cell-wall exists they extend through pores in the latter. The *motion of cilia* consists alternately in a forcible contractile erection and a slower, more or less passive relaxing movement. The position of the cilium in the former case is perpendicular to the general surface of the cell, and in the latter more or less parallel to it. It is largely through the difference in the velocity of these two phases of motion that their motor function is possible. The movement of a surface of the cilia shows a perfect rhythm, best described by the partly schematic figure (Verworn). In many cases the movements of the cilia, and of the flagella especially, are complicated combinations of spiral, funnel-shaped, whip-movements and of others too complex to be indicated. The principle of action is in all cases similar—namely, according to Verworn, that "a contractile side (of a cilium) contracts from the cell-body outward, and thereby the opposite side is extended; in the phase of expansion (or relaxation) the latter by its elasticity brings the cilium back into the position of rest. According to the relative positions of the contractile and the passively extended substances, there results a movement in a plane or a more complicated form." The mechanism by which the rhythm of movement on a surface of ciliated epithelium is kept up with such perfect regularity and adaptation to the needs is not understood. The existence of a nervous coördinating apparatus has not been proved, so that it depends on impulses passing, in manner and route unknown, through the protoplasm itself, and from cell to cell indefinitely. Such subjects as this, the typical movements of the basal protoplasms, which are almost impossible of being understood by mere description, at once illustrate and prove the importance of actual laboratory work in elementary biology as a part of every course in physiology.

The third variety of active contraction-relaxation movement exhibited by protoplasm that may be mentioned is muscular movement. The needs of the evolving animal world rapidly became complex at an early period, and demanded evidently a closer, stronger, and more adaptable means of motion than was possible from any sort of bioplasm then existing. Thus (so runs the teleological theory of evolution) muscle was made to develop, with its complex and extraordinary functions. In general terms this function is always either to draw closer together two parts of an organism or else to diminish the caliber of a tube or of a hollow viscus. Among the lower and simpler animals various transition-stages between epithelium and muscle cells may be found. Sometimes, for example, one sees the upper part of an epithelial cell developed into a structure which is essentially a smooth muscle cell. Within this minute organ very fine contractile fibers are to be found, known as myoids, and it is this elementary thread-like mass of protoplasm, capable of shortening, which seems to be characteristic of all the varied sorts of muscle described in a separate chapter below.

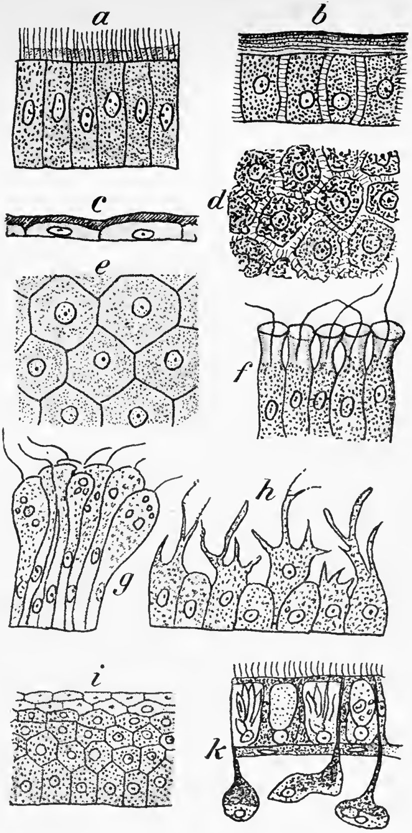
Besides movements due to active contraction and the passive relaxation of protoplasm, there are others of much less frequent occurrence, and therefore of less importance. One of these is caused by changes in the specific gravity, the animal cell being made lighter by the secretion of a bubble of carbon dioxide, and then at another time heavier than water by the expulsion of this bubble of gas. Again, certain forms progress by the continuous secretion of a viscid substance from the end of the body which is in contact with the surface along which it moves.

FIG. 14



Epithelial cells from the human trachea, ciliated and goblet cells: a,^{3} a,^{2} and a^1, various stages in the development of the ciliated cells; b and b^1, goblet cells; d, the upper ends of two developed goblet cells. (Behrens, Kossel, and Schiefferdecker.)

FIG. 15

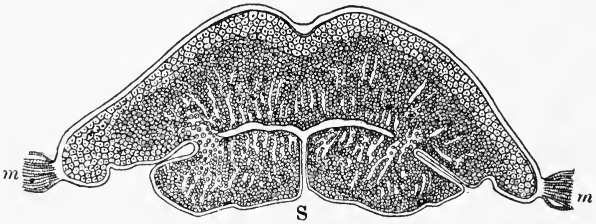


Some different types of epithelial cells: a, ciliated epithelium; b, cylindrical, seen in profile; d, the same seen on the end; f, cells with flagellæ and "collarettes;" g, flagellate cells; h, digestive cells with ameboid projections (as in hydra); i, stratified epithelium; k, external epithelium of a marine planarian with pigment-cells, epithelial cells, and gland-cells beneath. (Dubois.)

SECRETION.—Another manifestation of the irritability of protoplasm is to be seen in the general function of secretion. In some form or other this is a universal activity in protoplasm. Secretion may be said to be the process by which protoplasm produces within itself by its own activity some substance—gaseous, liquid, or solid. It is obvious that in any process a definition as general as this may be both widespread and various in its details. These details will be described in another chapter. Here it is necessary only to note that the process, however various in man, does not differ in its essentials from the process in the lower order of animals.

The Production of Energy.—Still another manifestation of irritability in protoplasm is the production of energy. Energy is that which may give rise to change in the properties of matter or in its location. Work in the gross, mechanical sense, involving visible space, need not, however, be concerned in the biological varieties of expenditure of energy. We have already discussed one variety, the kinetic sort, as employed in some of the movements of protoplasm. Besides the power to move, there are resident in protoplasm the power to produce (2) chemism, (3) heat, (4) electricity, (5) light, while it is an undetermined matter at present whether (6) inhibition is considered another manifestation of energy. These are all expenditures on the part of protoplasm, different modes of reaction to a stimulus.

Fig. 16

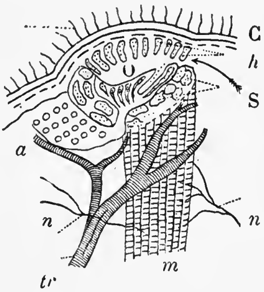


A transverse section in the ventral light-organ of pyrophorus: *m*, *m*, muscles on the edges of the blood-sinus whose opening is at *S*. The influx of blood into the mass of cells, under pressure from the muscles, gives rise to the light. (Dubois.)

Conductivity.—Conductivity is yet another important manifestation of irritability. This is a universal property of living matter, although one reduced to its logical minimum in some of the tissues—enamel, for example. But this is scarcely alive any more than is a clam-shell or the quartz sheath of the caddis-fly lava of our aquaria. At the same time, as we have suggested, even enamel is technically a tissue made of "protoplasm." The power which protoplasm has of conducting through its substance any adequate stimulus may be seen practically in any of the common unicells—for example, paramecian, ameba, or even in plants, such as the leaf of the famous plant Dionea (Venus' flytrap). If any part of one of these animals or leaves is touched, it is obvious that the whole organism is immediately affected—in other words, the stimulus is conducted throughout the protoplasm. This is about all that can be said on this subject in the way of explanation, for the means of communication through the protoplasm from molecule to molecule is absolutely unknown. So important, however, is this function of conveyance of a stimulus from one part of an animal to another that a special tissue, nerve, has evolved so that it may be done more promptly and more accurately. The nervous system, then, aside from the important supposed relation to spontaneity and consciousness, is only an immensely complicated series of protoplasmic paths through the various parts, large and small, of the body, and connecting by means of the sense organs the individual animal with its environment. This main function of conduction is discussed in the chapter on the Nervous System.

Taxes.—This term is used to indicate several sorts of reactions to the stimulation of protoplasm. It has largely replaced the older word tropism. The term is from the Greek *taxeo,* to arrange, and in physiology indicates a tendency which various animals and plants exhibit of arranging or coördinating themselves in various ways to different sorts of stimuli or conditions in their environments. Especially does the word taxis indicate the attraction toward the places where these conditions or stimuli are, or away from them. The most important of the taxes, only recently investigated, and then with not very important results, are chemotaxis, attraction toward certain substances; thermotaxis, toward heat; phototaxis, toward light; electrotaxis, toward electricity; and barotaxis, toward pressure, including thigmotaxis, rheotaxis, and geotaxis. Though they are interesting, and possibly of some importance in explaining the behavior of animals, space does not allow a further discussion of these reactions in this place.

Fig. 17



A diagrammatic section through the photogenic organ of a lightning-bug (Pyrophorus noctilucus): *C*, cuticle; *h*, hypodermis; *O*, luminous organ; *S*, blood-sinus of the organ; *a*, adipose body; *tr*, tracheæ; *m*, muscles; *n*, nerves. (Dubois.)

Consciousness has such a close relation to the living substance that it may be mentioned here, for convenience, without in any sense giving it classification as a manifestation of the irritability of protoplasm. Whatever consciousness or mental activity may be (and it cannot be defined except as experience), it has a relation to protoplasm such that, so far as we actually *know,* it does not exist apart from bioplasm. No one at present considers it a function of protoplasm or a product of protoplasmic life. Thought is no longer said to be "the secretion of the brain, as urine is of the kidney," but it is in some quite unknown way related to the irritability of protoplasm, and is at once master and servant of the living substance of animals and an accompaniment of its life. The chief usefulness of consciousness (if for the sake of system we must find a biological "function" for it) is probably resident chiefly in memory. It is the means by which experiences are acquired for preservation in memory to be of further use to the individual. (See Chapter XII.)

Reproduction and Growth.—The fourth and last of the classes of functions of protoplasm deals with the means by which the races of animals are continued, as the three other classes discuss some of the protoplasmic functions as means of continuance of the individual organism. Chapter XIII is devoted to the physiology of mammalian and especially of human reproduction. In this connection, therefore, we shall confine ourselves to the underlying principles of cell-division and of cell-growth, and of what might almost be called protoplasmic reproduction.

Fig. 18

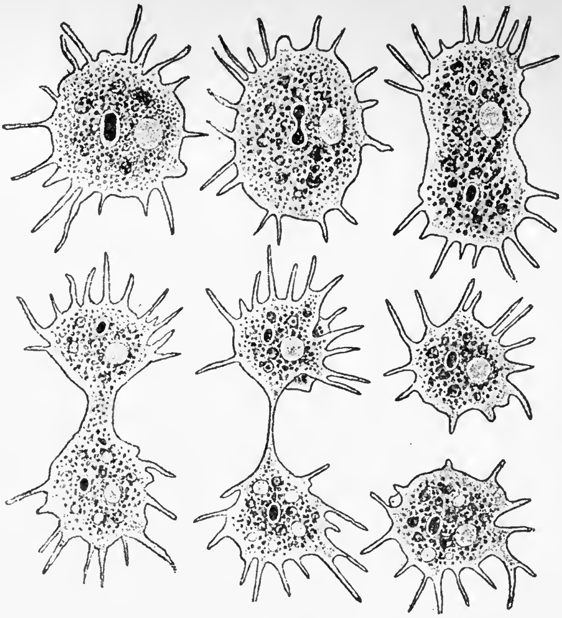


Diagram of amitotic cell-division, showing an Ameba polypodia becoming two. (F. E. Schulze.)

Amitosis.—Amitosis is direct cell-division or direct nuclear division. This mode of division has been seen to occur in leukocytes and in epithelial cells, especially those of arthropods. It occurs also in the protista, and in other forms. The process of amitosis is, so far as the microscope shows, very simple; none of the complex, minute organs (spindles, radiations, asters, chromosomes, etc.), soon to be described, are apparently employed in this process. In amitosis the nucleus simply flows apart, and this is followed by a similar active division of the cytoplasm, the whole cell thus being made two. First, the nucleus elongates, and then by active protoplasmic streaming one-half separates gradually from the other in the cytoplasm. Meanwhile, the latter has begun the same process and slowly becomes constricted between the separated nuclei. This constriction becomes gradually more slender and lengthened, until perhaps only a thread connects the two new daughter-cells. Finally, this is cut quite through and the process is complete, requiring in ameba, where it may in rare instances be observed, about three hours. Sometimes the course of the division is interrupted and much disturbed, as it were, by confusion or disagreement among different parts of the cytoplasm, and there may be long delays seemingly at any stage of the process, but especially during its later stages. From this or some other cause, the nucleus often breaks up into many daughter-nuclei, as, for example, in the giant-cells, which may break up then into several new cells containing the nuclei near their peripheries (Arnold).

MITOSIS.—Mitosis, karyokinesis, indirect nuclear or cell-division, or nuclear segmentation, is the complicated process by which the great multitude of cells divide, for amitosis is decidedly the exception in the animal world. The simple purpose of this marvellously complex process is to divide equally the essential parts of the nucleus and of the cytoplasm of the mother-cell among the two daughter-cells. As will be recalled (see page 23), a typical cell-nucleus has, besides its linin reticulum and nuclear sap or enchylema, numerous masses of nuclein irregular in shape (but usually elongated), of chromatin termed *chromosomes*, and one or more nucleoli. The cytoplasm, besides its foam-like probable reticulum and enchylema, has in it (at least during its periods of reproductive activity and perhaps at all times) a small body called the attraction-sphere, at the centre of which is a minute round body known as the *centrosome*. Yatsu has shown this to be an organ independent structurally of both nucleus and cytoplasm, although derived from the latter, a third constituent of the cell; and it is thus that we have classed it above. Its exact status is still in doubt.

The process of mitosis, remarkably constant in the thousands of animal species and cells, may be seen graphically represented in the diagrammatic Fig. 19, taken from Flemming. The *attraction-sphere* is, in the resting cell not about to divide, either in the nucleus or close to the nucleus in the cytoplasm, and inconspicuous probably outside and at one end of the latter. When the process of mitosis is about to begin the *centrosomes* separate within the attraction-sphere and soon divide the latter into two parts, connected by fibrils. Each becomes the center of numerous rays which extend outward in all directions, conspicuously through the cytoplasm, the whole of each being called an *aster*. Meanwhile the masses of chromatin of the nucleus have arranged themselves into lines or threads (*A*) (hence the name mitosis, given by Flemming), or perhaps into one thread, coiled on itself within the nucleus. This soon breaks up into particles called *chromosomes*. The number of these chromosomes is constant for one animal species—twenty-four in the mouse, salamander, and trout; sixteen in the guinea-pig, ox, and man; sometimes they are only four, or even two. O. Hertwig is of the opinion that the nucleolus or nucleoli divide into parts and are distributed about the chromatin masses. By the time that the chromatin thread (*skein*) is divided into chromosomes, these latter have arranged themselves around the nucleus in a broken ring (*B*), and the centrosomes, still connected by the conspicuous rays of the asters, are on opposite sides of the nucleus. The nuclear reticulum, arranged in parallel lines, helps to connect them through the mass of the now fast dividing nucleus. This whole structure, the two asters and the nucleus, called the *diaster;* the connecting fibrils (possibly contractile), the *nuclear spindle.* So far no actual division of any structure has taken place, the process up to this point consisting only of the separation and proper preliminary arrangement of structures, either dual or numerous. These processes together, then, make up the "prophases" of mitosis

Fig. 19

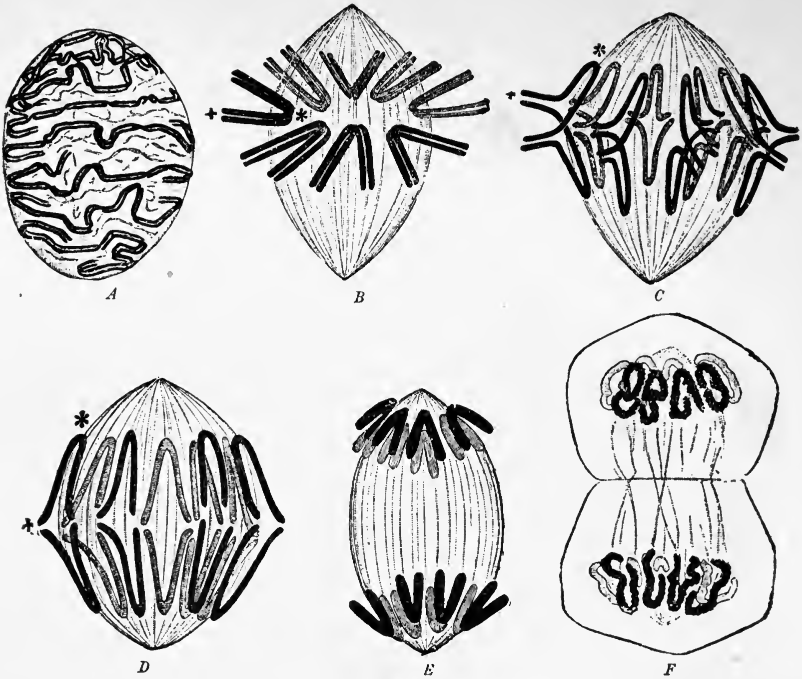


Diagram of mitotic cell-division. (Flemming.

The next step, the most difficult to explain (although not to describe) in the whole marvellous mitotic process, consists in the longitudinal halving of each of the chromosomes, each lateral half of each particle of chromatin "thread" then beginning to separate from its former half (*C*). It gradually makes its way outward (*D*) through what was formerly the mother-nucleus, now called the *nuclear spindle,* to its centrosome and aster, one of which still remains on each side. This separation (*E*) of the chromosomes into lateral halves is called the "metaphase" and the succeeding events the "anaphases" of mitosis. As the new chromatin-masses approach the centrosomes on either side a constriction (*F*) is taking place around the periphery of the cytoplasm in a plane half-way between the asters, and this constriction, deepening, finally cuts the mother-cell completely into two parts, the new daughter-cells. The chromatin masses, thickening, now gradually arrange themselves apparently on the reticulum about the new attraction spheres, the rays disappear, a nuclear membrane forms, the periphery of the cytoplasm rounds itself, and the two new cells are become miniature replicas of their mother-cell.

HEREDITY AND ADAPTATION.—Heredity and adaptation are two opposed phases of the phylogenic or continued racial life of animals. *Heredity* may be defined as that protoplasmic principle or faculty by which cells tend to be like the parent-cells from which they spring. *Adaptation* is the tendency of new protoplasm to adjust itself structurally and functionally to the conditions of its environment. It is only by the constant interaction of these two tendencies of all protoplasm that life can continue unendingly. If only heredity determined the characters of offspring, life would soon be overcome by an ever-changing physical environment.

On the other hand, were protoplasm too plastic, living forms would lack that constancy of characteristics which marks each of them off from the rest of the world. These two indispensable and interdependent tendencies are, therefore, functions inherent in all protoplasm. Like the other dispositions already considered, they are immediately dependent (1) on the *fluidity,* (2) on the atomic or molecular *complexity,* and (3) on the extreme *instability* of the living substance. These qualities of protoplasm have already been described and explained. They are, in fact, probably only different views or statements of the leading property of biogen—its extreme *plasticity.* By this property protoplasm is capable of receiving on the one hand all the qualities of its parent protoplasm, and on the other hand of accepting an impression from every surrounding influence, great or small.

It is not difficult to imagine in regard to heredity that which has no actual biological existence, and yet herein is apparently one of the greatest mysteries of all of Nature's secrets. At the present time we cannot well imagine how a body of jelly-like matter so minute as to be invisible to the naked eye should be the sole means of transmitting from a man to his son not only, sometimes, the whole physical constitution of that man, but his mental and moral nature as well, habits of speech, tendencies appearing perhaps scores of years after the heredity-conveying speck of protoplasm from the parent is gone. The whole matter is enormously complex and inwrought with speculation and skepticism.

An Example of Relatively Simple Protoplasm: Ameba.—Perhaps the best way to give the reader an idea of the appearance and functions of relatively undifferentiated or primal protoplasm is to describe one of the more simple animals, in fact, the most simple animal known; unless we suppose with Häckel that there lives an animal still more simple in that it lacks a nucleus—namely, the monera.

The ameba is generally taken as the most typical and the most simple of animal cells. It has for us additional value for the reason that it is endowed with more functions than many sorts of tissue-cells, because it is an independent and separate animal. It is not a part of a tissue with only one or two processes to accomplish—*e. g.*, an epithelial cell in a mammal. There are several species of the genus ameba, but the one most typical, largest, and best adapted for description is ameba proteus, classed zoölogically as a protozoan rhizopod. These animals are often large enough to be seen by the unaided eye, but more usually are only a small fraction of a millimeter in diameter, and therefore require much magnification for study. When enlarged about three hundred diameters there can be seen a mass, irregular in shape, of a substance which looks like granular jelly in the bottom of the water drop on the slide of the microscope. Around the edges of the mass the jelly-like protoplasm is freer of granules than it is within. This more or less transparent temporary edge of the animal is called the ectoplasm, and the inner and more granular portion the endoplasm, distinctions which are of slight significance. Near the centre of the animal is a small spherical body, often darker than the surrounding protoplasm, which may be encircled by a more or less transparent ring. This rounded mass is the nucleoplasm or *nucleus*. The rest of the cell is called the *cytoplasm*. Within the nucleus there is, although exceeding small, a still darker dot, which is the *nucleolus*, of unknown significance. About the nucleus, or here and there through the cytoplasm generally, are seen, sometimes prominently, what appear like bubbles, but which are spaces filled with clear liquid, but not a gas. Most of these *vacuoles*, as they are mistakenly called, are constant and unchangeable in size, and are termed *permanent vacuoles*. One, larger than the rest ordinarily, may be seen to grow slowly and to disappear suddenly (by bursting) when it has reached a certain size; this is the *contractile vacuole*. Close examination shows the whole nucleus to be pervaded with small masses of a more opaque substance called *chromatin*, while with a very high magnification, the cytoplasm, apparently homogeneous with a low power, shows a minute reticular structure, as if made up of a mass of liquid foam. The status of the distinct *granules* is not yet clear. Despite their name, metaplasm, they probably are a part of the protoplasm. These, then, are the "organs" of ameba in its normal condition. Sometimes other objects within its mass may be noted. For example, there may be seen particles of food (a vegetable cell or a diatom) or a piece of the waste left from the digestion of such a meal. These particles, while in process of digestion, may be surrounded by visible vacuoles, in which case the latter are filled with digestive juices. The finer structure and significance of these various organs will be described later, our endeavor now being to gain an understanding of how protoplasm appears and what animals made of it do. (See Fig. 1.)

It would be difficult to distinguish an ameba from the multifarious debris of the pool-bottom in which it is to be found were it not that observation suggests that the granular ameboid mass (unlike the others) is moving, without apparently being disturbed from the outside. Amebæ are continually shifting, in fact, with a sort of slow motion characteristic of themselves. If the animal be in water at a temperature lower than 15° C., the movement may not be perceptible except when one repeatedly draws the outlines of the cell at intervals of several minutes and compares the drawings. When this is done, it is at once obvious that the creature changes in shape if not in position. This spontaneous movement of this minute drop of protoplasm is a wondrous thing, but to its wonder we are accustomed, and call it life. The pseudopod ("false foot"), as it is called, may be on a smaller scale and extend only a little way, almost as a point of protoplasm, soon withdrawing again or else remaining, while others, larger or smaller, push out in various places and directions. Several of these may be extending themselves at one time, some large, some small, some dull, some pointed, all of different shapes, some upward, toward the objective point of the microscope so as to be little noticed, the size or bulk of the cell meanwhile not changing, but only its shape. It is evident that a large pseudopod is made always at the expense of some other part of the creature. When the flowing occurs in one direction continually the animal advances, and in this way, hither and thither, it creeps, especially out of open spaces, very slowly and indirectly, over the bottom of the drop in which it lies. (See Movement, page 38.)

The fluidity of the ameba is its most conspicuous property; without it all these curious "ameboid movements" would be impossible. This is true of almost all protoplasm. The mode of this motion in detail is characteristic. With a high-power microscope it may be readily seen that it consists of a curious combination of rolling, streaming, and pushing particles, the movement of the different parts of the bioplasm being made clear by the metaplasmic granules which are so conspicuous in ameba. This liquid motion is technically known as *protoplasmic streaming*. When stimulated, as by a jarring, the movement ceases and the animal, contracting its pseudopodia, takes a shape more closely approaching a sphere than it had before. This shape, however, if the animal be left unstimulated, soon vanishes in the ceaseless pseudopod-making and unmaking just described.

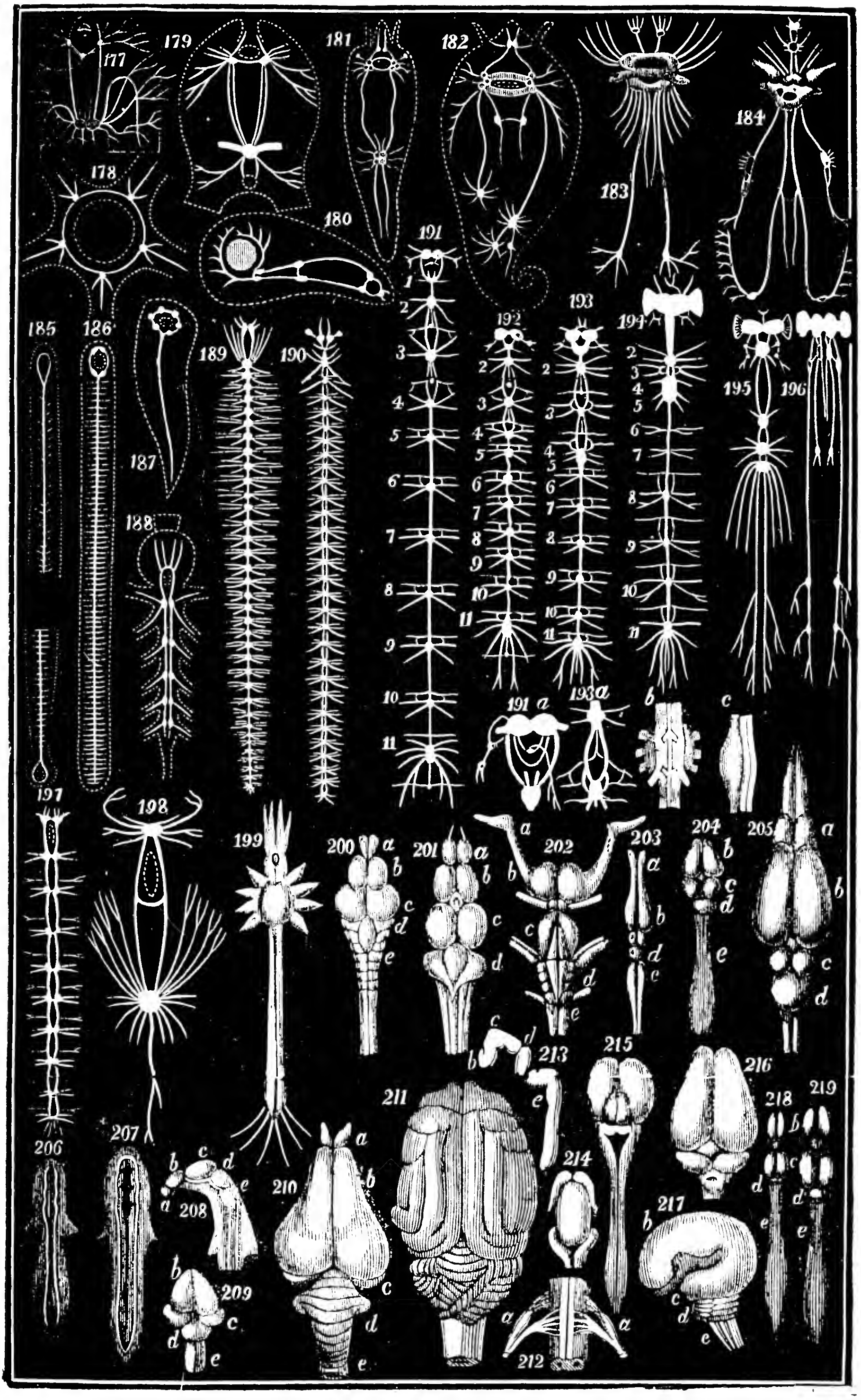
Patience in observation would show how the ameba gets its food and how it swallows and digests it. The animal appears not to have sense of smell or taste or sight, by which more complex animals may recognize their food at a distance. It has some sort of sense, however, such that on contact with a bit of quartz and then with a bit of nutriment, it will reject the quartz and ingest the food. When in its aimless pseudopodial creeping the animal has come in contact with a particle which it can digest and use as a source of tissue and of energy, the animal at once, but in its characteristically slow way, sets about ingesting it. This is often a difficult task. One side of the particle is surrounded by a pseudopod, and if the food does not slip away, another on the opposite side slowly flows out. These coalesce, and thus the piece of nutritious matter is surrounded by a living net. Sometimes living animals are thus entrapped. The cytoplasm then flows in upon it closely, and the particle is soon in the interior of the ameba. Soon a vacuole is produced about the particle, probably by a process of secretion from the immediately surrounding protoplasm. The product of this secretion, which fills the vacuole it has made, is undoubtedly a proteolytic enzyme in a solution such as that which digests proteids in the more highly evolved animals. While digestion is going on the nutritious part of the food is absorbed and assimilated to the ameba's protoplasm. The waste is excreted by a method homologous to that by which the food was ingested—the waste particles are flowed away from after they have been gradually worked to the periphery of the animal.

The effects of various physical agents on an ameba are instructive. We may examine first as to *heat*. Reduction of the temperature of ameba causes a decided slowing of the ameboid movements, and they cease some few degrees above 0° C. When raised above 20° C. or so, an average room-temperature, the quickness and size of the movements increase, reaching a maximum at about 30° C. At about 35° C. the protoplasm goes into what is called heat-rigor, the coagulation being completed when the temperature is at 40° C. or a trifle higher. To *light*, the ameba reacts under ordinary aquarium conditions, but seeks to avoid it when too strong. It discriminates between degrees of light and shade, and this is only a general protoplasmic function. If a weak current of *electricity* be passed through the water surrounding the animal, its protoplasm elongates(by electrotaxis) and turns its long axis in the direction of the current. Pointed pseudopodia of small size extend outward, usually toward the anode. If the voltage of the electricity be excessive, the protoplasm of the animal is broken up, disintegrated, and scattered in a characteristic manner.

Like all protoplasm, that of ameba requires *oxygen* for its metabolism. It is regularly attracted by an excess of the gas, while if its oxygen supply be cut off, the pseudopodial movements gradually cease and the animal becomes more or less spherical, and enters into the condition known as necrobiosis, or death-in-life, in which the vital functions surely but gradually cease. Occasionally an ameba may be seen to *reproduce* itself—a process lasting two or three hours—by its usual method of amitosis or simple nuclear division. (See page 44.) The nucleus may be seen to be constricting in one diameter. This is followed by a similar process in the cytoplasm in the same plane. Finally, after only a thread of cytoplasm connects them, the daughter-cells wholly separate. These new cells, which are like their parent save in size, proceed in their functions seemingly as the mother did before them—links of a chain which theoretically has no end—the protoplasm composing them being in this limited sense immortal. The ameba also has to conjugate at times with another individual in order to maintain continuously the descent.

We are now able to summarize some of the underlying facts and ideas

PLATE II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which an observation of the ameba has given us, the characteristics of this animal by which it is the most typical of cells, the type of protoplasm. In the first place, the protoplasm of the ameba has a certain consistence, fluid yet capable of form. It has structure and organs, nucleus, cytoplasm, nucleolus, a contractile vacuole, one or more permanent vacuoles, and chromatin masses in the nucleus; it is, then, a morphological thing and concept. The ameba moves spontaneously and in a peculiar way—namely, by flowing slowly or streaming back and forth into pseudopods and out again, rolling, pouring, streaming slowly over the ground. Heat, up to a certain temperature, makes protoplasm more active, while cold makes it less so; light affects it in this animal, and electricity influences it peculiarly. The protoplasm of the ameba requires oxygen, food, and water in order to live; it absorbs the oxygen, digests and assimilates the food, and moves only by its inherent water. Finally, a drop of protoplasm in this animal form reproduces by dividing itself into two substantially equal parts, which thereupon are immediately capable of all the ameba's functions.

EXPLANATION OF PLATE II.

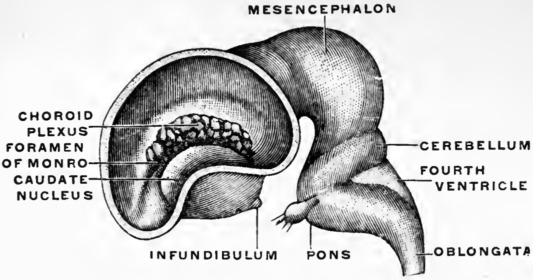
Plans of the nervous systems and brains of animals of widely varying complexity. Nervous systems of 177, scallop (Pecten); 178, starfish (Asterias); 179, mollusc (Unio); 180, sea-mussel (Mytilus); 181, a mollusc (Carinaria); 182, a mollusc (Bullea); 183, argonaut (Nautilus); 184, cuttle-fish (Sepia); 185, a parasitic worm (Strongylus); 186, earthworm (Lumbricus); 187, a rotifer (Hydatina); 188, barnacle (Lepas); 189, a marine worm (Aphroditea); 190, a myriapod insect (Scolopendra); 191, larva of a moth-insect (Sphinx ligustri): *A*, cephalic ganglia; 192, same at time of the first change: *A*, portion of thoracic cord, showing respiratory nerves; *B*, view of ganglion from above; *C*, from the side; 193, nervous system of the pupa of Sphinx; 194, of the imago of the same insect; 195, of the cockchaffer (Melolontha); 196, enteric system of the locust (Gryllus migratorius); 197, nervous system of the sand-hopper (Talitrus); 198, crab (Maia); 199, spider. In the following figures *a* points to the olfactory ganglia; *b*, to cerebral hemispheres or ganglia; *c*, to optic lobes or ganglia; *d*, to the cerebellum, and *e*, to the spinal cord: 200, brain of gurnard (fish, Trigla); 201, conger eel (Murena); 202, ray-fish (Raia); 203, gray lizard; 204, frog (Rana); 205, green turtle (Testudo mydas); 206–209, development of nervous system of the chick; 210, brain of cassowary; 211, lion; 212, origins of spinal nerves; 213, nervous system of human embryo at seven weeks; 214, brain of human embryo at nine weeks; 215, twelve weeks; 216, fifteen weeks; 217, twenty-seven weeks; 218, 219, brain and cord of frog-tadpole. (Carpenter, from many sources.)

CHAPTER II.

THE NERVOUS SYSTEM.

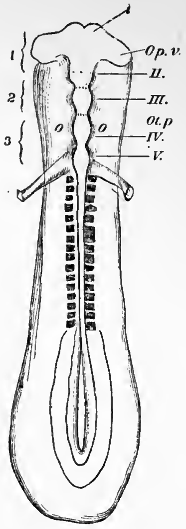
We have examined into the basal nature of the substance composing animal bodies so far as it may readily be studied, and have noted its activities. We can now discuss the functions of the human body systematically and with as much detail as our space allows. In this description of bodily processes we must first understand the ways by which the various parts and functions of the body are coördinated so as to constitute an individual. Animals exist only as individuals, and in part at least, as the name implies, are separate from each other and more or less independent. Without a proper understanding of the means of unification of the various functions we should miss the full meaning of many of them and fail utterly to take that broad view of animal life which is so essential to knowledge and invaluable in treating diseased conditions. We should never think of the animal, then, as a group of organs but as one integral organism, though necessarily made up of parts more or less different in their structure and uses. It is exceedingly important to keep in mind this inherent unification and to remember that it is for descriptive purposes only that we should separate the organs and describe them one at a time. In reality, as they live, they are in no sense independent of each other. One of the means

Fig. 20



Brain of calf-embryo of 5 cm., to show the bendings of the originally straight neural axis. Lateral view of left side, the outer wall of the hemisphere being removed. (Hertwig.)

Fig. 21

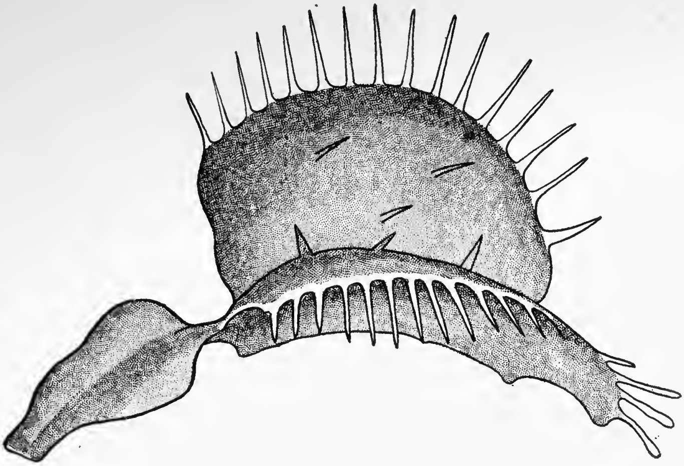


Very early state of the central nervous system of man: 1, 2, 3, forebrain, midbrain, and hindbrain, respectively; *I*, telencephalon; *Op. v.*, optic vesicle; *II*, diencephalon; *III*, mesencephalon; *IV*, metencephalon; *V*, myelencephalon. Farther down the neural groove one sees the somites and medullary groove of the spinal cord. (Häckel.)

by which the organs of the body are coördinated is the complex and nearly all-pervasive system of bloodvessels and of lymphatics. The other chief means is the nervous system, and this is still more complex. (See the experiments and the theoretical notes on them in the Appendix.)

The nervous system, then, is that fabric of linear structures which serves to connect in a functional manner the various parts of the body, coördinating them into an individual, just as the connective-tissue anatomically binds the organs and parts together. The nervous tissue comprises physiologically a vastly complex "protoplasmic bridge" (Loeb) between cells and between organs, and transmits (more or less changed perhaps) the myriad influences which originate in these organic units. The nerve-fabric only takes up and perfects in the biological division of labor one of the functions of all protoplasm, conductivity. If we omit for the present the relations of the nervous system to the mental process, we may say in advance that the function of the nervous system is almost wholly conduction, using this term in a broad way to include coördination.

Fig. 22

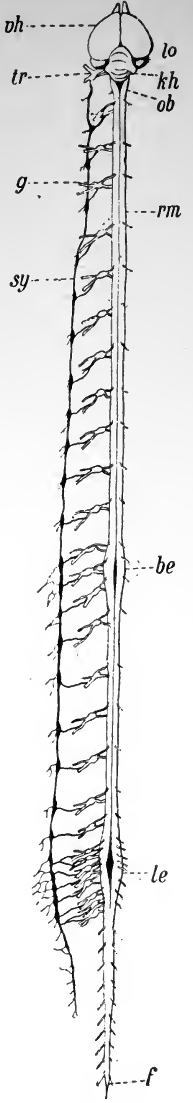


A leaf of Venus' fly-trap (Dionea), much enlarged. Conductivity, the basal function of the nervous system, and a process common to all protoplasm, is seen well-developed even in certain plants. A stimulus (from an insect, for example) applied to the hair-like projections on the edge of the leaf is promptly conveyed to the (motor) hinge and occasions there a quick approximation of the two halves. There are present here, then, all the essentials of a reflex action (see below) and of a useful neuro-muscular mechanism—the immediate agent of all the world's advancement.

THE GENERAL FUNCTIONS OF THE NERVOUS SYSTEM.

The general functions of the nervous system may be classified as follows: (1) To represent consciousness, at least as a connector or coördinator; (2) to receive and to transmit impulses "inward," afferently; (3) to direct muscular function: (*a*) actuating it, (*b*) inhibiting

Fig. 23



The brain, cord, and sympathetic chain of the dove: *vh*, forebrain (hemispheres); *lo*, optic lobe; *kh*, cerebellum; *ob*, medulla oblongata ("bulb"); *tr*, trigeminal (fifth cranial) nerve; *g*, spinal ganglion; *rm*, spinal cord; *sy*, sympathetic; *be*, dorsal enlargement; *le*, lumbar enlargement; *f*, filum terminale. (B. Haller.)

it; (4) to direct glandular function: (*a*) actuating it, (*b*) inhibiting it; (5) to direct tissue-nutrition: trophism.

1. The nervous system, in representing *consciousness*, as the general though careless presumption is, performs its most mysterious function. Yet were it not for the fact that a blow on the brain destroys consciousness, while one on a mass of muscle does not, we could not perhaps claim that the nervous system transmits consciousness any more than does the muscular tissue, or the bones, or the protoplasm of the liver. Consciousness and living bodies, so far as we know, are inseparable; more than this cannot be said. How completely the nerves represent the mind, then, we do not know, but they apparently do so by unifying the functions of the organism, and by coördinating the protoplasmic activities into the "physical basis" of a personality.

2. The animal body, like the mind, is a part of Nature, and as such is in the closest possible relation with its *environment*. The nervous system has to adapt the organism to this environment, especially to changes, among others, in the kind and amount of its nutrients and in its amount of moisture, heat, pressure, light, and oxygen. All these and numerous other conditions help to determine the reactions of the body, and should be regarded by the dyschophysical organism every moment of its life. It is the inward (afferent or centripetal) impulses which convey to the reflex and voluntary centers of the nervous system knowledge of these and many other conditions of the environment.

3. In the direction of *muscular contractions*, producing both molecular and molar movements, the nervous system controls and coördinates the deliberate voluntary movements, and the instinctive and emotional (reflex) reactions of the organism. It does this both by actuating them

(setting them in motion) and by inhibiting or checking them. From an area of the cerebral cortex around or in front of the Rolandic fissure and less than 7 cm. by 3 cm. in size, millions of muscle-fibers throughout the opposite side of the body are directed to contract or not to contract. The millions of possible combinations of these numberless muscle-fibers produce in various degrees all the intricate muscular movements and adjustments of civilized man. Every one of these many thousands of muscle fibers should be made to contract in the proper sequence, long enough and not too long, fast enough yet not too fast, and hard enough and not too hard, to serve the intended purpose. We are but now, with the developing knowledge of the conducting mesh which seems to make up the more essential part of the neural tissue, beginning to realize adequately the extreme complexity and perfection of this function of the nervous system. The neurone has something of a new aspect. Perhaps the cerebellum has more to do with actuating the movements than has the Rolandic area; so, at least, some investigators have recently claimed.

Fig. 24

The nervous net about a ciliated cell from a dog's trachea. (Ploschko.)

Muscular movements are classified as (1) deliberately voluntary; (2) reflex; and (3) "automatic" or autochthonic. *Voluntary* muscular movements are those made with the immediate choice or will of the individual. Some biologists consider these the primary movements in the evolving series of life. When they had been performed often enough and generation after generation long enough, they became *reflex*, and no longer required an act of will for each performance; they were controlled then by centers situated especially in the spinal cord. Those movements, however (*e. g.*, the heart-beat, peristalsis), which are of universal need and occurrence, have gone a step farther and have become "automatic," though requiring actuation from the central nervous system for control. The law of habit, then, has determined the status of the various muscular viscera. These, or some of them, have, it is possible, learned to act perfectly as long as supplied with the needful amounts of nutriment, heat, etc. Thoracic respiration is an exceptional sort of automatic series of movements in which the dominating center (in the medulla oblongata) is actuated by the varying quality of the blood flowing through it. In this case the nerve-center is automatic rather than the muscular mechanism.

4. In controlling *glandular action* (that is, epithelial metabolism, which usually acts to produce a secretion or an excretion) the nervous system works in a manner similar to its action on the muscles. The epithelial

cells are organs made to produce atomic movements just as the muscles are instruments of molar movement. Every epithelial cell is a tiny laboratory for the elaboration of some new substance, and the nervous influence coming to it starts or stops its secretion. Whether or not it has any qualitative control over the metabolism is still somewhat in doubt. Whatever the nervous authority over a single gland-cell accomplishes, it certainly (*a*) coördinates the actions of the myriad separate cells, and (*b*) adapts their collective action to the needs of the organism as a whole.

5. Concerning the *trophic function* of nerves, the influence over tissue-nutrition, little can at present be definitely stated, save that such control undoubtedly exists. Whether the nerves immediately direct the nutrition of any tissue is not determined, but the function of coördinating the nutrition of parts is surely performed by the nervous system. In normal conditions there are some signs of this, but pathology shows us numerous instances in which a disease of a brain-part results in trophic disaster in some portion of the organism (*e. g.*, acromegaly). This trophic control may prove to be identical with that overglandular action, since all protoplasm appears more and more to be the site of complex chemical production. The nervous energy, whatever it is, actually stimulates the energetic processes of protoplasm. When cut nerves are regenerated, the first function to recur is the trophic function: the part slowly regains its lost flesh-color, its warmth, and its firm tone. Its resistance to disease increases. These, then, are the most conspicuous elements of "trophism." (Sensation next appears, then reflex movement, and lastly voluntary movement.) It is probably through this trophic control over tissue-metabolism exerted by the central nervous system that the chronic emotion of worry exerts its baleful influence over health. (See Chapter XII.)

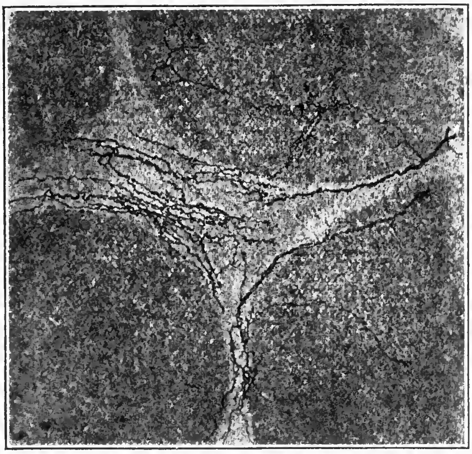
FEATURES OF THE NEURAL STRUCTURE.

The chief function of the nervous system is coördination, and it accomplishes this by the conduction of various influences between large or small parts of the body and between the organism as a whole and its environment. For this conduction fibers are necessary, and accordingly we find the nervous system essentially a network of fibers or of fibrils extending almost everywhere in the body. The relations of these fibers or fibrils making up the neural "reticulum" are not yet fully understood, nor are its relations to the nerve-cells which are so numerously connected with it. It is not certain that the fibril rather than the fiber (neuraxone, neurite, neuraxis, fibril-bundle, axis-cylinder) is the conducting unit (that is, that each fibril bears a separate impulse), but the probability of this belief is increasing.

Throughout most of their length the supposed fibrils are gathered in bundles (the fibers, axones), and these are of several different sorts, classified according to their coverings. The essential fiber made up of fibrils varies little, so far as is known, save in diameter. Two chief types, however, are commonly described, the medullated and the non-medullated. In both of these the fiber consists of the essential fibrils embedded probably in a clear substance called the neuroplasm, while according to a few observers a delicate reticulum is also present in the fiber.

In the *medullated fibers* the bundle of fibrils, often more or less flattened and irregular, is surrounded by the axolemma and then by a relatively thick covering of a highly refractive substance of a fatty nature called myelin, this covering being the medullary sheath or myelin sheath. The contained myelin is kept in place by a neurokeratin network. The sheath is divided into segments by oblique fissures, the incisures of Schmidt, the segments bearing the name of Lantermann. As usually studied, the myelin sheath is colored black by osmic acid. In the peripheral nerves (mostly cerebrospinal, but also sympathetic in part) the myelin sheath is in turn covered by a transparent structureless membrane called the neurilemma, or sheath of Schwann. At intervals varying with the diameter of the fibril-bundle or fiber the myelin sheath is interrupted, these interruptions being the nodes of Ranvier, and it is through these nodes, apparently, that the fiber receives its nutriment from the lymph and excretes its katabolic waste. They are from 80 to 900 mmm. apart, these extremes corresponding to fiber-diameters of about 2 and 25 mmm. respectively. Each of Lantermann's segments in man contains one neurilemma-nucleus, surrounded by a small amount of protoplasm. At the nodes the neurilemma or sheath of Schwann is thickened, being thus continuous along the fiber, oftentimes from close to its "origin" in the nerve-cell nearly to its termination.

FIG. 25



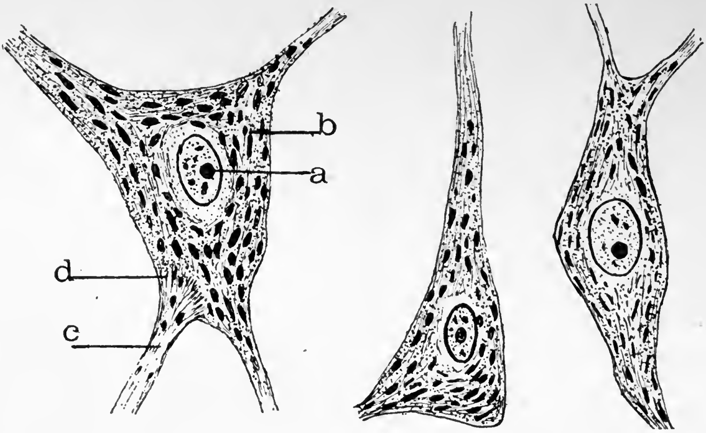
Nerves of a mesenteric lymph-gland from a new-born dog. (Manouélian.)

Non-medullated fibers (Remak's) lack the myelin sheath. Usually they are surrounded by the neurilemma, and are then from about 4 to

7 mmm. in diameter. In the prolongations from certain ganglion-cells even this covering is apparently lacking. The non-medullated fibers have a grayish color. They are generally in the sympathetic system.

Nerve-cells are the other elements of the nervous system besides the conducting fibers or fibrils. They vary greatly in size, for while the motor cells of man's spinal cord may be 150 mmm. in diameter (ranging upward from 75), some of the nerve-cells in the granular layer of the cerebellum have a diameter of not over 4 mmm., while others are twice as large. Nerve-cells have large nuclei and nucleoli, but relatively little chromatin. There is usually about the periphery of the cell a non-granular layer, and probably a similar clear layer around the nucleus. The principal fiber, the neuraxis, or axis-cylinder, joining a nerve-cell spreads out into a cone-shaped mass (the implantation cone) in the cell, which is also free of granules. In other parts of the cells there are fibrils doubtless continuous with those of the prolongation from the cell; very fine, highly refractive biogenic granules, and the so-called chromatophile granules (Nissl bodies, tigroid substance), which are coarse granules or flakes especially abundant about the nucleus, and continuous into some of the cell's branches. About these three elements of the nerve-cells, and others (*e. g.*, pigment) which it is needless to mention, there is at present no little discussion among histologists. Their exact respective functions are still more obscure; in fact, little is definitely known of the use of any of the many parts of a nerve-cell.

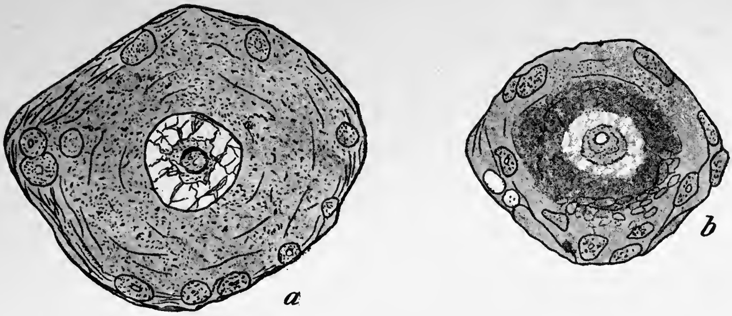
Fig. 26



Motor nerve-cells from the anterior horns of the spinal cord: *a*, nucleus with its conspicuous nucleosus; *b*, stainable substance of Nissl; *c*, neurite; *d*, implantation cone. Note the neurofibrils. (Bates.)

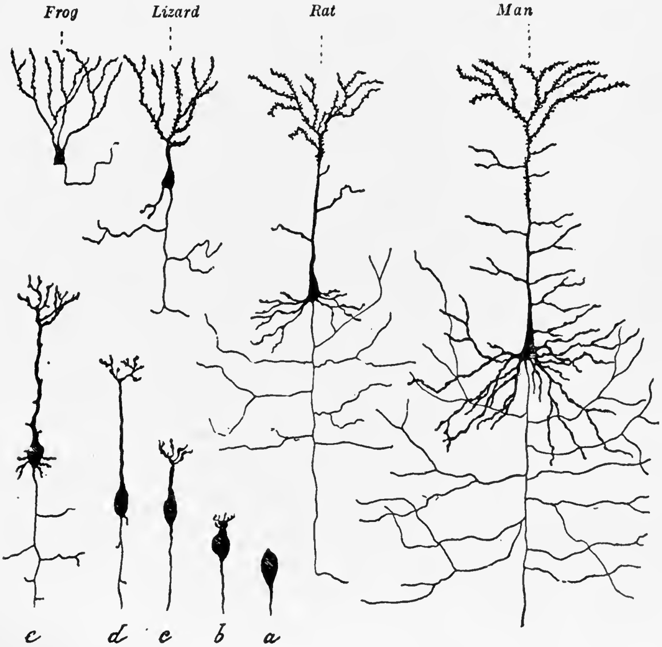
In the brain the cells of the cerebellum, of the retina, and of many other parts are small. So are those of the posterior horns of the cord, while those of the anterior horns, as already stated, are many times larger. Some competent neurologists (*e. g.*, Campbell) claim that on sectioning and staining the cortex its numerous functional divisions are at once obvious by the differences in the cells and fibers. The brain-cells have no obvious capsule. In the ganglia of the peripheral nerves are medium-sized nerve-cells which have around them the neurilemma. In the sympathetic system and in other places are cells surrounded by "baskets" of nerve-fibrils, connecting with a more or less distant cell.

FIG. 27



The effects of overstimulation (fatigue?) on the motor nerve-cells of a cat: *a*, normal; *b*, after five hours' continual stimulation. (Hodge.)

FIG. 28



The phylogenic and the ontogenic evolutions of the pyramidal nerve-cell and the neurone. The top row of neurones (from left to right) are those of the frog, the lizard, the rat, and man, respectively: *a*, *b*, *c*, *d*, *e* are stages in the embryological development of the pyramidal cell. (Ramon y Cajal.)

These important networks are now under active discussion; their function is by no means understood.

The *neurone theory* of the structure and action of the nervous system supposes that even in the adult this system is made up entirely of distinct units called neurones, which do not connect structurally save by contact. Between them are the recondite gaps called synapses, to which some investigators attribute a psychical nature. A neurone consists of a nerve-cell and nerve-fibers, of various numbers and lengths and modes of branching, extending from it. One of these projections is usually longer and more definite and direct than the others, and is called the neuraxis or neuraxone. This neuraxis, marked also by its uniform diameter,

Fig. 29

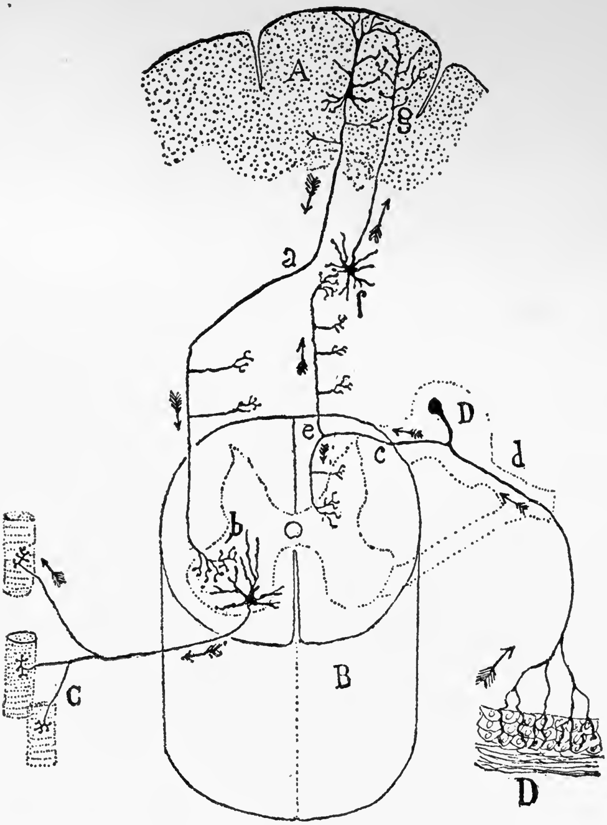
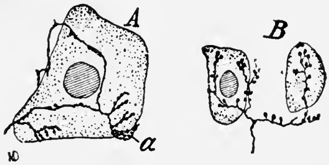


Diagram of some of the neurones concerned in the central nervous system: *A*, cortex cerebri; *B*, spinal cord; *C*, muscle-cells and the teleodendrites of a motor spinal neurone; *D*, a peripheral afferent (sensory?) surface; *G*, spinal ganglion; *a*, the neuraxone of a corticospinal neurone; *b*, the teleodendrites of the same in the anterior gray horn; *c*, the neuraxone of an afferent spinal neurone; *d*, the peripheral process of the same; *e*, the bifurcation of the same; *f*, the teleodendrites of the same connecting with the dendrites of another neurone, *g*, in the brain somewhere. (Ramon y Cajal.)

arises generally from an implantation-cone, but sometimes from one of the other branches (dendrites) close to or at some distance from the cell-body of the neurone. From the neuraxes of the Purkinje cells of the cerebellum, of the pyramidal cells of the cortex cerebri, of certain cells of the cord, etc., fine branches or collaterals are given off, usually at right angles to the neuraxis. Sometimes the neuraxes are very long (for example, they may extend from the cord to the feet), and much less often they break up soon into arborizations. At the peripheral extremities of all those which do not so divide, there is a tuft of fibrils called teleodendrites. In the course of a nerve the neuraxes seldom branch (save as the fine collaterals), but near their terminations they frequently divide into two, three, or more fibers of a size similar to that of the neuraxis. It is part of the neurone theory that the axis-cylinder is the centrifugal path—*i. e.*, the fiber along which impulses pass outward from the cell-body. Besides this "centrifugal" branch, most neurones have "centripetal" projections called dendrites. These may be only few in number or very numerous, and often, as in Purkinje's cells of the cerebellum, have arborizations of great extent and complexity. Sometimes the dendrites appear like collaterals, or even like neuraxes, and may then have terminal claw-like teleodendria like those of the latter. In some cases the dendrites are arranged like a basket closely around the nerve-cell of the next neurone in the functional series. But the respective uses of all these structures are not well understood.

Fig. 30



Neuronal terminations in secreting epithelium: *A*, a cell from a rabbit's parotid gland; *B*, a cell from mammary gland of a cat during gestation. Observe that the nerve-endings do not connect with the nuclei. (Morat.)

Fig. 31

Perivascular plexus of nerve-fibrils. (Ramon y Cajal.)

THE CHEMICAL COMPOSITION OF NERVE-TISSUE.

The facts as to neural composition are clearly of more and more importance as they become better understood. Sooner or later the chemistry of the nervous system will throw much light on the real nature of its activity, about which so little is now known with certainty. Many things in physiology, as in psychology, depend, for example, on the nature of the nervous impulse, and this depends on the chemical composition and on the metabolism of the neural tissue.

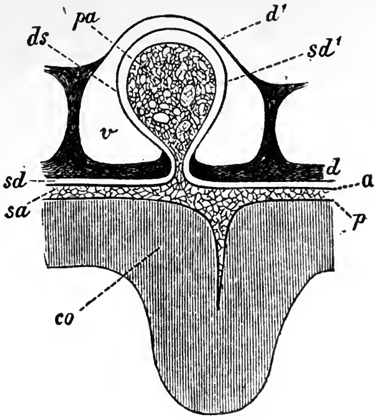
The amount of water in the nervous system and in the white and gray matter varies greatly according to age. In a fetus the white matter appears to contain about 87 per cent. of water and the gray matter 92 per cent. In adults the percentage of water in the white matter is about 69, and in the gray matter about 83; while in old age the percentages of both are somewhat higher. From this it will be seen that nervous tissue is about four-fifths water, and that the gray matter (cells and unmedullated fibers) contains more water than white matter, especially in the prime of life. The gray matter contains less than 17 per cent. of solid materials, and we see herein the physical basis of its great activity. Among the solids of the nervous system may be noted proteids, nuclein, neurokeratin, cerebrins, cholesterin, various extractives (such as creatin, xanthin, lactic acid, uric acid), gelatin from the adherent connective tissue, and inorganic salts. Of the proteids, the gray matter has the largest proportion, 51 per cent., according to Halliburton. These are a nucleoproteid and two cell-globulins, one of which coagulates at a temperature as low as 47° C. (a possible cause of death from sunstroke and from high fever). The cerebrospinal liquid is much like lymph in the matter of inorganic salts, but it contains only a trace of proteid. One of its constituents is a substance (perhaps dextrose) that will reduce Fehling's solution.

THE BLOOD-SUPPLY OF THE NERVOUS SYSTEM.

The nervous system receives proportionally more blood than do most of the organs of the body, as the unique circle of Willis at the base of the brain and the ample sinuses about the hemispheres indicate. At present little is definitely known about the vasomotor system of the nerves and the brain, but that it is elaborate is becoming more and more evident. Recent researches by Weber, Bourgery, and Cavazani have shown by anatomical and physiological experiments that a vasomotor mechanism exists in the brain, while Obersteiner has worked out somewhat systematically its nerve-fibers. The ventricles of the cerebrum are portions of an hydraulic system, parts of which surround the brain and the cord. About the whole brain is the pia mater, lining the skull is the dura mater, while between these is the arachnoid, which is probably an important osmotic membrane. The hydraulic cavity in question is the space beteen the pia mater and this membrane. The liquid filling it (a very thin lymph) communicates freely with the ventricles in the brain through many canals, the largest of which are the foramens of Luschka and Majendie. By osmosis the lymph of this subarachnoid space communicates with the venous blood in the subdural sinus. Thus, there is a set of large vascular cavities in the interior and about the periphery of the brain, and the different parts of these can exert on the brain all degrees of local or general pressure, as normal function demands. Osmosis may have much to do with these adaptive movements of liquid. Only few details, however, of these vasomotor activities have so far been obtained, but there is little doubt that the conditions are complex and important. Perhaps the pituitary body has chemical control over the blood-supply of the brain, for it seems to contain a vasoconstrictor principle thirty times as strong as adrenalin. (See Chapter on Nutrition.) The reciprocal vasomotor action between the trunk and limbs and the blood-supply of the head has long been a well-known fact.

Another function of this "water jacket" of the brain is to protect it from injury by blows on the skull. The spinal cord is supplied with blood by arterioles extending inward from the pia mater. Capillaries are especially abundant about the nerve-cells, especially in the cortex cerebri. The immediate dependence of the brain's function on ample and continuous blood-supply is the most complete found in the body. When the flow of blood ceases or even slows greatly the central functions cease. Illustrations of this fact are seen in the instant dropping dead of people when the heart stops beating or bursts.

Fig. 32



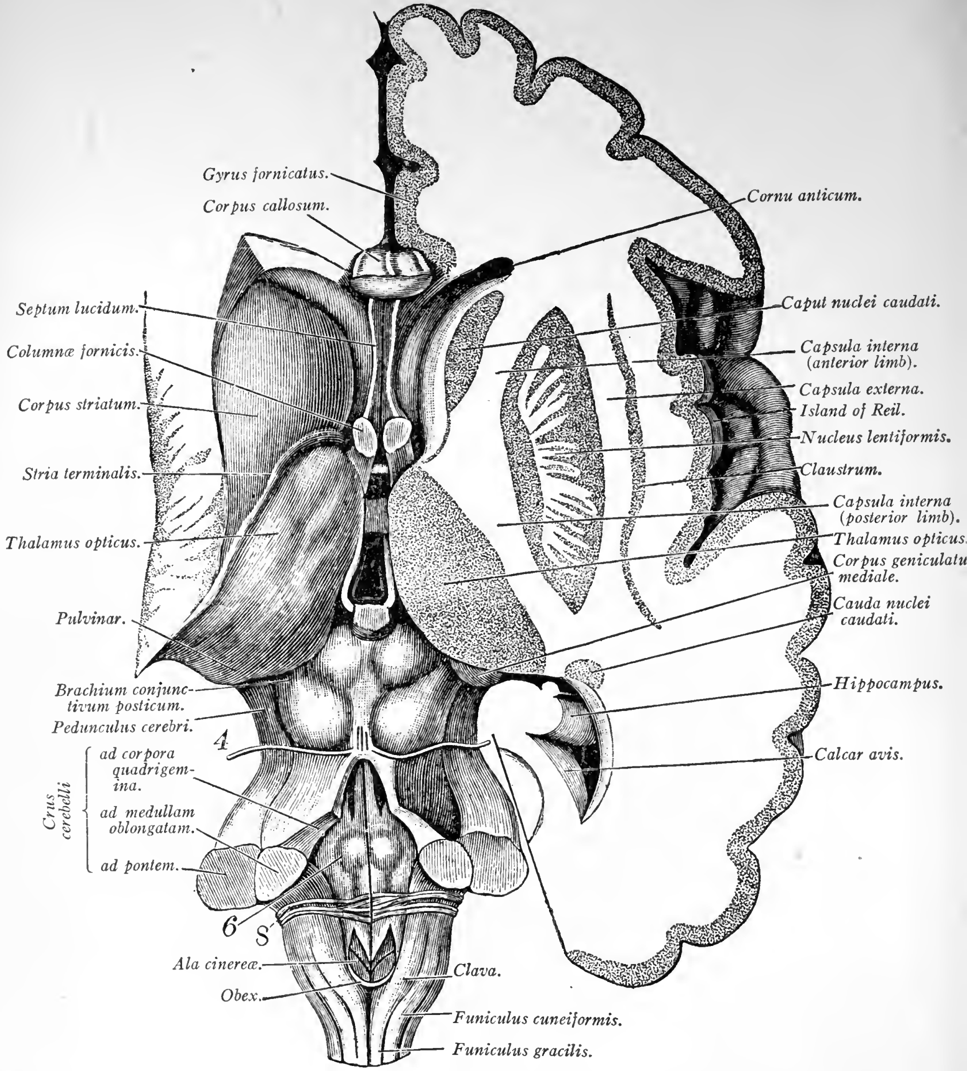
Diagrammatic suggestion of an arachnoidal villus and its coverings: *co*, gray cortex of the hemisphere; *p*, pia intima; *sa*, subarachnoidal space continuous with the villus, *pa;* *a*, arachnoid; *sd*, subdural space, continuous with that of the villus, *sd';* *d*, inner layer of the dura mater separated from the upper layer, (*d'*) by the venous space, *v;* *ds*, dural covering of the arachnoidal villus. (Rauber.)

FUNCTIONAL PARTS OF THE NERVOUS SYSTEM.

Certain portions of the nervous system should be especially studied because of their diagnostic importance if for no other reason, though little is known about some of them. We will consider briefly the uses of the hemispheres (including their much-discussed cortex), the cerebellum, the medulla oblongata, the optic thalami, the corpora striata, and the pons.

The Hemispheres.—The hemispheres, or cerebrum, as they are sometimes called, are the large convoluted, seamed masses of white protoplasm which are seen in the opened skull when the tough dura mater and the thin arachnoid and pia mater ("meninges" of the brain) have been cut through. The hemispheres in man cover over all the remainder of the brain—a fact of instructive contrast with all animals below the mammalian complexity, for in them it remains anterior to the rest of the brain. In a young human embryo this same anterior position prevails,

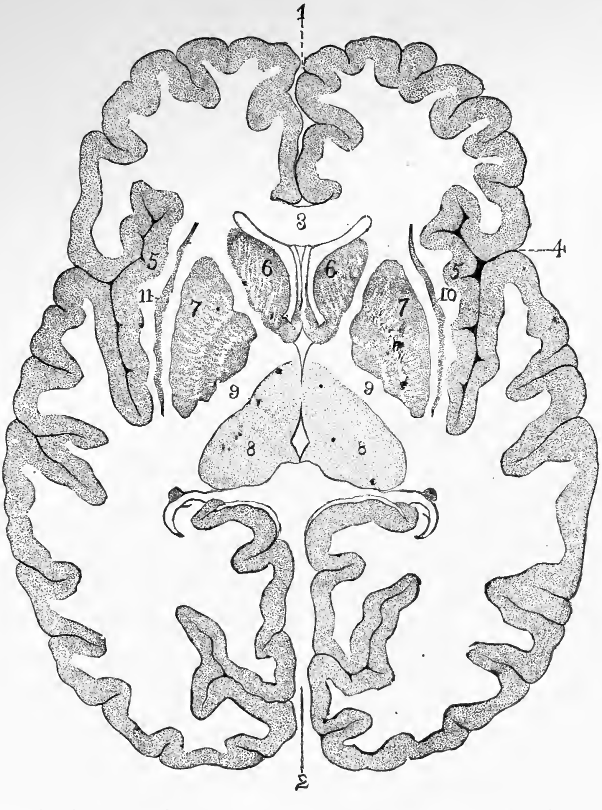
Fig. 33



The human brain, within.

but what is then only a small protuberance in front on each side gradually grows outward and backward until at birth the "lobes" of the cerebrum cover over all the rest. This preponderance is doubtless an index of the superior complexity, capability, and intelligence of man. Exactly in what way, however, the two facts are connected cannot be precisely told. Perhaps the excess in the human brain over the brute's brain is taken up in paths for the *association* of organic events of many sorts, this increased association making possible a much larger number of actions, bodily and mental, than the small-hemisphered simpler animal can perform. At any rate, the relative size of the cerebrum usually, but in a general way and with many exceptions, corresponds to the complexity of the animal's life. Thus, *e. g.*, women and ants have relatively large brains.

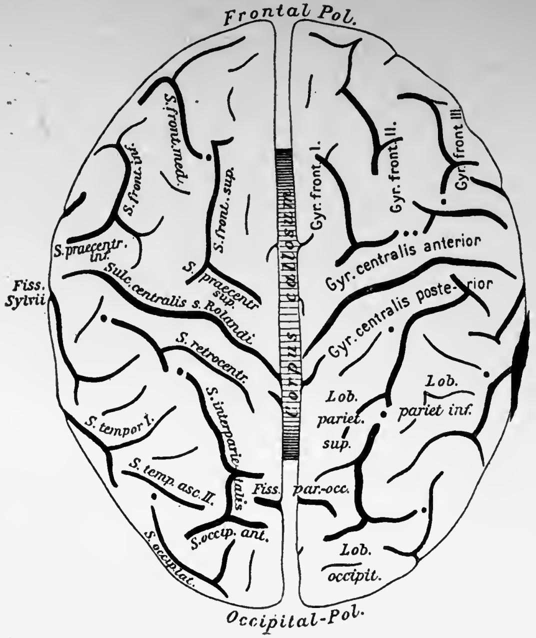
Fig. 34



Horizontal section in the hemispheres through the ganglia: 1, 2, longitudinal fissures, former between frontal lobes, latter between occipital lobes; 3, anterior part of corpus callosum; 4, fissure of Sylvius; 5, island of Reil; 6, caudate nucleus of the corpus striatum; 7, the lenticular nucleus of the same; 8, optic thalamus; 9, internal capsule; 10, external capsule; 11, claustrum. (Dalton.)

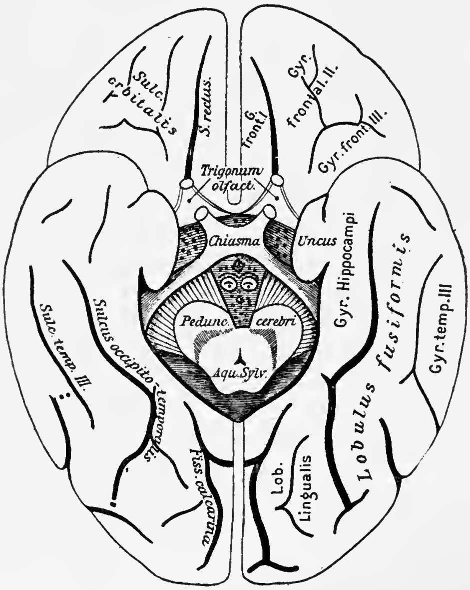
The hemispheres, like the nervous system in general, are composed of gray matter (nerve-centers) and white matter (fibers). The way in which these two sorts of tissue are disposed is best shown by a transverse horizontal section such as is illustrated in Fig. 34. Above the level of the

Fig. 35



Hemispheres from above. (Eberstaller.)

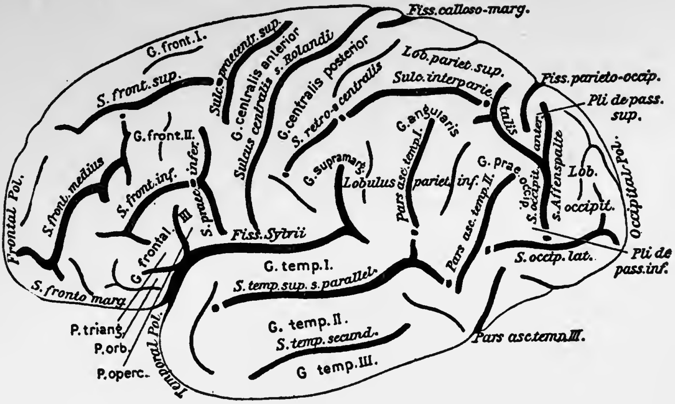
Fig. 36



Hemispheres from below. (Eberstaller.)

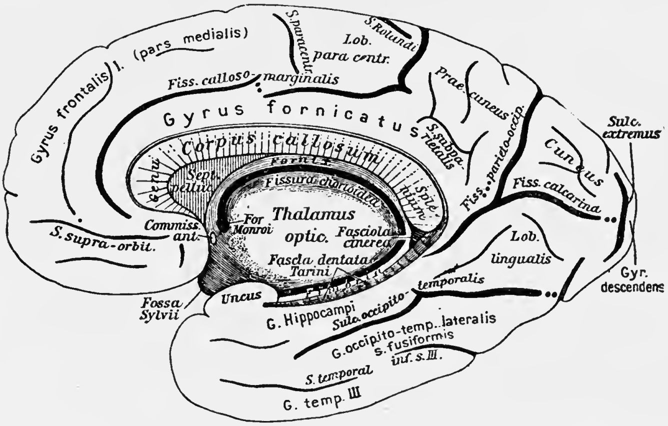
corpus callosum the *gray matter* lies wholly in the cortex, but below that level the gray matter constitutes the corpora striata, the optic thalami, the lenticular nuclei, etc., as well as the cortex. The functions of these various nuclear regions will be considered later. The *white matter* of the cerebrum seems to be made up of fibers which conduct impulses from one part of the brain to another, and especially from the cortex on all sides, inward and downward, and which constitute more or less directly the spinal cord and the cranial nerves passing outward within the skull. Above, these fibers, converging toward the pons, start from the cortex as the corona radiata, and farther down they are called, misleadingly,

Fig. 37



Left hemisphere, dorsolateral surface. (Eberstaller.)

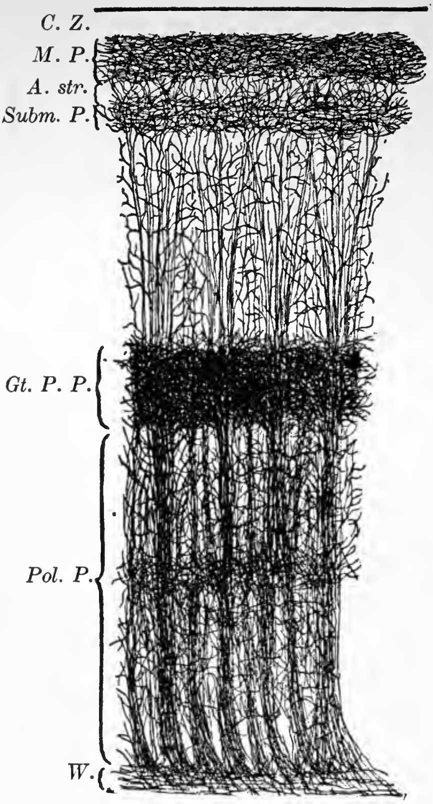
Fig. 38



Right hemisphere, mesial surface. (Eberstaller.)

the internal capsule. This is simply the laterally bent and flattened sheaf of fibers from the cortex where they pass between the lenticular nucleus on the outside and the corpora striata and optic thalami within, as the illustration shows. Similarly, the mysterious corpus callosum is a thick, hard bundle of fibers connecting intimately the two hemispheres. Not infrequently, however, it is absent altogether without obvious functional defect in the individual. In an homologous way the lower or temporal convolutions exhibit converging fans of fibers passing inward and upward into the crura of the brain. What sorts of impulses, and in what directions, these various fibers conduct will be somewhat better understood when the functions of the cortex cerebri and the nuclei which they serve have been described.

Fig. 39

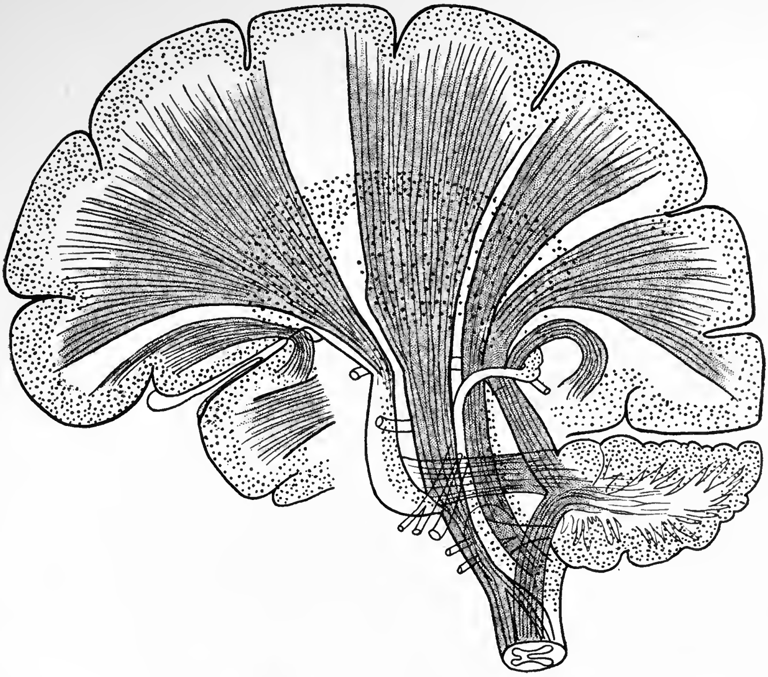


Section of human cerebral cortex, to suggest especially the immense complexity of the neuronal relations (methods of Weigert and Golgi): *C. Z.*, clear zone having no nerve fibers; *M. P.*, Exner's plexus in the molecular layer; *A. str.*, ambiguous cell stratum; *Subm. P.*, submolecular plexus; *Gt. P. P.*, great pyramidal plexus; *Pol. P.*, polymorphic plexus; *W.*, white matter. (Andriezen.)

The Cerebral Cortex.—This is the outermost or bounding layer of the hemispheres, and is from 2 to 4 mm. in thickness in different parts. The area of the cortex is increased two or three times at least by the numerous sulci and fissures, 2 or 3 cm. deep, in the surface of the hemispheres. The cortex dips down into these sulci in all cases and lines them on both sides and on the bottom. Indeed, these sulci appear to be present for the purpose of increasing the area of the cortex, and they are more numerous and deeper the more highly evolved and the more skilful and intelligent the animal. The cortex is composed of various layers of nerve-cells and the fibers connecting them. A recent estimate of the number of these cells in the human cortex is 9,200,000,000; other estimates state that the number of these cells is several times as small. They weigh, however, only about seventeen grams. The rounded masses of brain between the sulci and fissures are the gyri or convolutions, and each of these has a name corresponding to its position and shape.

Aside from the great longitudinal fissure separating the hemispheres down to the corpus callosum, two others merit special notice in Physiology—namely, the central fissure, or fissure of Rolando, and the fissure of Sylvius. The *Rolandic fissure* divides the frontal lobe from the parietal, and extends nearly straight from about the middle of the summit of the hemisphere outward, downward, and forward to a point more or less close to the fissure of Sylvius. The *Sylvian fissure* divides the frontal lobe from the temporosphenoidal lobe. It extends from the anterior perforated space on the base of the brain outward to the lateral surface of the hemisphere, and thence backward, upward, and inward; a short branch, the ascending limb, extends anteriorly a little distance from below the lower end of the fissure of Rolando. Besides these there are several others nearly as large anatomically which divide the various lobes into convolutions, and there are many smaller fissures.

Fig. 40



The chief paths from the cortex to the cord. (Starr.)

The old-time phrenology, so largely a subject of discussion in the early part of the nineteenth century, is no longer thought of, save historically. It was based on a wrong psychology. Even today, however, neurology has no facts which can take the place of this system of brain localization. We are not sure, even, whether in any given mental process the whole cortex does not act in one way or another. The more recent division of the cortical surface into motor areas, sensory areas, and association areas is still incomplete, and there is doubt as to its substantial value. It is, however, customary and so provisionally proper, to describe certain areas of the cortex as motor and sensory, the latter especially having a definite and more or less certain value. Other regions are called association-areas.

The Motor Areas of the Human Cerebrum, in which it has been supposed that voluntary or deliberate muscular movements are actuated; are thought at present to be the convolutions anterior to the fissure of Rolando, the adjoining posterior part of the frontal lobe, and that portion of this general region to be seen on the mesial surface of the hemispheres. In the earlier work of Ferrier, Horsley, Munk, and others on monkeys the motor area was found to occupy the posterior central convolution also, but it has lately been made probable by Sherrington and Grünbaum, working on the chimpanzee (the brute most like man), and by the embryological studies of Flechsig, that the area just posterior to the Rolandic fissure represents in man cutaneous sensation. Farther back the important muscular and joint sensations, known as the kinesthetic impulses, are represented. These facts, however, are simply the products of stimulation of the cortex and of the other modes of experimental study largely on speechless animals. It is likely, on the whole, that the kinesthetic sensations of a muscular part have their "centers" in the same brain-areas as do the movements of these parts. We are not then certain at the present time what we mean by "a motor area," since all sorts of sensations, feelings, ideas, etc., are closely related to the contraction of muscles. Adamkiewicz has recently claimed, as a result of four years of careful research, that the whole cerebral cortex is, properly speaking, psychical, or at least psychomotor, in its functions. He supposes, accordingly, that it is the function of the cerebellum to conduct unconscious movements. Still, stimulation of the Rolandic area above defined causes contraction of the cross-striated muscles in different parts of the body.

The motor area of each side of the brain represents the muscles of the other side of the body, for a large proportion (90 per cent.) of the efferent paths that run thence cross to the opposite side in the lower part of the medulla. Another sort of reversal is present in the Rolandic motor area. The higher in the erect human body a muscular group is, the lower in general is its center along the lateral surface of the anterior central convolution. The muscles of the face are thus represented in front of the lower end of the fissure of Rolando and those of the toes at its upper end. Above the centers for the head muscles are those of the neck, then upward those of the wrist, arm, shoulder, trunk, and hip. The centers of the leg extend in reverse order thence to the median longitudinal fissure, on or near which are situated the motor nuclei of the toes.

When this region of the cortex is stimulated with any suitable agent, as, for example, a weak alternating induced electric current, contraction takes place in the corresponding muscle or muscle-group on the other side of the body. If the stimulus be too strong or continued too long, the contractions become more and more spasmodic and radiate to surrounding muscles, until, finally, general convulsions, such as one sees in epilepsy ("grand mal"), occur and put an end to this demonstration of the motor centers. When these overlapping areas are destroyed in any natural or artificial way, the corresponding muscles are paralyzed, and most often permanently. Just what occurs in this cortical region when the normal animal wills to make a muscular movement is not definitely known. It is likely that incoming messages from the muscles, joints, and skin direct in someway the continued innervation of the particular outward motor paths to be employed in the movement, but just how we cannot say. Morat supposes that there is a continual circulation of nervous energy in the sensorimotor paths which store up stimuli for the voluntary movements. Of the original stimulus to deliberate movements we know nothing. In this sense these centers are not wholly motor, but, as often called, sensorimotor. We have thus already taken a step here toward considering the cortex essentially a network that is actuated as a unit, at least in performing its motor functions.

There is one aspect of the relations of the motor cortex, so called, to muscular function which is attaining increased prominence—namely, the relations of the flexor movements to the extensor movements. There is evidently a basal contrast between these sorts of movements related not only to the method of balance in voluntary control, but at the foundation also of emotional expression. Flexion is more characteristic of the unpleasant emotions, while extensor movements are common in pleasant emotions. This contrast appears to be far-reaching, involving perhaps the whole matter of inhibition. Thus, Wedensky, in 1897, saw in stimulation experiments on the motor cortex that excitation, for example, of the motor center for extension on one side of the brain, augmented the excitability of the flexor center of the other hemisphere and diminished the excitability of the flexor center of the same side of the brain—and vice versa. Such a suggestion introduces interesting possibilities as to the complexity of the arrangement of the nuclei controlling the coördination of the various muscle-groups. This reciprocal mode of action is not unknown in other parts of the organism and in widely differing functions. Like many other problems, this one awaits more exact knowledge as to the relation of the brain-paths and centers.

THE SENSORY AREAS.—The sensory areas of the cortex are more numerous and more extensive than are the motor areas. The kinesthetic sensations, concerned with the control of the muscles, as already noted, are situated in the posterior central convolution just behind the fissure of Rolando, in the region posterior to this, and in the anterior central convolution. These are co-extensive with the centers of voluntary movement. In addition, the mesial cortex seems to represent, in some regions, these important afferent impulses, part of the frontal lobe and the upper and posterior part of the gyrus fornicatus being also concerned. On the lateral surface of the hemisphere still farther back is probably the center which controls the stereognostic sense, by which the limbs, especially the hands, give a sense of shape in space without help from vision. Thus the whole middle and upper part of the lateral aspect of the hemispheres seems to be connected with the general bodily sensitivity. The somesthetic areas, which may be defined as those representing the visceral and dermal sensations as well as the sensations arising in the muscles (touch plus kinesthesia), have not been definitely determined. Indeed, frequent injuries to the motor areas, accompanied with no lessening or derangement of general sensitivity (somesthesia), suggest that the whole matter is still indefinite. When this knowledge is attained, the workings of the nervous system will become clear.

The cortical representations of the other four of the "five senses" ("feeling" has just been discussed) are somewhat more definite. The *visual centers* seem to be on both sides of the calcarine fissure in the mesial surface of the occipital lobe, and affect an area in the cortex of the lateral aspect of the occipital lobe in the first convolution. We should suppose that one ill-defined region represented that part of the retina, the macula lutea, concerned with the *ever-changing focus* of sight. Schäfer (also Henschen) thinks that this spot is at the anterior end of the calcarine fissure on the mesial surface. We should look for another center for *color-vision,* but so far none has been found. We might suppose that other small regions were interested merely with perception of *light,* and that still another, as Wilbrand suggests, was concerned with the appreciation of *perspective.* At present, however, the visual cortical area cannot be thus divided.

Schäfer concisely summarizes somewhat as follows the probable relations between the cortical areas of both hemispheres and the retina: The visual area of one hemisphere is connected with the corresponding lateral half of both retinæ, while the upper, lower, and intermediate zones of the area represent the zones of the corresponding lateral halves of both retinæ; the focal point of the area, located as above defined, is connected with more than the corresponding half of the macula lutea of each retina. Thus, the areas for the focus of seeing are each concerned with both foveæ centrales. This fact enables one to understand why the movements of the two eyes in focusing on a new point are so perfectly controlled and also the perfection of sight when this particular retinal region of the fovea is concerned.

The *auditory centers* in man are in the superior temporal gyrus and also in the island of Reil within the Sylvian fissure. It is probable that each center represents both cochleæ, for when these areas of only one hemisphere are destroyed both ears are made partially deaf. The superior temporal convolution of the left hemisphere is concerned with the hearing of words, and the form of aphasia known as word-deafness is associated with disturbance or removal of the posterior two-thirds (Naunyn) of this gyrus. (See page 396 and Chapter XI.)

The sound of the speaking voice is heard, but the words are not recognized, nor appreciated as having any meaning. Thus the speech-center is in the left hemisphere in right-handed persons. It remains to be learned where the speech-center is located in children properly trained from the first in ambidexterity.

The *olfactory center* of the cortex in man is on the mesial surface in front of and below the corpus callosum. It is situated in the uncinate convolution, the anterior part of the gyrus fornicatus, and posteriorly on the base of the frontal lobe. In those lower animals in which the sense of smell is more developed than in man, there exist large special olfactory lobes extending forward from the hemispheres. In many of the brutes smell is the sense which, next to the kinesthesia, tells them most about their environment. In man it is relatively unimportant, for vision and hearing (owing to the evolution of speech) have superseded this sense. There appears to be only a small amount of neural crossing from one side to the other in the case of smell.

The *gustatory center* also was thought by Ferrier to be located in part in the anterior portion of the gyrus fornicatus on the mesial cortex (Bechterew), the first and second gyri. Smell and taste are closely associated functionally in some cases (*e. g.*, in eating), and it is likely that this phenomenon may depend partly on the situation of the gustatory center low down on the mesial surface of the temporal lobe close to (but below) one of the centers of smell. Taste-buds, however, have recently been found in the nose. In the anterior portion of this temporal area in the monkey and cat stimulation produces movements of the lips and tongue such as are naturally associated with tasting (Ferrier). Bechterew obtained similar results in dogs from a corresponding spot on the cortex of the brain, and in apes from the operculum.

THE "ASSOCIATION-AREAS."—The so-called association-areas of the human cortex take up more than two-thirds of its surface. There are three: the frontal area, the parietotemporal area, and the island of Reil. So far as direct experimental evidence goes, we know practically nothing as to any special sensory or motor function of these regions, for they seem to be inexcitable by the means which actively stimulate the motor and sensory areas about them. Actual removal of these areas, under the proper and extremely delicate conditions necessary, produces proportional loss of mental faculty. At present, however, the particulars of this loss cannot be given. Flechsig cites cases which show that loss in the frontal areas is apt to be accompanied by a lessening of the inhibitory habits of the individual, so that he becomes, like one of the lower animals, deficient in cultural human control over the organic tendencies.

The name association-areas implies that they are the place where the functions of the brain are associated by means of nerve-fibers and nerve-cells. This may be seen, for example, in the loss of recognition exhibited by animals that have had this area removed. Munk calls it "soul-blindness." These "association-areas" are the portions of the cortex about which least is known. Their function is largely psychological and of a complex nature, if one may judge by the facts concerning these regions so far discovered.

The Optic Thalami.—These large nuclei in the middle of each hemisphere have shown in experiments and in natural lesions so large a variety of apparent functions that to name their general purpose or purposes in the nervous system is at present impossible. They seem to be centers of correlation between afferent impulses and those which produce movement. Perhaps, as their name implies, vision is especially concerned, for they are in the nature of nerve-currents passing from the eyes to the nerve-centers in the occipital lobes, and when an eye is destroyed the thalamus of the opposite side degenerates somewhat. Lesions in these nuclei produce undoubtedly a rise of body-temperature. They also disturb severely emotional expression. Thus, in one case a man who was found after death to have a large tumor of one thalamus could imitate a smile perfectly well (by using probably his voluntary motor cortex), but on hearing anything humorous that side of his face opposite to the tumor remained blank, although the other side of his face smiled naturally. Such cases prove that one of the functions of the thalami is coördination in the muscular expression of the emotions. These nuclei intervene between the incoming afferent impulses and the cortex of the brain around them, but exactly what they do to these impulses is not yet fully understood.

The Corpora Striata.—These consist of two parts: The lenticular nucleus and the caudate nucleus. Lines of white fibers extend through the gray mass of the corpus (giving it its name). Little is known about the function of these bodies, less than about any other part of the brain. Stimulation of one mechanically or electrically causes convulsions of the muscles on the opposite side of the body, while destruction of one corpus gives rise to paralysis of these muscles. This paralysis appears to be transitory if only the gray part of the organ is destroyed. Several experimenters have seen a rise of body-temperature follow irritation of the gray matter, but this follows also from stimulation of various regions of the cortex cerebri. The fact, however, is suggestive of a possibility that the corpora striata may be concerned in the regulation of the muscular metabolism, and this largely determines the heat-production of the body.

Nothnagel and Rezek have recently corroborated the conclusions of Magendie that the corpora striata are organs concerned in the reflex coördination of the muscles of locomotion. Destruction of part of the caudate nucleus causes rabbits to go in circles rather than straight ahead. This part of the nucleus Nothnagel names the nodus cursorius.

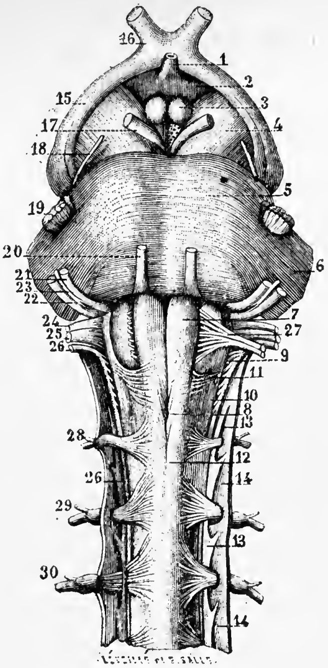
The Corpora Quadrigemina.—These are in the roof of the aqueduct of Sylvius, above the cerebellum, and in front of the lower posterior part of the corpus callosum. They are composed of white fibers outside and of gray matter within. Two of the four small bodies are anterior and two posterior. They apparently differ much in function. Through the anterior pair the internal capsule is connected with the optic tract from the retina to the occipital lobe, while similarly the posterior pair connects the internal capsule with the paths between the cochlea and temporosphenoidal cortex. Monakow showed the connection of the cortex of the temporal lobe with the posterior body. They seem to be unconnected with the afferent fibers of the cord.

It is possible that the anterior corpora are concerned in regulating the movements of the body and of the eyes under the influence of vision. The posterior pair have probably some sort of control over the muscular movements of producing the voice. On removing them from dogs and apes the voice is lost, and when one of them in man is diseased the hearing of the contralateral ear is lessened. Removal of the four causes the interesting "forced movements" in which the animal on attempting to move makes various sorts of circular motions or rolls over. This indicates that the function of equilibrium is involved, and we know that their connection with the cerebellum is intimate.

The Hypophysis Cerebri (pineal body) is discussed under the Internal Secretions on page 218.

The Pons.—The pons, as its name and position both imply, is primarily a bridge connecting by its gray and its white nueral structures the different parts of the nervous system, coördinating the sensory and the motor tracts, and furthering generally the association of impulses of many sorts. The sense-organs of the skin and mucous membranes send impulses into the pons, as do also those of the muscles and joints. It seems especially to connect the cortex of the hemisphere with that of the opposite side of the cerebellum, its middle portions laterally being the great middle peduncles of the cerebellum. With the equilibrium of the head (and thereby of the body) it has much to do by its connection with the vestibular branch of the auditory nerve and with the cerebellum. The muscular movements of that part of the alimentary canal within and above the pharynx appear to be controlled via the fifth nerve partly within the pons. Efferent (muscular and

Fig. 41



Ventral (anterior) aspect of the medulla and of the parts above it: 1, infundibulum; 2, tuber cinereum; 3, corpora albicantia; 4, cerebral peduncle; 5, annular tubercle; 6, place of origin of the middle cerebellar peduncle; 7, anterior pyramids of the bulb; 8, decussation of these pyramids; 9, olivary bodies; 10, restiform bodies; 11, arciform fibers; 12, upper end of the spinal cord; 13, denticulate ligament; 14, the cord's dura mater; 15, optic tracts; 16, chiasma; 17, motor oculi nerve; 18, pathetic; 19, trigeminal; 20, abducens; 21, facial; 22, auditory, etc.; 23, nerve of Wrisberg; 24, glossopharyngeal; 25, pneumogastric; 26, spinal accessory; 27, hypoglossal; 28, 29, 30, spinal nerves. (Sappey.)

glandular) impulses may pass from the gray nuclei of the organ to many parts of the body besides the head by way of the closely connected medulla below and the internal capsule above.

The Medulla Oblongata.—The medulla oblongata, or bulb, as it is sometimes called, is understood as compared with the nuclei just above it on the base of the brain, though the actual details of the structure and functions of the medulla are, however, not well known. In general, the medulla is largely a conducting organ, with many small, but important "centers" (neuronal regions) scattered in the interior of its 8 or 9 c.c. It gives rise to seven or eight of the twelve so-called cranial nerves (page 88).

The white matter of the medulla is arranged in four bundles or columns—namely, the anterior pyramid, the lateral tract, the restiform body, and the posterior pyramid—on each side.

The *anterior pyramid* is composed of fibers extending upward from the direct pyramidal tract of the spinal cord and from the crossed pyramidal tract. Some of these continue upward into the crus of the cerebrum, others are lost in the pons, while still others pass to the cerebellum as part of the restiform bundle. In a similar way the *lateral tract*, continuous below with the lateral column of the cord, divides itself between the cerebellum and the cerebrum, joining partly with the anterior pyramid. The *restiform body* is made up largely of fibers from part of the posterior column below, and having received fibers within the medulla in a complex way, divides, part going to the cerebellum, and part upward farther into the hemisphere. The *posterior pyramid* comes upward also from the posterior column of the cord (Goll's column) and with a portion of the preceding continues into the cerebrum as part of the fasciculi teretes. Near the broad upper end of the medulla is the *olivary body*, containing the gray nucleus called the corpus dentatum, and conspicuous ventrally (anteriorly) on the medulla's surface. Fibers from this gray matter join with part of the anterior column to form the olivary bundle ascending into the crus of the hemisphere.

The gray matter of the medulla, situated largely beneath (*i. e.*, ventral or anterior to the floor of the fourth ventricle), performs two general functions. It is concerned with the cranial nerves (which will be mentioned later—see page 88), as already noted, and (as nuclei) with important reflex activities. It is because the medulla connects and coördinates these two important systems of nerves (those of special sense and motion with those of the great reflex vegetative movements of the body), that this portion of the spinal cord is of such unexcelled usefulness in the organism. It is from the medulla more than from any other part of the nerve-scheme that the vital functions are controlled and made to work together, thus insuring the inherent unity of the individual animal. Such basal functions as respiration, nutrition, circulation, and thermotaxis depend directly on the duties of the medulla. Here are controlled the many varied secretions and movements of the whole complex alimentary canal, the heart's action, the distribution of blood, the adapted move-

FIG. 42

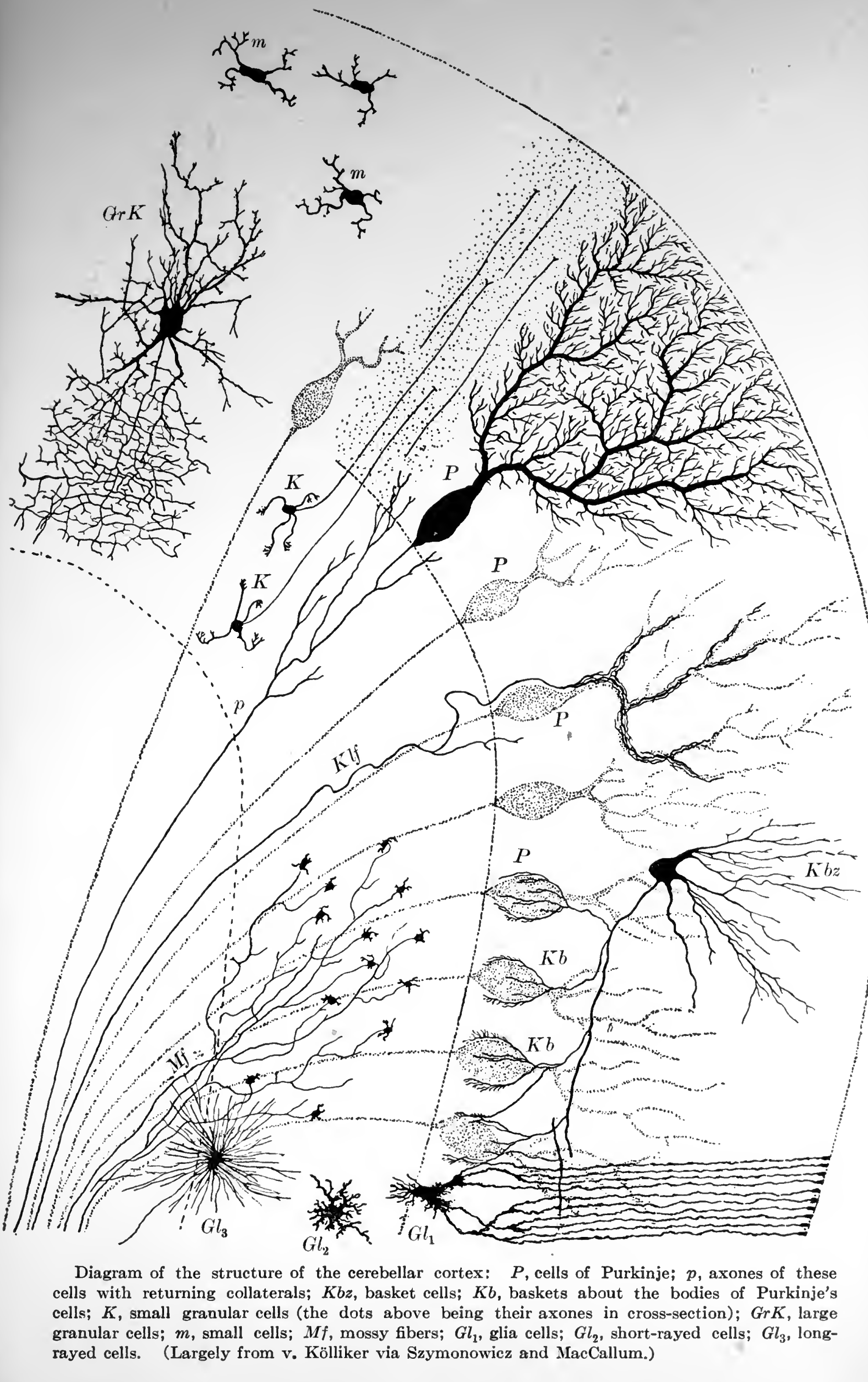


Diagram of the structure of the cerebellar cortex: *P*, cells of Purkinje; *p*, axones of these cells with returning collaterals; *Kbz*, basket cells; *Kb*, baskets about the bodies of Purkinje's cells; *K*, small granular cells (the dots above being their axones in cross-section); *GrK*, large granular cells; *m*, small cells; *Mf*, mossy fibers; *Gl*$_1$, glia cells; *Gl*$_2$, short-rayed cells; *Gl*$_3$, long-rayed cells. (Largely from v. Kölliker via Szymonowicz and MacCallum.)

ments of the thoracic walls, and many other functions the action of which demands this complex sort of coördinating control. These actions of the medulla are not only reflex like those of the cord farther down (*i. e.*, dependent for action on an immediately preceding nervous stimulus), but to a greater degree than elsewhere (especially as concerns respiration); the activity here is "automatic," that is, subject to stimuli not coming from afar over a nerve, but acting on the central nerve-cells directly. Thus, the term autochthonic is more exact and probably less misleading than is "automatic," for it implies that the actuation comes from the immediate environment of the cell, a theory quite in line with the most advanced ideas of tissue-metabolism. In point of fact, stimuli which actuate automatic centers are the physicochemical conditions of the blood flowing through the gray matter of the medulla.

Some of the medullary centers are more reflex than autochthonic. For example, those of vomiting, swallowing, sneezing, coughing, sucking, eye and mouth movements, as well as those centers which control the secretion of sweat, saliva, and of the numerous other digestive juices found within the alimentary canal, are of this reflex nature. In brute animals there is also in the medulla a reflex center which actuates the muscles productive of vocal sounds. Most of the centers so far named produce their effects over the complicated cranial nerves.

As essential as the foregoing functions are those which follow; they too are directed by "automatically acting" medullary centers: inspiration, expiration, cardio-inhibition, cardio-augmentation, vasoconstriction, vasodilatation, and thermotaxis. Heubel, Nothnagel, and others have called attention to a spot at the extreme upper end of the medulla the chemical stimulation of which gives rise to the universal muscular spasms such as are seen in the *grand mal* of epilepsy. What the function of this arrangement of motor nerve-cells may be it is difficult to say; it may be related to the thermotactic center and be concerned in regulating the metabolic activity of the muscles short of their actual gross shortening by contraction. Of this kind of muscular action fibrillary contraction is an extreme degree. All these functions may be set in activity reflexly as well as autochthonically, for these two modes in practice merge into each other. All of these, besides most of the reflex centers proper, are of necessity intimately connected within the gray tissue of the medulla, as, indeed, a brief consideration of their interrelation in the bodily functions demonstrates.

The Cerebellum.—The cerebellum is situated in man above the overhanging occipital lobes of the hemispheres and dorsal to the pons and the medulla, and consists, like the hemispheres, of a rind or cortex of gray matter enclosing white matter made up of nerve-fibers. As in the case of the cerebral lobes, part of these fibers are engaged in associating intimately all parts of the organ, while others convey impulses inward to or outward from the cerebellum, connecting it most closely with the great conducting organs just described that lie ventrally to it. In general terms, the function of the cerebellum is to coördinate the muscular movements of the body. It probably has less to do with sensation than any other part of the brain. Luciani, indeed, claims that the cerebellum may be called the organ of subconsciousness, coördinating the bodily functions independently of the deliberate will and without the consciousness of the individual. It may be supposed, then, that the movements which are directly under the control of the spinal cord are properly coördinated by the cerebellum with each other and with the multitude of influences which come from the cerebrum. The function that has long been accorded to the cerebellum (maintenance of the equilibrium of the body) is only one of many similar functions, for all involve coördination.

FIG. 43

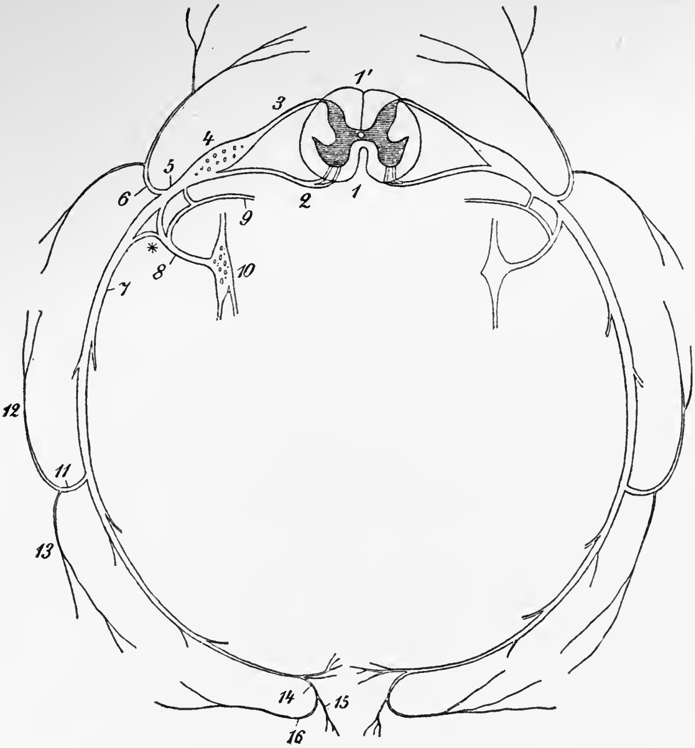


Diagram of a human neural "segment:" 1, the cord's ventral (anterior) median fissure; 1^1, dorsal (posterior) median fissure; 2, ventral root (efferent and perhaps motor); 3, dorsal root (afferent and perhaps sensory); 4, spinal ganglion; 5, trunk of the spinal nerve; 6, dorsal limb of the same; 7, ventral limb of the same; 8, ramus communicans; 9, meningeal branch; 10, sympathetic ganglion; 11, lateral cutaneous branch; 12, dorsal limb, and 13, ventral limb of the same; 14, ventral cutaneous branch; 15, medial limb, and 16, lateral limb of the same. (Rauber.)

The Spinal Cord.—The spinal cord is the great distributing and conducting portion of the nervous system, and is the seat also of many reflexes. It extends from the top of the medulla oblongata (the medulla is usually considered a part of the cord), downward in the canal of the spinal column, to a point opposite the body of the second lumbar vertebra; thence its large sacral roots continue as the cauda equina. The cord, as a whole, is cylindrical, but there are two prominent enlargements laterally, one in the cervical and the other in the lumbar region. The former swelling is due to the presence of the nerves of the arms, the latter to those of the legs. The cord is also made up of gray matter and white matter, the former within the latter, but passing outward through it as the anterior and the posterior roots. The gray matter, as seen on cross-section of the cord, is shaped much like the two extended wings of a moth connected by a narrow commissure. In the center of the latter is the canal of the cord, a minute tube (sometimes called the sixth ventricle), lined with ciliated epithelium (beating upward) and filled with the cerebrospinal lymph. The posterior end of each of these gray-matter wings is relatively slender and long, and is continuous with the posterior (afferent) spinal roots extending outward through the white matter. The anterior end of each wing is rounded and short and is surrounded by white matter except where the anterior (efferent) spinal roots pass outward. Thus these two pairs of roots divide each half of the cord into three unequal columns called anterior, lateral, and posterior. The whole cord is nearly divided dorsoventrally by two fissures, the dorsal being deeper but narrower than the ventral or anterior fissure, and without a commissure of white matter intervening between its inner end and the gray commissure.

Conduction.—Let us look in turn at the three general functions of the cord: conduction, distribution and collection, and reflexion. The cord is the great highway between the legs and the lower part of the trunk and the upper parts of the central nervous system. Numberless impulses passing upward and downward between these regions go directly in the white matter, and sometimes without alteration or loss, probably, the whole length of the cord. In general terms those impulses passing upward (called afferent, centripetal, or "sensory") go in the posterior or dorsal parts of the cord, while those that go downward (efferent, centrifugal, or "motor") pass in some part or other of the anterior or ventral regions. Owing to this and other far-extended divisions of labor, not only are there present the three gross columns already noted, made accidentally as it were by the roots passing through the white matter, but there are present in each of these numerous smaller bundles of fibers. Only a few of these, doubtless, have been located without question and named. The methods by which these tracts have been made out (they need be only mentioned here) are chiefly four: by embryological study of the paths, which develop at different times; by the observation of their degeneration when cut, away from their trophic central cells; by observation of pathological cases (tumors, stabbings, etc.); and by direct vivisectional experiment on animals similar to man. How large the number of tracts through the white matter from the numberless functional regions of the body we have as yet no means of estimating, but they are very numerous. As elsewhere in anatomical nomenclature, the discoverer's or exploiter's name is attached to some of the columns, but here, fortunately, there are other and preferable names besides. In the anterior portion of the cord, close to the median fissure, is the *direct pyramidal tract* (Türck's), containing those fibers leading from the motor cortex cerebri which do not decussate (cross over) in the medulla. This extends downward only about half-way through the thoracic cord because the axones have been continually giving off collaterals which cross to the anterior horn of the opposite side of the cord. Surrounding this horn of the gray matter is the anterior association-bundle, the so-called *antero-lateral ground-bundle*. The fibers composing this tract are not long like those of the preceding column, but extend only a short distance each. They are supposed to connect cells of the gray matter. They are the association-fibers, in short, of the cord. Some connect different segments of the cord and so have a vertical course. Others are horizontal in direction and connect the cells of the anterior horn with the anterior nerve-roots (Starr). External to this tract is the narrow *antero-lateral column* (Löwenthal's) of *descending* fibers coming in part from the posterior bundle of the medulla and probably from the cerebellum. Vaso-motor impulses may pass downward in this column (Starr). Lateral to this and on the periphery of the cord is the *antero-lateral column* (Gowers') of *ascending* fibers, a long tract conveying messages probably from the cord's gray matter to the cerebellum. This column varies much in shape in different parts of the cord; its fibers are more or less confused with those of the descending column; it is called also sometimes the anterior cerebellar tract. In the neck externally between these two last-named columns is the *bundle of Helweg*, conducting impulses apparently from the olivary body of the medulla. Within the curve of the lateral edge of the gray matter is another association-column, the *mixed lateral zone* of short fibers. This probably connects minute centers in the gray matter which, although separated spatially, require close functional connection. Outside and posterior to this ill-understood zone is the great *crossed pyramidal tract* (Türck's). This column is smaller and nearer the periphery farther down in the cord because of its gradual loss of fibers into the gray matter of the anterior horns and roots. The two tracts communicate with each other through the cord. It is made up of the 90 per cent. of the efferent motor fibers from the "motor" cortex of the hemisphere which cross over in the medulla. Each tract, therefore, represents the opposite hemisphere. In front of this column is a *bundle* called *Monakow's*, which conducts impulses from the red nucleus of the medulla to the gray matter of the cord.

On the periphery of the cord and external to the column just considered is the *direct cerebellar tract* (Flechsig's). The impulses which pass up this column (muscle and joint "sensations" in part) arise more or less directly from the gray matter on the outer side of the posterior horn (Clark's column) and pass to the upper worm of both sides of the cerebellum by way of the restiform body. This is the vegetative tract of

Starr, so called because up this column pass the impulses coming from the basal or vegetative organs of the body, by which impulses, reflexly, the centers above control their actions. Posteriorly lies the *posterior external column* (Burdach's) on the inner side of the posterior horns. Some of these fibers end about the cuneate nucleus of the medulla. They conduct tactile and muscular impulses afferently from the posterior roots connected with the arms and neck. Others are association-fibers between various spinal segments, while others still, more or less horizontal in direction, convey messages from posterior roots to cells in the gray matter of the cord. Medial to this column and bounded within by the posterior fissure is the *posterior-median column* (Goll's) which more or less similarly conveys important (sensory, afferent) impulses from the skin, muscles, and joints of the legs and the lower part of the trunk, upward to the gray nuclei of the medulla's nucleus gracilis. The paths of this tract communicate more or less with the gray horn of the same side of the cord. A distinct fibrous septum, especially above, separates this column from the preceding. On the medial side of this tract are two smaller tracts bordering on the posterior fissure: posteriorly the *septo-marginal bundle,* and just anterior to it, and sometimes extending to the posterior commissure, the so-called *oval bundle.* These are probably association-paths, as is also the so-called *comma-tract* (afferent) in the anterior part of the posterior external column. Close to and within the place of exit of the posterior roots from the cord is the *posterior marginal tract* (Lissauer's), a small bundle composed of fibers rising in the posterior horns and extending both upward and downward to connect with the posterior columns and with other posterior roots. This, then, is also an association-bundle. It is likely that in addition to these more or less well-defined tracts there are others and especially many small association-paths. The latter are particularly on the cord's periphery, and serve to unify to an unknown extent all the various parts of the cord, as similar fibers unify the brain. The functional facts demand this supposition, and many experiments, especially those of Sherrington and of Flechsig, indicate strongly their existence.

Distribution and Collection.—These are together functions general to the spinal cord, and we have seen well enough in the last few paragraphs how they are brought about. The cord has as its major part thick conducting columns composed of numberless fibers and fibrils which often run completely through the trunk from end to end. Within this layer of white columns is a mass of gray matter composed in part of nerve-cells and of short but complicated neurones. These, as we have seen, associate freely, by means of their dendrites, neuraxones, and countless collaterals. Down the cord so constituted come numberless and most various impulses, to be distributed wherever normal function demands, but what determines just where, and what determines where not (Morat calls this viatility), we do not as yet know. In like manner countless impulses pass into the cord, to be distributed in a way more or less similar. Again, numerous influences enter the cord and are made to concentrate or to collect so that their combined message goes in only one direction, perhaps to one region for the performance perhaps of a single end. How all these things are done in particular we do not know, but we see well-nigh universal interconnection, and we observe continually the results in living animals of these processes of adapted collection and distribution by the long and complicated spinal cord. This viatility of the nerve-centers is one of the functional marvels of biology.

REFLEXION, OR REFLEX ACTION.—Reflexes are actions of the body carried on by the spinal cord (and perhaps by the cerebellum) without the immediate volition or even knowledge of the individual. In a typical reflex action, as the name implies, there is a turning-backward of the nerve-current. The impulse originates in some sense-organ, passes through some nerve-cell or nerve-cells, and goes out of the central nervous system to the muscle or gland, or possibly to exert trophic action on some portion of the tissue. The influence which passes from the sense-organ to the central nerve-organ is called the afferent or centripetal impulse. Its passage through the gray matter is called the central process. It should not be thought that the afferent sense-organ must be on the periphery of the body or that the efferent instrument (muscle or gland usually), must be far away from the reflecting center, because the impulse might and often does originate very close to or even within the spinal column and pass to a muscle cell or gland alveolus close by. The terms afferent and efferent were derived from typical instances of reflex action, such as occurs when a touch on the foot, for example, causes it to be withdrawn. The central process, properly speaking, does not have to be in the spinal cord, but may occur in one of the numerous gray nuclei elsewhere in the body. Matters are so complicated in nerve-action that seldom are processes limited to that which their names denote.

In general terms, the afferent or centripetal impulse goes into the spinal cord through the posterior roots. Here it is associated, mainly in the gray alæ of the cord, with many other impulses, perhaps passing up and down in connected neurones. It then passes out, properly adapted to its purpose, in the anterior spinal roots on its way to the muscle or the gland. Matters in fact, however, are very much more complicated than such a mere formula implies, especially as regards the association which abounds in the gray matter. The greatest mystery concerned with the reflex movements of the body is as to how the necessary distribution and selection of paths (viatility) is made. A single unexpected touch, for example, on the back of the neck causes the exactly adapted and coordinated contraction of scores of complicated muscles of the trunk, neck, and legs. The centers in the cord, consisting of knots of neurones, are somehow able to distribute an impulse among the neurones so as to make the succeeding act exactly the one out of possible thousands which is most useful to the animal. This is the great mystery about all neuromuscular actions, and when the problem is complicated by trying to imagine how the influences from the brain above are connected with those proper to the spinal cord, the problem is obviously a most complicated one. The facts are comparatively simple; it is only how they are accomplished that physiology does not as yet explain. There are thousands of unitary muscular bundles whose arithmetic combination would make millions of possibilities of action. There are, too, thousands of possible outgoing nerve-paths whose possible combination would make other millions of possibilities of action. All these millions combine in the neuro-muscular mechanism, yet out of them normally the one right path is chosen!

For the most part reflex actions are conducted without much influence from the brain, especially from the cortex, but it appears certain that impulses regularly do pass from the reflex spinal centers upward into the brain. In general, it may be said that the cortex of the brain, during waking hours at least, exerts a controlling influence over most of the reflexes. Those movements are largely concerned with the purely vegetative processes, such as the movements of the alimentary canal and of the heart. These have, however, become so nearly "automatic" that in their normal condition they occur quite without the knowledge of the individual, the nerve-impulses not being correlated with consciousness. Still, it needs only some inflammation in these parts or disturbance in their nervous mechanisms to show that, so far as the nervous impulses are concerned, there is a very close constant relation between even these organs and the cortex of the brain.

The more highly developed the animal, the smaller the proportion of his activity controlled by the spinal cord. In worms, for example, there is no brain worthy to be called such, and the animal is wholly a "spinal animal," such as, for example, the frog becomes when its fore-brain and mid-brain are destroyed. In future chapters we shall discuss more in detail the relations of reflex actions to voluntary actions and to mental function or consciousness.

Although of many various sorts, the human spinal reflexes are not very satisfactorily classifiable. We may think of them, however, as either vegetative or non-vegetative, although every normal reflex has more or less of a vegetative or basal value to the organism. For convenience, however, we may arrange the spinal reflex-actions, including those of the medulla, in these two classes. The former class, *vegetative reflexions*, includes those which are essential to the life of the organism. Among them are inspiration, expiration, sneezing, coughing, cardio-inhibition, cardio-augmentation, vaso-dilation, vaso-constriction, thermogenesis, thermolysis, sucking, mammillary erection, mastication, salivation, deglutition, digestive secretion, digestive motion, vomiting, sweating, urination, copulation, erection, ejaculation, parturition, winking, and pupillary motion. The *non-vegetative* reflexes are very numerous if we include many actions which merge indistinguishably into voluntary movements. These are such actions as movements of self-defence, of withdrawal from injury, walking, running, swimming, and speaking. Included in this class are a number of skin-reflexes, the so-called superficial spinal reflexes: the gluteal, plantar, cremasteric, epigastric, abdominal, and scapular reflexes. These are of much practical use to neurologists and surgeons in determining especially the upper limits of spinal-cord lesions. Some of these reflexes have concern only with a small knot of neurones in the medulla oblongata or with cells in one spinal segment, while others involve neurones scattered far up and down the cord through many segments and by multitudes of cells and pathways. Their two common aspects are that their centers are located in some part of the spinal cord, including the medulla; and that they are in some degree slightly or wholly controlled by afferent impulses coming from a less or a greater distance.

We quote from Hall the following table, showing the location in the spinal cord of forty-three reflexes. It is useful not only as a summary of the reflex functions of the cord, but for diagnostic purposes in many diseases of the nervous system:

Reflex.	Location of Center.
Plantar	1st and 2d sacral segments.
Gluteal	4th and 5th lumbar.
Cremasteric	1st to 3d lumbar.
Erectile of penis	1st and 2d lumbar.
Abdominal	7th to 11th dorsal.
Epigastric	4th to 7th dorsal.
Mammary	2d to 12th dorsal.
Scapular	5th cervical to 1st dorsal.
Palmar	7th cervical to 1st dorsal.
Laryngeal	10th cranial nerve, bulb.
Pharyngeal	9th cranial nerve, bulb.
Nasal	5th cranial nerve, bulb.
Conjunctival	5th cranial nerve, bulb.
Tendo-Achillis	3d to 5th sacral.
Ankle-clonus	5th lumbar.
Patellar	2d lumbar.
Extensors of hand	6th cervical.
Flexors of hand	7th and 8th cervical.
Pronator of hand	8th cervical.
Triceps	6th cervical.
Supinator of hand	5th cervical.
Biceps	4th and 5th cervical.
Inferior maxillary	5th cranial nerve, bulb.
Defecation	4th lumbar.
Micturition	3d lumbar.
Seminal emission	4th lumbar to 3d sacral.
Parturition	1st and 2d lumbar.
Intestinal movements	10th cranial nerve, bulb.
Duodenal regurgitation	1st to 4th dorsal (splanchnic).
Pylorus	10th cranial nerve, bulb.
Gastric movements	10th cranial nerve, bulb.
Emesis	10th cranial nerve, bulb.
Deglutition	9th and 10th cranial nerves, bulb.
Sucking	5th, 7th, and 11th cranial nerves, bulb.
Respiration	Tip of calamus scriptorius, bulb.
Expiration	10th cranial nerve, bulb.
Inspiration	10th cranial nerve, bulb.
Circulation:	
Cardiac acceleration	2d and 3d et seq. dorsal.
Cardiac inhibition	10th cranial nerve, bulb.
Vaso-motor dilatation, blush	7th cranial to 3d sacral.
Vaso-motor constriction, pallor	2d dorsal to 2d lumbar, inclusive.
Pupillary	4th cervical to 3d dorsal.
Vaso-motor	Floor of the 4th ventricle.
Salivary secretion	7th cranial nerve, bulb (chorda tympani).

The brain can exert normally almost any degree of inhibitory control over the reflex actions. It commonly acts in this way provided it has been made aware that the reflex influences are to pass, and provided also that the neuro-muscular mechanism has not passed by long-inherited habit into a condition of practical atomatism such as is observed, for example, in the heart and intestines. Inhibition is one of the great problems of the day in physiology; about its cause, its actual mode of working, and its limits of influence we still know but very little.

Coördination.—Coördination of movements is accomplished through the meeting of the separate nerve-paths in cells, in plexuses, or in the "centers" of the central nervous system. According to the neurone-theory, each fiber (axone) being the unit of conduction, coördination can scarcely be supposed to take place within the cell, but rather in the groups of neurones called centers. Various kinds of centers have been already described. If, however, we consider the fibril within the fiber as the conducting unit, we might suppose that the various impulses coming in over the hundreds of fibrils may be arranged and connected within the body of the cell, the better to serve the various actions of muscles, the secretion of glands, the functions of the sense-organs, or other functions. We cannot as yet decide between these opposed points of view of the nervous system because of the histological uncertainty.

In its function of unifying the different actions of the body, the coördinating process is essential, as is readily seen from any one of numerous complex muscular acts. Take, for example, speech. (See page 394.) This complicated process in its mechanical aspects is essentially produced by draughts of air to and from the lungs which cause vibration of the vocal cords, while the throat, tongue, lips, teeth, etc., are adapted at the same time to the requirements of word-enunciation. To produce the requisite draughts of air the whole respiratory muscular-mechansim has to act in an exactly suitable way, inspiration and expiration being carefully adapted in force, frequency, and continuance to the exact needs. This means not only numerous afferent impulses passing continually to the speech-center in the temporal lobe of the brain, but hundreds and probably thousands of efferent impulses passing thence indirectly (by way of the respiratory center) to the numerous muscles of respiration. None of these cross-striated muscles and no portion of any will work by itself, but every part must be directed in exactly the proper way to produce the precise movements demanded of them. Similarly in the larynx, numerous small muscles must be made to act together as they have acted in producing similar sounds since the individual learned to talk. This mechanism is by itself one of the most complex of muscular coördinations. The soft palate must be innervated in a certain way, and the tongue must be made to select out of its multitude of movements just those, and none others, required for the particular words expressed. The lips take part also and involve exactly the right innervation of many small muscles, while the muscles of the jaw must at the same time so act as to make use both of the mouth and the teeth in the one proper manner. All of these parts meanwhile are sending inward to the brain and spinal cord a continual stream of afferent, sensory (kinesthetic) impulses by which alone the centers can guide the muscles to contract to the requisite extent. The mental aspects of speech (the one human function) require a multitude of other impulses of which we know essentially nothing. Thus complicated is the function of nervous coördination going on continually all over the body for hundreds of complex acts. The details of the nervous currents cannot be made out in any case, but the principle is now sufficiently clear.

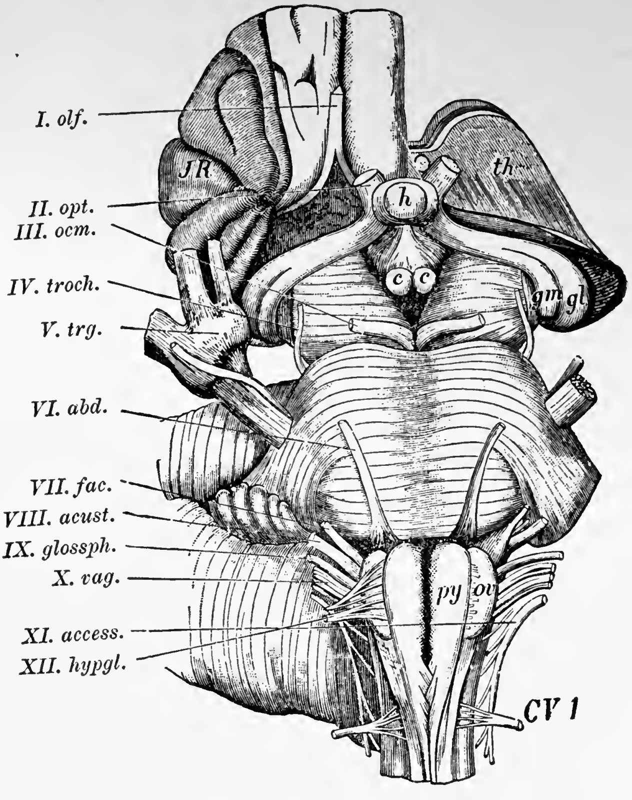
In the illustration just given there is one dominant center, that of speech, but it exerts control over a number of coördinating centers corresponding to the organs employed in the act. Besides the respiratory center, that of the tongue is regulated and that portion of the nervous system directing mastication, in itself a complicated act. In the process of swallowing nearly the same organs (save in part for the larynx) are involved. The movements of each are then different, however, and the center of deglutition is the dominant center while that of speech is affected in part only as subsidiary.

Thus continually all through the body a vast but exactly ordered multitude of impulses is passing to and fro between all the parts. The complexity of these groups of influences along nerves cannot be even imagined unless one impresses on his mind the number and the variety of interests and of purposes of the body's sense-organs and of its muscular and glandular and metabolic units. Uncoördinated these would make a chaos, but coördinated by the nervous system they are the essential part of a living animal body.

CERTAIN SETS OF NERVES.

Forty-three pairs of nerves connect the body-tissues of man with his central nervous system, one of each pair going outward on each side. Twelve of these pairs arise from the base of the brain and the medulla oblongata; these are called, therefore, *cranial nerves*. The other thirty-one pairs arise from the various segments of the cord; these are hence known as *spinal nerves*. Besides these, numerous sets of ganglia and nerves exist in the body and perform various vegetative functions; these ganglia and nerves are (but none too well) termed the *sympathetic "system,"* as if they in some way were distinct from the rest of the nervous system. This, of course, they are not, but rather an important portion of the common neural fabric and very intimately related to all its parts in many ways. If we speak of these three "sets" of nerves as separate, it is only for convenience and because they have been thus unduly and arbitrarily separated in anatomical treatises for many years and have so in a sense really become to the science sets of nerves. Functionally, however, it must be continually remembered they are only to a very limited degree separated from the rest and are combined with it to form the unity of the organism. We describe them separately, but in life these three sets of nerves act invariably more or less together. These same considerations are true also of the "separate" nerves—separate only anatomically.

Fig. 44

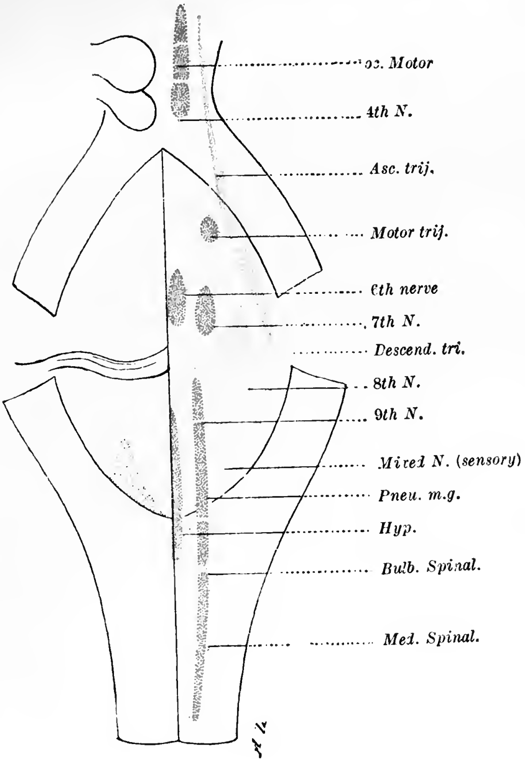


The base of the brain, showing especially the apparent origins of the cranial nerves: *I–XII*, the respective cranial nerves; *JR*, island of Reil; *h*, hypophysis cerebri; *th*, optic thalamus; *cc*, corpora albicantia; *gm*, mesial geniculate body; *gl*, lateral geniculate body; *py*, pyramid; *ov*, olivary body; *CV*1, first spinal nerve (cervical). (Schwalbe.)

The Cranial Nerves.—These are twelve in number in each side of the body. They are known by their respective names, but often, especially in the newer books, also by numerals, according to this list:

Olfactory, or first.
Optic, or second.
Motor oculi, or third.
Pathetic, or fourth.
Trigeminal, or fifth.
Abducens, or sixth.
Facial, or seventh.
Auditory, or eighth.
Glosso-pharyngeal, or ninth.
Vagus (pneumogastric), or tenth
Spinal accessory, or eleventh.
Hypoglossal, or twelfth.

PLATE III



Topography of the Cranial Nerve-nuclei of the Floor of the Fourth Ventricle. (Morat.)

The efferent nuclei are in red and the afferent nuclei in blue.

Of these, three, the olfactory, optic, and auditory, are (mostly afferent) nerves of special sense; five, the motor oculi, pathetic, abducens, facial, and hypoglossal, are chiefly efferent or motor nerves; while the remaining four, the trigeminal, glosso-pharyngeal, vagus, and spinal accessory, are of mixed functions—special sense, general sensibility, (touch, pain, myesthesia, heat, cold, etc.), trophism, motion, and vasomotion in various combinations, whose details are not yet in all cases sure. For detailed information as to the cerebral origins, the distribution, and the functions of these complex groups of afferent and efferent nerve-paths the reader is referred to text-books of anatomy and of the physiology of the nervous system.

FIG. 45

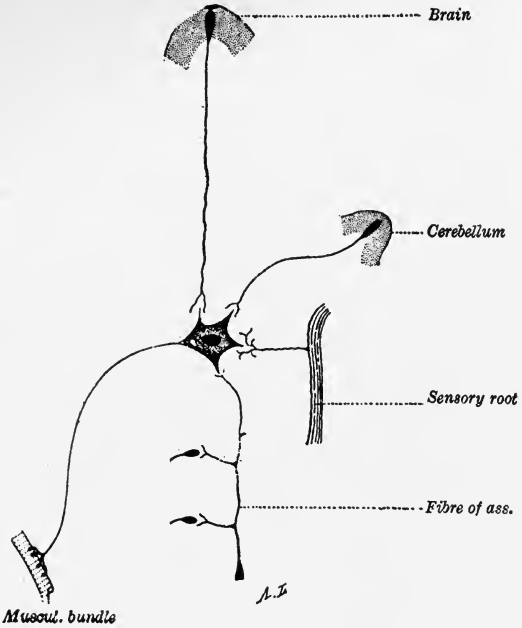


Diagram showing the collection of different sorts of influence by a motor root nerve-cell. (Morat.)

The Spinal Nerves.—These are thirty-one in number, on either side of the body. Each arises by two roots, an anterior and a posterior. The former root is mostly motor, vaso-dilator, "secretory," and "trophic"; the latter mostly sensory. Each divides into two trunks, one leading to the tissues of the back, and the other, much the larger, to the remaining parts of the body-trunk and to the limbs. We need do no more than to explain some of the principles of action of these afferent, inward, and efferent, outward, impulses and to summarize for reference purposes the basis of distribution of the motor nerves, showing the sensory distribution so far as it is dermal by an illustration. The process here outlined is on the basis of the neurone theory; should the nerve-cells be proved to be only trophic centers, material changes would of necessity result in our notions as to the mode of action of the spinal cord and especially regarding its relations to the spinal nerves.

The anterior roots, mostly efferent in action, receive their impulses from many-branched neurones situated in the gray matter of the cord, and more usually in the anterior (ventral) horns of this gray matter. In the most complex animals each ventral root is made up by combination of a row of rootlets, and each rootlet represents in miniature the whole root, the spinal cells in connection with them coming from slightly different levels of the cord. By this arrangement it is brought about that no root or rootlet represents a single muscle, but rather in part all the muscles of a functional group. Each muscle, moreover, is thus innervated from several (three or four) segments. In some parts of the cord, notably those representing the neck- and limb-muscles, the anterior root-cells are distinctly collected into groups, each group probably innervating collectively a group of muscles. The largest motor cells probably control cross-striated (skeletal) muscles, while the smaller ones may innervate the muscle-fibers ("unstriated") of the bloodvessels and of the viscera. Cells for flexion and cells for extension of a joint, for example, seem to lie intermingled in the same segments of gray matter. Both sorts of cells are probably (Sherrington) actuated at every movement of the joint, flexor or extensor, one set being stimulated to actuate and the other to inhibit. Sherrington notes the discovery by Golgi that from the neuraxones of some spinal efferent root-cells "side-fibers" are given near their origins. These may conduct efferently into the axone, but for what purpose is not known; von Lenhossek terms them axo-dendrites.

Fig. 46

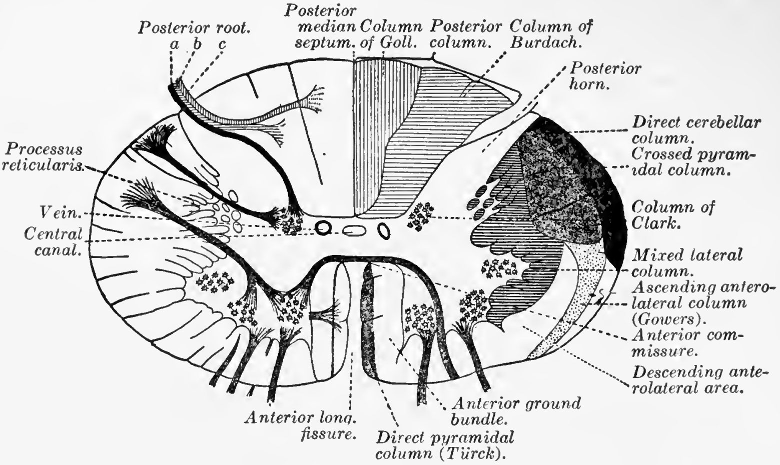


Diagram of the physiological structure of the spinal cord. (Ziehen, von Bardeleben, and H. Häckel.)

The functions of the impulses passing in the anterior roots are various but not yet definitely understood. Most conspicuous is their function of *controlling the cross-striated muscles* of the body, these impulses being perhaps of two phases, actuating and inhibitory. The starting-point of these influences is probably in the cortex of the hemispheres anterior to the Rolandic fissure. These impulses, then, are productive of voluntary or deliberate movements. It is possible that many of these impulses start in the cerebellar cortex. In the case of reflexions, the incitement of the motor neurones comes from other neurones interlacing with them and thereby usually from the periphery. As we have just seen, each muscle is innervated by the fibers of several roots and so controls in part a whole functional group of muscles, especially in the hands and feet. *Smooth muscles* in the hollow viscera are in part actuated through the anterior roots, notably those of the uterus, urinary bladder, and the skin. Another sort of influence passing outward in the ventral roots is that of *vaso-motor action and tone,* the probably two-phased influence which so essentially adapts the size of the arteries to the body's requirements both local and general. One phase is vaso-constrictor while the other is vaso-dilator. Whether the latter is an inhibitory influence on the former or a contractile effect is not yet certain. Impulses which bring about the *secretion of sweat* pass out of the spinal cord in the anterior roots. This stimulus is either secretory in the proper sense of the term or only an effect of vaso-dilatation. Which, it is still undecided, largely because of the slight histological doubt as to whether nerve-fibers enter epithelial cells in all cases. Similar uncertainty sometimes exists about a supposed "*trophic*" (chemic?) *influence* exerted by the central nerve-system. Whatever the nature of this undoubted control (proved by a host of pathological cases as well as by the phenomena following nerve-suturing), the ventral, anterior, roots are the paths of its conveyance outward.

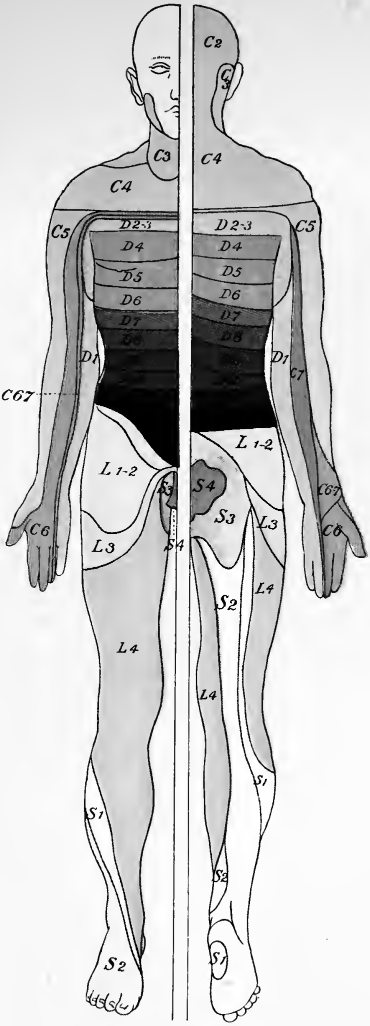
The *posterior spinal roots* (so far as their nerve-cells at present imply) have their origin in ganglia, more or less ellipsoidal in shape, to be found one on each dorsal root close to its junction with the ventral root. The accompanying diagram (Fig. 46) indicates the probable finer structure of these ganglia and the relations of the ventral and dorsal fibers to them. The afferent, "sensory," nerve-cells for the most part have two axones. Each of these divides into two medullated branches, one having grown from the cells of the "neural crests" into the posterior horn of the cord's gray matter, and the other centrifugally into the body's tissues and periphery. Some of the ganglion-cells are multipolar, like those of the sympathetic, while others are bipolar, but with short branching axones which communicate (Dogiel) with the other sort of bipolar cells. Fibers, not numerous, from the sympathetic ganglia communicate freely with the cells of these spinal ganglia. In the cord's gray matter the dendrites of these neurones associate freely with hosts of nerve-cells and neurones, motor and sensory, as well as with many of a purely associative function and position. Fibers from the ventral ("sensory") root pass round through the ganglion and centripetally into the anterior root. This gives the so-called recurrent sensibility of the anterior roots observed in mammals and birds; it does not obtain in the frog.

For diagnostic purposes, the following table of the relations of the skeletal muscles and the spinal anterior roots as compiled by Kocher from human clinical material is of importance:

Roots.	Muscles.
Cervical I.	Small neck-muscles, sterno-hyoideus, sterno-thyroideus, omohyoideus.
“ II.	Sterno-cleido-mastoideus, trapezius.
“ III.	Platysma myoides.
“ IV.	Scaleni, diaphragma.
“ V.	Rhomboidei, supra- and infra-spinatus, coraco-brachialis, biceps, brachialis anticus, deltoideus, supinator longus and brevis.
“ VI.	Subscapularis, pectorialis major and minor, pronator radii teres, pronator quadratus, latissimus dorsi, teres major, triceps, serratus magnus.
“ VII.	Flexors and extensors of the wrist.
“ VIII.	Long flexors and extensors of the fingers.
Dorsal I.	All the small muscles of the hand and fingers.
“ I–XII.	Muscles of the back.
“ I–XI.	Intercostals.
“ VII–XII.	Muscles of the abdomen.
Lumbar I.	Lower abdominal muscles, quadratus lumborum.
“ II.	Cremaster.
“ III.	Psoas, sartorius, iliacus, pectineus, adductors of the thighs.
“ IV.	Quadriceps femoris, gracilis, obturator externus (?).
“ V.	Gluteus medias and minimus, tensor fasciæ latæ, semitendinosus, semimembranosus, biceps femoris.
Sacral I.	Pyriformis, obturator internus, gemelli, quadratus femoris, gluteus maximus, long extensors of the foot and of the toes, peroneus longus and brevis.
“ II.	Long flexors of the foot and of the toes, large calf-muscles, small foot-muscles.
“ III.	Ejaculatory and verumontanum muscles.
“ IV.	Sphincter and detrusor vesicæ, sphincter ani.
“ V.	Levator ani.

The exact varieties of afferent messages which the posterior roots conduct into the cord and so to the cortex cerebri and elsewhere in the brain have not been defined. Whatever "sensations" arrive at all, peripherally started, come into the great highway and coördinating center through these roots (save for those which come by way of the afferent cranial nerves). Touch, pain, muscle and joint-sense, heat-sense, cold-sense, and that ill-defined sensibility which the viscera have, are among the sorts of impressions (some conscious, but many more certainly at least subconscious) conveyed inward by these ventral roots. Much as in case of the efferent roots, the areas supplied by different roots overlap, especially in the extremities, so that every portion, at least of the skin, is supplied with sensation by at least two roots. In some cases the area supplied by the roots of one side extend somewhat into the other side of the body. Head and Dana have shown how certain visceral areas are in close connection with certain regions of the surface of the body—the so-called principle of referred pain. Thus, for example, in the same direction, hip-joint disease produces pain at the inside of the knee, and

PLATE IV



Scheme of the Various Areas of Sensibility Represented by Spinal Segments (the front of the body on the left of the picture, the back on the right). (Kocher.)

The letters *C*, *D*, *L*, and *S* refer to the cervical, dorsal, lumbar, and sacral segments respectively, as indicated further by the numbers.

many similar relations are being gradually worked out clinically. Landois gives the following as the general spinal distribution of the viscera: The heart and lungs are represented by the tenth cranial and by the upper thoracic nerves; the stomach, small intestine, liver, spleen, and pancreas by the vagus and the middle inferior thoracic and upper lumbar nerves; the adrenals, kidneys, testicles, ovaries, and uterus by the middle and lower thoracic and the upper lumbar nerves; the rectum, prostate, penis, uterus, and vagina by the sacral nerves and the hypogastric plexus, which last in turn is supplied from the lower dorsal and upper lumbar cord. In certain animals some motor fibers pass out through the dorsal roots (Morat and Bonne) and in some mammals the vaso-dilators, for certain parts at least, go by the same unsymmetrical paths. If these conditions obtain in man, however, their details have not as yet been made out.

FIG. 47

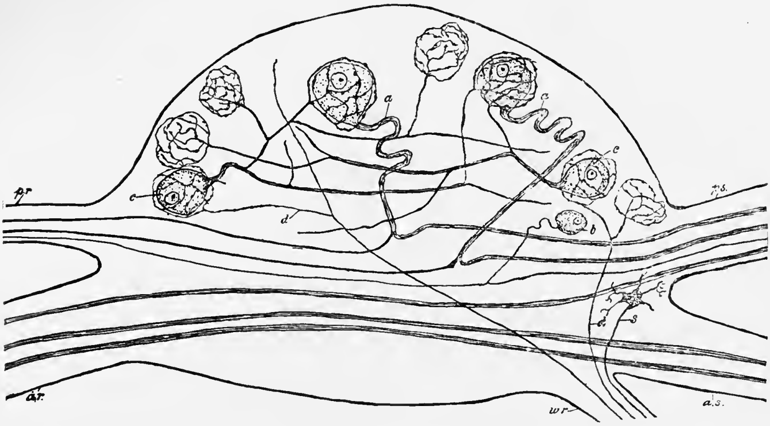


Diagram of the neurones of a spinal ganglion, showing their relations: *p.r.*, posterior root; *a.r.*, anterior root; *p.s.*, posterior branch, and *a.s.*, anterior branch of a spinal nerve; *w.r.*, white ramus communicans; *a*, large, and *b*, small spinal ganglion cells with bifurcations; *c*, one of Dogiel's types of ganglion cells; *s*, multipolar cell; *d*, nerve-fiber from a sympathetic ganglion terminating in pericellular plexuses. (Dogiel and Böhm, and Davidoff and Huber.)

In Plate IV is given the distribution of the spinal posterior roots, according to Kocher as he finds it indicated by human pathological inquiry, the two halves of the picture representing respectively the front and the back of a man. A similar map made by Head mostly corresponds.

The Sympathetic Nerves.—The quasi-system of neural structures known by the name sympathetic, consists of three sets of ganglia and the fibers connecting and serving them. The first set of ganglia are those of the *gangliated cord,* about twenty-two in number on each side. They extend from the base of the skull to the coccyx, and are classed as cervical, dorsal, lumbar, and sacral. The second set are the ganglia (solar, hypogastric, pelvic, etc.) of the *prevertebral* plexuses. The third set are the much smaller *peripheral* groups of cells situated in the various viscera (*e. g.*, in the plexuses of Auerbach and the no less essential ganglia of the uterus and the heart). The cells of these various nuclei connect directly by contact with the medullated, white neuraxones of cells seated probably in the lateral horn of the spinal cord or in the homologous region of the brain (Hüber). The cells of the *gangliated cord* (but not those of the prevertebral ganglia) send outward fibers (known as those of Remak) which are "gray," *i. e.*, non-medullated. These are distributed exclusively to smooth muscle-fibers and perhaps to epithelium all over the body by way of the spinal nerve-trunks. The branches to the spinal nerves and beyond are the so-called gray rami communicantes, while the fibers arising in the gangliated cord above referred to are the white rami. The latter are found only from the dorsal and first one or two lumbar spinal nerves, but the gray rami extend to each of the spinal nerves, each ganglion sending inward axones to two or three of them. The *prevertebral ganglia* send non-medullated fibers to the viscera of the thorax and the abdomen, continuing, doubtless more or less altered, the messages they receive from the gray matter of the cord or from the small much-branched cells of the ganglia of the gangliated cord. The *peripheral ganglia* in similar manner retail to the tissues in which they are situated the motor (and secretory?) influence they receive from the cord's gray matter direct, from the ganglia of the gangliated cord, or from the prevertebral ganglia. Dogiel's recent work on the heart-action well illustrates the work of these peripheral ganglia.

Fig. 48

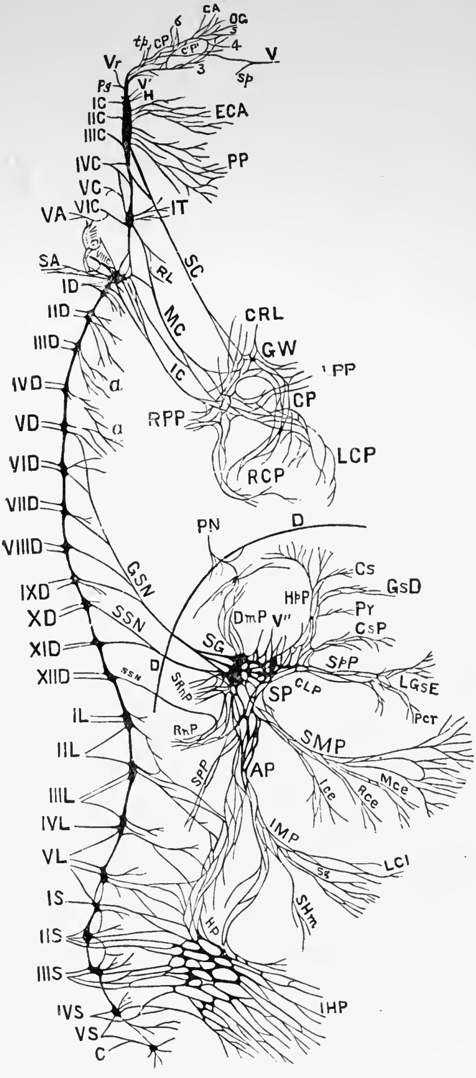


Diagram of the sympathetic. (Flower.)

The pre-ganglionic fibers are those which connect the cord and the ganglion-cell, while the post-ganglionic fibers are peripheral to the latter. It appears that all the impulses given out by sympathetic fibers pass over both of these paths. In other and more direct terms, it is not apparent on the neurone theory that impulses originate in the sympathetic ganglia, the presumption being rather that the exciting influence always comes more or less directly from the central nervous system proper. Perhaps, nevertheless, influences do originate in these ganglia as well as in other knots of neuro-fibrils or masses of nerve-cell tissue. This problem is still unsolved. The fact that, under abnormal conditions, the heart, for example, may continue its beat after all "nerves" attached to it have been "cut," does not prove that normally the organ does not receive continually influences from the complex medulla, through these peripheral ganglion-cells. On the other hand, the same phenomena demonstrate that either the heart-muscle or the nerve-cells within it have automatic powers dependent on their own metabolism, at least for a time. Between these two theoretic drifts the exact balance has not yet been made: we do not know, in fine, how much or how little in the way of actual energy-liberation the nervous system performs. If it liberates much exciting energy we have no reason to deny to the cells of the sympathetic their proportion of this essential work (*e. g.*, in the heart or the uterus).

The sympathetic, unaided by other autonomic nerves (see below) actuates the bloodvessels, glands, and smooth muscles of the skin, the bloodvessels of that part of the intestine between the mouth and the rectum, of the glands opening into this portion of the gut, and possibly also the spleen and the internal generative organs. In general terms, then, if we may accept this estimate tentatively as correct, it is the function of the sympathetic to innervate much of the body's smooth muscle tissue wherever its fabric, extending so widely through the body, occurs.

For example, the pilomotors, the tiny muscles whose contraction erects the hairs, are under this kind of influence. This suggests one conspicuous way in which the sympathetic is controlled—namely, from the midbrain, at least in emotional conditions. The inhibitory effects of the sympathetic action are as important, if not as widespread, as those of the actual production of movement. A second possible immediate duty of these nerves is still somewhat in doubt histologically—namely, the actuation of secretion directly by innervation of the secretory protoplasm. If this connection between nerve and cell interior regularly occurs, the sympathetic is the agent of the control. Where it does not occur, on the other hand, secretory control is brought about through vasomotion. As the sympathetic surely directs this process, secretion in any case is under the management of this "system."

But besides these two efferent functions (whether from the central nerve-system or only from the sympathetic's vertebral or prevertebral or peripheral ganglia) the sympathetic has minor afferent functions of various sorts. These impulses pass inward apparently on both the gray and the white rami, although only the latter, according to Langley, has been actually proved to contain them. It is through these afferent fibers that the viscera possess that indefinite sort of touch sense which they have, and their pain sensations. The afferent fibers are only few compared with those which are efferent: Langley and Anderson found one-tenth of the medullated axones in the hypogastric nerves to be afferent. It is by these latter fibers that the phenomena of referred pain are brought about. It cannot be doubted that the afferent nerves of the sympathetic are more widespread than at present we actually know them to be.

The functions of the sympathetic and of the other autonomic nerves are tabulated nearly thus by Langley:

	Sympathetic.	Other Autonomous Nerves.
Midbrain's autonomous nerves.	Contraction of the iris dilators. Contraction of the smooth orbital muscles. Contraction of the ocular arteries.	Contraction of the iris. Contraction of the ciliary muscles.
Bulbar autonomous nerves.	Acceleration of the heart and contraction of the bloodvessels of the mucous membranes of the head. Inhibitory and motor action on the smooth musculature of the gut from the œsophagus to the descending colon. ? Secretion in the stomach, liver and pancreas. Contraction of the bloodvessels from the œsophagus to the descending colon. ? Contraction of the bloodvessels of the lung. Contraction of the bloodvessels of the intestines. Contraction of the smooth musculature of the spleen, ureters, and internal sexual organs. Contraction of the smooth muscles and arteries, and secretion in the skin.	Inhibition of the heart and (dilatation) of the bloodvessels in the mucous membranes of the head. Motor and inhibitory action on the smooth musculature of the gut from the œsophagus to the descending colon. (?) Secretion in the stomach, liver, and pancreas.
Sacral autonomous nerves.	Contraction of the arteries of the rectum, anus, and external sexual organs. Inhibition and contraction of the smooth muscle of the descending colon, rectum, and anus. Inhibition and contraction of the bladder. Contraction (and ? inhibition) of the urethra. Contraction of the muscles of the external sexual organs.	Inhibition of the arteries of the rectum, anus, and external sexual organs. Contraction of the smooth musculature of the descending colon, rectum, and anus. Contraction of the smooth muscle of the anus. Contraction of the urinary bladder. Inhibition (and ? contraction) of the urethra. Inhibition of the muscles of the external sexual organs.

Other Autonomic Nerves.—Langley has introduced the term autonomic to include "the contractile cells, unstriated muscle, cardiac muscle, and gland cells of the body, together with the nerve cells and fibers in connection with them. The autonomic nervous system consists of the sympathetic system, which we have already in part considered, of the cranial autonomic system, the sacral autonomic system, and the enteric system." The nerves supplying the sorts of tissue first-named above not supplied by the sympathetic come from the other autonomic nerves, cranial, sacral, and enteric. In the most general terms the *cranial autonomic nerves* (the third, seventh, ninth, tenth, and eleventh) supply certain parts and functions at the upper end of the alimentary canal. The *sacral autonomic system* (which are all fibers connected with the pelvic nerve, "nervus erigens") serves various parts near the lower end of the same canal—rectal muscles, generative muscles, vasomotor muscles, etc. The *enteric system* consists of the plexuses of Auerbach and of Meissner. These are unique neural nets extending from the middle of the esophagus to the anus. Whether these two systems of nerve-cells and fibers are connected with the cord and brain by sympathetic or by cranial and sacral autonomic fibers, is as yet not known. They are so unlike the other nerves of the sympathetic that they may be properly classed separately.

This division of what used to be known as the "sympathetic system" into the sympathetic, cranial, sacral, and enteric systems is a step in the important direction of unravelling the set of nerve-fibers whose general functions we have just suggested. The danger is rather of too little analysis and classification than of too much, for scarcely yet is the complexity of the nerve-fibrils necessary to the actually observed complexity of function adequately realized.

THE NERVOUS IMPULSE.

Despite the large amount of work put upon it, the real nature of the nervous impulse is today as uncertain as ever it was. There have been many speculations as to the means by which the nervous influence is transferred along the nerve. Some of these now appear absurd indeed to us. For example, it was at one time supposed that the nerve-fiber was in effect a string which was in some way pulled on by the brain, much as a boy pulls a jumping-jack. Another supposition was that the nerve was a tube and that the impulse passed literally in a stream through it. Some thought that the movement along the nerve was a mechanical vibration, as others still think that it may be a vibration of a molecular sort. More recent suppositions have been that the impulse is of an electrical nature, such as runs along a telegraph wire. A still more recent supposition is that it is a progressive coagulation of a colloidal material of the nerve tissue brought about by ionic influences. Finally, we may note that it is commonly thought that the impulse is a chemical change of some sort passing along the nerve. As is well recognized, there is a tendency in Physics today to unify so-called molecular, electrical, and chemical changes. It becomes more certain continually, therefore, that the nervous impulse is of a nature somewhat akin to these. That it is any one of them alone, we cannot at present say. Whatever be the nature of the impulse, it can be shown that it passes progressively from one portion of a nerve to the next at a rate not very rapid, and that it produces various changes on its way, especially of an electrical nature. Whether there is an electrical variation during the passage along a nerve which is absolutely normal in an unharmed animal, we are not certain. It is probable that an exceedingly small amount of heat also is produced by the process of nervous conduction, although all attempts to measure it have so far proved futile, even with very delicate electrical thermometers.

Whatever its nature, the nervous impulse conveys exciting energy rather than efficient energy. It is the protoplasm of the muscle or the epithelium which provides the energy for its work—the nervous impulse only activates it and changes it from potential to kinetic. The nerve-energy is many millions of times the smaller in amount.

The speed of the nervous impulse varies in different conditions and in different nerves. Thus, in general, heat somewhat accelerates this as it does most other functions, and we find the rate higher in the so-called warm-blooded animals (homotherms) than in cold-blooded animals (poikilotherms). A frog's sciatic shows a rate varying between 10 and 27 meters per second, according to the time of year, etc. In the afferent nerves of man the speed is 45 or even 50 meters per second. In the efferent channels the rate of conduction is less, and ranges from 30 to 35 meters per second. It seems to vary not a little in different nerves even of the same general sort. (See Appendix, Experiment 79.)

Nerves conduct their currents in *both directions*, in the abnormal as well as in the normal direction. This is readily shown in the common laboratory experiments with the sartorius muscle split at its iliac end. (See Appendix, Experiment 77.) Whether or not the nerves of the uninjured animal ever transmit impulses in two directions is not known. The ordinary presumption is that they do not, because of the arrangement of their terminal connections, if for no other reason.

Chemical agents effect the conductivity of nerves in various complicated ways. (See the experiments in the Appendix.) For example, carbon dioxide poured about an isolated frog's sciatic lessens the excitability of the nerve but does not change its conductivity. On the other hand, the vapor of ethyl alcohol stops the transmission of the nervous impulse but does not lessen the irritability of the nerve-protoplasm. From work by Overton and by Myer it appears likely that this action of alcoholic vapor is the type of the action of all anesthetics on the nervous system.

Electricity in constant current acts in a more complicated way, for at the anode the excitability is lessened (anelectrotonus), while at the cathode it is increased (catelectrotonus). The conductivity is diminished.

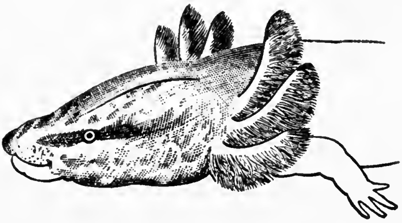
By these effects of electricity and of the agents mentioned before, it is clear that while conduction is the specialized function of nerve, the tissue still retains the irritability common to all protoplasm, and the two may vary independently of each other. The conductivity of the nerve, then, whatever its specific process, is something different from the irritability of other tissues. The nervous impulse is readily actuated not only by electricity, but also by rapid changes of temperature either way, by mechanical impact, or by irritating chemical substances. However set in movement, the nervous impulse is accompanied or preceded by currents which are truly electrical, as may be readily shown by instruments for the indication and measurement only of electricity. It has never been proved yet that nerves originate the impulses which pass over them. The energy necessary for starting the impulse comes probably either from the bodily tissues (mechanically, thermally, chemically, or electrically acting) or else from outside the organism altogether. This must not be stated, however, too absolutely, for the nerve-tissue has metabolism as well as the other tissues, and an amount of energy proportional to the mass of the nervous system may be generated within it. Probably this energy or part of it goes to the origination of nervous impulses as well as to supporting them. Although so important, this question has as yet no sort of certain answer.

CHAPTER III.

RESPIRATION.

Of all the functions of living animals, respiration perhaps is the most general. The union of oxygen with the tissues and the removal of the consequent oxidation-products is at the basis of metabolism. We may define respiration then as essentially an interchange of oxygen and of carbon dioxide between the tissue-protoplasm and the atmosphere. So long as these requirements are fulfilled, whatever the means, however superficial or deep the tissues lie, respiration is going on. In man it is obvious that almost all of his tissue-cells are so far away from the atmosphere that there can be no direct interchange between them and the oxygen and carbon dioxide in the air. Even the skin in the case of man performs no respiration directly with the atmosphere, for its outer layers are essentially dead, while its inner layers are supplied much as are the inmost tissues of the body. Francke estimates that an average human body is made up of 400,000,000,000,000 cells, while another estimate makes the number 26,500,000,000,000. Every one of these requires oxygen, and exhales carbon dioxide. The biological problem then in the case of man is how to supply an abundance of oxygen to all these cells and how to remove the products of their combustion. Thus, in practice the conspicuous part of respiration is the mechanical means of taking in and giving out respiratory gases. The essential process, however, is the interchange of these gases between the living protoplasm and the atmosphere. The pulmonary part of the process is called external respiration, while the essential intercellular interchange is called internal respiration.

Fig. 49



Head and gills of the mud-puppy (Necturus), to show direct respiration in a relatively highly developed animal. (Dalton.)

The Chemistry of Respiration Proper.—Before taking up a systematic description of the respiratory process as a unified system of events, the chemical relations of the tissues to the atmosphere must be briefly discussed, and in a most general way the biochemistry of oxidation.

Oxidation is a process probably more nearly universal on the planet Earth than any other chemical reaction with which we are familiar. One-half of the crust of the world is oxygen, as is more than one-fifth of the atmosphere and about four-fifths of all the water. Oxygen is the source of all "combustion," and furnishes to organisms one of their sources of energy. Not only all animals but also all plants (a few indirectly) are dependent on oxygen for their living. Oxygen combines with all "elements" so far isolated (except fluorine). This fact partly accounts for its very wide distribution in nature. The protein particle contains oxygen, and so does the carbohydrate molecule, the molecule of fat, and that of albuminoid. Moreover, each of these molecules contains carbon, with a strong affinity for oxygen, and this, when satisfied, gives rise to carbon dioxide. Later on, in the chapter on Nutrition, we shall study somewhat more in detail the metabolic processes of the body. The important fact now is that the atmosphere and the food contain both oxygen and carbon, and that these are prominent also in the animal tissues. Life in its basis is but a physiological succession of anabolism (building-up), and of katabolism (tearing-down), the vital animal energies being made kinetic, apparent, useful, in the latter or katabolic process. Even tissues excised from the body of an animal respire, that is, absorb oxygen and give off carbon dioxide. Thus, Bert obtained from the tissues of a dog recently killed an interchange of the two gases in twenty-four hours as follows:

RESPIRATION OF EXCISED TISSUES.

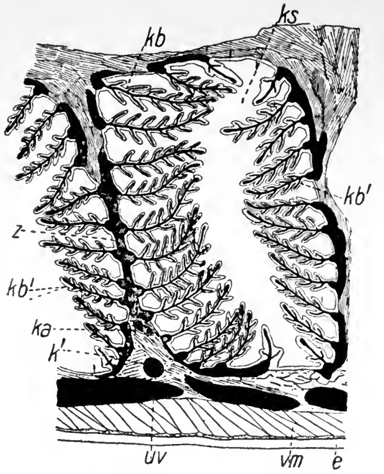
Cubic centimeters of gas per 100 grams of tissue.

Tissue.	Oxygen absorbed.	Carbon dioxide excreted.
Muscle	50.8	56.8
Brain	45.8	42.8
Kidney	37.0	15.6
Spleen	27.3	15.4
Testis	18.3	27.5
Broken bone and marrow	17.2	8.1

These quantities are interesting because they prove, among other things, that respiration is inherent in living tissues. A molecule of protoplasm in the dying muscle from a dog respires quite as does a molecule of the protoplasm of an ameba or of a human spermatozoön. Nothing further is needed to prove that the animal combustion which requires the oxygen and produces the carbon-dioxide takes place in the tissues themselves, and not for the most part in the circulating blood, as was formerly supposed. The blood is a tissue and has its share of direct oxidation, but most of the oxygen absorbed into the body goes as directly into the protoplasmic cells of the tissues as the complexity of the structural conditions will allow.

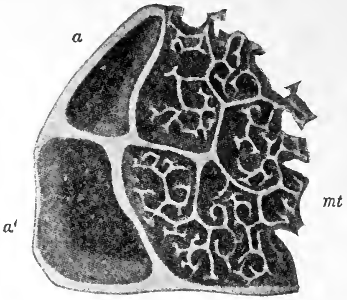
The oxygen absorbed furnishes one of the elements of the combustive katabolism by which life is manifested. Partial katabolism is apparently always primary and oxidation secondary—namely, in the combustion of the first products of the katabolism. About the details of this union of the oxygen and the tissue-molecules we know but very little. We are sure what some of the end-products of these complicated chemical reactions are, as will be seen later in the chapter on Nutrition; and we know that carbon dioxide is the chief of these end-products, the most universal in the tissues. It is the one representative of the actual combustion of the cells, especially of the fats and carbohydrates of the tissues and of the still circulating food as well. When wood or coal is burned in the air, oxygen is used up and carbon dioxide, the union-product of the carbon and the oxygen, is given off. Moreover, heat is liberated, and, with the proper mechanisms attached, energy of several forms. In these respects, at least, bio-metabolism is like the oxidation in a steam-engine's furnace. Because of these similarities it has long been customary to speak of the combustion going on in the body, of the "life-giving oxygen," of the food as the

FIG. 50



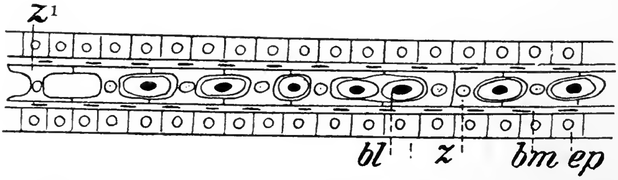
Section through the gills of the lamprey (Ammocaetes): *ks*, gill-cavity; *kb*, anterior, and kb^1, posterior gill-plates; *z*, septum; *ka*, gill-artery; *uv*, vein; *vm*, ventral body-muscle; *e*, epithelium. (B. Haller.)

FIG. 51



Section through the nasal cavities of the duck-bill (Ornithorhynchus). (Zuckerkandl.)

FIG. 52

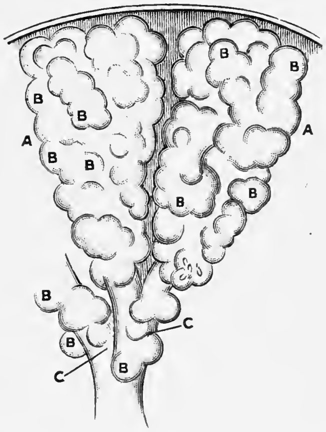


Diagrammatic section of the gill-plate of a fish: *ep*, epithelium; *bl*, erythrocytes; *z*, cells of the bloodvessels; *bm*, basal membrane; *z'*, bloodvessel. (Marianne Plehn.)

fuel of the organism, of the lungs as the chimney, etc. Such similes are instructive and fairly well represent the facts so far as they go.

A living organism, however, is very different in its working conditions from a steam-engine plant. It is more automatic, less dependent on external conditions, has principles and tendencies of its own, and habits structural and functional, in a much greater degree than has the steam-engine and its boilers. One unlikeness is fundamental and must be specifically noted here. Whereas in the boiler-furnaces the draft, that is the relative abundance of oxygen, determines directly the speed and vigor of the combustion, in organisms the combustion or *metabolism* is largely the controlling agent, and not the oxygen. It is not possible by a "forced draft" to hasten beyond its normal maximum the combustive metabolism in living tissues. They absorb no more oxygen when the animal breathes only this gas than they do from the ordinary, average-pure atmosphere to which the tissues are adapted by evolution. Indeed, when the arterial blood has been forced to absorb one-third more than its normal quantity of oxygen by subjecting the animal to an oxygen-pressure of six atmospheres the animal dies, from a lowering of the vital metabolism of some or other of the tissues (Paul Bert). The metabolism then determines the amount of oxygen needed by the tissues, rather than that the supply of the gas normally affects the tissue-metabolism.

Fig. 53

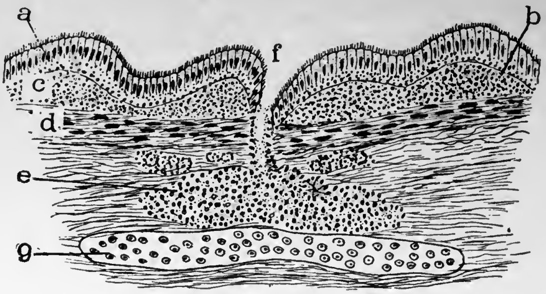


Two infundibula of human lung: *a* and *b*, air-sacs; *c c*, two ultimate bronchi. (Kölliker.)

Various conditions help to determine the amount of oxygen consumed by the tissues as also the amount of carbon dioxide excreted. Anything in general which increases the metabolism either in intensity or in extent enlarges the respiratory exchange. Voit and Pettenkofer showed that in a man of average weight, say 70 kg., about 700 gm. of oxygen are required in twenty-four hours, while about 800 gm. of carbon dioxide are given off. But during rest the 700 gm. required in average activity may decline to 600 gm. and the 800 gm. of carbon dioxide excreted may decrease even more than 100 gm. On the other hand, during hard muscular work the consumption of oxygen may arise to 1100 gm. daily and the amount of carbon dioxide to nearly 1300 gm. As an average for the adult's demand for oxygen, Zuntz states about 14.5 gm. per kilo of body weight in twenty-four hours.

The Respiratory Mechanism.—There is no space here for a description of the gross and microscopic anatomy of the respiratory mechanism. This must, however, be thoroughly kept in mind in all its details if the breathing function is to be really understood. The reader must have in mind the structure of this functional system, from the outer edge of the nostrils to the diaphragm—the nasal fossæ, larynx, trachea, bronchi, lungs, pleural cavities, thorax, diaphragm, and the nerves which are concerned in the movements of all of these. We can here mention a few only of the conditions which are the most essential for our purpose. The nose, in man, is very largely a respiratory organ.

Fig. 54



Section of trachea: *a*, ciliated epithelium of inner wall; *b*, basement membrane; *c*, elastic connective-tissue layer; *d*, muscular layer; *e*, gland; *f*, gland-duct; *g*, cartilage lying in the fibrous coat. (Bates.)

Fig. 55

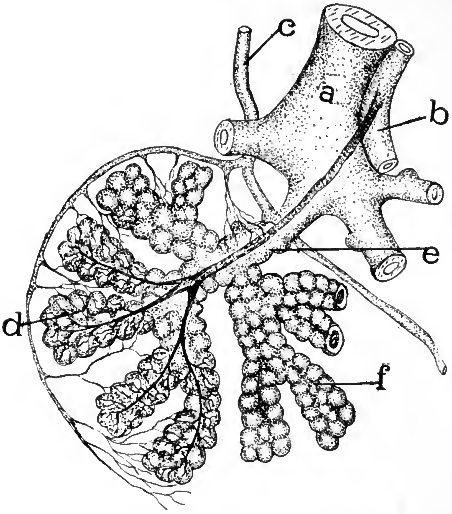


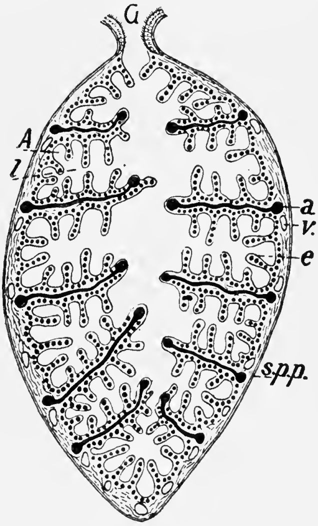
Diagram of a lung lobule: *a*, is placed in a bronchial tube; *b*, branch of pulmonary artery; from this a branch passes to be distributed to the alveoli of the lobule as seen at *d;* *e*, vein which passes on the outside of the lobule to come into relation with the arterial capillaries in the lobule; *e*, lobar bronchiole; *f*, infundibulum in which are seen the alveoli. (Bates, modified from Stoehr.)

Its vibrissæ (the hairs) strain out large foreign particles in the draughts of air. The organ of smell not only warns us of some sorts of unwholesome air, but makes us breathe more deeply when the air is sweet and fresh. The nasal fossæ are larger and more complex than is commonly supposed, and are lined with very thick vascular mucosa, which warms to the body temperature and saturates with moisture the incoming air. Both of these modifications are necessary to prevent injury to the sensitive bronchi and the lungs. The larynx is the organ of the voice, and is discussed later on. It is rather a hindrance to respiration in the long run than a respiratory organ, although the closing-down of the epiglottis over the trachea and bronchi at each act of swallowing protects the latter from frequent danger. The trachea is ample in diameter, and kept so by strong cartilaginous rings. The ramifying bronchi finally becomes muscular to a certain extent, and so somewhat control the air-supply to the lungs.

The Lungs.—These are the proper organs of respiration, and must be fully understood in their structure and mode of action. The two lungs are separated by the mediastinum. The right lung weighs about 625 gm. and the left not far from 565 gm. The specific gravity of the lung-tissue, according to Gray, is from 345 to 746, water being 1000. To the touch, it is a highly elastic, spongy, and crepitating mass; and in appearance it ranges from a light pink at birth to almost black in old age, darkening largely from the coal- and other dust slowly collecting in it.

According to Rainey, the small bronchi after entering a lobule of the lung subdivide from four to nine times conformably to the size of the lobule, the smallest branches being about two-thirds of a millimeter (0.63 mm.) in diameter, or smaller. These smallest subdivisions of the air-tubes then lose their cylindrical shape and structure and continue onward a short way as *infundibula.* These are irregular tubes from which the short alveoli dilate in various places and directions. Indeed, bronchioles of 2 mm. diameter often have alveoli extending outward from them, as shallow and rounded vesicles. Those are the ultimate chambers for air in the lungs, and it is from them and through their walls that the two respiratory gases osmose and diffuse in their respective directions, inward and outward.

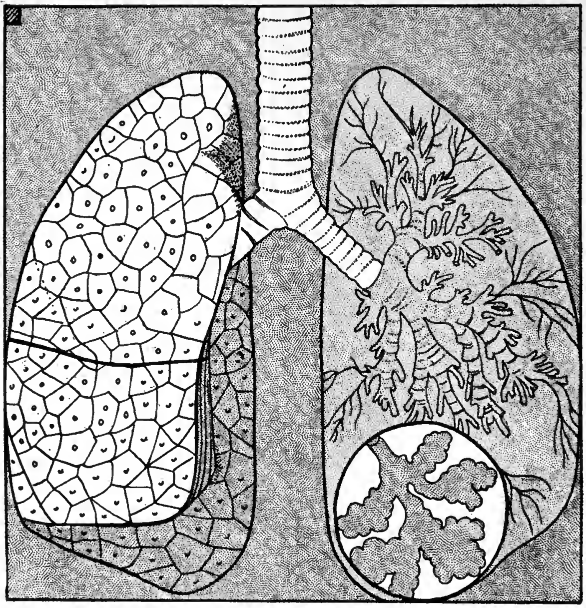
Fig. 56



Scheme of the lung of a frog to show its relatively simple lobulation: *G*, glottis; *l*, lobules; *A*, alveoli; *e*, lung-epithelium; *a*, afferent artery; *v*, vein; *s.p.p.*, serous covering. (Renaut.)

The *alveoli* or air-cells vary in diameter from $\frac{1}{8}$ to $\frac{1}{3}$ mm. They are composed of epithelium, strengthened with a thick network of elastic connective tissue. The epithelium is of two sorts, a large, flat, thin-celled variety like endothelium, and a kind composed of small flat polygonal nucleated cells. The latter lie singly or in small groups scattered among the cells of the former variety, and are, it is supposed, substitutes ready, after differentiation, to take the places of destroyed cells of the other variety. Otherwise their special purpose is quite unknown. It is possible that they may have some specific osmotic powers, as probably have the different sorts of epithelium of the uriniferous (kidney) tubules. (See page 246). The number of the respiratory alveoli in adult human beings has been estimated at 725,000,000. Bearing in mind the vastness of this multitude, it is easier to believe, what appears to be true, that the combined concave area of the alveoli is about 200 square meters, or more than one hundred times the entire superficial area of the body. This is the size of the air-layer exposed on what is functionally the periphery of the lungs. Its great size makes it possible to understand how the gaseous interchange can take place, for, as we shall see, the forces which bring about the osmosis back and forth through the alveolar wall are slight and can have, therefore, small intensive action. This lack of intensity is made up by

Fig. 57



Magnification of the lung-area by the alveoli. Were the lungs plain sacs instead of organs made up of 725,000,000 alveoli, their respiratory capacity would be only about one two-thousandth of what it is. This ratio is that of the small square to the large.

abundant extensity, as has just been seen and as is shown graphically in the diagram. A layer of air 200 square meters in size separated from a like extent of rapidly moving blood by only two layers of highly

FIG. 58

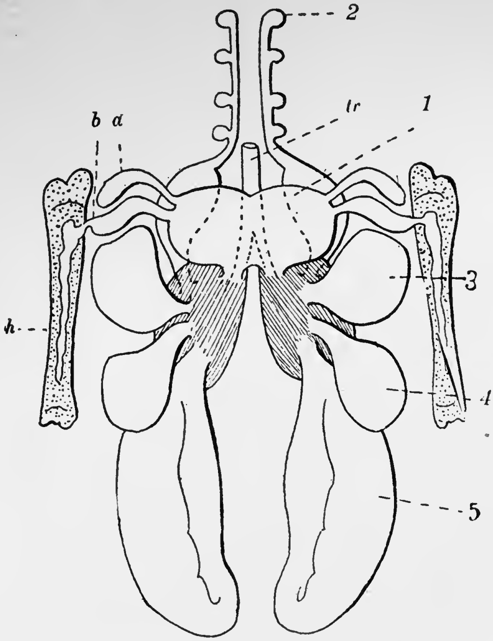
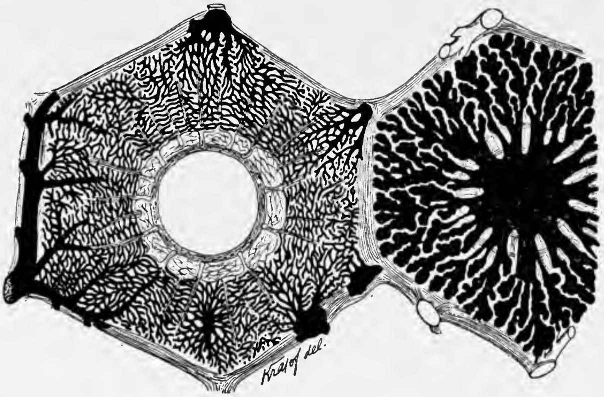


Diagram to show the relations of the air-chambers to the lungs in a carinate bird (*e. g.*, any American bird). The lungs are the shaded portion of the picture: 1, clavicular air-sacs; 2, cervical sacs; 3, anterior, and 4, posterior diaphragmatic sacs; 5, abdominal sac; *h*, air sac in the humerus. (B. Haller.)

FIG. 59

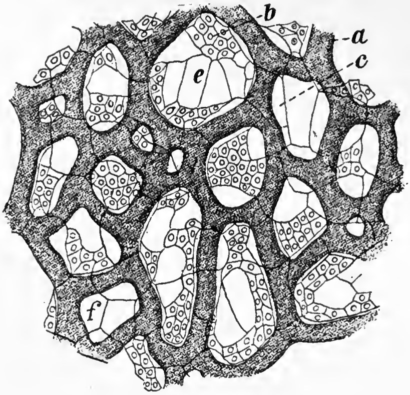


Two alveoli from the lung of a goose. The right-hand picture shows the air-spaces injected (black), while the left-hand view is that of the injected arterioles. (F. E. Schulze.)

permeable epithelium each $\frac{1}{1000}$ mm. thick, with a thin layer of lymph between them, might well serve as an organ with great capabilities! So closely are the alveoli packed together in the lung that besides them in these large organs there is little else except the capillaries.

The Capillaries.—From Fig. 57, representing the histology of the lung, the relation of the capillaries to the alveoli is obvious. The wall of these tubelets (the ultimate bloodvessels, and those which alone immediately supply the tissues) is simply one layer of flat epithelial cells, here called endothelium, cemented edge to edge so as to constitute a tube. Sihler claims that a plexus of fine nerve-fibrils surrounds the capillaries in all parts of the body. This layer of protoplasm is often less than one micron in thickness, and it practically lies in apposition to the alveolar wall. So crowded are these capillaries, however, all over the periphery of the alveoli that it is functionally almost a continuous surface. This endothelial layer, together with the alveolar surface (in contact with each other save for the universal moistening lymph), constitutes the osmotic animal membrane through which the processes of external respiration take place. This is the living protoplasmic layer to which the respiratory tubes conduct air and from which they lead it away into the atmosphere. We will next inquire as to the motor power of this ceaseless ebb and flow of waste and life-giving gases.

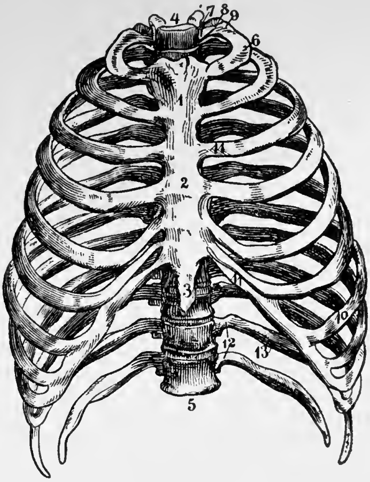
Fig. 60



The pulmonary epithelium of a young dove: *a*, capillary; *b*, cell-groups in the capillary flexus; *c*, contours of the larger epithelial cells; *d*, a capillary mesh-opening with two cell-islands; *f*, capillary opening without any cell-groups. (Elenz.)

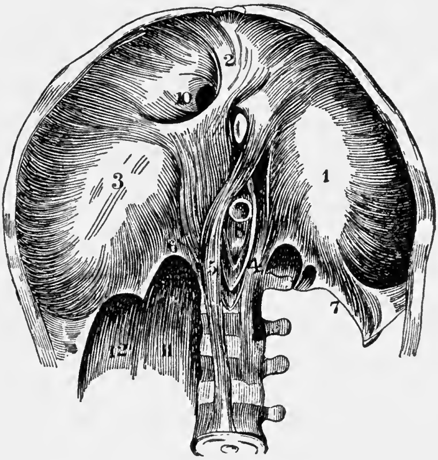
The Thorax.—This is a muscular, bony, and cartilaginous box adapted as a motor organ of respiration. The sides and bottom of this flattened and conical bellows are all more or less movable by means of muscles, of which the diaphragm is, functionally, the most important. The ribs are so shaped that when they are raised, largely by the external intercostal muscles, the capacity of the chest is increased laterally, antero-posteriorly, and to a slight extent upward. The fibers of the external intercostal muscles are arranged obliquely between the ribs in such a way that when the fibers shorten the ribs are drawn closer together. Thus, all except the top ribs are raised, as the accompanying diagram makes plain. The muscles which aid these intercostals are the levatores costarum, the scaleni, and the serrati postici. The quadratus lumborum connects the pelvis with the last rib, and by its tonic resistance holds the

Fig. 61



Anterior view of the thorax.

Fig. 62



Diaphragm as seen from below: 1, 2, 3, the three lobes of the central tendon connecting the muscular fasciculi extending from the lower edge of the thorax, the crura (4, 5), and the arcuate ligaments (6, 7); 8, aorta; 9, esophagus; 10, quadrate foramen; 11, psoas muscle; 12, quadratus lumborum muscle. The convexity is upward.

latter down when other muscles, especially the diaphragm, tend to raise it during inspiration. The diaphragm is by far the most important of the muscles of respiration. When it contracts, its dome-shape central portion flattens out somewhat. This increases the contents of the thorax. The

Fig. 63

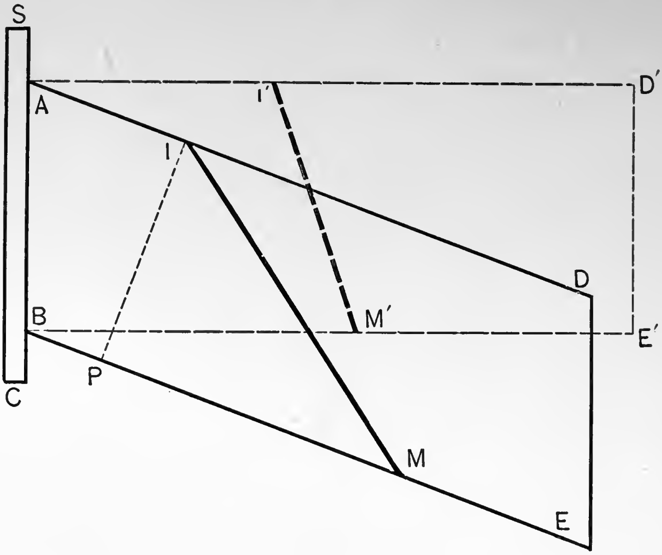
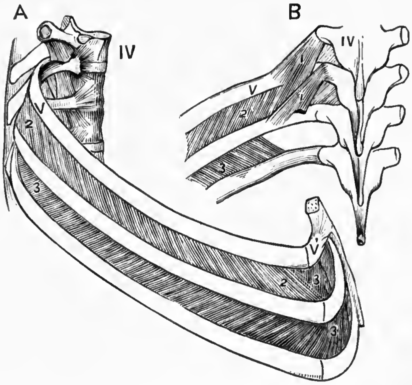


Diagram to show the actions of the intercostal muscles: *S C*, spinal column; *D E*, sternum; *A D*, one rib; *B E*, the next rib; *I M*, an external intercostal muscle-fiber in its relaxed state; *I′ M′*, the same in its contracted condition. Its shortening helps to raise the ribs and advance the sternum into the position *A D′ E′ B*. The internal intercostals act on the same principle, their contraction lowering the ribs.

Fig. 64

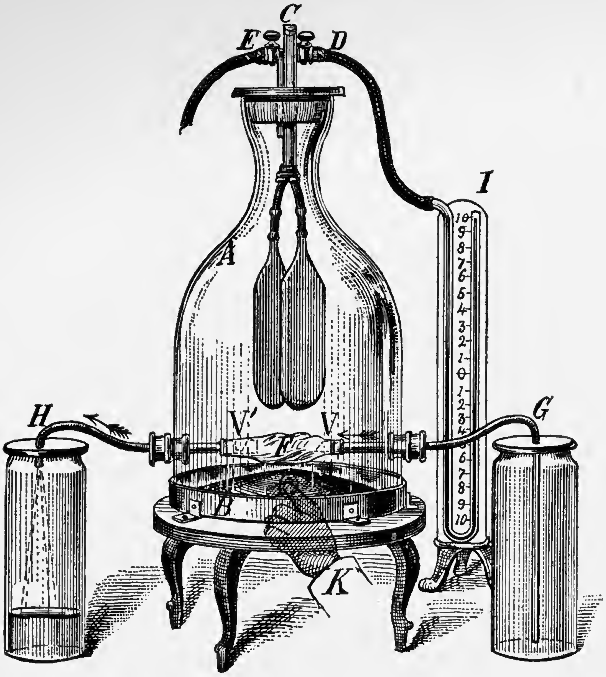


The intercostal muscles, etc.: *A*, lateral view; *B*, rear view; 1, the levatores costarum, short and long; 2, the external intercostals; 3, the internal intercostals seen on removal of the external set. The internal layer is seen to be deficient toward the spine. (Cloquet.)

amount of this depression varies between 1 cm. in ordinary respiration to 2 or 3 cm. in deep inspiration.

The expiratory muscles are far less important than the inspiratory because the process of expiration is largely a passive recoil of tissues twisted or stretched in inspiration. The lungs also, as we have seen, are highly elastic and tend ever to contract to a size much smaller than that when they are full. The muscles of the abdominal wall also aid expiration by contracting to a slight extent, pressing the abdominal contents against the diaphragm.

Fig. 65

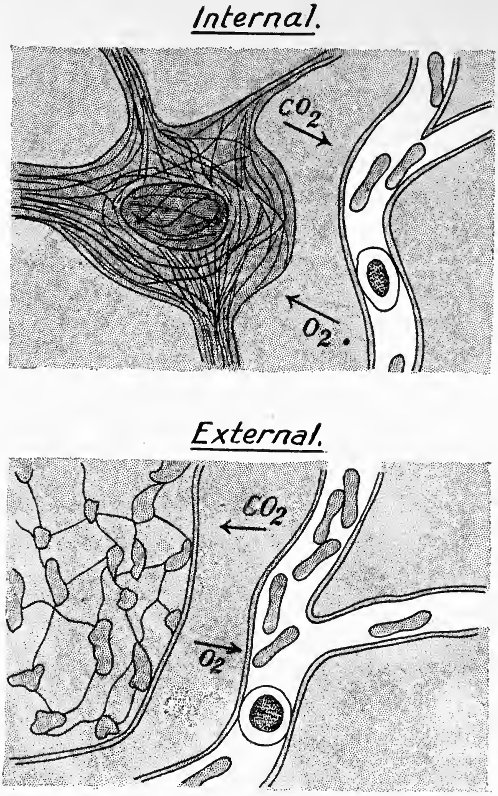


Apparatus to show the pneumatic relations of the respiration and of the circulation: *A*, represents the thorax; *B*, the diaphragm; *C*, the glottis; *D* is a tube leading to the manometer, *I*, indicating the intrathoracic pressure (while *E* runs to another manometer (not shown) indicating the intrapulmonary pressure); *G* is a reservoir (veins), and *H* a receiver, connected in part by the thin loose tube *F;* at *V* and *V′* are valves; *K* represents the muscles which lower the diaphragm in inspiration. When this occurs the heart is distended and the suction helps to draw the blood from *G* toward the heart *F*, the valve *V′* preventing suction also on *H*. The same suction draws apart the suspended rubber bags (lungs), and to fill this increased space air falls in through the opening *C* (glottis). When the diaphragm ascends in expiration the reverse processes occur. (Hering.) (See Experiment 30 in the Appendix.)

The internal intercostal muscles, put on stretch by inspiration, tend to contract in expiration, although in ordinary breathing they are used apparently mostly to complete the thoracic wall between the ribs. In dyspnea (difficult breathing), the abdominal muscles, especially the recti, contract and press the abdominal contents upward against the diaphragm. The pectoral muscles also aid in forced respiration, as do, indeed, at times, in one way or another, nearly all the muscles attached to the thorax.

The Nerves.—The nerves employed in respiration are a very important part of the mechanism. It is necessary that the parts of the apparatus should work perfectly together, and essential that the respiratory function should be adapted to the many changing conditions of the rest of the organism. The afferent nerves of respiration pass from different parts of the respiratory tract to the breath-center in the medulla oblongata. Among these are the fifth cranial (the trigeminal), the first (olfactory), the laryngeal, glosso-pharyngeal, and the vagus. Everyone is aware how easily a sneeze may be produced by a sharp stimulation of the nostrils, and inhibited by pressure on the upper lip. The afferent branches of the vagal nerves probably ramify in the walls of the lungs of

Fig. 66



True respiration. Internal respiration is the interchange between the tissue-cells and the blood. External respiration is the interchange between the blood and the lung-alveoli.

the alveoli and so continually keep the movements of the lungs delicately in touch with the means of their ventilation.

The respiratory center is a portion of the gray matter of the brain which controls the actions of the respiratory mechanism. It was discovered by Flourens. He observed that puncture or destruction in a certain small spot in the medulla oblongata was followed immediately by cessation of respiration, which could not be recovered from. This switch-board for incoming and outgoing respiratory nervous impulses is now known to be bilateral, below the vaso-motor center, and near the point of the calamus scriptorius in the floor of the fourth ventricle in the medulla. It appears also that one part of this minute knot of neurones is concerned in inspiration, and another part with expiration. It is in close connection with the center of the vagus. Some authorities doubt the precisely definite location which used to be described, and say that we cannot locate it more closely than in the lower portion of the medulla.

This center is unique in the body so far as known, in that it is controlled by certain definite substances present in the blood-stream which flows through it and around its nerve-cells. This fact makes it in technical terms an "automatic center." There has been much discussion as to whether it is the lack of oxygen or the excess of carbon dioxide in the blood which stimulates it. The fact seems to be that it may be both of these; but the excess of carbon dioxide stimulates it much more actively it is probable than does a deficiency of oxygen. Pflüger has suggested that some easily oxidized substance may be the actual stimulant, this being usually absent from well-oxygenated blood. Recent work by Plavec and by Laulanié makes it still more probable that the immediate stimulant is carbon dioxide. The center has an intimate association with about all the other important nuclei in the medulla. One sees this readily in the great sensitivity of respiration to almost all conditions, emotional, morbid, etc.

The efferent nerves of respiration are chiefly the phrenics, certain of the intercostals, and the vagus. Of these, the phrenics are perhaps most essential because they actuate the diaphragm, which is the essential respiratory motor organ.

The Process and the Mechanism of Internal Respiration.—The means by which internal respiration is carried on, the essential portion of the whole process, is in part physical without being mechanical, and in part the mechanism of another functional system—namely, the circulation. Internal respiration is the interchange of the two respiratory gases between the blood and the tissue-protoplasm. The mechanism of the blood's movement is one part of this process and the passage through the animal membranes intervening between the interior of a capillary and the interior of a tissue-cell is the other part. The circulatory mechanism will be described in a chapter by itself. (See page 278.) First, then, we must here inquire by exactly what carrying agents the oxygen and the carbon dioxide are conveyed between the alveoli and the tissues, and then as to the physical principles and the physiological conditions which are concerned in the passing inward of the oxygen to the cells of the tissues and the passage of the carbon dioxide from the tissues to the deporting blood.

Of the 60 volumes of gas which, by means of the mercurial air pump, may be removed from 100 volumes of the blood of the dog, the average composition is as follows (Halliburton):

	Arterial blood.	Venous blood.
Oxygen	20	8 to 12
Carbon dioxide	40	46
Nitrogen	1 to 2	1 to 2

The oxygen while being carried in the distributing blood is nearly all in loose chemical combination with the hemoglobin of the erythrocytes or red blood corpuscles. The average amount of oxygen present in arterial blood is about 22 per cent. by volume, while Pflüger found that plasma or serum (the corpuscles being absent) would absorb no more than 9.26 per cent. by volume. Crystals of hemoglobin have the power of absorbing large amounts of this gas. Hüfner found in 100 gm. of ox-blood crystals, as a mean of ten analyses, 134 c.c. Hemoglobin (see page 256 for its physical and chemical description) will from its nature absorb certainly more than its bulk of oxygen. From the evolutionary viewpoint it has been evolved for the sole purpose of carrying a large amount of this gas from the lungs to the tissues, for taking it readily and rapidly, and for giving it up quickly and easily. Hemoglobin is, in fact, an excellent example of a substance developed to a high perfection apparently for a single purpose. The hemoglobin of animals and the chlorophyll or plant-green of the vegetable kingdom are very similar chemically, if not identical in their composition, and their functions are certainly homologous.

The place and condition of the carbon dioxide, while it is being excreted from the protoplasm into the lungs by the blood, are not so easily described as are these same matters in regard to oxygen. The former gas is carried apparently by the leukocytes, the erythrocytes, and the plasma, two-thirds of it being contained in the last of these. While it is true that blood-plasma, owing to the presence of indifferent substances, cannot hold in simple solution as much of any gas as water can, still plasma holds much more of carbon dioxide than of oxygen. Setschenow calculated that of the carbon dioxide in the dog's serum, one-tenth was in simple solution in the liquid. Most of this gas in the blood is undoubtedly contained in the plasma rather than in the corpuscles. It is in two sorts of union with the various chemicals of the plasma—namely, in loose and in firm chemical combination. These distinctions are purely empirical, the portion in loose combination being removable with a vacuum, but not that in firm combination. Bunge by analyzing out the sodium content of dog's serum, calculated that a liter of such plasma could hold 632 c.c. in chemical union, or 63.2 volumes per cent. Most of the carbon dioxide of the plasma is in combination with those dissolved salts that render the plasma alkaline—namely, sodium carbonate and sodium phosphate. Walter found in the blood of rabbits poisoned with hydrochloric acid (thus rendering the plasma acid) only 2.5 volumes per cent. of carbon dioxide. According to Fernet and to Heidenhain, the dioxide is also combined in part with sodium acid phosphate, Na_2HPO_4, but only to a small extent. Serum globulin is another substance of the plasma which undoubtedly holds some of the carbon dioxide during its transit to the lungs. The corpuscles contain about a third of the carbon dioxide, it being "in loose chemical combination probably with the alkali of the phosphates, globulin, and hemoglobin of the corpuscles, and directly with the hemoglobin." (Starling.) Setschenow found in the erythrocytes 10 per cent. by volume of carbon dioxide and in the leukocytes 2.5 per cent.

There is a small amount (about 1.8 per cent.) of nitrogen simply dissolved in the blood, but as it appears not to have any respiratory function, its further consideration need not detain us. It is absorbed by the blood in the lungs on purely physical principles, and does not enter into chemical combination when in its free gaseous state, being only a diluent of the oxygen of the atmosphere.

Having summarized now the chemical information as to the relation of the respiratory gases in the blood to and from the lungs and the tissues, let us see in general terms the mechanism of this transit.

The blood circulating in its closed system of tubes and transuding (as lymph) through the capillary walls is the means of the distribution of oxygen and of the excretion of the carbon dioxide into air in the alveoli. As the arterial blood-current moves a meter or less in a second, and the venous current somewhat more slowly (the capillaries are only $\frac{1}{2}$ mm. long), a complete circulation from any point through the heart and the lungs and back again to the point of starting might occur in thirty seconds. This fact shows how prompt a carrier the blood (plasma and corpuscles) is, and as it is a continual flow, unceasing for an instant during life, the service is very efficient. Owing to the minute caliber of the capillaries of the lungs and tissues generally, the speed of the blood through them is small, $\frac{1}{2}$ mm. per second. The capillaries average $\frac{1}{2}$ mm. in length, and there is just a second, therefore, on the average, for the plasma, its dissolved sodium carbonate and phosphate, and the two main sorts of corpuscles floating in its stream to dissolve and absorb from the lungs their load of oxygen and from the tissues their load of carbon dioxide. During this second also the respective burdens must be dropped when they have made their transits.

The structures through which the two respiratory gases pass in internal respiration—that is, between the tissue-capillaries and the interior of tissue-cells—are not unlike the homologous structures of external respiration in the lungs. A molecule of oxygen bound from the blood for a tissue-cell must pass through the plasma intervening between the red corpuscle from which it starts and the capillary wall; through the endothelium constituting the latter; through a layer of lymph, practically plasma, outside the capillary; through the cell's wall, if it has one; and then through a larger or smaller layer of protoplasm into the interior of the cell. All these are either liquid or semiliquid protoplasm, and hence each offers a minimum resistance to the progress of the two respiratory gases. As is the case with the mechanism of external respiration also, these tissues together constitute an animal membrane, in reality complex both structurally and probably functionally. Yet this may be considered as a simple membrane in studying the forces and other conditions which determine the passage through it of the oxygen and the carbon dioxide. What the different layers of this living partition between the blood and the tissues have to do with this transit of the two gases is at present undetermined. We can study it only as a whole, and even then the precise functional conditions are none too certain.

The Sequence and the Causes of the Respiratory Events.—Let us now systematically trace an imagined portion of oxygen from the atmosphere inward to some tissue-cell and a portion of carbon dioxide outward from a cell to the open air. We will note in the progress the process itself and the causes which bring it about; we will see what actually happens to and about the supposed molecules of oxygen and of carbon dioxide as they pass in and out respectively. By "causes" we here may understand the physical and chemical forces which combine to produce the orderly sequence of respiration. This viewing of the events in order will serve at once to make the actual process clear and to summarize the facts already stated of its mechanism and chemistry. The description of these events naturally divides into two parts, the course and the causes of the movements of the two respiratory gases respectively.

THE COURSE AND THE KINETICS OF THE OXYGEN INWARD.—Pressing in all directions at the nostrils is the atmosphere under a pressure of about 1032 grams on every square centimeter of surface. This is the weight of a column of the atmosphere of that size many miles high above us. Thus, gravity is the force which causes the air to pass inward in inspiration. Before entrance can be made, however, space has to be provided for it to move into. This space is furnished, as we have seen, at the expense of crowding downward the abdominal viscera, the distending of the abdominal walls, and by an enlargement of the thorax forward, upward, and laterally, as well as downward. The mechanism of this enlargement produced by muscular contraction has already been suggested.

As anyone at all familiar with the thoracic viscera realizes, however, the matter is not in its physics so simple as this. The thorax is not a space bounded by elastic walls which expand and so enlarge the "cavity of the thorax." The only variable cavities in the thorax connected with respiration are those minute spaces contained within the complicated and highly elastic lungs—namely, the alveoli and the terminations of the numerous bronchi. Moreover, nearly surrounding the lungs are the pleuræ, and these are reflexed so as to line not only the outer surface of the lungs, but also the inner surface of the thoracic wall proper. Thus, between the outer surface of the lung and the thoracic wall on each side is the so-called "pleural cavity." Physiologically speaking, this is a misleading misnomer. Each of the pleuræ is a sac, one of whose sides lines the ribs and intercostal muscles, while the other encloses a lung. It is only because this sac is completely closed, air-tight, that the thoracic wall on expanding outward does not draw apart its two sides and leave the lung unenlarged. Boys sometimes amuse themselves with a scientific toy made of a circular piece of stout leather five or six inches in diameter, through the center of which is knotted a strong string. The leather being wet and pressed carefully over the smooth surface of a boulder, a considerable rock can be lifted by drawing upward on the string. Theoretically about as many pounds of rock can be raised as there are square inches of leather multiplied by 14.7, which is the weight in pounds of the atmosphere over a square inch of this sucker. The boy's muscles lift the rock, but the weight of the air keeps the leather meanwhile in contact with the stone. Exactly so in inspiration: the muscles (external intercostals chiefly) horizontally enlarge the thorax, but the atmospheric pressure keeps the outer surface of the lungs in contact with the expanding thoracic wall, thus distending the lungs against their elasticity. Thus, two forces combine to draw the air through the nostrils and into the larger bronchi, *muscular contraction* providing space into which the atmosphere is forced by its own weight (*gravitation*).

The essential importance of the air-tightness of the pleural cavities, so-called, is demonstrated only too often by accidents to people in which the pleural sac is punctured in a way that the tissues cannot immediately close. By a bullet, a dagger, or a corroding ulcer, air is let into a pleural "cavity"—which then for the first time becomes a real cavity. The elasticity of the lung-tissue now draws together the lung in a collapsed condition, and it no longer enlarges in inspiration, no longer ventilates. The two surfaces, visceral and parietal, of the pleura are drawn apart and separated by air instead of by a mere lubricating layer of lymph or plasma such as alone is present in the uninjured animal. If inflammation does not occur the opening in the thoracic wall soon heals together, the air in the cavity is absorbed by the tissues, and the lung gradually resumes its bellows-like expansion and contraction and its normal functions. If both pleural "cavities" are punctured, and skilled and unusual means be not close at hand, the patient promptly dies of asphyxia, both lungs being then undilatable. This is the condition known in surgery as pneumothorax, single and double respectively.

The force which causes the oxygen of the bronchial tidal air to continue its course to the alveoli on its way to the capillary blood there, seems to be an addition to this the physical force of *diffusion*. In respiration this force may be said to be the preëminent physical principle, if the term be used to include osmosis, the passage through a membrane. The diffusion of gases is that process by which two gases which do not chemically interact mix into a homogeneous mass when brought together. Thus, if a large bottle be half-filled with carbon dioxide and then the upper half filled with hydrogen, in a short time the bottle will contain a homogeneous mixture, although the carbon dioxide is many times heavier than the hydrogen. Again, if one bottle be filled with oxygen, a tube 1 meter long and only 1 cm. in diameter connected with it and inserted into a similar bottle above containing hydrogen, in a few hours both bottles will contain a homogeneous mixture of the hydrogen and oxygen; although the light hydrogen has to pass downward through a narrow tube in doing its part of the diffusion. This phenomenon is brought about by the fact that the molecules of gases are continually and rapidly moving in straight lines as far as they can go—namely, until they meet with obstacles, whether other molecules or the walls of the vessel containing the gas. As the rate of the molecular movements of a gas increases with its temperature, diffusion takes place faster in a warm environment, *e. g.*, in the lung, than in cool surroundings. The rate varies also with the density of the gases, in exact terms inversely as the square root of the density (Graham's law). If a vessel be filled with oxygen and hydrogen each on one side of a porous and thin earthenware partition dividing the vessel equally, the two gases will pass through this diaphragm at very different rates; 4 c.c. of hydrogen will work its way through the pores of the earthenware and into the other half of the vessel while 1 c.c. of oxygen is passing in the opposite direction. This process of admixture, whether or not through a dry partition, is *diffusion*, and is the process in part which obtains in the small bronchi of the lungs. It must be discriminated carefully from the phenomena which occur when gases mix through an organic membrane, such as one made of skin, rubber, or epithelium; the process then is *osmosis*. In diffusion there is immediate mixture or else the passage of the gases through minute tubes such as those of the earthenware partition or the smallest bronchi, the conditions being relatively simple. In gaseous osmosis, on the other hand, the rate of interchange depends not alone on the natures of the passing gases and their passageways, but more on the nature of the dividing membrane. Among the determining factors in osmosis are the relative diffusibilities of the two gases: their respective densities; the different degrees exerted by the membrane on the different gases by virtue of which the gas which adheres the most strongly penetrates the diaphragm most easily; and the degree of actual liquefaction of the two gases sometimes, which may thus penetrate the membrane and evaporate to gases again on the other side. Osmosis is the process which obtains in external and internal respiration. The "membrane" in this case is, of course, the complex and protoplasmic epithelial layers of the alveolar wall and that of the capillaries, plus the layers of intervening organic liquid, already described.

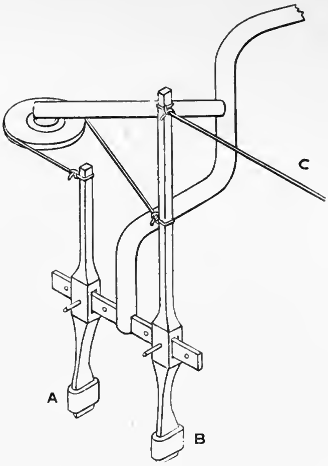
THE COURSE AND THE KINETICS OF THE CARBON DIOXIDE OUTWARD. —This can be described much more briefly than was the corresponding treatment of the oxygen, because these two homologous series of events are very similar in their natures, and only their differences need to be noted.

On an average, the partial pressure of carbon dioxide in the tissues is about 58 mm. of mercury, while in arterial blood it is not much over 21 mm. Because, therefore, arterial blood practically saturates the tissues everywhere, the carbon dioxide, poured out unceasingly by the tissue-protoplasm, takes this, the path of least resistance. It goes through with a pressure represented by the difference of these numbers, 37 mm. of mercury. Thus, it passes everywhere into the capillary blood, which is thereby made venous. Here, again, the process perhaps is one combined of osmosis, chemical affinity, solution, and secretory selection, and thereby the carbon dioxide passes into the plasma of the blood and into the leukocytes in proportions already described. The blood is constantly streaming backward from all directions to the right auricle, whence when pumped by the right ventricle it is hurried into the pulmonary capillaries. There it becomes revitalized by the acquisition of more oxygen and the giving up of its large burden of waste carbon dioxide. The deliverance of this latter gas occurs partly doubtless on the same familiar principles. Sometimes, at least, the living protoplasmic membrane separating it from the air aids and actively draws and pushes it through. It goes partly, too, because the tension of carbon dioxide in the venous blood of the capillaries is about 41 mm. of mercury, while that of the alveoli is only 29. Gases, like water, always tend to run down the hill of the gradient of pressures, to take the path of the lesser resistance. Such is the adaptation of the respiratory protoplasm, however, that in case the pressure-gradient declines in the direction prejudicial to the life of the animal, there are automatic means, already noted, of forcing the carbon dioxide, so to say, up hill in the life-preserving direction. In more direct terms, the lung-epithelium draws the gas out of the blood and thus out of the organism. The metabolism of plants may then make it over, liberating its oxygen for animals to breathe again.

The progress from the alveoli to the tidal air-current in the larger bronchi occurs under simpler conditions. It is caused partly by gaseous diffusion, partly by muscular contraction of the bronchioles, and partly by the compression of the lungs by the heart each time it expands in diastole. That diffusion is an active agent of this transfer may be seen from the differences in partial pressures of the carbon dioxide in the alveoli (about 29 mm. of mercury) and that in the open air (not over 0.3 mm.). This pressure-gradient, combined with that of the oxygen opposed (159 mm. to 100 mm.) sets up two streams in opposite directions, and keeps the excreting carbon dioxide pouring outward into the larger bronchi. There, as part of the expiratory tidal air, it is forced out through the trachea, larynx, nares, and nostrils seventeen times or so every minute.

The expiratory process, already described, is largely in normal respiration a *passive* one. It is a complex movement of recoil in tissues variously stretched, twisted, displaced, or bent, and of the fall of more or less heavy tissues raised, by the active muscular movements of inspiration. All of these strains together force the tidal air, 500 c.c. at a breath, upward and outward. The expiratory movement follows the completion of the inspiratory movement normally without appreciable pause. Expiration requires normally one-fifth more time than does inspiration. The pressure of the air in the trachea during expiration, according to Donders, is about 2 mm. of mercury, which may be increased in forced expiration to 100 mm. As the air passes upward the larynx rises slightly, raised partly by the expanding lungs and partly as the effect of contraction of the thyrohyoid muscles.

FIG. 67

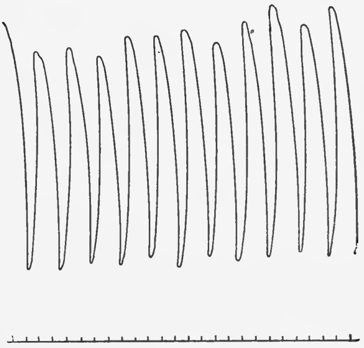


The Anolis stethograph: the padded arms of the levers at *A* and *B* partly enclose the chameleon, mouse, or other vertebrate of proper size (fixed by its legs to the frog-board), just behind its forelegs; *C* is the thread by which the respiratory movements are conveyed to a light aluminum lever for record on the smoked kymograph-drum.

The Respiratory Rhythm.—One of the most conspicuous elements in both the bodily movements and the sensation-mass of man is the rhythmic rise and fall of the chest walls in respiration. We have already considered the probable cause of this complicated system of movements, finding that it is regulated by a compound center in the medulla, which is in turn actuated by certain lacks or excesses in the constituents of the capillary blood flowing through it. There are certain elements in the rhythm itself which are of scientific interest and practical importance. Among these are its time-relations and its rate under various organic conditions. Many researches have been carried out on men, as well as on animals, in the study of the respiratory rhythm and its derangements. One method of registering these movements is by means of the pneumograph devised by Marey and improved by Fitz. By the use of this instrument pneumatic negative pressure actuates the lever of a recording tambour. Another apparatus for recording the time-relations, etc., of the respiratory rhythm is the stethograph, a variety of which adapted to study the respiratory movements of the common Southern lizard Anolis ("chameleon") is shown in Fig. 67. It consists of levers resting against the sides of the thorax of the little animal, which when separated lift a light lever writing as before on a smoked drum rotating by clockwork. A third way of studying the respiratory rhythm is to record by means of levers as before the movements up and down of the reservoir which receives the air expired by the animal. This is perhaps the least useful of the methods so far devised, for the reason that the conditions are complicated by chemical as well as by merely mechanical relations. The last of the methods invented, and one which has told us much concerning the respiration of the smaller mammals and of the movements of the diaphragm especially, is that of Head, who employed slips of the rabbit's diaphragm to directly actuate levers recording as before described.

By these means, and by others more or less similar, the chief characteristics of the gross respiratory movements have been accurately studied. It has been learned that in man the time of inspiration is shorter than that of expiration, the former being to the latter about as 6 to 7. In women, children, and old people the difference is greater than this. There is normally no pause between the cessation of inspiration and the commencement of expiration, for the parts put on stretch instantly recoil in their various ways when the active contractile pressure stops at the end of inspiration. Between the end of one expiration and the beginning of the next inspiration there is normally a short pause. In duration this may be about one-fifth of the time required for a complete respiration. Observation of any normal stethogram, for example, that of Fig. 68, shows well the respective characteristics of the inspiratory and of the expiratory movements. The inspiratory phase is at first quick (as is shown by the nearly vertical direction of the tracing), and then slightly slows to its end; it is also steady and interrupted less often than is the expiratory phase. The expiratory movement is somewhat slower and more variable in its different parts, as is shown by the tracing's obliquity and relative irregularity. In looking over a number of stethograms traced from

Fig. 68



The Anolis stethogram. This shows one type of the breath-movements of the common Southern "chameleon." The right-hand line in each curve is the inspiratory movement. To be read from right to left. Original size. The time-line is in seconds. (See other Anolis stethograms in the Appendix.)

different animals, these qualities would be much more emphatically noticed than in that of the figure made from Anolis.

The respiratory movements, except so far as stopping them for a long time is concerned, are very perfectly under the control of the animal's will. This we shall see more fully in studying speech. Thus, stethograms have many more arbitrary interruptions in their course than have, for example, sphygmograms, or tracings made from the pulse of the heart, which is only rarely under voluntary control. Men by practice can learn to stop their breathing for five minutes or so, as do the pearl- and sponge-divers of the South Sea islands. No man can commit suicide by this means, however, unless it be those rare individuals who have some voluntary control of their hearts and respiration together. In this case death is caused by stopping for too long a period the heart rather than the respiratory mechanism.

The relation between these two rhythms, the cardiac and the respiratory, is close and tends to keep up the ratio of 4 to 1, whatever, within limits, be the condition of either rhythm. As the breath-rate goes high, as, for example, in pneumonia, the pulse-rate oftentimes fails to keep up this its normal ratio.

The Breath-rate.—Few things in human function are more normally variable within normal limits than is the number of respirations per minute. The reason for this is that respiration is more closely related to other functional conditions and more sensitive to mental influence than almost any other of the basal functions. This may in turn be due to the wide and, indeed, almost universal connections of the vagus, the nerve which has so much to do with respiration.

The breath-rate varies, for example, according to sex, age, season, time of day, muscular and mental activity, temperature of the air, body-temperature, recency of digestion, volition, atmospheric pressure, emotion, composition of inspired air, depth of breathing, pulse-rate, sleep, and posture. These sixteen or seventeen conditions, at least, besides the protoplasmic structure of the respiratory central neurones and the respiratory state of the blood, determine the number of breaths per minute in man.

We need hardly do more than to point out the direction in which each of these influences acts. Because the nervous system of the female is more unstable than that of the male, women appear to breathe oftentimes much more rapidly than do men. The average excess is really small, and in childhood nearly nil; indeed, Milne Edwards supposed that young men breathe somewhat more rapidly than young women. On the average, it may be said that women breathe twice or thrice a minute more than do men. The variation according to age is large, and of much practical importance in medicine. From three hundred countings, Quetelet derived the following numbers:

VARIATIONS IN BREATH-RATE WITH AGE.

Average Number of Respirations per Minute.

Years of age.	Respirations.	Years of age.	Respirations.
0 to 1	44	20 to 25	18.7
1 to 5	26	25 to 30	16.0
15 to 20	20	30 to 50	18.1

Season of the year has a distinct influence, the rate being greater in spring than in fall. The variation according to the hour of the day nearly follows that of the pulse, the breath-rate being less at night, when metabolism is also less. Muscular exertion has very marked influence on the rate, respiration being more sensitive even than the circulation, and hastening sooner after the exercise begins. Only a very small increase in the muscular exertion is required to distinctly accelerate the breathing, the stimulation being due probably to excitation of the center by acid products of muscular activity. Mental exercise has a similar effect, but less in amount; respiration is apt to be inhibited more or less and made irregular by many sorts of mental activity. The influence of atmospheric temperature is slight, but a rise of the temperature somewhat lowers the rate. Body-temperature, on the other hand, is of marked influence on the respiratory rate, a matter of clinical and diagnostic importance. Thus, fever from whatever cause increases the rate, while in coma and in collapse the rate is lessened. The process of digestion slightly increases the breath-rate, especially dinner at noon (Vierordt), the increase being apparently due to the forced increase in metabolism due to the temporary feeding of the blood. The will, of course, has great influence over the rate, for we can breathe more rapidly than normally, if we so choose, until the inspiratory muscles become too painful or exhausted. Likewise we can breathe more slowly than normally, provided we breathe more deeply. Atmospheric pressure exerts little influence unless excessive, in which case greater pressure decreases the rate and rarefaction increases it. This is in order that the respiratory ventilation may remain the more nearly constant. Dwellers on high mountains breathe faster than do persons on the sea level. The various emotions have characteristic influences on the breath-rate, some hastening it and some slowing it. In general the sthenic or strength-giving and pleasant emotions quicken the rate, while the asthenic and unpleasant emotions retard it. If the air to be breathed becomes deficient in oxygen (below 13 per cent. by volume) or excessive in carbon dioxide, the breath-rate is increased to restore the normal conditions in the body. The rate of breathing is in inverse ratio to the depth of breathing. This is conspicuous in pneumonia, for example, in which case parts of the lungs may be thrown out of their function. As has been said before, the respiratory rate tends to keep a constant ratio of 1 to 4 with the pulse-rate, save in fever and other abnormal conditions. On this account conditions which affect directly only the frequency of the heart often indirectly increase the breath-rate also.

In sleep, because the metabolism is lessened, the rate is less; the decrease in muscular activity during sleep probably helps the effect. The decrease is, on the average, about 20 per cent. of the waking rate. Finally, posture may affect the rate aside from the variations of muscular exercise in the different postures. In standing, the respiration is faster than in sitting, and faster in sitting than in lying down. This, perhaps, is due to mechanical interference with the depth of the inspirations, which, as we noted above, increases the rate.

The breath-rate varies widely in different animals, and a tabulation of the rates of many genera gives little clue to the reason for some of the variations.

BREATH-RATES OF VARIOUS ANIMALS (BERT).

Complete Respirations per Minute.

Hippopotamus	1	Panther	18
Snake	5	Canary	18
Tiger	6	Cat	24
Condor	6	Pigeon	30
Rhinoceros	6 to 10	Mollusca	14 to 65
Ass	7	Perch	30
Giraffe	8 to 10	Hippocampus	33
Lion	10	Raja	50
Jaguar	11	Eel	50
Dromedary	11	Torpedo	51
Horse	10 to 12	Rabbit	55
Tortoise	12	Mullet	60
Crab	12	Sparrow	90
Dog	15	Siskin	100
Ox	15 to 18	Rat (asleep)	100
Man	18	Rat (awake)	up to 210

Why the rhinoceros should breathe, say, eight times as often as the hippopotamus, or the sparrow five times as frequently as the canary, it is difficult to satisfactorily explain. The physiology of other differences is obvious, and leads to rather fundamental considerations of importance. The most basal criterion of difference is probably that of difference in degree of the body-metabolism based either on difference in the activity of the animal or on its size. Moreover, the heat lost is determined largely by surface in ratio to mass, or as square to cube, which, of course, gives the smaller animal the larger proportional surface, and so the larger proportional loss of energy. More oxygen is needed to correspond to this additional metabolism. The same explanation probably applies to the difference in the respiratory ratio of the cat and the tiger, two felines much alike save in size. The difference in rate of the rat's breathing and in that of the tortoise is largely one of metabolism, arising from inherent differences in habits and nature, the rat being active and homothermous, the tortoise "cold-blooded" and proverbially slow. In general the breath-rates of the birds are high because of their lively metabolism, which is dependent in turn on their great bodily activity. In the case of the condor, however, a bird at once large and lazy, we see a very low rate, on the principles already suggested.

Special Functions Connected with Respiration.—There are a number of complex processes, variously useful, and more or less normal, which involve the respiratory mechanism more than that of any other functional system. These are, among others, speaking, singing, coughing, sneezing, hawking, sniffing, yawning, sighing, laughing, sobbing, snoring, sucking, and hiccoughing, thirteen functions less formidable to understand than one might fear. The first two are so important and complex that they require special discussion in the proper place immediately below. The next four—coughing, sneezing, hawking, and sniffing—are movements habitual to many mammals for the purpose of clearing the respiratory passages of mucus and other obstructions and irritants. The next one—yawning—is a mode of muscular relief. The next three—sighing, laughing, and sobbing—are emotional expressions. The general nature and the purpose of the next—sucking and snoring—are known to everyone. Hiccoughing alone seems to be strictly abnormal. Here we need discuss only two of these processes.

Coughing is an essentially protective process in catarrhal inflammation of the respiratory passages and useful for removing from them accidental particles, as of food. When both vagus nerves are cut in the neck, the afferent impulses to coughing are cut off, and the animal usually dies in a few weeks or months from foreign-body pneumonia. Coughing may be either a voluntary action or one reflexly started. It consists first of a very deep and full inspiration, with the closure of the glottis, followed by a forced expiration. When the increasing pressure in the larynx is sufficient the glottis is burst open and the current of air passing violently out through the previously opened mouth tends to remove the irritating substances. Stirling enumerates eight sources of stimulation of reflexly produced coughs: (1) The respiratory mucous membrane, especially of the larynx, the afferent impulses of the reflex arc going in over the vagus and the superior laryngeal. Kohts determined that a cough-stimulus could come from only the glottis respiratoria, not from the true vocal cords nor from the trachea down to the bifurcation. (2) The skin, especially of the upper part of the body, a cold draught on which produces a congestion of the air-passages, which in turn excites coughing. (3) The external auditory meatus, where a foreign body may start impulses inward over the auricular branch of the vagus. (4) The mucosa of the stomach, the afferent nerves being again in the vagus. (5) The costal pleura and (Kohts) the esophagus. (6) The nose. (7) The pharynx. (8) The liver, spleen, and generative organs in diseased condition when pressure is applied over them.

Sneezing is similar to coughing save that the blast of air from the trachea passes out through the nose instead of the mouth, the latter being tightly closed. Sneezing is much more reflex than is coughing. A bright light even may occasion a sneeze. The remainder of these subsidiary respiratory processes are of interest, but do not need special description.

The Respiratory Sounds.—As might be expected in a process where currents of air rush in and out through a series of tubes and chambers more or less obstructed in various ways, the function of respiration is accompanied by various sounds. These are audible either by the unaided ear or by means of magnifying instruments, such as the stethoscope or phonendoscope. Accompanying normal breathing through average respiratory organs is a set of sounds called by the diagnostician "normal." When either the function or the organs are materially altered the sounds also are changed and thus become valuable means of diagnosticating and locating disease. This is the important art of auscultation.

Two sounds made in normal breathing—bronchial breathing and vesicular murmur—are especially important.

Bronchial breathing is the sound natural to the passage of a current of air over imperfectly vibrating strings within a tube. It is caused by the rapid movement of the air passing through the glottis. It is heard during both inspiration and expiration, and best over the larynx and the trachea. It can also be distinguished below the trachea, but not unmixed with sound produced in the lung-tissue proper. Between the scapulæ, behind, it is somewhat less distinct than over the trachea. The pitch of bronchial respiration is high, that of expiration being somewhat higher than that of inspiration. The intensity is about equal in the two phases, as is also the duration.

Fig. 69

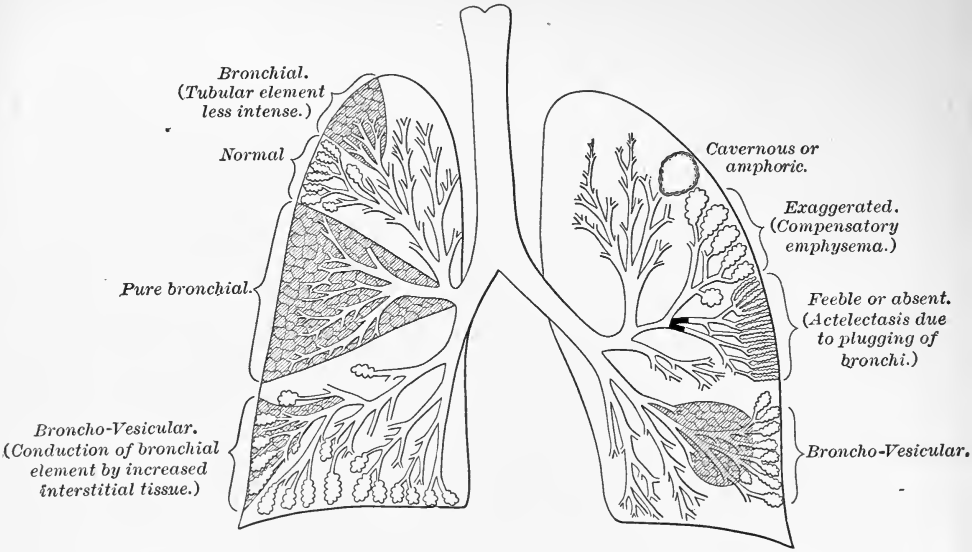


Diagram of the modification of breath-sounds as heard on auscultation. (Le Fevre.)

The vesicular murmur is so called because it is largely caused by the expansion and recoil of the air-vesicles or alveoli, complicated, however, with the tubular sounds produced in the bronchioles. The murmur of the inspiratory phase is about four times as long in duration as that of expiration, gradually increasing to a maximum and decreasing again by degrees. A slight pause intervenes between the sounds of the two phases. In quiet breathing the expiratory murmur may be difficult to hear. It is hard to describe the nature of this sound, and its description is not necessary when the sound itself is so readily available. It is produced by the friction of the air entering the alveoli plus the slight crepitation of the alternately expanding and lessening bronchioles and alveoli. It may be heard at its best below the left clavicle. In most parts of the lungs this sound is mixed, more or less in different places, with the bronchial sound.

Nasal sounds of various sorts are to be heard externally, their quality and intensity depending on the configuration of the nares and the nasal cavities.

The various *abnormal* respiratory sounds are of extreme importance to the clinician in the diagnosis of the diseases of the chest, throat, and nose, and moreover, have much physiological interest because they serve to illustrate and to emphasize the mechanical conditions both in the structure and the function of the whole respiratory tract above the diaphragm. For the technical description and names of these numerous abnormal sounds the student is referred to the special works on physical diagnosis. We here look briefly only at a few abnormal mechanical conditions in the breathing apparatus from which the sounds arise. When some of the alveoli and bronchioles are filled up by exudate, as in pneumonia, the respiratory sounds may be absent altogether from that part of the chest, save as they are conveyed from elsewhere. To compensate for such diminution in the acting lung-tissue, the functioning portions work more vigorously, and the more or less normal sounds are increased beyond the normal intensity ("puerile breathing"). This comes also from collapse or compression of a lung, as in empyema, pneumothorax, or pleurisy with effusion.

Sometimes, most often from tuberculosis, there is a cavity in the lung, and this may be of any size, up to that of a whole lung. Such a cavity gives rise to cavernous sounds or to amphoric breathing when of moderate or large size, the breath echoing or resounding more or less as it enters and passes by the openings into it. If the cavity be of small size, the first third or so of inspiration may be harsh (as the air forces a way into it). When the lung-tissue is solidified it serves as a much better conductor of the bronchial sounds than when normal, and so the latter may be heard in an abnormal intensity and in places where in health they are faint; on the other hand, the vesicular murmur is quite absent. When there is fluid in the bronchioles one may hear the crepitating sound always made by air bubbling through a small quantity of a liquid. This is the condition in the first stage of pneumonia. The same condition in the larger bronchi causes mucous rales. When the bronchioles are obstructed (as by mucus) in just the right degree, an occasional inspiration only penetrates them and there is what is called cog-wheel breathing in that region of the chest. If the bronchioles are mostly filled with tough mucus, the air has to tear its way through, causing the harsh, rough sounds technically known as rhonchi. When this condition is extreme the whole adjacent chest-wall may be set into a sort of vibration, producing the effect called fremitus, which may be felt even with the finger. Rarely there are in a cavity both air and liquid, and we hear the sound arising from the shaking together of these two sorts of fluids in a vessel (succussion).

Anything which lessens the tone or elasticity of the lung-tissue prolongs expiration, this process being one of passive recoil. Such a condition obtains in emphysema. When the contiguous surfaces of the pleura (the pulmonary and the costal), instead of being very smooth and well lubricated, are covered more or less with exudated solid materials, there is friction which gives rise to easily heard and characteristic sounds. This happens often in pleurisy and in tuberculosis. Sometimes, as in pneumothorax, for example, the conditions in the lungs are such that drops of liquid fall into a cavity. Then there is a peculiar sound known often as metallic tinkling. It may be produced by drops of secretion falling from the end of a bronchus into a cavity.

Some Respiratory Quantities.—The capacity of the lungs and the relations of the various volumes of air and of gases remaining and passing in and out under various circumstances have a certain interest and importance both theroretically and therapeutically as well as for the purposes of athletic measurement. The first of these that we need to consider is *the tidal air*. This is that volume of air which goes out and in at every breath. On the average in the adult man its quantity is about 500 c.c., or about 7 c.c. per kilo of body-weight. Perhaps the most noteworthy fact about the tidal air is its small amount compared with the lung-capacity, for only about 15 per cent. of the air in the lungs under normal conditions passes out at each breath. This fraction is called the co-efficient of ventilation. The *vital capacity* of any individual is the volume of air he can, by the greatest effort, expire after the most complete inspiration. A more accurate term for this quantity would be respiratory capacity, its importance to life being somewhat less than the inventor of the term "vital capacity" supposed. Vierordt states that for man on the average it is 3400 c.c., and for woman 2500 c.c., a marked and important sexual difference. These quantities, however, may be raised a good deal by practice and by general athletic training, especially by running. This shows probably that the muscles of the bronchioles may be developed by exercising them, so that more air than before can enter the alveoli.

Other respiratory quantities are the so-called supplemental air, the complemental air, the stationary air, the residual air, the bronchial capacity, the alveolar capacity, and the lung-capacity. What these are in general can be made out from their names.

The Respiration of the Fetus.—Unlike the circulatory organs, the fetal mechanism of respiration does not begin its work until after birth, when for the first time it can have air with which to inflate the lungs. The fetus, however, breathes, but oxygen and not air, and it excretes the carbon dioxide, inevitable product of its tissue-metabolism, into the maternal blood instead of into the atmosphere. Fetal respiration, then, is wholly internal respiration. The respiratory mode of mammalian embryos is practically the same as that of fishes, for although the former have no proper gills, still the gases interchange (through layers of maternal and fetal epithelium) between the liquid blood of the embryo and the liquid environment. In this case the environment is the circulation in the placenta of the mother. The fecal chorionic villi and the blood-filled sinuses of the decidua serotina of the placenta, extending inward from the uterine fundus, interknit with the greatest closeness. Thus, the villi of the fetal circulation, made up largely of capillaries, are quite surrounded by the large blood-sinuses filled with maternal blood. The circulation of the fetus, then, exchanges its two respiratory gases through the walls of capillaries just as does the adult circulation, save that instead of exchanging them with the alveoli the fetal blood takes its oxygen and excretes its carbon dioxide second-hand, as it were, from and into the maternal circulation. The essence of these facts was understood by Mayow in England as early as 1674.

The sinuses of the maternal circulation in the placenta are large, and the blood-current through them correspondingly slow, thus allowing ample time for the respiratory exchange. Diffusion would partly account for the interchange, but probably here as elsewhere the protoplasmic powers of the septa have more or less to do with the passage through. Unlike the adult's hemoglobin, that of the fetus is never saturated with oxygen. An estimate of the oxygen consumed by the human fetus was 0.169 gm. daily per kilo of body-weight, compared with the 14 gm. or so used by the adult per kilo, or about 1.2 per cent. of the adult's requirement. This low demand for oxygen depends on a correspondingly low metabolism, which in turn is due to the relative inactivity of the fetus, its protection from loss of heat, etc.

Respiration through the Skin.—The lungs are not the only organs by which oxygen is absorbed into the organism and carbon dioxide given off, for the skin and the intestines are also media for a small amount of this interchange, even in mammals. This is not difficult to understand, for a part of the tissues of the body, constantly producing carbon dioxide and requiring oxygen, are separated from the atmosphere, the great reservoir of both these gases, only by the thin upper layers of the skin. This important organ, the skin, is in some respects an admirable osmotic membrane, being moist, thin, and vascular. The structure of its outer layer, the epidermis, however, is not so favorable to respiration, the epidermis being, indeed, evolved to be negative and protective.

Cruikshank more than a century ago proved that a clean hand or foot immersed in lime-water (a solution of calcium oxide) for an hour rendered the water milky by the production of the insoluble calcium carbonate—the ordinary test for carbon dioxide. Abernethy thereupon showed that in ordinary air oxygen was absorbed and carbon dioxide discharged by a hand as readily as in pure oxygen. Gerlach, from experiments on a part of a man's skin, calculated that 8.4 gm. of carbon dioxide were given off in twenty-four hours from the entire bodily surface. Scharling, Röhrig, and others proved that carbon dioxide was given off from all parts of the body, but at very various rates in different portions. Anything which increases the vascularity of the skin increases also the respiration through it. As in case of the pulmonary interchange, heightened metabolism causes a livelier respiration through the skin; so, according to Fubini and Rouchi, do food and light. In general, cutaneous respiration seems to be about $\frac{1}{200}$ (0.5 per cent.) of the pulmonary respiration in quantity. Trial demonstrates that the human skin will absorb, besides oxygen and carbon dioxide, carbon monoxide, sulphuretted hydrogen, and the vapors of chloroform and of ether.

In *amphibians,* dermal respiration, especially the absorption of oxygen, is a much more important process than in mammals. Frogs, for example, during a third or more of the year in temperate climates, are buried in the mud at the bottom of ponds and streams, and the use of their lungs must, then, for mechanical reasons be only nominal. But metabolism goes on during these months and requires oxygen as it does in the summer time. The carbon dioxide produced must be given off too, or the animal would soon die of asphyxia. Klug found that the body-surface of the frog exclusive of the head excreted three or four times as much carbon dioxide as did the lungs and the skin of the head—namely, about 0.2 gm. in the three hours of the experiment. In the summer the opposite ratio obtains, the lungs then being the more important. Dissard, however, proved that the frog dies when either of these respiratory organs (the skin or the lungs) are thrown out of function. There is need, then, of experiment in this direction on various classes of hibernating animals as well as on the fakirs of India, who seem to be practically hibernating men, their hearts and lungs being nearly at a standstill.

Respiration through the Wall of the Alimentary Canal.—Just as gases pass outward through the skin from the underlying tissues, so a similar and more varied respiratory interchange takes place into and out of the alimentary canal. Ruge found carbon dioxide, hydrogen, nitrogen, methane, and hydrogen sulphide in the rectum of a man, but no oxygen. The carbon dioxide, methane, and hydrogen sulphide were most abundant on a vegetable diet, the nitrogen on an animal diet, and the hydrogen on a milk diet. The proportion of carbon dioxide in the intestines varies from 20 to 90 per cent. of the total gas content (Tappeiner). Its partial pressure would be greater than that of the tissues, whether solid or liquid, about the gut. The carbon dioxide of the intestines, therefore, would soon make its way into the circulation and be excreted by way of the lungs.

Oxygen is promptly absorbed from the alimentary canal by the surrounding tissues and largely by the capillary blood. It can seldom be found below the duodenum, for most of it is absorbed by the wall of the stomach. Pembrey relates that swimmers who are in the habit of staying under water an exceptionally long time swallow air into their stomachs, in order that the oxygen so taken in may be utilized as well as that of the lungs. A kitten with clamped trachea will die in thirteen minutes, but if a current of air be passed through the intestine after closure of the trachea it will live 61 per cent. longer. In fish, intestinal respiration is probably as important as dermal respiration is to amphibians.

In the frog, at least, the mucous membrane of the mouth and pharynx is an important respiratory organ, and in a species of salamander more respiratory exchange takes place in these localities than is conducted by the skin on the whole surface of the body.

The Quantity and Quality of Air Required for Respiration.—In order that respiration may be conducted normally and with an expenditure of only a minimum amount of energy, it is necessary that the air to be breathed should be pure within certain physiological limits—that is, that it should contain enough oxygen and not too much carbon dioxide. The atmosphere being for all respiratory purposes a boundless reservoir of oxygen and an infinite absorber of carbon dioxide, the most natural way of maintaining the requirements inside our dwellings and assembly rooms is to let in fresh air in the required amount. As it enters this necessarily drives out an equal amount of air already present, but more or less vitiated. This is the simple-enough principle of *ventilation.* The problems then are to determine how much air per hour a person needs for perfect breathing, and then to so provide this quantity of air from the atmosphere under all its varying conditions that the supply, without draughts of a harmful intensity, may be certain, economical, and constant. The former part of this problem has been solved satisfactorily; the latter part in everyday life is not so easy.

The ratio of required oxygen to carbon dioxide cast out is so fairly constant that it is customary to measure the purity of a given mass of air to be breathed by the percentage of carbon dioxide it contains. Each adult man or woman is found to expire about 0.6 cubic foot of carbon dioxide on the average every hour. In a room of ten feet cube this would make the proportion of carbon dioxide at the end of the hour 0.06 per cent., and this proportion is taken as the proper maximum of vitiation by this gas. It is an index also of the oxygen required. In ordinary dwellings, on average days, if there be but one person to this space—namely, to every thousand cubic feet—ventilation will take care of itself through the cracks about the windows and the doors, draughts in the chimneys, and by the opening and closing of the doors. When, however, more than one person breathes from this thousand cubic feet of air the problem is complicated, and chiefly by the fact that in winter a draught of air at once cools off a room and imposes on the occupants, at least indirectly, some slight risk of a catarrhal inflammation of the nose or chest, of neuralgia, etc.—in short of "taking cold."

The ideal mode of ventilation undoubtedly is by means of an open-grate fire in every room, and modern dwellings of the better class are fast meeting this ideal. Even if no fire be burning in the grate, there is a draught of considerable proportions constantly passing up the chimney.

This draws an equivalent volume of air, moist and cool, through the cracks about the doors and windows, if not from a supply provided by some system of ventilating apparatus.

Perhaps the next best form of heating, so far as ventilation is concerned, is the hot-air furnace. When properly built and run, it provides a current of fresh air from out of doors warmed and humid enough to be breathed. Steam and hot water have so great mechanical advantages that their use is becoming very widespread. Neither of these methods, however, provides any ventilation nor any mode of moistening the air. The heating-stove has these disadvantages in an exaggerated form because of the extreme temperatures they often reach, while the small basin of water sometimes attached to the stove above, intended to moisten the air, is almost ludicrously inadequate. Whatever the mode of heating, the matter of direct ventilation by means of open windows will seem to the next generation a very simple matter, and children now being born will look back, we may imagine, with mild amazement on the fear many of their parents and grandparents now have of a current of air. Education is advancing rapidly in this important regard, and it is a common experience that toleration even of cold draughts may be readily acquired without any sort of harm and with great benefit to everyone; and with life itself to the millions of every century who else would die of tuberculosis of the lungs.

Diffusion also assists ventilation everywhere to no small extent, quickly evening up the composition of the air in an open space. Difference in temperature and consequent density of air is another cause of the air's movement. A fair allowance of air space in the large cities is 1500 cubic feet, and 4500 cubic feet of air hourly per capita. The floor-space should be one-tenth of the cubic space.

A method of public school-room ventilation especially that commends itself on many accounts is the free opening of the windows for five minutes every half-hour, the pupils meanwhile marching about the room. This would keep the air pure at a low monetary cost. It would relieve the brain of its congestion by vaso-motor rearrangement of the blood, and it would accustom the child to small changes in the temperature of the air. Under such a system, harmful over-strain of the mind, eyes, etc., would be much rarer than now, and the supply of respiratory oxygen greatly increased.

Save in the hospitals, the problem of ventilation certainly will be a simpler one continually as more and more of the mass of the people hear and believe the gospel of fresh air as taught them in the schools—that oxygen is as food and drink and, unlike them, free; and to take it in great abundance day and night is to ward off multiform disease and to add to the length and happiness of their lives.

CHAPTER IV.

FOODS.

In studying respiration we saw in some of its bearings the status of oxygen as one of the indispensable supplies of the organism. The discussion demonstrated that living protoplasm requires oxygen for its metabolism, and it showed furthermore how the protoplasm which makes up the human body gets its oxygen, and what finally becomes of it. In the present chapter we begin the description of the same sort of acquiring and disposing process for the remainder of the material provisions on which the body subsists and in the metabolism of which it lives. Oxygen is a sort of food, but as it is a gas it requires special means for receiving it and for excreting the products of its use. All food other than oxygen is either solid or liquid in its density, and because of this difference has required the evolution and action of a mechanism peculiar to itself.

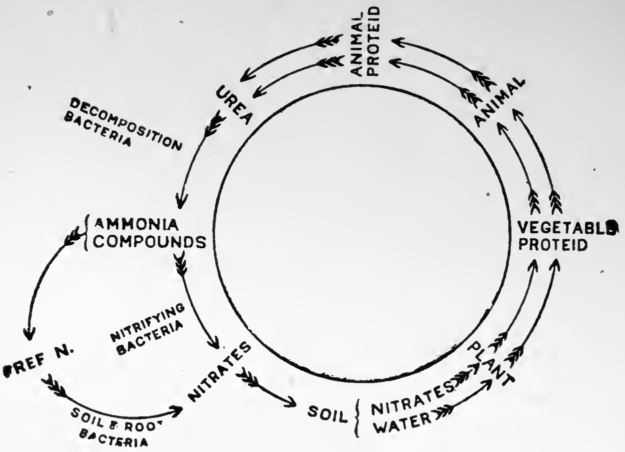
In describing the natural history of food proper and its organic use we need to understand the nature of the various classes of alimentary substances and their general relations to the organism.

THE GENERAL NATURE OF A FOOD.

A food or nutrient may be defined as anything which, taken into an organism, is capable of supplying it with tissue or of producing energy. Let us as a preliminary to our study of the nutrients see of what materials an average animal body is made up, in order that we may know in advance what substances will be required in the food for supplying tissue, whether in the growing young animal, or in the replacement of the normal loss by wear and tear. We have already learned what chemical elements combine to make up an animal organism.

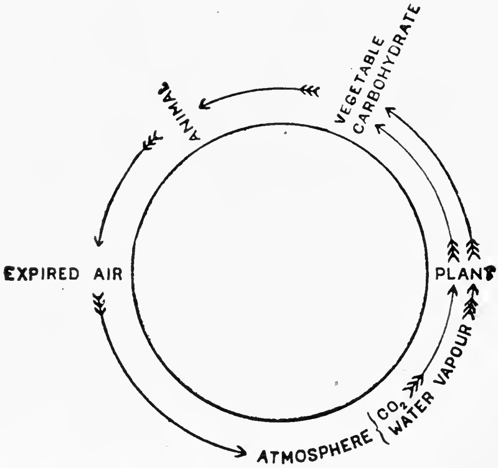
The Animal Organism's Proximate Principles.—The table on page 30 is given partly as a place for reference to the names and classification of the chief constituent compounds so far known to exist in an average animal body of high development, and partly to suggest the need of very various materials in the food which is to reproduce all these substances as they bit by bit wear away. The iron, manganese, ammonia, and carbon dioxide mentioned, and probably the nitrogen and hydrogen, exist only to a minute extent in free uncombined form in the body. The others, and doubtless many more proteid forms, and especially enzymes and salts of the alkaline metals, seem to be present as such in large or small quantities. The proportion of water given, 65 per cent., is constantly changing, but is approximately correct as an average. The relatively large proportion of water, approximately two-thirds of the body, again reminds us of the fact, important in understanding the *movements* of the tissues, that the body, apparently solid, is made up largely of *liquid* protoplasm—in the ancient medical dictum, *corpora non agunt nisi fluida.*

Fig. 70



The nitrogen food-cycle. (Hutchison.)

Fig. 71



The carbon food-cycle. (Hutchison.)

Through the agency of light, plants have the power of combining the water of the soil and the carbon dioxide of the air into sugar. Furthermore, plants make from this sugar starch and cellulose and fats, and combine it with nitrogen-bearing radicles of the soil to form proteids. It is then the chlorophyll, very like hemoglobin, which *synthesizes* certain inorganic elements into more complex substances, protein, fats, and carbohydrates. These three with water and inorganic salts make up the necessary food of all animals. These proteids, fats, and carbohydrates, stored with the potential energy coming from the sun, expended in making them, animals again *analyze* into simpler compounds, and these are essentially those with which the plants again begin their work. The stored energy thus liberated is the originator of the movements which life, especially animal life, essentially is. The formula

$$(6CO_2 + 5H_2O)_n = (C_6H_{10}O_5) + O_n$$

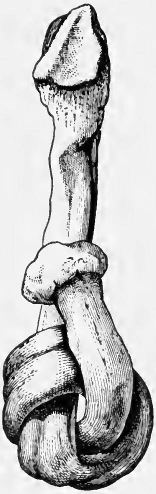
is, therefore, typical for the synthesizing function of plants, and its reversal—

$$(C_6H_{10}O_5)_n + O_n = (6CO_2 + 5H_2O)_n$$

is characteristic of the analyzing, energy-liberating function of animals. Plants and animals in this way are mutually dependent, and thus runs the eternal round of matter. It is the essence of vegetable life, so far as we are at present concerned with it, to synthesize the molecule of starch, but it does this only through the obscure agency of the chlorophyll of its verdure. This substance, it is interesting to note, is largely a *proteid*, the baffling nature of whose life-mystery has already been pointed out.

Nutrient Proximate Principles.—The table of chemical compounds (page 30), already isolated from a highly evolved animal body, is made up chiefly of six classes of substances: protein, fats, carbohydrates, albuminoids, inorganic salts, and water. Each one of these classes is probably represented, at least in minute amount, in any particle of living matter, for analysis of masses of the purest protoplasm obtainable always shows the presence of at least the first three of these and water. Logically, then, these determine what foods animals require as supplyers of tissue, and we find, in fact, that all actual nutrients used by man the world over may be divided into the six classes—*proteids, albuminoids, fats, carbohydrates, inorganic salts,* and *water.* If we are guided by empirical conditions of actual diets, we must add to these two other classes, *stimulants* and *condiments,* the latter of essential importance.

Fig. 72



A fibula tied in a knot, after maceration in acid to remove its lime, etc. (From a specimen in the College of Physicians and Surgeons, New York.) (Dalton.)

General Requirements in a Food.—The total food of an animal at different periods of his life must meet three requirements (as, indeed, Aristotle long ago pointed out), each indispensable: (1) Throughout life the food must be able to supply energy, by expending which the animal lives. Previous to its birth this energy, like the body-tissues, was derived ready-made from the maternal organism. (2) Until maturity the food must afford the materials for constant bodily growth—that is, the tissues must be built up faster than they are worn away by use. (3) At all periods of life the food must furnish a continuation of the tissue-material used up and worn out by the universal wear and tear to which all material objects are subject in some degree or other.

All food taken into the body and digested is reduced to the simplest terms in which it can retain its characteristics. These food-elements are then reconstructed by the eating animal into his own sort of tissues or proximate principles. In other words, there is never any direct transference of food-materials from the flesh of one animal to that of another. When a man eats pork, his tissues do not become more like those of a pig; and sheep-fat is never to be found in a dog's adipose tissue after being fed even wholly on mutton (except under the abnormal conditions of forced feeding far beyond the limits of normal digestion). Just as in a paper-mill all sorts of paper and rags are macerated together and then run out as one fresh homogeneous product, so in organisms protein, fat, carbohydrate, albuminoid, inorganic salts, and water are run through the mechanism of the individual's digestion and absorption and are assimilated to the special likenesses of the particular tissues of which perhaps they are to form a part. Chemically as well as histologically the muscle of no two sorts of animals is exactly alike, yet every one of them may serve in part as the chief and adequate food of any other carnivorous animal. If the flesh of seagulls tastes like that of fish it is because these birds at times gorge themselves with fish far beyond even their powers of assimilation, although not beyond their digestive powers. Only recently has it been learned how complete is the tearing-down of food in the alimentary canal. The absorbing wall of the intestines has, therefore, powers of recombining these food-elements, "proximate principles," to a degree much greater than was a few years ago suspected.

By the definition in common use, any substance which produces in an organism animal tissue and energy or either of these is a food. Neither of these results, however, can be effected until the nutrient has been actually absorbed, after its digestion, at least into the circulating fluid of the body, the blood, and has thus become a part of the organism. Thus, a food is really a food only after it has been absorbed. Two requisites of a food, then, are digestibility and absorbability. The prerequisite of digestibility is obviously essential. No substance, candidate for use as a food, unless directly soluble in water or the normal alkaline salines of the body (saliva, the blood and lymph, etc.), can be digested except those proximate principles of nutrients so often rehearsed—namely, proteids, fats, carbohydrates, and albuminoids. These predominant components of various foods vary widely, however, in the degree of their respective absorbability which is so essential. Atwater calculated from a large amount of data that from a mixed diet the following proportions of nutrient components are on the average absorbed:

PERCENTAGES OF ABSORPTION.

Nutrients.	Proteid.	Fat.	Carbobydrates.
Animal foods . . .	98%	97%	100%
Cereals and sugars . .	85%	90%	98%
Vegetables and fruits .	80%	90%	95%

Another characteristic of foods is that they should require digestion. This is on the universal principle that lack of exercise allows an organ to degenerate. If the muscular and chemical arrangements of the intestine are not employed actively they tend to lose their vigor. This is the objection to the large use of partly predigested foods.

THE GENERAL NATURE OF DIET.

A diet is a selection of nutrients so arranged as to meet continuously the requirements of an organism. This selection may be almost unconscious, as was formerly that, for example, of an average farmer's family. It may be, on the other hand, the exactly defined choice like that of the army, or of a modern scientific research, like that, for instance, conducted by the Department of Agriculture on the harmfulness of commercial food-preservatives. The selection may be, in case of the wealthy, from the whole artistic menu of the chef of a great hotel, or, at the other logical extreme, in reality no choice at all, on which basis was once the diet of potatoes of the Irish peasant and the rice of the Chinese. Still, the leading notions in the term "diet" are those of a set arrangement of nutrients for a considerable space of time, sufficient, at least, to allow of observation of its effect, good or bad, general or special, on an organism.

Of the general requirements of a normal or ideal diet, so understood, there are at least six which should be noted: (1) A diet must contain both energizers and tissue-builders; (2) it must be sufficient in quantity to support the organism in normal condition, but no larger in amount; (3) it must have the alimentary proximate principles or components in nearly the proportions which best suit the needs of the organism; (4) it must contain a variety of nutrients both for each meal and from day to day; (5) it must be adapted more or less accurately in a quantitative way to the particular use of the organism under its specific conditions at the time; (6) it must be adapted also qualitatively to the organism's needs in certain physiological (and pathological) periods.

A Source Both of Energy and of Tissue.—Of the six alimentary components already frequently mentioned (proteids, albuminoids, fats, carbohydrates, inorganic salts, and water), five, all except water, are *sources of energy* by their metabolism, chiefly katabolism, in the body. It is possible that the ingested water also may be in part decomposed, or, more probably, may unite with the simple products of katabolism in anabolic processes, thus producing energy; of this little is definitely known. Of the familiar six, three only are *sources of tissue* considered as active bioplasm (that is, excluding fat)—namely, proteids, inorganic salts, and water. Carbohydrates and fats are sources of tissue-fat, but the latter is relatively, at least, unimportant in the actual life of the animal in health, and in this relation is not considered as tissue-protoplasm. It is a tissue, but one of a special sort.

THE GRAND DIVISION OF NUTRIENTS.

Sources of bioplasm.	Sources of energy.
Proteids.	Proteids.
Inorganic salts.	Inorganic salts.
Water	Fats.
	Carbohydrates.
	Albuminoids.
	Water (?).

Of the three sources of protoplasm, proteids alone are by themselves producers of protoplasm, for, of course, feeding inorganic salts or water, or both together, and nothing else, could do nothing toward continuously supporting life. Actual starvation is, however, excepted, for then water will prolong vitality; in case of the higher animals entire lack of water kills much more quickly than entire lack of other nutrients. (Lack of all sleep destroys life sooner than lack of either food or drink.)

This division of the proximate principle of foods into two classes, one of which supplies to the animal both active tissue and energy, and the other of which furnishes only energy, is of the largest importance in the physiology of nutrition. Notwithstanding, the division is far from absolute, in that even a carnivorous animal requires for continued existence at least a very small proportion of fats and carbohydrates as well as the proteids, the mineral salts, and water mentioned in the table. The reason for this is, as has already been stated, the composition of the living substance. As will be recalled, it seems always to contain some fat and especially some carbohydrate. The characteristically vital particle probably consists of all of these molecules in some sort of combination or other—proteid, carbohydrate, fat, salts, and water in one unstable vital mass. However, in general terms, an animal can live on proteids, inorganic salts, and water, but not on fats, carbohydrates, salts, and water, singly or in any combination. This gives proteid a preëminence as an alimentary component, a preëminence which men in general as well as physiologists appreciate. The immediate reason for this superiority, of course, is obvious: the proteids alone (save as noted below) contain *nitrogen*, available for the building of new albumin in the ever-wasting animal tissues. In the nitrogen most probably, as was seen in our first chapter, perhaps in the cyanogen-combination, lies the vital nexus. Why animal organisms cannot take this nitrogen from albuminoids or from salts containing nitrogen, science at present cannot tell us. The hemoglobin-like bioplasm of the vegetal kingdom seems to do this paramount work for all living organisms.

The five food-components which are surely sources of energy in the body (proteids, albuminoids, fats, carbohydrates, and mineral salts, with the possible addition of water) produce this energy in a multiplicity of ways of chemical reaction. These methods are mostly katabolic in trend, but some are partly anabolic. Some, too, of the reactions doubtless occur in other ways which could be classed technically as neither anabolic nor katabolic, since the large majority of chemical processes are productive of some degree of heat. In the case of fats and carbohydrates the general reaction is doubtless *oxidation*, a good part of the energy produced chemically in animals being derived from this source. The katabolism of proteids and of albuminoids is more complex than that of fats and carbohydrates, but especially in case of the tissue-proteids (as distinguished from the circulating proteids, mostly serum albumin and serum globulin), is partly a process of oxidation also. One must not lose sight of the simple parallelism between an organism and a steam-engine in that in both cases the actual burning of fuel, largely carbonaceous, is necessary for the production of energy. This is expended partly as work, "the overcoming of resistance," and partly as heat, which latter is quite essential in the organism, but not in the steam-engine. There are, besides these, other modes of vital energy-expense, mentioned in the chapter on Nutrition. We shall soon see (under Calorimetry, p. 140) how accurately the total energy set free in an organism can now be measured, and how fully the combustion-values, although not too strictly the *organic* energy-production, of any nutrient can be estimated and allowed for in the study of diets.

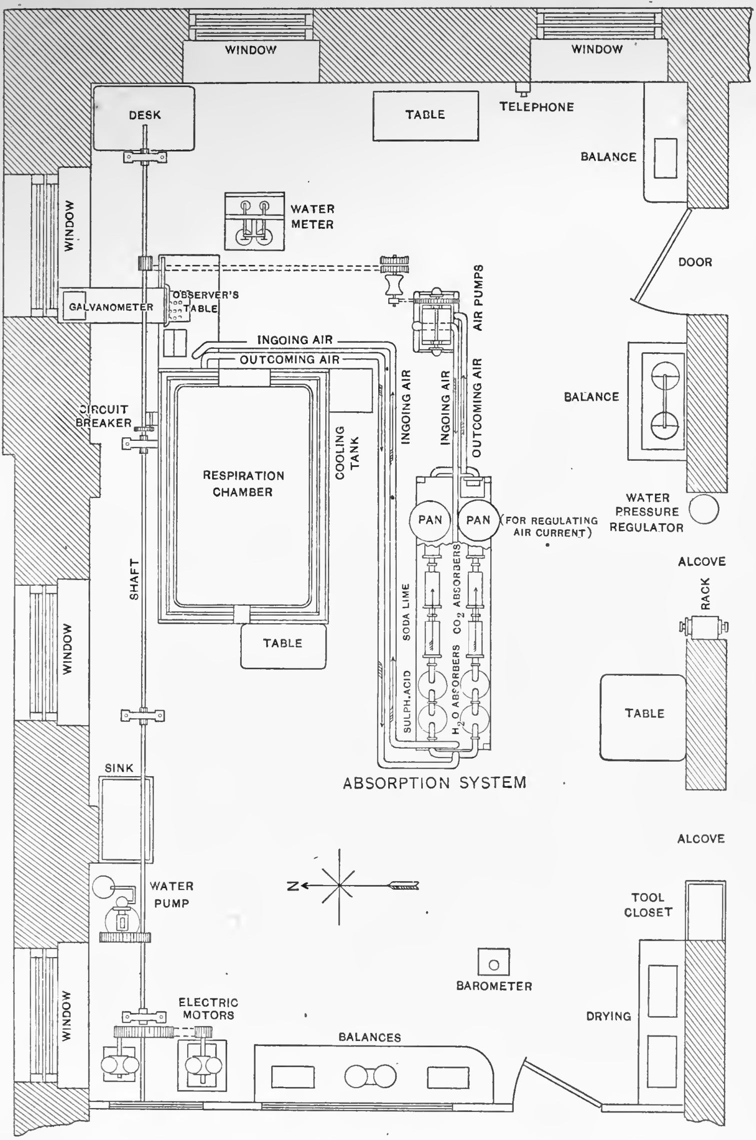
Most foods in actual use contain both energizers and tissue-producers, but some important foods do not. No animal, no man, for instance, could live on pure sugar, butter, or starch, for these contain nothing which could replace the wasting protein muscles whereby his body and its organs are moved. Man could not live on gelatin, for although it contains the needful nitrogen, the latter is for some reason locked up in unavailable combination. On simple bread, potateos, rice, corn, oatmeal, or flesh (water being added in each case) a person could, if necessary, live a long time, for each of these contains proteids, carbohydrates, fat, and inorganic salts, although in very various proportions. On eggs alone or on milk alone life endures in theory for an unlimited time, for these are, of course, the sole diet of young birds before hatching and of all young mammals. In practice, however, it is doubtful if a normal human adult could stand the strain of living solely on either of these for many years—surely not in a well-nourished condition. Our first requirement of an adequate diet is that it contains both tissue-builders and sources of vital energy, but considerations other than this are essential.

The Right Quantity is Important.—Our second ideal requirement is that the quantity of the food should be sufficient for the normal needs of the organism, but not excessive. This is well-nigh axiomatic, and yet its scientific meaning demands expression and the average limits of a normal diet, maximal and minimal, require some discussion. If a diet be too small in amount, short of fasting or its continuance into starvation, the consequences are a diminution both of tissue-repair and of the energy of the body. The organism which is living or has lived on its own tissue-fat to help meet the deficiency of income shows that bony angularity most of us are familiar with, unfortunately, sooner or later, in all localities. The individual is obviously weak, and exertion, either physical or mental, requires an unusual effort. The deficiency in heat-production is felt in cold weather in that sense of continual chill to which very poor folk strive in vain to become used, the thermometer showing perhaps half a degree's depression of the body-temperature.

The determination of the quantity of food in an average diet has been and is a matter of much research and of more discussion. The explanation of this indeterminateness is to be found in the very widely differing needs and habits of the classes and divisions of mankind. Physiology has been heretofore very largely a descriptive science, analyzing and systematizing what it finds in Nature, and only gradually is it becoming a normative science which sets ideals or tells what ought to be. In this case, therefore, we can but describe what people actually do eat, and if the science declares what men should eat, how their diets ought to be composed, it will be only by taking as a basis the best average of actual diets used by any class of persons that can be arrived at. It is only the faddists and the "cranks" who, on any other basis than this which is natural and actual, say what men should eat. Still, of late, quantitative researches have been made by methods soon to be described, which, independently of actual dietary conditions, have more or less well established the proper amount of food for persons under various circumstances of metabolic expenditure, climate, etc. To a great extent these experimental products and the data derived from observations of actual corresponding diets very closely agree in all essential respects. It is agreements of this sort which give encouragement in the often slow progress of a science.

THE ENERGY-VALUES OF FOODS.—The quantitative work referred to has been accomplished by a method of accurate measurements of the energy-values of nutrients in relation to the income and expenditure of energy by animal organism. This method is termed *calorimetry*, literally "heat-measurement," for the process was developed in studying animal heat, its sources and modes of loss. At the present time calorimetry means the accurate measurement of the energy-values of the ingesta of organisms, oftentimes in relation to the heating-energy and the moving-energy of the organisms. In its theory it is a simple method, for it merely attempts to measure the income and expenditure of animals (and latterly of plants sometimes) and to determine the combustion-value of their various nutrients. In its practice elaborate and very extensive apparatus is sometimes required, and the conduct of the experiments involves much careful complex chemical analysis and attention to the finer points of several branches of physics.

Fig. 73



General plan of the respiration-calorimeter laboratory of the United States Department of Agriculture, Washington. This diagram is self-explanatory, so far as the principles of the action of the calorimeter are concerned. The details are very complex. (Atwater.)

The unit of measurement in all researches of this sort, very necessary to be well understood, is the *calorie* or, formerly, the *millecalorie* ($\frac{1}{1000}$ part of the calorie proper). Sometimes one unit and sometimes the other is used, but they are so unlike in size that confusion can scarcely arise. A calorie is the quantity of energy, expressed as heat, necessary to raise the temperature of one kilo (1000 gm., 1000 c.c., or one liter) of pure water 1° C. A millecalorie is the energy in the form of heat needful to raise 1 c.c. of water 1° C. The absolute combustion- or heat-value of any nutrient is, then, the number of calories of energy liberated by its complete union with oxygen. It matters not a bit whether it be in a furnace of the laboratory or in the circulation and tissues of an animal. To be exact, however, oxidation in the organism might not extend to every particle of any ingested mass of food even if all were absorbed, and all of any food is seldom wholly absorbed. There is invariably waste of one sort and another, as the composition of the feces shows. Still, in general terms, for theory's sake, we may say that any given quantity of food gives out as much energy when consumed by the body as when burned in an ignition-tube. It has been one of the tasks of calorimetrists to ascertain by experiment the "combustion-equivalents" of all important articles of diet, the differences between their laboratory combustion-values and their intra-organic energy-values being so small as to be negligible. A complete table of such determinations has less interest and physiological value, however, than it would have were the conditions of organic usefulness in oxidation as simple and as certain as those methods by which these tables are derived.

A few examples will suffice. The number of calories of heat liberated in the burning of 1 gm. of average dried bacon is 8.86, that is, in the union of oxygen with 1 gm. of bacon just enough heat is liberated to raise the temperature of 8.86 liters of water 1° C. Similarly, the combustion-equivalent of fat mutton is 4.03 calories; of fat beef, 3.27; of white bread, 2.74; of eggs, 1.59; of lean beef, 0.98; of potatoes, also 0.98; of milk, 0.70; of apples, 0.74; while lettuce yields only 0.20 calories of heat per gram. Thus, bacon is adapted to be wisely eaten on an active day in winter, and lettuce, apples, and milk on lazy days in summer. Experience inherited as instinct very early taught many animals this dietetic principle, and today among human beings it has become settled in universal custom. Thus, the natives of the tropics live largely on juicy fruits and vegetables, while the inhabitants far north and south of the equator eat great amounts of fatty meat and even, it is said, oils and fat in quantities which would be nauseating to the majority of mankind nearer the equator.

Just as every actual article of food has its combustion-equivalent, so have the alimentary proximate principles, proteid, fat, and carbohydrate. Rubner found by actual calorimetric experiments on the tissues (so avoiding the more uncertain methods of calculation), allowing for energy still in the excreted urea, etc., that the following three food-components had combustion-values about as given below. These determinations approximately are in general use for the calculation of diets.

COMBUSTION-EQUIVALENTS (PER GRAM).

Average proteid	4.1 calories.
Average fat	9.3 calories.
Average carbohydrate	4.1 calories.

It is useful to know, as a basis of comparison, that the combustion-equivalent of 1 gm. of hydrogen is 34.622, and of carbon 8.08. In order now to find the approximate energy-value of any given mass of a man's food it is necessary to know only the percentage-proportion of average proteid, fat, and carbohydrate in it. We do not at present know enough quantitatively about the katabolism of the inorganic salts and the water to calculate or allow for them, while comparatively few foods contain albuminoids in important amount. Having learned from one of the standard tables (for example those of the U. S. Agricultural Department) the percentages of fat, proteid, and carbohydrate present, it is necessary, in order to estimate the energy-value of the composite food, only to multiply each component by its combustion-equivalent and add the products. This will give the number of energy-calories in 100 gm. of the food, disregarding salts, water, and albuminoid if present. As an illustration, take a kilo (two-pound) loaf of white wheat bread: what is its value to a hunter, for example, as nutriment? In every 100 gm. of the bread there are about 8 gm. of average proteid, 49.2 gm. of carbohydrate, and only 1.5 gm. of fat (hence people "naturally" eat butter with bread). The salts and water as energizers we disregard. The combustion-equivalent of average proteid is, from Rubner's table above, 4.1 of carbohydrate 4.1, and of fat 9.3.

8.0	multiplied by	4.1	equals	32.80
49.2	"	" 4.1	"	201.72
1.5	"	" 9.3	"	13.95
The products' sum equals				248.47

In every 100 gm. then of the bread-sample there are probably available for the eater's warmth and strength and tissue-repair 248.47 calories of energy. Reduced to heat, this is enough to raise 248.47 liters of water 1° C. in temperature. In the supposed kilo-loaf there are ten times as many calories, or a total of 2484.70 calories, or about two-thirds the "fuel," which a very active hunter would require in winter for his personal "engine." If the man eats 100 gm. of butter with this loaf of bread he increases his food materially, and both in a pleasant and an easily available way. A dekagram of butter properly made consists of 0.3 gm. of proteid, 91 gm. of fat, besides water and salts, but no carbohydrate. From the 0.3 gm. of proteid (0.3 × 4.1) would come 1.23 calories of energy, and from the 91 gm. of fat

(91 × 9.3) 846.30 calories, or a total of 847.53 calories from 100 gm. of butter. This is more than one-third as much energy as was afforded by the bread, ten times as heavy. The following table, compiled by Atwater, gives a fair estimate of the calorie-needs of men performing various degrees of labor.

DIETETIC NEEDS FOR VARIOUS DEGREES OF LABOR.

Conditions.	Proteid.	Fat.	Carbohydrate.	Energy in calories.
Man at light work	110	60	390	2634.2
Man at light outdoor work	110	100	400	3052.0
Man at moderate outdoor work	125	125	450	3556.0
Man at hard outdoor work	150	150	500	4105.0
Man at very hard outdoor work in winter	180	200	600	5008.0
United States army ration	120	161	454	3851.0
United States navy ration	143	184	520	4998.0
College football team	181	292	557	5742.0
Teamsters and marble-cutters in Boston, Mass.	254	363	826	7804.0
Laborers of Lombardy, Italy	82	40	362	2192.0

We shall have a little more discussion of the quantitative adaptation of diets later on (p. 151). Even the last two diets summarized in the above table are not the extremes of actual diets in the overcivilized countries of Europe and of America. Playfair reported, about thirty-five years ago, a London sewing-girl with weekly earnings of three shillings ninepence, who subsisted on 53 gm. of proteid, 33 gm. of fat, and 316 gm. of carbohydrate, a diet theoretically worth only 1820 calories. The physiological conditions which made life on so little fuel possible are obvious. The individual was a female, doubtless not tall, certainly very thin, with a relatively small amount, therefore, of tissue-waste. Her labor had in it almost a minimum of both bodily and mental exercise, and was carried on almost if not quite wholly indoors. It was done doubtless in that spiritless and feeble way characteristic of any machine, natural or artificial, with little power behind it. At the other extreme, Atwater found in Cambridge, Massachusetts, brickmakers who daily consumed 180 gm. of proteid, 365 gm. fat, and 1150 gm. of carbohydrate, giving altogether 8848 calories of energy. These are indeed extremes—that of the little seamstress almost a starvation, indoor diet barely enough to keep body and soul together, while that of the brickmakers is the almost gluttonous diet of well-paid workmen, in one of the most laborious of outdoor trades.

Using the combustion values of proteid, fat, and carbohydrate already given, the average food-requirements as estimated by seven older authorities, give the following averages: Of dry proteid, according to these older figures, about 121 gm. is required, of dry fat about 59 gm., and of dry carbohydrate 510 gm. To these numbers should be added 30 gm. of inorganic salts and 3 liters of water. The recent work by Chittenden and some others makes it fairly probable that these amounts are excessive as a grand average requirement for the average adult human being. It has lately been claimed that man does not masticate his food sufficiently, and that if he chewed it more he would get from it much nutriment which is now wasted. These more recent researches would tend to cut down the average requirements of proteid 40 per cent., or even more. It is believed by many physiologists, however, that to do this would so decrease the working surplus, so to say, of the individual's food-income that emergencies, such as illness, would be much more dangerous to a person who had lived on this quantity of food. It remains to be seen, then, by further research on a much larger scale and lasting a much longer time how much food an average adult actually needs. Here as elsewhere the relations are more widespread and more complicated than the experimental conditions take account of.

The Right Proportion of the Diet's Components is Important.—The third general requirement of diet is that its proximate principles should be in nearly the proportion best suited to the organism's needs. In the average published heretofore by these seven authorities recently mentioned, the proteid was about 17 per cent., the fat about 8.5 per cent., and the carbohydrate about 74 per cent., if we neglect the inorganic salts and the water. The whole principle underlying the right proportion of proximate principles in food is that an excess of one of them in the diet necessitates the useless expense of energy to digest and absorb this excess. In general terms, only milk and eggs contain the proximate principles in just the right proportion. White bread perhaps approaches this condition next best. Rice, for example, contains about one-third the ideal proportion of nitrogen. The person who is compelled to live upon it continually, therefore, has to burden his digestive apparatus with a large excess of carbohydrate (almost wholly starch). In some South American tribes the diet was formerly, at least, almost wholly meat. These people would have to eat a large excess of the flesh to get a sufficient amount of carbohydrate. In the Arctic regions the diet, on the other hand, is largely fat, and carbohydrate might often be lacking in a diet in this region. In order to obtain these deficient proximate principles, an excess of the others must be digested and absorbed, only to be excreted again unused. All of these processes (mastication, deglutition, digestion, absorption, excretion, etc.) use up many varied forms of energy which might be better employed.

Variety in the Diet is Necessary.—A fourth requirement of a proper diet is that it should consist of a considerable variety of foods. This exaction of Nature in its effects on the world's diet is not unlike the preceding demand that the proportions of the alimentary components should not depart too far from the composition of the consumer's body. The ingestion of a large variety of foods in practice assures this right proportion. But several other things involved in the matter of variety are as yet unconsidered, and especially the preparation of food-materials for being eaten by man.

It is not enough that an animal's diet should contain both energizers and sources of tissue-replacement, or that it should consist of a sufficient quantity of the proximate principles of the animal tissues, even if nearly or quite in their proper proportions. Most of the brutes, to be sure, would continue to live very well on a diet thus describable. By force of poverty or other adverse conditions millions even of men and women subsist their lives through on a very few of the staple articles of food, such as rice and other starchy nutrients. We are trying to become familiar, however, with an ideal diet physiologically adapted to such men, women, and children as most of us are concerned with in civilized (perhaps overcivilized) modern lands. To men who are more than the victims of an unkind nativity and more than animals, variety in their food is important, indeed practically essential. We might even go farther and maintain that the basal requirements of composition being always satisfied, the greater the variety in the food the better is the organism served by it. In obtaining an understanding of the facts and principles of digestion, in the next chaper we shall see that the conditions under which the softening and hydrolyzing secretions of the alimentary canal are augmented or, on the other hand, inhibited are very intricate. This might be expected in an organism as uniquely complex as that of man, combining in its functions mind as well as body. Even if the tissue-cells are supplied with what they demand of food quantitatively as well as qualitatively, the mechanism which immediately furnishes to them this nutriment is discriminative. Because, perhaps, of its close connection with the sensitive brain it soon demands a change in the quality of its supplies when forced to work on a small series of foods. We tire of almost all sorts of food eaten to excess, and the more quickly the greater the sameness and the stronger the flavors. The organism's requirements are in this respect, out of many, self-regulating, and on the one side demand that the foods shall be not too much alike in taste (and to a less extent in odor), and, on the other hand, that they shall be not too strongly flavored. So, as a practical outcome of this natural tendency, we see that wheat-bread and the staple sorts of meat, eggs, milk, plain soups, and vegetables, feebly flavored, constitute the great bulk of our usual diet. Sugar is an important nutrient which is almost an exception to this rule, for exceedingly few or no individuals of the animal kingdom, from insects to man, young or old, seem ever to weary of its sweetness. Indeed, this is a word in all languages adopted metaphorically for delight and pleasantness. It is of small account if any new article of food has an unpleasant flavor, for when familiar, such a flavor becomes pleasant. As no two articles of food taste quite alike, the natural way to obtain this variety of flavor with its consequent and more important variety of composition, is to use as nutrients many sorts of substances, mineral, vegetable, and animal, from many various places, earth and air and sea. The organism naturally is after a wide variety of elementary and compound materials which in their union in the gut shall always form an average pabulum ample and nearly invariable in its absorbable products. By this wide-gathering of many substances whose limits of strangeness are guarded by taste and smell and the sense of nausea, the organism best secures its ends in this respect. We have seen already the chemical basis of this unity-in-variety, and it needs no further elaboration.

The variety required is not only the diversity of a day or a week, but also of each meal, as is the custom more or less everywhere. A large variety at a meal is necessitated more by the pleasure arising from the varied flavors than from the precise needs of the organism from hour to hour. Let us look a little, then, at the nature of the diversity in a well-cooked meal as regards its chemical components, its digestibility, its flavors, and its odor. We may take for this purpose a dinner such as is served at an average American hotel; this will answer several purposes at once. The first thing most people from habit wish after being seated at the table is two or three swallows of cold water, and this, undoubtedly, slightly stimulates the salivary glands and the mucosa of the stomach and prepares the taste-organs for better action. The first food brought, we will suppose, is bouillon and bread and butter. This soup is at once nutritious, tasteful, and of pleasant odor, the two latter qualities coming largely from the "extractives," salts, and soluble albumins which it contains, the nutritive value from its richness in most of the proteids of beef. Soup serves by its heat, liquidity, and salts to warm and stimulate gently the glands and walls of the stomach and duodenum in preparation for solid food. The bread adds physical substantiality to the liquid food, while, as already noted, the butter adds the fat lacking in the bread, makes the latter more pleasant to the taste, and, when melted in the mouth, more easily swallowed. Between the soup and the fish the short interval of waiting is an advantage, a distressing sense of hurry, leading to indigestion, being thus avoided when time for eating is normally abundant. Fish contains mostly proteids and fat, and potatoes are eaten with it to supply the lacking carbohydrate. A little of some strongly flavored condiment or relish, a pickle or an olive or two, often serves at this point in a dinner to still more vigorously stimulate the digestive glands (by means of the pepper, mustard, horseradish, acid, etc., which they contain) in readiness for the *pièce de résistance,* the flesh-meat, more difficult of digestion than ordinary fish. This also, as in case of the fish and for like reason, is served with potatoes, most often baked, and if properly cooked is to most persons the most pleasant as well as the most substantial portion of the meal. The seasonable vegetables, peas, beans, spinach, squash, or what not, add each its flavor, its salts, its juice, and its quota of starch and proteid to the food; these are best handled by the digestive mechanism while in the full vigor of the meal's solution. Two or three glasses or even more of cool but not ice-cold water may have been drunk during the meal thus far with pleasant effect. The pastry and dessert and a cup of coffee are now served. The second if not the first usually contains much sugar, and being in other ways intended to be delicious to the taste, thus adds almost the finishing touches to the pleasant sense of "fulness" or satiety which usually accompanies the satisfaction of basal organic needs by normal functioning. A cup of coffee adds still more to the liquid and heat of the digesting meal, both beneficial factors, while its essential alkaloid, caffeine, stimulates gently the whole organism, especially the nerves and the muscles. If a mild cigar be smoked after the dinner, as an incentive to social chat with genial companions, the organism is, thereby, still further stimulated into a condition of quiet digestive activity, with mental musing and muscular rest, the condition best adapted for the quick and pleasant digestion of a meal.

The feeling of satiety which follows the eating of a full dinner or other repast has some little physiological interest. It is especially noticeable when a large quantity of food has been taken slowly, accompanied by hot tea, coffee, or cocoa, and ending with a sweet dessert. It arises doubtless from the functional congestion of the stomach and small intestine with its accompanying internal warmth; the muscular and glandular activity add that tone of pleasantness which exercise of whatever sort always produces in a normal organ. This feeling, however, cannot be regarded as the necessary criterion of a sufficient meal, for long before the stomach is so full as to occasion this sensation the needs of the body, if supplied three times a day, have been satisfied. It may be taken, however, to some degree, apparently as the index or criterion of a properly balanced meal, all parts of the digestive mechanism proper being then put in activity.

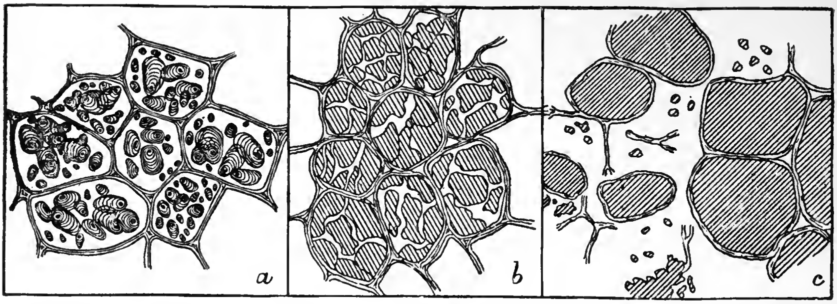
As in other human affairs, the common-sense usefulness of ordinary diet is at times disturbed for even a considerable number of persons by the influence of new and radical theories and fads, not to mention the host of proprietary foods which are continually appearing. Certain that actually new nutrients are little apt to appear, scientific dietetics pays little heed to the extreme theories, save to combat them. It welcomes, however, every new form of adequate nutriment as one further addition to the variety of foods, all useful at some time or other. For example, the recent large number of brands of prepared cereals, etc., is a distinct advantage to the public who can buy them, for they make it certain that almost anyone can eat month after month, as part of their breakfast, some delectable and substantial grain-product, whereas not so many years ago to be tired of three or four was to be tired of them all.

The most usual dietetic objection to eating-fads generally is that, even if the methods or the foods suggested supply the needful nutrients, their use tends to decrease the variety and, by consequence, the value of one's diet. They foster the harmful and disturbing habit of attending to the digestive process, and, like other fads, direct the individual more or less toward the unbalance of fixed or of imperative ideas. The most widespread of the diet-fads is *vegetarianism.* It arose in the Eastern countries apparently because of the influence brought from Buddhistic India, which makes it seem murder to kill the brute-animals because supposedly animated by transmigrated human souls. Hereabouts, by Christian people, it is construed merely as a belief in the sacredness of brute-life or as a feeling of natural pity. One sees the same point of view as an innate emotion in young children sometimes, an exaggeration of the validity of the purely sentimental over that of the valuable and the practical. Vegetarians are of two sorts, real and self-fancied, consistent vegetarians and mock-vegetarians, as they are termed. The latter we need not here notice, for they are mere zoöphilic pretenders in that they eat the two most characteristic of all animal foods, eggs and milk. Consistent vegetarians are omnivorous animals, who try to make themselves into herbivora. Some of them, so far as the source of their food is concerned, succeed in this endeavor, but only at no little cost in force to themselves. For this extravagance of organic force there are three main causes: (1) The relative great difficulty in general of masticating and digesting the proteid out of cereals, lentils, vegetables, and fruits, as compared with that from fish and meat, eggs, and milk. (2) The relatively small absorbability of the alimentary proximate principles derived from foodstuffs other than animal. The table compiled by Atwater (page 137) shows the second of these objections well, and in particular the fact that from animal foods 98 per cent. of the proteid, 97 per cent. of the fat, and 100 per cent. of the carbohydrates is absorbed into the circulation and utilized, while from other sorts of foods an average of only 82.5 per cent. of proteid is absorbed, 90 per cent. of the fat, and 96.5 per cent. of the carbohydrate. The greatest loss, then, is in proteid, and in the struggle for existence of the multitude of men this actual loss of 15.5 per cent. is of considerable importance, of far greater moment certainly than are the lives of certain animals which never would have lived at all unless raised solely for this high and biological purpose of feeding man and other animals. One has only to glance at the teeth of man, comparing them with those of cattle and of dogs (page 165), and to understand the rudiments of the digestive chemistry of the various sorts of animals, to be assured that the whole human organism is naturally omnivorous: carnivorous quite as much as herbivorous.

Cookery.—The variety of foods which most of the brutes naturally use is small. What they shall eat is largely predetermined by instinct, by the chance of what happens to be near and by habits originated by these other two conditions. The food-range of carnivora is doubtless larger than that of herbivora, while naturally the range of omnivora, like many fishes and birds and man, is larger than that of those species which use only plants or only animals. Man's intelligence doubtless would have led him directly to have tried many sorts of food, but it certainly has taught him one great art which has accomplished the same important result indirectly, and which, as much as any other thing, biologically differentiates him from his "poor relations," the brutes. This art is that of *cookery*, of preparing food for the pleasurable nourishment of man and other animals. In this definition of cookery three words are emphatic: "Preparing," indicating the wide range of the art; "pleasurable," suggesting one of its important purposes; and "nourishment," indicating its basal usefulness, and the essential requisite of all proper cookery. The range of the art of the cook is wide, physiologically at least, for it includes as certainly the proper care of milk and the sterile cleansing of lettuce as the concoction of a seashore chowder or the proper roasting of a turkey. It is the cook's proper business to be in a position to guarantee to his trustful clients the adequate nourishment, the pleasant flavor, and the entire safety of the food he prepares for them. The last requirement is seemingly often overlooked, and with dire effect. The importance of the art of cookery to mankind can scarcely be overestimated. To the trained nurse, the nursery-maid, and the physician few things are more important, but at present the last learns scarcely more about it than the second, and not nearly as much as does the first. In many diseases, and for more and more with the increasing number of antitoxins, the proper feeding of the patient is three-quarters of his proper treatment, and to direct this proper feeding intelligently, the physician requires a practical as well as a theoretical knowledge of foods and their ideal preparation. Every medical curriculum might not improperly include a demonstration-course in actual cookery to complete its discussion of food and dietetics.

The preparation of food for man includes the boiling, stewing, roasting, baking, broiling, frying, preserving, freezing, brewing, and arranging of soups, meats, breads, vegetables, salads, pastry, desserts, preserves, ices, fruits, and beverages. We will consider the chief of these culinary processes, and especially their relations to the physiological value of food.

Fig. 74



Changes of starch-cells in cooking: *a*, cells of raw potato with starch-grains in natural condition; *b*, cells of a partially cooked potato; *c*, cells of a thoroughly boiled potato. (United States Department of Agriculture Year-book, 1900.

In general, the application of heat to food more or less (1) destroys the cellulose shell about the grains of starch in carbohydrates, coagulates some proteids and dissolves others, and softens the fat; (2) macerates and makes more easily masticable flesh and vegetables; (3) destroys parasites of nearly all sorts; (4) renders the food more grateful both to the taste and to the intestines by its warmth; and (5) develops flavors, especially in meats.

Of all modes of cooking, *boiling* is undoubtedly the most common, it being easiest and cheapest. Boiling differs from *stewing* only in degree, for the latter process is boiling continued until the food falls apart from solution of the connective-tissue of meats or of the rough cellulose framework of vegetables. The boiling water penetrates the mass of food and cooks it homogeneously, and so differs much in its effects from roasting or broiling. Boiled meats are less easily digestible than those roasted or broiled, for the soluble proteids are coagulated and rendered hard and relatively tasteless, while the salts and savory extractives pass largely into the water. Prolonged boiling may redissolve some of the coagulated proteids. In boiling, unless under pressure, the temperature does not exceed 100° C. Boiling is chiefly important as a means of cooking vegetables, for it makes starchy foods available as food which raw would be quite indigestible and even irritating to the gut. In the processes of *roasting* and *broiling*, essentially alike in action, the material should be at first subjected to a high degree of heat, 200° or higher. This coagulates the outside of the mass into a sort of shell, which retains, more or less unchanged, the juices and, in case of meat, the salts, extractives, and soluble albumins. Flesh which has been heated not above 70° is the most digestible, for even this degree of heat changes the connective-tissue which binds the muscle-bundles together to gelatin and renders the meat more easily masticated. The high heat of the first part of roasting also develops in the fats of the meat several very savory fatty acids, and thus provides useful flavors not otherwise obtained. In *frying*, the heat is conveyed to the interior of the food by means of melted fat of various sorts, commonly lard, butter, or suet. This provides a very high degree of heat which more or less penetrates the mass and produces effects somewhat like those of prolonged and excessive baking or roasting. The fat, however, tends to surround with a film each particle of the meat or vegetable, and so renders it relatively indigestible. The excessive use of fried food, caused by its relative ease and cheapness, is one of the curses of American habits of cooking, it being often used when broiling would be very much better for the consumer. *Preserving* is a mode of preparing food so that it will keep indefinitely. It consists usually of some process of sterilizing (commonly by heat), the material being then sealed from the putrefactive germs of the air. In jellies the sugar acts as a preservative. Almost every sort of meat, vegetable, and fruit is now thus prepared in glass or in tin, and so made for indefinite periods of time available in any part of the world. In some cases the use of artificial preservative substances renders the foods so prepared difficult of digestion, but most of the objections made on this score seem unfounded. The elaborate test-experiments made by the United States Government chemists tended to the principle that while boric acid, for example, would probably irritate a digestive apparatus unduly if taken in considerable quantities continuously, in the amount apt to be ingested by the average person on an average diet practically no harm would ensue. The cold-storage problem (fowls, for example, often being kept, it is said, two years or more) is in practice a more important question. However low the temperature, in time protoplasm probably undergoes degeneration, which makes it more and more unsuitable for human food. The smoking of flesh-meats, including fish, and the drying of meats, vegetables, and fruits is a valuable mode of preserving food for a shorter period than in case of hermetical sealing from the air. Nutrients so prepared are liable to be infested by worms and by mould, and, in many cases, at least, are relatively lacking in flavor, except that of salt or of the volatile substances of smoke. The *brewing* of beverages, such as coffee, tea, cocoa, and beers, consists either in the making of a decoction (as in tea and coffee); of a solution which is then *cooked* (cocoa and chocolate); or in the fermentation of the sugars in many vegetable substances (of which barley is typical) under the influence of yeast (*Saccharomycetes cerevisiæ*). *Freezing* is a culinary method which has come into common use only of late years, but it affords many desserts nourishing and grateful to the well, and often very valuable in febrile disorders. The use of ices is rapidly increasing in Europe as well as in America, where the art originated.

Quantitative Adaptation to its Service is Essential.—Another requirement in an ideal diet is that it should be adapted quantitatively in some degree to the conditions under which it is employed. As has already been emphasized, a food provides energy for the warming and the moving of the body and materials for the replacement of wornout and excreted tissue. The greater then (*a*) the amount of muscular and neural exercise, the greater (*b*) the atmospheric opposition for keeping warm, and the greater (*c*) the need of new tissue, whether for growth or for tissue-waste, the greater the amount of food required. This is axiomatic, but it is important in dietetics. The only reason, in practice, that there is observed no greater differences in the amount of food consumed by, say, the idle "society woman" and the street-laborer is that the former probably eats far too much, while the latter, owing chiefly to his small income, perhaps eats somewhat too little. The status of mental labor as regards the amount of food required is at present in a somewhat uncertain condition theoretically. We do not know exactly how much energy and tissue the brain's activity actually consumes. Researches now being performed on men with balances large enough to support a man and yet exceedingly delicate, will doubtless determine the amount of tissue lost in mental work. Calorimetric measurements of the energy expended in mental activity have given thus far no important results. So far, then, we cannot make as close a correlation between the amount of brainwork and the food-requirements as is made between muscle-work and the necessary amount of food. The cortex cerebri in the average man weighs about 17 gm., while the muscles in an average sized man weigh about 33,000 gm. This, obviously, is the cause of the difference noted. It is likely that the nervous system per gram wastes faster and gives out more energy than does muscle. (For an estimate of the work done by the human heart see page 279.)

The colder the atmosphere in which an organism lives the more heating fuel it will require, and the quantity of food needs adaptation to this condition to some extent. Part of the body-heat comes from muscular exercise, so that the metabolism in general tends to be more active in a cold atmosphere, and tissue-waste is thus increased. Again, heat is lost by radiation and conduction from the skin more rapidly on a cold day than on a warm day, and this excess of loss the food must supply. Of the 2500 calories of energy which an average man daily receives from his food, at least five-sixths are expended in warming the body to its constant temperature. A large part of this is expended from the skin. Any variation in the radiation, conduction, and evaporation from the skin, therefore, would markedly affect the amount of food required. In bodies of the same general shape, but of different size, the surface area is much larger in proportion to the mass in a smaller body than in a larger one. It is by the mass that the heat is produced, and by the surface area that it is largely lost. It is on this principle partly that a child requires proportionally much more food than does an adult. A male baby of one year requires nearly twice as much food proportionally to his weight as does the man twenty years old doing moderate muscular work. Another factor in this difference is the greater activity of the metabolism in children. Moreover, in early life the body is growing larger, and more food is required on this account.

In general terms, then, the man who works with his muscles outdoors in winter requires the largest amount of food, while the man who works with his brains indoors requires proportionally the smallest amount of food. As we have noted, however, the latter individual consumes more nearly the food that the former consumes than what we might expect theoretically. It remains to be seen by further research whether the indoor brain-worker in particular actually eats on the average more than he needs.

Qualitative Adaptation in Certain Physiological Conditions is Valuable.—The last demand in an ideal diet which was suggested was that the food during certain physiological periods and conditions should be adapted *qualitatively* to their respective needs.

Stating the matter in this way, the implication is conspicuous that, save in these circumstances, diet should *not* be adapted qualitatively. Such undoubtedly is the case. From considerations already discussed, it is obvious that it is part of the power peculiar to protoplasm to select for itself out of the circulation's general store of pabulum that which it needs for its own, perhaps unique, purposes, and to reject what it has no use for. This selective capacity of bioplasm is everywhere conspicuous, and forms one of the most marked characteristics of the living substance. A less specialized selection of nutritious material is made by the absorptive mechanism of the gut, and this determines what shall enter the circulation. A still more general choice is made by the digestive enzymes, and they determine, probably ionically, what things shall and what shall not gain access to the absorptive selecting cells. The most general selecting agent of all is the will of the individual at large, and his choice of food is guided by convenience and by his intelligence plus his appetite, and bids him eat what is good for him by general consent. He learns, unconsciously perhaps, that in order to live he must eat proteid, fat, carbohydrate, salts, and water, each and all, and that the proportions of these and their total amount must both be approximately right. Further than this, the individual makes no selection other than that which his appetite's caprice or habit may command. He leaves it to the delicately elaborated organs within him to do that careful and complicated selecting which he could not do otherwise than through them if he would. The day has long gone by, for example, when physiology could say to a brainworker, "Eat more fish than muscle-workers eat, for fish contains phosphorus, which your brain, consuming phosphorus, needs." Science today would say, rather, "If the brain needs phosphorus, you may be sure that the brain-bioplasm knows how to absorb it from the general store of food circulating so rapidly and constantly through it." And this is the principle all through the average conditions of average animals. Voluntary selection of foods extends only to the right quantity of a mixture of proteids, fats, carbohydrates, salts, and water suitably prepared for being eaten. Trained protoplasm automatically does the rest.

There are, however, at least five conditions common to animals which do require more or less *qualitative* adaptation of diet to their respective needs. These conditions are infancy, pregnancy and lactation, senility, idiosyncrasy, and a few special forms of disease. Three of these, the first three, are physiological, one, the last, pathological, and the other is as yet undetermined, whether normal or abnormal. Let us consider these in turn, so far as their discussion properly forms a part of a general treatise on physiology. The last condition, disease, however, is largely outside our present province.

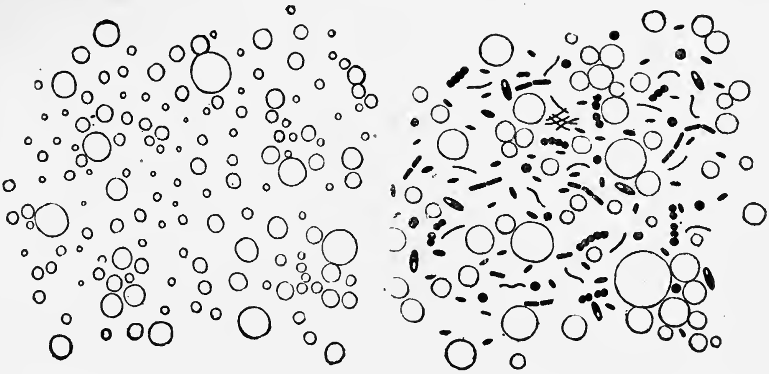
INFANCY.—*The feeding of infants* is a matter which only in very recent years is beginning to receive the careful attention it deserves. Few subjects are more vital to society. In America and Europe, on the average, nearly one-third of all children born die before before they are five years old, and largely from disease more or less dependent on improper or inadequate food. The infant during the first seven or eight months of its extra-uterine life needs nothing but *milk*. The comparative compositions of ten kinds of milk are given in this table:

PERCENTAL COMPOSITIONS OF VARIOUS SORTS OF MILK (König).

Kinds of Milk.	Proteids.			Fats.	Carbo-hydrates (milk-sugar).	Mineral matters.	Water.
	Casein.	Albumins.	Total proteids.				
Woman . . .	1.0	1.3	2.3	3.8	6.2	0.3	87.4
Cow	3.0	0.5	3.5	3.7	4.9	0.7	87.2
Goat	3.2	1.1	4.3	4.8	4.4	0.8	85.7
Ass	0.7	1.6	2.3	1.6	6.0	0.5	89.6
Mare	1.2	0.1	1.3	1.2	5.7	0.3	91.5
Ewe	5.0	1.5	6.5	6.9	4.9	0.9	80.8
Buffalo . . .	5.8	0.3	6.1	7.5	4.1	0.9	81.4
Llama . . .	3.0	0.9	3.9	3.2	5.6	0.8	86.5
Dog	6.1	5.1	11.2	9.6	3.1	0.7	75.4
Cat	3.1	6.0	9.1	3.3	4.9	0.6	82.1

Human milk contains 2.3 per cent. of proteid, 3.8 per cent. of fat, and 6.2 per cent. of carbohydrate, almost wholly lactose or milk-sugar, while cows' milk has about 3.5 per cent. proteid 3.7 per cent. fat, and only 4.9 per cent. sugar. The inorganic salts and water are practically the same in both. When necessity compels an infant to be "brought up on the bottle," that is, fed with cows' milk, usually, instead of its mother's milk, the former should be modified so as to more closely resemble human milk. As seen from the above figures, cows' milk has almost 50 per cent. more proteid (largely in caseinogen) than woman's milk has. To reduce this proportion water is added, at first considerable of it. The proportion of water is gradually decreased, month by month. The caseinogen of cows' milk coagulates in the child's stomach in small lumps, while that of human milk solidifies in a flocculent mass easily permeated by the digestive enzymes; this is a reason other than the proteid disproportion why cows' milk used by infants needs diluting with water. To compensate for the proportional reduction of fat by this dilution, cream is added. To make up the deficiency of the cows' milk in the carbohydrate, lactose, (milk-sugar) is added, or even cane-sugar. To insure its alkalinity usually a small proportion of lime-water is used—a saturated aqueous solution of calcic hydrate. Provided it is fresh and free of disease germs, warmed cows' milk so prepared (the proportions varying with the child's age) is a very good imitation of woman's milk. To insure that it is free of the germs of disease (tuberculosis especially, diphtheria, scarlatina, typhoid, etc.), it is at present customary and necessary to pasteurize all milk bought in the open market by heating it in a steam bath to 75° C. (167° F.) for a few minutes. To insure average composition it is better to have mixed milk rather than that from a single cow. Milk sterilized by boiling is rather indigestible (some of the digestive enzymes contained being thus destroyed); but it will keep in a cool place thus prepared for a week or over, and is, therefore, at times a great convenience, for example, in necessary travelling.

Fig. 75



Pure milk and milk after standing in a warm room for a few hours in a dirty dish. Many forms of bacteria are to be seen. (Moore.)

Rotch recommends the following percentages for the composition of cows' milk modified to suit various ages. It will be observed that the proportion of each of the chief proximate principles of the prepared food is less at first than in average human milk:

Composition of Cows' Milk Modified for Various Ages (Rotch).
Percentages.

Age.	Proteid.	Fat.	Sugar.	Mineral matter.	Reaction.
1 to 2 weeks . .	0.75	2.0	5.0	At least 0.15	Always alkaline.
2 to 3 " . .	1.00	2.5	6.0	"	
3 to 4 " . .	1.00	3.0	6.0	"	"
4 to 6 " . .	1.00	3.5	6.5	"	"
6 to 8 " . .	1.50	3.5	6.5	"	"
2 to 5 months . .	1.50	4.0	7.0	"	"
4 to 8 " . .	2.00	4.0	7.0	"	"
8 to 9 " . .	2.50	4.0	7.0	"	"
9 to 10 " . .	3.00	4.0	7.0	"	"
10 to 10.5 " . .	3.25	4.0	5.0	"	"
10.5 to 11 " . .	3.50	4.0	4.5	"	"
11 to 11.5 " . .	unmodified.				

The milk of the ass, common in some Oriental lands, is very similar to human milk save in its small proportion of fat.

In general, milk is an opaque, bluish-white or yellowish-white liquid, of a specific gravity of from 1027 to 1035, the larger the quantity of cream the lower, of course, being the density of the milk. It is the most perfect emulsion known, consisting of a plasma holding in permanent suspension innumerable globules of fat (butter), each from 2 to 5 mmm. in diameter. The *plasma*, easily separated from the oil by dialysis, is a somewhat opalescent, transparent fluid. It contains as proteids caseinogen, lactalbumin, an albumose-like substance (sometimes called lacto-protein), some nuclein, and (in human milk) a small amount of a diastatic enzyme, referred to above. The caseinogen is allied to the alkali albumins, and contains iron; it does not coagulate on heating unless the milk becomes acid; it seems to act as the emulsifying agent of the milk. The plasma also contains lactose, lecithin, cholesterin, traces of lactic acid (from the natural fermentation of the lactose), and of kreatinin and urea, besides the important salts, calcium, magnesium, sodium, and potassium phosphates, chlorides, sulphates, and carbonates, with traces of iron, fluorine, silicon, oxygen, nitrogen, and carbonic dioxide. Of these, calcium phosphate is the most abundant. The newborn body being very rich in iron, the milk contains little, so little in fact, as Bunge has pointed out, that infants weaned too late are apt to suffer from anemia due to lack of this iron. The *cream* or fat of milk consists of the triglycerides of palmitic, stearic, and oleic acids, together with small quantities of butyric acid (giving butter its flavor), and of others in still smaller traces, such as caproic, myristic, and formic acids. Olein is most abundant (about three-sevenths) and plamitin next (about one-third), while the stearin is present in the proportion of about one-sixth; these are all about as in body-fat. A pigment, lipochrome, gives butter its characteristic yellowness.

Colostrum is the first milk secreted during and for a few days following parturition. The mammary acini have then been rapidly proliferating, and it is natural that the first milk produced should be loaded more or less with the debris of this activity. Besides this, the so-called "colostrum-corpuscles" may be seen under the microscope; these consist of modified leukocytes or perhaps of milk-cells, with the butter-droplets to be seen within them. Perfect leukocytes also are sometimes found. The chemical composition is different from that of the milk coming later, colostrum containing much more lactalbumin and more of a material often described as a globulin, the "lactoprotein" or lactoglobulin mentioned above. The colostrum is said to act as a purgative partly in the newborn child, cleansing and preparing the intestinal mucosa for its work.

The *coagulation* of milk (very like that of blood), commonly called "curdling," consists in the formation of a clot composed of casein entangling much of the fat. In the presence of salts of calcium, the enzyme rennin acts on the caseinogen in solution in the milk-plasma, splitting it into two parts, one, soluble in the plasma, called whey-proteid, the other caseinogen, which is insoluble. This is a process of hydrolysis, and occurs only in the presence of calcium phosphate. This substance, casein, with its included fat constitutes the curd. The caseinogen in solution in the whole milk seems to be a combination of a nucleoproteid (nuclein) and a somewhat globulin-like proteid. This is the present most-accepted theory of the coagulation of milk, but not yet proved; compare the coagulation of blood.

The coagulating enzyme, rennin, is secreted by the glands of the stomach and of the pancreas. For the manufacture of cheese an impure briny infusion called rennet has long been in use, made from the fourth stomach of the calf. One part of rennet will coagulate nearly 1,000,000 parts of caseinogen.

The *souring* of milk consists of the acid-fermentation of its lactose from the influence of special bacilli which are present everywhere in the air and in the large intestine. The lactose, absorbing water, becomes lactic acid, which then breaks up into butyric acid, carbon dioxide, and hydrogen. This acid is very apt to injure the digestive process, if not the digestive organs, of young children. Hence the harm from sour or souring milk. The latter, being in a state of active bacterial change, is worse than the former.

It appears that the hydrolyzing enzymes of the alimentary canal, the digestive "ferments," as they used to be called, do not develop in the infant all at once, nor are they all actively strong in the child less than seven months old. After that period the use of some solid food is properly begun, although milk should form a considerable part of the aliment of the child the first five years at least. No solid nutrients are better adapted to early use in the first year than lightly boiled eggs and buttered stale wheat bread. The yolk of the eggs is especially valuable, as it contains much iron, and also fat and proteid in a combination perfectly adapted to the child's first year or two. Gradually the list of common articles of diet is enlarged, great stress being laid upon easily digested proteids and on ripe, juicy, fresh fruits and well-cooked fresh vegetables. These foods combine to furnish in forms easily available to the as yet feeble digestion the energy and the tissue demanded by the growing bones and organs and muscles. It is easier to overdo the feeding of fats and of carbohydrates than to underdo it, fat but "flabby" babies being often supposed to be well nourished when in reality much less weight made up of firm bones, solid muscles, and vigorous glands is of much greater worth. The latter part of the third year is early enough to begin to give to the child the general variety of always easily digested nutrients of the adult diet. The limit of proteid-feeding should be in its stimulating effects on the preponderant nervous system of the child, the "beef-fed," wheat-fed, and oat-fed boys and girls being, other things equal, those with the best bodily start in life. Sugar should be, if possible, used very sparingly, and in the form of candy given only immediately after meals. As a muscle-energizer, sugar is unexcelled (page 383), but during the first three or four years its use is apt to destroy the appetite for substantial foods not so attractive to the taste.

PREGNANCY AND LACTATION.—A second physiological condition which properly demands some qualitative adaptation of diet is that of *pregnancy and lactation.* In this case the changes from the average diet required are very much less than in the feeding of infants, but they are, nevertheless, of considerable importance.

The fetus requires for its nourishment food which will furnish it especially with tissue, much kinetic energy not yet being required. This nutriment it gets from the circulating proteids of its mother, largely serum-albumin and serum-globulin. The mother needs, therefore, as food an ample supply of both tissue-builders and energizers. The one sort builds up the fetus, the rapidly growing uterus, mammary glands, heart, and in general supplies the active anabolic functions characteristic of pregnancy. The other, the energizers of the food, are necessary in increased amount to supply the force the augmented work of the organism requires. Proteids of animal origin supply these materials better than ony other nutrients, supplemented by a generous, abundant diet, otherwise average in composition. During lactation a somewhat similar excess of proteids over the average is apparently beneficial, together with a normal excess of water. Milk is richest and most copious on an abundant proteid diet, especially meat. Thereby also is solved the problem of storing iron in the fetus in sufficient amount to last until solid food begins to be taken, for milk is deficient in this essential element.

SENILITY.—In *senility,* or old age, the adaptation of diet qualitatively is, as in the other extreme of life, largely in the way of using foods which are easily digested. Laxative and easily digested foods are especially indicated

IDIOSYNCRASY.—The term *idiosyncrasy* (from a very similar Greek word meaning peculiarity or temperament) is an interesting one in physiology. Little is known, however, as to the causes and conditions of these individual differences between persons. For our present purpose, that is as concerns diet, the sense of the term is expressed very well by the ancient adage, "One man's meat is another man's poison." After having discounted these supposed marked differences as mostly imaginary, accidental, or merely as habits of thinking, whatever the habits' origin, there certainly does remain a residuum of differences, often striking, in the way in which various nutrients affect the organisms of different persons. Some persons are regularly made sick by clams, others suffer from a dermatitis after eating strawberries, tomatoes, etc. The liking or disliking of flavors, proverbially unaccountable, concerns the subject little or not at all. Chemical and other differences in the tissues, circulating liquids, or digestive processes are probably at the bottom of these idiosyncrasies of diet, but in detail most of these differences are quite unknown. These conditions are facts, and often not less important or more easily remedied because sometimes partly imaginary. When fully established in an individual they must be complied with and the diet accommodated to them qualitatively.

DISEASE.—In certain forms of *disease* due to digestive or metabolic derangement, adaptation of diet is more or less useful or even curative. In invalid-feeding the aim is usually merely to support the tissues and the strength of the patient. One employs for this purpose every device for inducing the individual and his digestion to accept and digest all the nourishment possible, adapting the means to the end.

In *diabetes*, however, there are occasional cases in which actual cure can be accomplished by diet of a certain sort, adapted to the special need both in quantity and quality. The indication is to reduce as far as practicable or even possible the ingested amount of carbohydrate, the disease being a serious disturbance consequent on the abnormal excretion of sugar in the urine. Meats (except liver), fish, shell-fish, and eggs are the staples of the required diet, cheese and butter being used as largely as possible. In mild cases, at least, milk is permissible, and such vegetables as cabbage, lettuce, spinach, cucumbers, mushrooms, cauliflower, asparagus, onions, and tomatoes, while beverages, such as water, tea, and coffee, are unobjectionable in any amount. *Nephritis*, or Bright's disease, is another disease in which diet is important more or less. In this case a diet of milk alone is usually prescribed, or one of milk extended by bread, vegetables, and fruit. In *tuberculosis* a special diet is sometimes of extreme importance, the object being to maintain the strength. In this case the adaptation of the diet is more quantitative than qualitative, the patient requiring to eat as much as he can possibly be made to digest rather than to have any particular articles of food. The patient's meals must be frequent and adapted in every other way to bring about the desired result of forcing, so to say, the nutritive anabolism. *Rachitis*, or rickets, is a children's disease characterized by defective nutrition, especially of the bones. The patient needs in this case a diet relatively rich in fats and proteids, and more or less lacking in carbohydrates. The meats contain the earthy salts most desired, and with the fats will furnish the deficient energy of the growing tissues. Carbohydrates usually lack most of the inorganic salts.

Coffee, Tea, Cocoa, Alcohol, and Tobacco.—We defined a food as any substance which when taken into an organism is capable of supplying it with tissue or of producing available energy. Stimulants, on the other hand, technically are agencies that only goad on the vital functions. In practice so-called stimulants partake in some degree of both these characters, excepting tobacco, which has no nutrient properties. Of all the substances of this general class, the above five are those that are in most general use over the world, but it is essential to note that there are many others, of which opium is perhaps the most important. We shall shortly see that of these "stimulants," alcohol is more properly a depressant, while tobacco and alcohol as well are used chiefly because of their preponderant sedative action on the emotional mental processes.

The importance, good and evil, of these five substances to the human race need not be described. We are in no sense and in no degree concerned here with ethics; we take things as we find them, and for scientific purposes state to scientific people the best we can the scientific truth. We, as students of physiology, do not even stop to inquire why many people (most, with one substance or another) so regularly stimulate their psychophysic organisms. We may note in passing, however, that they do so, and we may be confident that they always will do so despite the hysteria which some, and the wretched warning facts which others, lay before them. From the earliest recorded times and in all lands man has made from various vegetable materials "stimulants" of one sort or another. In the lapse of historic time thus far, say six thousand years, mankind shows no tendency to stop, or to lessen even, the stimulation of his body and mind with these and other products of natural and of human art. In a more enlightened age than ours they may go out of use.

Coffee has been in use as a stimulant by Europeans about three centuries, having been introduced a few years later than tea. It is a decoction of the roasted berry of a shrub, Coffea Arabica, indigenous in Brazil, Arabia, and in many other parts of the world. It contains at least two stimulating elements, an alkaloid of the vegetal-base class, called caffeine (methyl-theobromin or trimethyl xanthin), identical in composition with theine, having a formula $C_8H_{10}N_4O_2 + H_2O$; and two volatile oils, caffeol ($C_8H_{10}O_2$), source of coffee's aroma and of part of its flavor. Besides these, the most important constituent of coffee is caffetannic acid, astringent and inhibitory of hydrolysis in all parts of the alimentary canal. A 1 to 5000 solution of tannin will arrest, for example, the digestive action of ptyalin on starch completely, but it is less inhibitory of pancreatic digestion. As ordinarily made, when it is made well, a cup of coffee contains about 0.13 gram (2 grains) of caffeine and 0.22 gram (3.5 grains) of tannic acid, the amount of volatile oils present being dependent in general terms on the length of the time since the coffee-beans were roasted. The action of caffeine is largely on the nervous system, stimulating it. The mental process is hastened and supported, ennui and fatigue dispelled, mental work seeming almost a pleasure far beyond the limits of unstimulated endurance, while its quality is correspondingly improved.

One effect of this stimulation of the nerves is seen probably in its slight laxative action on many, especially "nervous" persons. The peristalsis of the gut is hastened, a result of the use of coffee which may, however, be due to the volatile oils etc., called collectively coffeol, rather than to the alkaloid caffeine.

That the brain is more or less functionally altered by coffee may be noted in the pain in the head which many persons experience when they omit for once their usual coffee at breakfast. A nervous restlessness and tremulousness follows the taking of two much coffee, the excitement of the nervous system having then gone beyond its normal intensity. That coffee increases metabolism is proved by the increased excretion of urea and of carbon dioxide during its use. Wood calls attention to the fact that coffee stimulates both the intellect and the imagination, while opium, another brain-stimulant under some conditions, acts largely to increase the latter and not the former. Caffeine in large doses has a distinctly diuretic action, increasing the urea to be excreted. As we saw above, caffeine is a xanthin, and it is now known that the nuclei of cells contain xanthin-like bodies. It is supposable, therefore, that coffee may actually feed the nerve-cells of the brain as well as stimulate them. Its action on the heart is to augment its force and frequency, but the effects on the blood-pressure are too complicated in various conditions to be stated here. Children are especially susceptible to the action of caffeine and hence to tea and coffee, the cerebral stimulation being evinced in them often by night-terrors and other harmful causes of insomnia. Over-use of coffee in adults leads sometimes to a depressive neurasthenia, which disappears when the occasioning substance is withdrawn. Its tendency to cause indigestion by checking hydrolysis is known to all—a slight attack of dyspepsia accompanied by unpleasant sensations in the head altogether known commonly as a "biliousness." These are the chief of the bad results accompanying the excessive use of the beverage, the proper amount for benefit having to be determined by every individual for himself. It must not be forgotten that the beverage coffee is usually accompanied by milk or cream and sugar, both of which are of course highly nutritious substances. The last of these, sugar, in particular is a supporter of muscular action and a banisher of muscular fatigue. Thus, in practice, for the great majority of cases, coffee as used is a distinct addition to a meal aside from its mentally stimulating action. Where there is a tendency to indigestion both of these additions to the decoction of the coffee-bean are apt to be harmful, the sugar because it is liable to ferment before its absorption as dextrose. The harmfulness of the milk is more obscure, but it is believed to be due to the formation of a chemical union between the alkaloid and the proteid caseinogen, the product of which for many individuals is very indigestible. Thus, black coffee is often less objectionable and more useful than when taken with cream and sugar.

Tea, as has been learned from our statements about caffeine, is much like coffee in its physiological action and effects, but, weight for weight, it contains more than twice as much both of caffeine (or theine) and of tannic acid as coffee does. Indian teas contain more theine and twice as much tannin as do Chinese teas. Ceylon tea is intermediate in its strength. Green tea contains more volatile oils than black tea and more tannic acid, but somewhat less of the alkaloid. In the United States the use of tea is proportionally decreasing, while that of coffee is increasing. In the British Empire, on the contrary, the reverse tendency obtains so that the one nation becomes ever more completely a coffee-drinking nation, and the other a race of tea-drinkers to even a greater degree than at present. In brewing tea it is important that it be used very soon after its infusion, for while the alkaloid dissolves into the hot water almost immediately, the harmful tannic acid dissolves much more slowly. For dyspeptic reasons, therefore, the habit, so common in some tea-drinking neighborhoods, of keeping the tea-pot on the nob all day is very pernicious, and the women who indulge in this hardly fail sooner or later to develop nervousness of a characteristic sort and a chronic gastritis and a leanness consequent on the constant interference with the action of their digestive enzymes which the excessive tannin exerts.

It is probable that for most persons tea is more harmful than coffee, while, furthermore, it somewhat lacks that genuine support of the nervous system, almost amounting to neural nutrition, so frequently observed in the case of coffee. Tea stimulates the brain and spinal cord, but oftentimes so to say in a more purposeless way. The effect is wakefulness and mental excitement, but not so much of a stimulation of the useful aspects of the mind. Another disadvantage of tea over coffee is the greater danger of its harmful adulteration and unhygienic manufacture, as well as the greater cost of a satisfactory quality of the substance.

The statements made above concerning the relations of coffee to milk and sugar apply equally well to tea—if anything, more emphatically, for tea contains much more tannin than does coffee.

Cocoa is a beverage made by mixing with hot water or milk the powdered seeds of the chocolate tree, Theobroma cacao (the former part of the name meaning "food for the gods"). Chocolate is of a similar nature, but usually contains more of the fat of the bean, cocoa butter. The chief alkaloid of cocoa, theobromine ($C_7H_8N_4O_2$), is nearly the same substance chemically as caffeine or theine. It is present in cocoa, however, in much smaller amount than it is in coffee or in tea. Unlike these latter stimulating substances, dry cocoa contains about half its weight, 40 to 54 per cent., of fat, about 20 per cent. of nitrogenous matters, in part (8 per cent.) proteid, and considerable starch; the alkaloids are present in proportion of from 1 to 2 per cent. Thus, cocoa is not only stimulating, but very nourishing, especially when the sugar and large proportion of milk usually employed, are added. A good-sized cup of cocoa so prepared is worth nearly 400 (large) calories.

Cocoa, by its alkaloid theobromine and its small amount of caffeine, affects the neuromuscular mechanism much as does coffee, but in a very much less degree. On the muscles, however, cocoa acts very powerfully to ward off fatigue, proportionally more strongly than does coffee. In some persons, in ordinary quantity, the effect is somnolent rather than stimulating to increased wakefulness. The only danger from an excessive use of cocoa is that of indigestion, which comes from the large proportion of fat it contains. Many persons quickly tire of cocoa, unfortunately, when they consume it frequently and regularly. That this tendency may be readily overcome, however, may be seen from its great and almost universal use in France, for example, where in concentrated solution it is nearly half of the common breakfast.

Maté and *Guarana* are beverages similar to these three used in South America to some extent. They are said to depend for their stimulative effect on the same alkaloids nearly as do coffee, tea, and cocoa, but in the strengths used by the natives generally they are weaker. All stimulants of this class are rich in inorganic salts (especially soluble compounds of iron, soda, and potassium), of value to the organism.

Alcohol.—From natural products as various as honey, grains, and cocoa-nuts, and from scores of others alcoholic beverages have been prepared in all times and by all sorts and conditions of men, by the most civilized as well as by the most savage and depraved. In America and Europe at the present time the alcoholic beverages are largely of three classes—liquors, wines, and beers. The first are made by distillation from a large variety of fermented substances all containing sugar; the second from grapes by fermentation; and the last by the brewing of malted grains. The proportion of alcohol in various beverages is approximately as follows: In *absolute alcohol*, 99.5 to 100 per cent., and in the *alcohol* official in the United States, 94 per cent. In *whiskey* there is from 35 to 50 per cent. by weight of alcohol; in *brandy*, from 25 to 55 per cent.; in *gin*, 30 to 45 per cent.; and in *rum*, from 25 to 45 per cent. *Red wines* and champagne have of alcohol from 9 to 12 per cent., bordeaux being somewhat the weakest, and burgundy the strongest. *White wines* contain from 10 to 14 per cent. of alcohol, and sparkling and sweet wines about the same proportion. Of the *fortified wines* with alcohol-content varying from 16 to 23 per cent., malaga is the weakest and sherry the strongest. *Ale* has from 4 to 8 per cent. of alcohol, and *cider* about the same proportion unless fresh from the press, while domestic (American) *beers* have from 2 to 6 per cent. of it. *Koumis* has in it, except when very fresh, about 2 per cent. of alcohol, and *kephyr* (similar to koumis, only made from cows' milk instead of from that of the mare) has in it 1 per cent. of alcohol. The popular *bitters* and other *patent medicines* are practically beverages of the most insidious sort, and often contain percentages of alcohol up to that of the strongest alcoholic liquors. The physiological effects of alcohol for purposes of description may be divided into influences on the neuromuscular mechanism, on the mental process, on digestion and nutrition (including metabolism and body-heat), and on the circulation.

On the nervous system and the muscular machines so closely connected with it alcohol exerts an effect all too familiar to everybody. In general terms the nervous system is disturbed, so that many movements are at first increased for a short time and hastened. Afterward, if the dose be large enough, they are made ataxic or incoördinate, vision double, for example, speech "thick," and the gait staggering, because the muscles do not pull together in the proper degree and sequence. When quantities of alcohol larger than this have been imbibed, an obviously depressive stuporous sleep may be caused, deepening perhaps after a time into a coma somewhat like that of chloroform-narcosis, in which the tendon-reflexes are lost. In this condition the muscles have little of their normal tone, but are relaxed, and death may follow from paralysis of the movements of respiration. It will be observed, then, that the general trend of the action of alcohol on the nervous system is asthenic or depressive and not excitatory. Some researchers in physiology, notably Meltzer, maintain that alcohol has no proper sthenic or stimulating effects on any sort of protoplasm, and that its effects are always *depressive* and devitalizing. They well account for the preliminary phenomena of exhilaration by postulating that at first and from small doses its action is wholly on the delicate repressive or inhibitory centers of the brain, depressing their action and so removing the inhibitory control which they normally exercise over the emotional activities. As we have seen in our discussion of brain-action and of the heart, inhibition is a function of great but unknown importance and extent in the nervous system, and more and more does this repressive aspect of its action become emphasized in different directions. As regards the action of alcohol, inhibition may be pre-eminently important; at present, however, we can not be actually certain that such is the case. The opposed way of explaining the action of alcohol on the nervous system is that the drug at first stimulates and then depresses the actual protoplasmic activities in the nerve-cells. How a substance can be supposed to act in this double way it is hard to define, especially when the two effects are of an opposite sort. Numerous elaborate researches have shown beyond doubt that while there is an initial stimulation of muscular movements arising from small doses, the general effect on both muscular accuracy and endurance is harmful rather than beneficial. For example, soldiers do arduous, long-continued labor much better without alcohol than with it. Exactly the same effect is observed when the muscular action is not that requiring long endurance, but of a sort necessitating fine adjustments. Alcohol removes the depressive feelings of fatigue following unusual exertion, and is often used as a beverage for this purpose. As Herter points out, however, the excessive exertion itself is harmful, and would probably not be undertaken could the pains of it not be removed by drinking—alcohol thus inciting sometimes to an abnormally exhausting mode of life.

On the mental process or mind the effect of alcohol is stimulating if it is so in any place. This comes through its probable action on the cells of the cortex cerebri, and is experienced as a sense of well-being and of happiness, of freedom from care, and in an increase in the workings of the imagination, and, in some individuals, not in others, in an increased capability of mental work for short periods of time. It is in doubt, however, whether the quality of this work is ever improved by alcohol, and there is much good experimental evidence (as that by Kraepelin) that it is not so improved, even for brief periods. For example, one research, done by Rudin, showed that 95 grams ingested by men unaccustomed to its use lengthened the time required to add columns of numbers, made more difficult and uncertain the learning of rows of figures, shortened reaction-time of some sorts and lengthened it in others. The influence on the mental powers lasted, as a rule, from twelve to twenty-four hours, but in one case forty-eight hours. Similar researches by several others interested in the question have given similarly complicated results. They agree, however, in the conclusion that alcohol deranges the neural and neuromuscular "basis" of mental activities.

Its power of abolishing the emotional over-stress of our hurried and complicated modern life is not easily explained. It is, however, to accomplish this very purpose that alcohol is most largely used—as a beverage—by the mass of mankind; they for the most part employ it as a sedative. Here too, perhaps, it is a depressive inhibitant, shutting out from present experience those finer cultural restraints represented probably in the cortex cerebri.

The action of alcohol on digestion and on the complicated processes of metabolism was of late in certain respects a vigorously, not to say rancorously, discussed question. This discussion is now, fortunately, nearly closed by decisive research conducted by scientists whom all may trust. Is or is not alcohol a food? Those opposed infallibly and emotionally to even the therapeutic use of alcohol in the saving of life and for the restoration of health, have bitterly opposed the presumption of physiological science that alcohol is under some narrow conditions a food, lest the drink-evil, one of the worst the world knows, be stimulated still more. Elaborate and costly work by the United States calorimetrist, Atwater, however, and by others, has shown conclusively that in amounts not over 50 or 60 cubic centimeters (40 grams) in twenty-four hours ethyl alcohol is oxidized by the body with the production of heat and other forms of energy. Furthermore, it has been shown that these oxidative processes take place in the tissues, and not in the gut alone, thus making the energy liberated available to the needs of organism as in the case of other foods. Hoppe-Seyler supposes that alcohol is formed in the normal katabolism of carbohydrate in the tissues, for he found traces of it in fresh tissues when they were distilled with water. Not more than 1 or 2 per cent. of the alcohol in the above-mentioned daily amount leaves the body unburned, in the urine and in the breath, for the greater part of the maximum quantity of 60 cubic centimeters (two ounces) is oxidized to carbon dioxide and water, the usual end-products of carbohydrate katabolism. It will be remembered (see page 143) that the combustion-equivalent of average proteid and of average carbohydrate is 4.1 calories per gram, and of average fat 9.3 calories. Alcohol, having no waste, is of higher calorie-value than the average carbohydrate, and has that of 7 calories per gram. The maximum food-allowance daily of alcohol, 60 cubic centimeters, with a specfic gravity of 0.820, weighs 49.2 grams, and would therefore furnish about 364.4 gross calories of energy. But another element enters into the food-question itself: Is alcohol a fat-sparer, a carbohydrate-sparer, and a proteid-sparer? In other words, when used for food (as, *e.g.*, in illness), does alcohol furnish only energy, or does it, as real foods do, also save the wearing-away of the proximate principles of the tissues and thus of the tissues themselves? If it does not, alcohol is of little use as a food in illness, for it does not replace or save loss of body-weight. Zunz and Geppert showed in 1887 that alcohol neither increased to any extent the consumption of oxygen nor changed the excreted amount of carbon dioxide. In other words, alcohol in the amount named does save the fats and carbohydrates of the tissues from consumption by the wear and tear of their living processes, for the alcohol itself furnished the energy required by the organism, leaving the tissue-fat and -carbohydrates nearly untouched. This work, repeated and corroborated by many other competent men since, establishes firmly the fact that alcohol spares at least the fat of the body-tissues and therefore may be of use as a real food in therapeutics.

But it does more than this as a food, for recent experiments, often elaborate and painstaking to an extreme degree, have shown that feeding alcohol spares the proteid of the tissues as well as the fat and carbohydrates (the latter existing only, of course, in comparatively small amount). This is now practically as certain as it is that alcohol spares fat; to open minds this important proposition is proved beyond a doubt. Atwater, for example, found that 72 grams of alcohol daily taken by a man spared 0.2 gram of nitrogen and spared also one-fifth of the carbon-excretion in respiration—two-thirds as much nitrogen as was spared by an isodynamic (equal-calorie) value of sugar, the latter being well known as a proteid-sparer. Ott showed that in the fever-condition also, alcohol acts as well as sugar as a proteid-sparer. Clopatt found that for the first five days of a twelve-day period it caused an increase of proteid katabolism, but acted as a proteid-sparer, decreasing, that is, the katabolism, for the other seven days. Again, Neumann, in elaborate measurements proved beyond a doubt that in doses of from 50 to 100 grams daily, it caused a noteworthy decrease in proteid katabolism, although not acting in quite the same way as fat in this respect. To have proved this sparing of proteid is even more important than to have shown it a fat-sparer, for while fat serves as a more or less dead and inactive store of material from which at need energy could be produced, the proteid of the body is all active and as such of vital importance to the organism either as muscle-cells, epithelium; or other essential organs.

On the body-temperature alcohol exerts in general a lowering effect, as was asserted first in 1848 by Duméril and Demarquay. Wendt recently showed that even small amounts of alcohol at first, for ten minutes only, raised the temperature 0.1° or 0.2°, followed by an equal lowering below its original position for twenty to thirty minutes. When the body was naked, the loss of heat was a degree instead of one-tenth or one-fifth of a degree. Large doses decrease the temperature markedly: as much as 3° or 5° C. The large majority of the persons of whom we read in the newspapers as being frozen to death are alcoholics. The reasons for this lowering of body-heat are at least two: Alcohol, in a manner not yet surely known, causes an increase in the diameter of the arterioles of the skin and of those just below it, thus occasioning a large increment of the heat-loss by radiation, conduction, and evaporation from the body-surface. Again, as we have seen, alcohol is probably a general depressant of organic function, and doubtless interferes with the heat-production of tissue-metabolism. The increased heat-production noted by Bevan Lewis, Wood, etc., was probably due to the combustion of the ingested alcohol itself, and not to any stimulation of the metabolism. The reason that alcohol gives a strong sensation of increased warmth is that the sense-organs providing the feeling of heat are situated in the skin, which is, of course, made actually warmer by the vasodilatation due to the alcohol.

On digestion and its mechanism the effects of alcohol are of great importance, for here a great part of the evil alcohol occasions is brought about if we include the liver in the digestive system (much of the harm done elsewhere being in the nervous system). Small amounts of alcohol, such as are contained in a bottle of koumis or of weak beer, taken with or just after meals, have in many persons little effect on digestion, although the appetite may be somewhat improved by its stimulation of the digestive juices. (When mixed with milk it makes the latter more rapidly digested and more quickly.) Sooner or later, however, the digestive process is certainly slowed and somewhat hindered even by such minimum amounts, owing probably to slight interference with the productive glands. When a moderate quantity of a beverage containing 4 or 5 per cent. of alcohol is taken regularly with meals the slowing-effect on digestion is more marked, but the ingestion of this amount, especially in beer, is soon followed by metabolic changes (particularly by an abnormal deposit of fat) which are of consequence. Some persons might drink for years daily with their dinners a glass of 8 or 10 per cent. claret or other wine with no obvious harm either to the digestive process or elsewhere. It is likely, none the less, that the foundation is being laid under such conditions for a chronic gastritis and enteritis later on. It is after all the frequent use of liquors containing from 30 to 50 per cent. of alcohol which causes the inevitably serious effects seen in the severe chronic or subacute gastritis, cirrhosis of the liver, degenerations in the nervous system, fatty degenerations in the circulatory system, and so forth. The hospitals show how very common and how very serious these poisonings are.

On the circulation alcohol exerts a generally stimulating effect, increasing the pulse-rate and the latitude of the vibrations of the arterial wall as felt by the finger or registered by the sphygmograph. This increase may be due to the muscular activity ordinarily great soon after ingesting alcohol. It is not always so caused. Sphygmograms made from man by Parkes and Wollowicz, and many since they worked, show an increased suddenness of ventricular systole and a shortening of the pause between the systoles. Zimmerberg showed that large doses depress both the rate and the power of the beat. Whether blood-pressure be increased or not depends in any case on the balance between the augmentation of the pumping-action by the heart and the size of the arterioles and capillaries through which the streams must pass. Sometimes, therefore, the pressure will be increased, sometimes decreased, sometimes, doubtless, unchanged by the ingestion of moderate doses of alcohol. Alcohol's harm on the heart is brought about partly, it appears, by the shortening of the rest-period which it produces, as mentioned above, for this soon leads to hypertrophy and general derangement, since no portion of an organism can work continuously.

Such are the chief of the physiological effects of alcohol on the animal economy as now understood by physiologists. They go to show to the student of medicine that alcohol may be of great use as a therapeutic agent in disease, feeding the body, sustaining the mind, improving digestion, supporting the heart when perhaps all that is necessary for saving a life is this feeding, sustaining, improving, or supporting for a brief period of time. But these physiological effects go to show to all men that alcohol, although a sedative, is an irritant and depressive poison generally inimical to life, with which a normal individual should have, even physiologically speaking, nothing to do.

Tobacco is so frequently practically a part of a meal, that it is not improper to consider its effects briefly in this place. The active principle of tobacco is an alkaloid nicotine, with the empirical formula $C_{10}H_{14}N_2$. Pictet and Rotschy claim to have discovered in tobacco three other alkaloids: "nicotimin," with composition like nicotine's; "nicoteïn," ($C_{10}H_{12}N_2$); and "nicotellin," ($C_{10}H_{18}N_2$). They find in ten kilos of tobacco-juice 1000 grams of nicotine, 20 grams of "nicoteïn," 5 grams of "nicotimin," and 1 gram of "nicotellin," and announce the action of the nicoteïn to be like that of nicotine, but more toxic. We shall look at the action of nicotine on the nervous system, on the mind, and on the circulation.

On the nervous system the action of nicotine is complicated. It has the peculiar power certainly of so disturbing the neurones as to block the afferent impulses leaving them. It also paralyzes the peripheral motor nerve-endings after a brief preliminary excitation of them. The convulsions which follow large doses of the alkaloid have been shown by Krocker to be quite independent of the brain, to be occasioned, then, in the cord. Sensory centers and nerves are not affected by nicotine. In what manner it affects the nervous system so as to abolish the general sensation and pain of hunger, one of its conspicuous effects, it is impossible at present to say, possibly by its peculiar sedative action, as in case of opium.

On the mind nicotine exerts a strong calming and quieting effect, while at the same time the brain is so stimulated that long-continued mental labor is less fatiguing. The same action is often noticed as regards muscular exertion. Tobacco is indeed often of great benefit in this fatigue-abolishing way to hunters, lumbermen, soldiers, and others who are liable to be obliged to undergo long periods of exertion. This sedative effect on the thoughts and fears and worries of life is the source of one of tobacco's benefits to humanity. It becomes, in these days of hurried eating especially, a conducer to good digestion by tending to make pleasant a quiet untroubled hour or half-hour after a meal, especially as the stimulating action on the mind makes toward sociability. In having thus the double and seemingly almost contradictory effects of quieting hurried anxiety and yet of stimulating mental action, tobacco stands closer to opium than does any other substance known. The action differs from opium's, however, in that it is the intellect and not alone the imagination that is stimulated by tobacco, while the sedative effects of the two plants are very similar, although that of opium is very much more powerful. In combination with coffee, tobacco exerts a very strong stimulation on the mind, sleeplessness being a frequent consequence.

The circulation and especially the heart is more strongly and injuriously influenced by the frequent taking of too much tobacco than any other system of the organism, for the rhythm of the heart is deranged by its excessive use and made irregular both in the force and the time of the heart-beats. This, the "tobacco-heart," is the most common effect of excess, but the results of its continuance are not cumulative to any considerable extent (as are those of alcohol and opium), and pass off in a relatively short time when the habit is broken. The immediate action of nicotine on the heart and peripheral vessels is not definitely known, the large number of experiments on various sorts of animals being to our present understanding contradictory.

Both the power and the disposition to do muscular work are undoubtedly lessened by the absorption of these alkaloids—an effect of which the physiological explanation is not as yet at hand. It is apparently a matter either of neural or of muscular metabolism,

On the mucous membrane of the mouth and throat tobacco sometimes exerts an injurious drying-action, leading to chronic inflammation of a mild type. Its nauseating effect is reflexly caused probably by stimulation by the nicotinized saliva of the unaccustomed nerve-endings in the stomach-wall. Were this nausea not so sharp and painful to the youthful mind, there would be even more smokers than there are. Nicotine is said to cause an increase in the urinary excretion of uric acid and of phosphoric acid; it does not affect the respiratory exchange. Excessive use of tobacco produces insomnia and great nervous irritability, besides the functional cardiac irregularity already noted. Each user of the herb must determine for his own particular organism the limits beyond which needless injury is done him.

To the evolving and unstable nervous systems of childhood and youth all of these substances usually known as stimulants are, of course, particularly poisonous.

CHAPTER V.

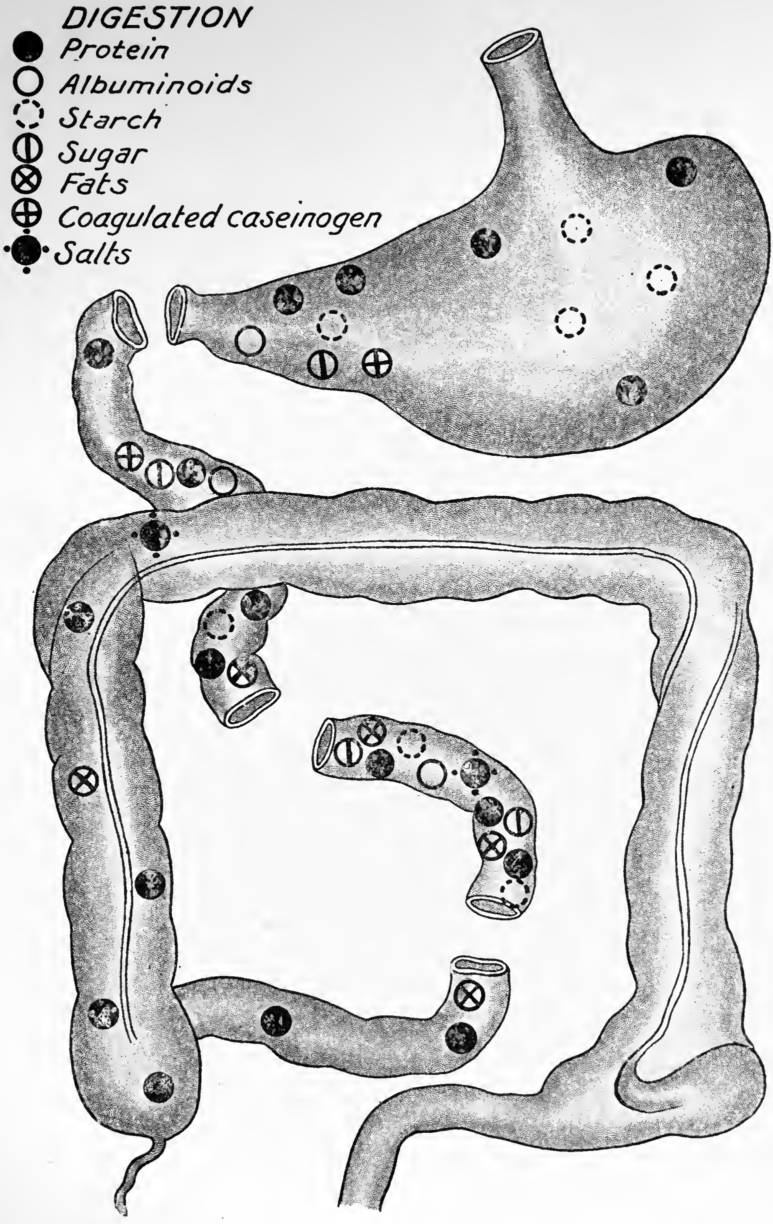
DIGESTION.

Having now seen in outline what the food of the body is and should be like, our next search is in what manner it becomes made into tissue-protoplasm which is alive again. Food, as we have seen, is largely either animal or vegetable. Substances of these origins are, by definition, forms of protoplasm. The present chapter, then, deals with that portion of the reanimation of food called digestion.

The whole process by which food proper is converted into tissue or made a source of energy to the organism may conveniently be divided for purposes of description into four stages, which we shall discuss under the arbitrary names digestion, absorption, nutrition, and excretion. The last process, excretion, is quite as essential as the others, for most of the products of katabolism are of such a nature that unless promptly removed, they quickly bring about protoplasmic and organic death. In our sketch of protoplasm we have already seen an outline of the general nature of this extensive vital function of nutrition. Here we extend it and apply it to man. So great is the complexity of animal function, whether taken as a whole, or in any of its parts, and so interdependent are its various portions, that sometimes, in fact, there is no such sharp discrimination between functions as, for convenience of description and ease of learning, we describe. We find an example of this circumstance, so common in science, in the latter limit of "digestion." Arbitrarily we shall leave the nutritive materials in this chapter when they are all ready to be absorbed into the complex circulation of the blood and lymph. It is the work of digestion proper to prepare the food for absorption. When, however, one considers that part of the work of digestion is apparently done as the nutritive substances pass through the thin wall of the intestine, and that in the villi both processes may take place, it is clear that the two subjects are much less sharply discriminated by the organism than by the analyzing mind describing them. This general interdependence of organic functions, this perfect unification, more or less evident, of the structural and functional multitude making up the individual, is an important matter for anyone to remember who would understand man in any way adequately. Only so, indeed, will his view be broad enough and accurate enough to rightly interpret things. We encounter repeatedly reminders of this principle that description implies a misleading separateness in structure and function when in reality the process is often a greatly involved continuity.

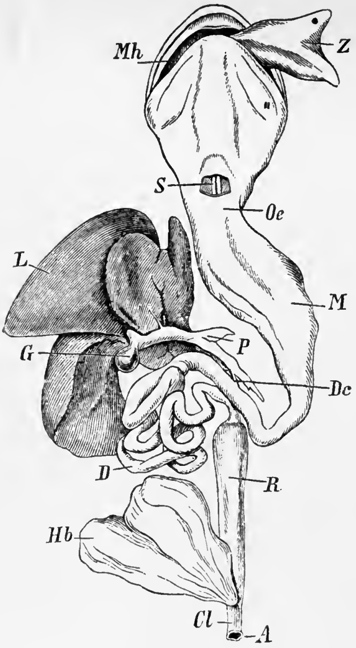
As was seen to be the case with the function of respiration, digestion is basally a necessary process of protoplasm either directly or indirectly, and hence is universal in the animal kingdom. It is, moreover, a process common enough, even as animals perform it, in the vegetable kingdom.

Fig. 76



Thus, the Venus' flytrap (Dionea), native to North Carolina, has an elaborate sensori-motor mechanism for catching its insect-prey and the essentials of a digestive apparatus for preparing it for absorption into the vital juices of the plant. The fly-catcher (Drosophyllum) of Morocco and Portugal and the pitcher-plant so common in New England bogs, catch insects which crawl into them in search of honey or of water by means of glandular hair-like organs that secrete a fluid at once viscid and digestive, and make good nutritional use of them. These are but examples of plants which have a true digestion by means of chemical-enzymes (hydrolyzing agents), while there are many others which in one way or another catch and hold living animals and other sorts of food and absorb the nutritive liquids from them either at once or as they decay. All plants are able to absorb prepared carbohydrate and proteid food-substances, but there are many genera that also digest them.

Fig. 77



Alimentary tract of the frog seen from in front: *Mh*, mouth; *Z*, extended tongue; *S*, opening into the larynx, showing the glottis; *Oe*, esophagus; *M*, stomach; *D*, small gut; *P*, pancreas; *L*, liver; *G*, gall-bladder; *Dc*, common place of emptying of the liver and pancreas into the gut; *R*, large gut; *Hb*, urinary bladder; *Cl*, cloaca; *A*, anus. (Claus.)

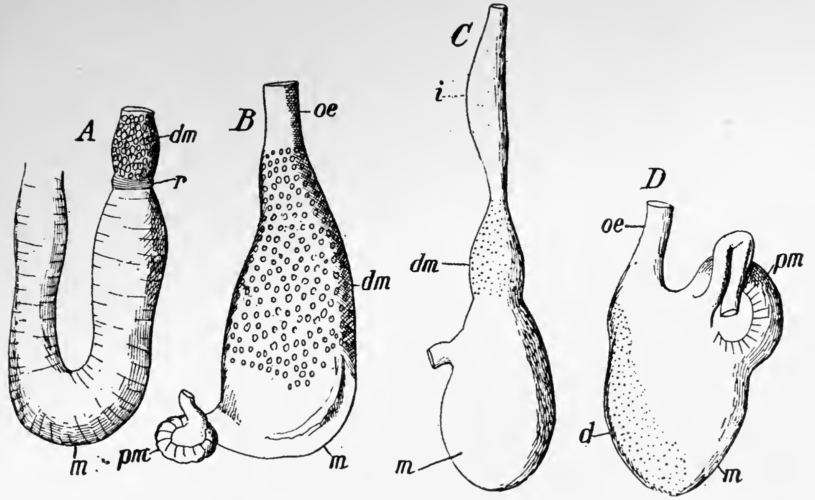
The Human Digestive Mechanism.—A knowledge of the anatomy and histology of the human digestive apparatus is obviously a prerequisite of an understanding of the digestion as a process. This information text-books other than those of Physiology fully supply, and to them the reader is earnestly referred.

The mouth or oral cavity is the receptacle into which the food is placed by the hands and the lips, and where it is masticated and insalivated. The tongue is an important organ of digestion, for by it almost alone the food is placed and kept between the two sets of teeth during its mastication. It is one of the most versatile organs of the body in that it has not only important motor functions, but because it bears also the end-organs of the sense of taste of so great importance in digestion.

The salivary glands empty their product into the mouth-cavity. Each of them produces to a certain minor extent mixed saliva, although for the most part the product of each is characteristic. The parotid gland is the largest of them, and weighs from 15 to 30 gm. This gland pours its saliva into the mouth through Stenson's duct, which is about 6 cm.

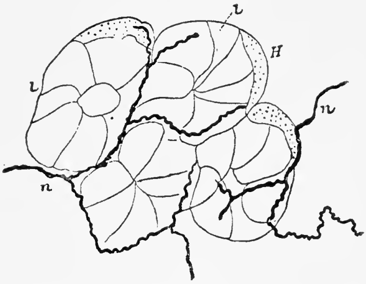
long and enters that cavity behind the second upper molar tooth. The saliva secreted by this gland is largely of a serous variety, that is, it is thin, albuminous, and highly lubricating. The submaxillary gland, weighing about 8 gm., sends its product into the mouth by Wharton's duct, which ends on both sides of the frenum linguæ. The sublingual gland opens by numerous small ducts (those of Rivini, from ten to twenty in number), directly into the mouth in various places. Besides these three major glands there are numerous others situated about the mouth-cavity. The product of these glands is largely of a mucous sort, whereas the submaxillary gland secretes both kinds of saliva in nearly equal proportions.

Fig. 78



The stomachs of four sorts of birds: *A*, pelican; *B*, tanager; *C*, hawk; *D*, ostrich; *oe*, esophagus; *dm*, chemical stomach; *r*, constrictor muscle; *m*, under part of stomach (reservoir); *pm*, antrum pylori. (Haller.)

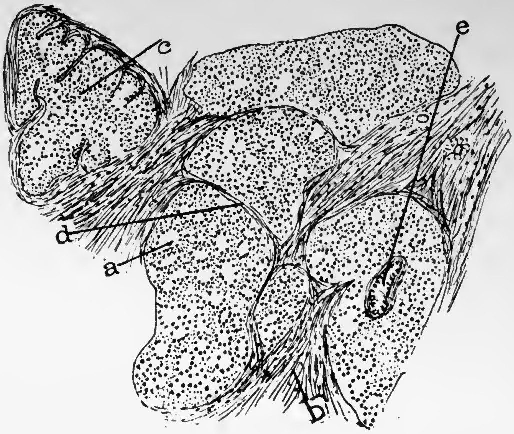
Fig. 79



The nerve-endings in the salivary glands: *l*, *l*, section in a column of cells; *H*, demilune-cell; *n*, *n*, nerve-fibers. (Retzius.)

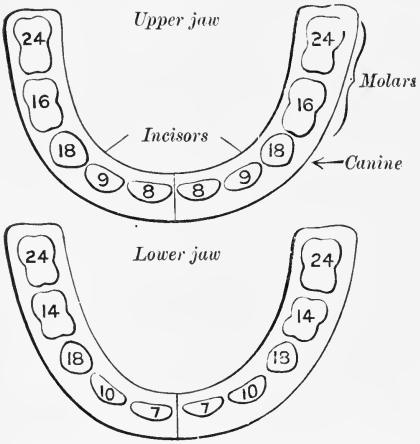
Mixed saliva as it pervades the walls of the mouth is an opalescent, somewhat glairy liquid, tasteless, and with a specific gravity of about 1005. Its chemical reaction is normally alkaline; but when not, the acidity is due to fermentation of bits of food in the mouth. In addition to the organic constituents of saliva (mucin, alkali-albumin, a globulin, serum-albumin, and ptyalin, which is the proper enzyme of saliva), this fluid contains several inorganic salts, notably potassium sulphocyanate. The quantity of saliva secreted in twenty-four hours in health appears to be rather more than a liter, the variation being large. Probably the three large glands, parotid, submaxillary, and sublingual, secrete the saliva into the mouth only during mastication. The other glands (the buccal, labial, lingual, and molar) are relied upon to keep the mouth, pharynx, and tongue moist, a condition necessary to mucous membranes.

Fig. 80



Section of salivary gland: *a*, alveolus; *b*, connective tissue which will be seen to penetrate the gland dividing it into lobes; *c*, points to the center of a lobe; *d*, septum between lobes; *e*, gland duct lined by columnar epithelium. (Bates.)

Fig. 81



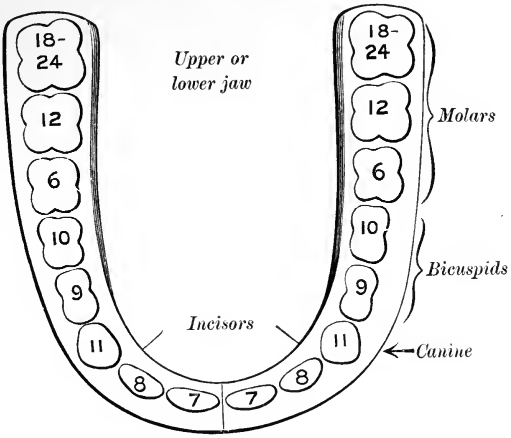
The temporary teeth. The numbers denote the respective times of their eruption in months. (Hall.)

The teeth are the organs by which the food that is in need of it is cut and ground into fine pieces, or a paste, preparatory to being swallowed and digested farther on in the alimentary canal. They are developed in two sets. On rare occasions a third set may be started.

The *temporary set* consists of twenty teeth, half of them in each jaw. Beginning in the middle line on either side of each jaw are two incisors, one canine, and two molars. These break through the gums nearly in pairs at intervals between the end of the first half-year after birth and the beginning of the third year. The order of their eruption, the periods, on the average, at which they come into view, is as follows: The lower central incisors appear at seven months, and the upper central incisors a little afterward; the upper lateral incisors show at nine months, and the lower lateral incisors somewhat later; the first molars in both jaws about the twelfth month; the canines at about the eighteenth month; and the second (that is, the posterior) molars at about the twenty-fourth month. The temporary teeth are similar in general shape to the permanent teeth, but are much smaller, bluer in tinge, and less firmly implanted.

The *permanent* set of teeth begin to displace the temporary teeth during the sixth or seventh year, although the sacs of all the permanent teeth, as well as those of the temporary set, are present in the jaw at birth. At the sixth year, therefore, the jaw contains forty-eight teeth—the whole of the deciduous set and all the permanent teeth except the third molars ("wisdom teeth"). The twenty teeth of the temporary set are replaced by a like number of somewhat similar permanent teeth, and these have similar names save that those replacing the temporary molar teeth are called bicuspids and have each two cusps instead of the molar's three. In addition three molars are added posteriorly on each side of each jaw, making the permanent teeth thirty-two in number. The first of the true molars (that is, that nearest the middle line), the earliest of the permanent teeth, appears at about the end of the sixth year, then the central incisors at seven years, the lateral incisors at eight years, the first bicuspids at nine years, the second bicuspids at ten years, the first canines at eleven years, the second canines at twelve years, the second molars between the twelfth and thirteenth years, and the unreliable third molars, or wisdom

Fig. 82



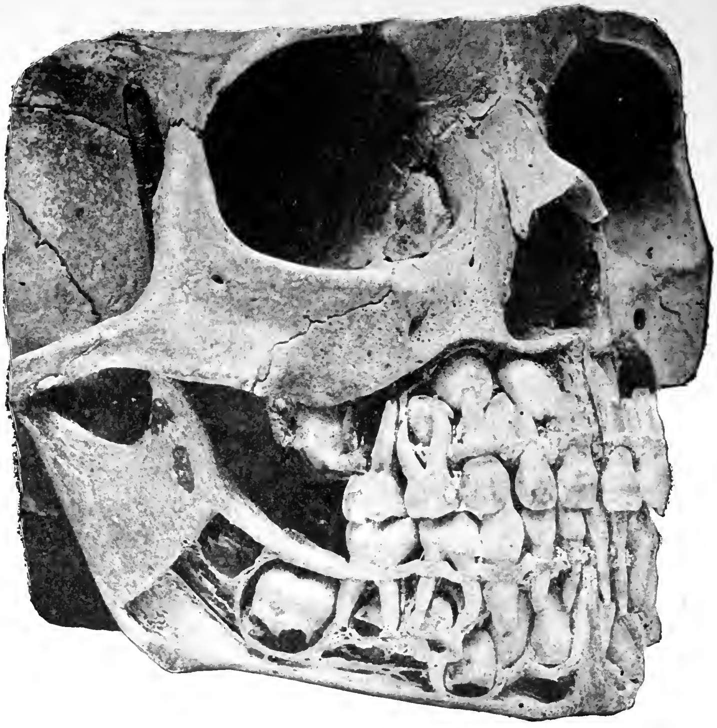
The permanent teeth. The numbers denote the respective times of their eruption in years. (Hall.)

teeth, only at a very variable time ranging from the seventeenth to the twenty-fifth year.

Mastication.—This is the first of the digestive processes if we neglect prehension of the food by the hands and lips. It is an habitual voluntary process carried on by a neuro-muscular mechanism, and once started goes on almost reflexly.

The masticatory muscles may be considered briefly in the following classes: Those which raise the lower jaw, those which move it laterally and forward, those which lower it, and those which keep the food in place between the opposed sets of teeth. (1) The elevators of the lower jaw are the masseter, the temporal, and the internal pterygoid. The masseter connects the molar process and the zygoma with the angle and ramus and coronoid process of the jaw with powerful contractile fibers, its action being, therefore, to draw the jaw both forward and backward as well as upward on the upper maxilla. The temporal muscle fills completely the temporal fossa of the skull and its fibers converge thence to the coronoid process of the jaw. By its contraction the latter is drawn powerfully upward, while at the same time the movement is somewhat

Fig. 83



The teeth of a seven-year-old child. The permanent teeth are already formed, and are waiting for positions in the jaws. (Litch.)

backward to help the grinding motions of the teeth and to keep the maxilla in its socket. The internal pterygoid muscle is in shape and direction much like the masseter, and acts to strongly press the lower jaw almost directly upward against the upper. The inferior maxillary nerve supplies these three muscles. These three muscles combined exert a pressure of several kilos as the crushing power of the molar teeth. (2) The lateral mover of the inferior maxilla is the external pterygoid muscle, whose powerful fibers pass horizontally backward and outward to the condyle of the jaw. When the muscle of the right side contracts the jaw is moved toward the left, and vice versa. Owing to the presence of the fibers which pass backward, when both external pterygoids contract together the jaw is drawn forward. This muscle also is supplied by the inferior maxillary branch of the fifth nerve. (3) The muscles which lower the jaw are the digastric, the mylo-hyoid, the genio-hyoid, and the platysma, of which the first two are the more important, while gravity is a force which in the mastication of ordinary food aids in the descent of the jaw.

The digastric muscle has two distinct bellies, the anterior and posterior, and only the latter has action in depressing the jaw. This anterior belly extends from the hyoid bone upward and forward to the inner surface of the lower jaw near the median-line. It is supplied by the inferior dental branch of the fifth nerve. The mylo-hyoid muscle is a flatter muscle than the preceding, and is placed just inside it, forming the muscular floor of the mouth. It extends between the hyoid bone and the mylo-hyoid ridge of the inferior maxilla. The inferior dental nerve supplies this muscle also. The genio-hyoid muscle is a slender bundle of fibers extending between the symphysis of the jaw and the middle portion of the hyoid bone. This muscle is supplied by the twelfth or hypoglossal nerve. When the hyoid bone is fixed from below by tonic contraction of the sterno-hyoid and other muscles, contraction of these three muscles depresses the jaw with considerable force. The platysma myoides muscle is a thin and superficial muscular fabric extending from the clavicle and acromion and superficial fascia of the upper part of the thorax to the whole length of the body of the jaw. Its contraction tends to depress the jaw.

Mastication employs these muscles, the tongue, and the muscles of the cheeks, these last being the active agents in keeping the food between the cutting and grinding teeth. In man the masticatory movements are largely vertical, the antero-posterior motion being slight, as are also the lateral movements of the jaw. As has been noted from our rehearsal of the actions of the various muscles, a large variety of jaw-movements are possible through the simultaneous operation of more than one muscle each with a different effect on the jaw. By this means, on a principle universal almost in muscular coördination, all the oblique motions of the jaw are to be observed during vigorous mastication unrestrained by the inhibiting conventionalities of culture. The tongue is at once the master and the servant of the mouth, and pervades it on occasion in nearly every part. In mastication its office is to gather up the portions of the food being chewed and to keep them sufficiently long between the teeth for complete mastication.

This directing, guiding, and restraining function of the versatile tongue would be impossible of its accomplishment, even with the muscles of the cheeks to aid, were it not for the saliva, with its sticky mucin, to fasten the crumbs together. The saliva is poured out into all portions of the mouth in a certain amount, but principally where it will be most useful to the grinding mechanism, behind the molar teeth, under the tongue, and on the floor of the mouth. Besides reducing the bite of food to a mass of fine particles easy of access by the digestive juices, mastication serves to mix thoroughly the bolus of food with this important amylolytic and alkaline digestant.

The saliva is, then, an essential substance. It has the power of chemically dissolving an important order of foodstuffs, and it alone makes possible adequate mastication and deglutition (passage of the food into the stomach from the mouth). Of these two sorts of function, the former, chemical solution, is apparently of the lesser importance, for saliva in this respect has perhaps a more efficient substitute in the pancreatic juice employed farther down the gut. Without the mechanical services of saliva, however, the swallowing of food is inconceivable, if not in liquid form or taken with a large quantity of liquid.

Saliva, then, (*a*) lubricates the tongue and keeps the mucosa of the mouth in normal condition. (*b*) It softens the food by its fluidity, makes it chewable, and renders it easily moved about by the tongue and cheeks. (*c*) It sticks together the food-particles by its mucin, so that a definite bolus suitable in size and shape to be swallowed is easily made by the tongue. (*d*) It lubricates this bolus by the serous element of its composition, so that it may be quickly passed into the esophagus and then painlessly down that narrow tube. (*e*) It starts at least the hydrolysis of starchy carbohydrates. (*f*) It dissolves such food as is soluble in a faintly alkaline liquid, and thus makes possible the important sense of taste (see page 357).

One of these uses of the saliva demands further description—namely, its solvent or digestive action on carbohydrates. This effect is brought about by a member of a class of bodies as yet in themselves little understood, called enzymes, or ferments, this particular enzyme (probably identical with the animal diastase or amylopsin of the pancreas) being called ptyalin. What ptyalin is, chemically speaking, is still unknown. It has been supposed that it is protein in its composition or a close derivative of a proteid. Recent researches, however, have made it necessary to deny that one enzyme, at least, is proteid substance, for an eminent chemist (Pekelharring) is sure that he has removed by repeated precipitation all traces of proteid from pepsin, a typical enzyme. Whatever the details of the actions set going by enzymes, the process, reduced to its simplest terms, seems to be one of hydrolysis. This term means the absorption of water by a molecule of the material acted upon and the latter's immediate splitting into simpler substances. These are found in practice to contain less latent energy than the molecule from which they originated. The hydrolytic process, then, is one of katabolism, the resulting chemical materials being more stable than their mother-substance. That water is required in the reaction is shown by the fact that no known enzyme acts save in its presence.

Various conditions determine the rate of digestive zymolysis, as has in part already been seen above. Among these are temperature (the normal body-temperature is the optimum), chemical reaction, fluidity or solidity of the substance acted on, the size of the particles of the latter, the concentration of the products of the zymolysis, the concentration of the enzyme, and whether or not the food-substance has been cooked (heated) or not. The necessity of promptly removing the products of the hydrolysis in order that the action of the enzyme may continue Brüche showed in 1862; it is a fact often demonstrated since. The impossibility of thus removing the products of the action when carried on artificially outside a living body is one of the chief difficulties in experiments on digestion under these circumstances. In the organism these products are promptly removed by absorption into the circulation. No explanation of this hindrance is at present available, but it is probably chemical and dependent on some sort of inhibiting reaction involving the enzyme. The slowing influence exerted by the excessive heating of the food-substance to be acted upon is probably a matter of general solubility; the heating of starch is clearly a step toward organic solution, but the cooking of proteids renders them in general somewhat less soluble. For the mode of action of ptyalin, see below (page 188), where hydrolysis in the stomach is briefly discussed.

Deglutition.—The next mechanism and set of movements which we have to consider in an orderly study of digestion are those of the process of swallowing, technically called deglutition. These have long been the subject of research on the part of anatomists and physiologists, for both the mechanism and its action are very complex.

The pharynx is a muscular, membranous, funnel-shaped tube connecting the mouth and nasal fossæ with the esophagus below it. The superior constrictor of the pharynx is composed of cross-striated fibers, the middle constrictor of both smooth and cross-striated fibers, and the inferior wholly of smooth or un-striated muscle. The esophagus, a muscular tube about 23 cm. long and 2 cm. in diameter, connects the pharynx above with the stomach below. The point at which it passes through the diaphragm is its narrowest part. Like the pharynx the esophagus has three coats, the outermost being muscular and consisting of two layers of fibers, of which the external are longitudinal and the internal circular. As in the pharynx also, the upper part of the esophagus is of cross-striated fibers chiefly and the lower part of smooth fibers. The muscles of the upper part are supplied by the recurrent laryngeal nerve, while the vagus supplies the muscles of the lower part of the tube. The pharyngeal muscles are supplied by branches from the pharyngeal plexus coming from the vagus, the glosso-pharyngeal, and the sympathetic.

The process of swallowing presents for consideration continuous series of muscular movements of a complex nature. They are one of the best examples of a highly developed and perfectly coördinated neuromuscular mechanism. The tongue arranges the bolus of food in the middle of its back surface and then tips up anteriorly. The bolus of food then partly drops and is partly squeezed backward between the tongue's dorsum and the hard palate and between the anterior pillars of the fauces. Meanwhile the soft palate has been raised and the posterior pillars have approximated, the uvula closing what little opening remains. This prevents the regurgitation of the food-mass into the mouth or into the nasal fossæ. By action of the upper pharyngeal muscles the pharynx is raised to meet the descending bolus. The larynx is also raised and at the same time closed above by the drawing forward of its posterior boundaries. As an extra safe-guard against drops of liquid falling into the lungs, the vocal cords are approximated at the same time. To the same end, and even more importantly, respiration is entirely suspended (reflexly by way of the glosso-pharyngeal nerve) during the entire swallowing process. Thus, the bolus of food drops into the grasp of the constrictors. These rapidly force it in the line of least resistance downward, where the inferior constrictors push it onward into the muscular esophagus. In the latter tube it moves at first rapidly and then more slowly by typical peristalsis. With a phonendoscope the thud made by the bolus dropping into the stomach can be often heard.

In the case of a large bolus this process of swallowing from the tongue to the stomach requires as much as six seconds. About five of these seconds are consumed in the esophagus. As Meltzer showed, when the mass of food swallowed is small or a liquid the process is simpler.

Deglutition appears to have a controlling center in the medulla oblongata apparently not far from the vagal center and closely related to the center of respiration. Deglutition is essentially a reflex process, but it may be initiated by the will. The act cannot be carried out completely however, unless there is some substance passing over the mucous membranes to reflexly actuate the apparatus. One cannot swallow several times in quick succession because after the first or second swallowing there is no saliva to furnish afferent nervous impulses. These nervous influences pass inward by branches of the superior maxillary of the fifth, of the superior laryngeal, of the tenth, and of the ninth cranial nerve. The efferent or motor nerves of deglutition are the twelfth, fifth, ninth, tenth, and eleventh.

The Stomach.—This viscus consists of two parts, functionally rather distinct—namely, the fundus and the antrum. The inlet of the stomach above is the cardia; its outlet below is the pylorus. Both are guarded by valves which consist of thickenings of the circular muscular fibers. The wall of the stomach is composed of four layers. The muscular part of the gastric wall consists of two complete and one incomplete layer of smooth fibers. The mucous membrane lines the entire stomach, but differs somewhat in the fundus and the antrum. It contains the cells which secrete the digestive juices of the organ. Judging by the varied nature of these juices, peptic, rennic, acrid, etc., there must be at least three sorts of cell-protoplasm present; it is not easy, however, to definitely discriminate more than two sorts of cells. The cells of the glands of the *fundus* have both these sorts of cells. One sort are irregular epithelial cells almost surrounding the capillary lumen of the straight tubular glands, and known as the central (or chief or principal) cells. The other sort, much less numerous, are irregular, polyhedral cells, peripheral to the central cells, lying on the parietes of the gland and hence called parietal cells. The latter variety are connected with the gland's lumen only by very fine channels running between the central cells (Fig. 84). These glands have wide mouths common to several tubules, and these openings give the stomach its reticulated appearance. They are lined by columnar epithelium and seem to be found in all parts of the stomach, but much less numerously in the antrum. It is by no means certain what the exact functions of these two kinds of cells are, but it is probable that the columnar central cells secrete by way of pepsinogen the enzyme pepsin, and that the parietal cells produce the free hydrochloric acid characteristic of the stomach.

Fig. 84

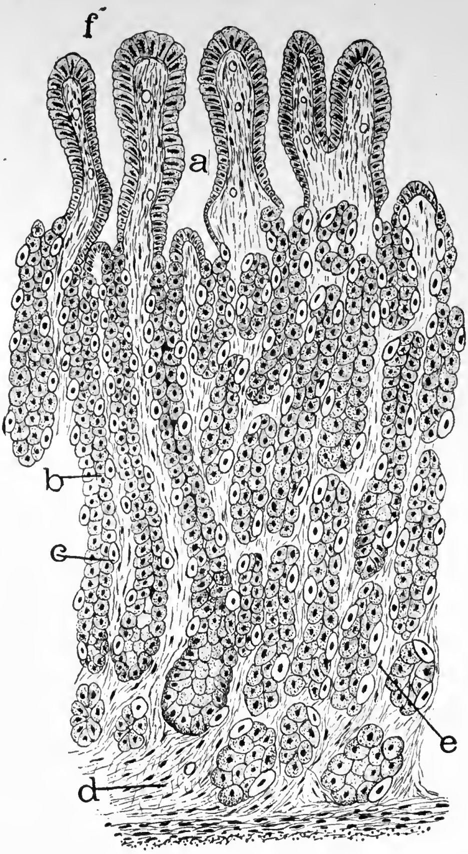
Longitudinal section of the stomach of the canary bird, to show the two parts, chemical and mechanical: *D*, the duodenum; *SDr*, small simple tubular glands; *Z Dr*, compound tubular glands. 5/1 (Oppel.)

The cells of the glands of the *antrum* are somewhat more cuboidal than those of the fundus, the lumens of the glands are longer and narrower and no polyhedral parietal cells are present. Toward the pyloric valve these glands become larger and similar in all apparent respects with Brunner's glands, so called, of the duodenum. It is likely that the columnar and cuboidal central cells all over the stomach secrete both pepsin and "rennin," but the details as to which secretes which are as yet undeveloped. Besides these three sorts of cells, small solitary lymph-follicles are scattered sparingly throughout the gastric mucosa. They are similar to those found in the intestine but smaller, and are like the follicles of lymph-nodes.

To summarize the functions so far as known at present of the various glands of the stomach: The central cells of the glands both in the fundus and in the antrum probably secrete pepsin and rennin, some of the granules (zymogens) apparent in these cells after resting being precursors of pepsin and some precursors of rennin. The glands of the antrum secrete a form of pepsin probably less complete and less active than that from the fundus. The parietal ("oxyntic") cells in the glands of the fundus probably prepare the free hydrochloric acid found in the stomach, and perhaps, as Maly supposes, from the sodium chloride of the blood by this reaction:

$$NaH_2PO_4 + NaCl = Na_2HPO_4 + HCl.$$

FIG. 85



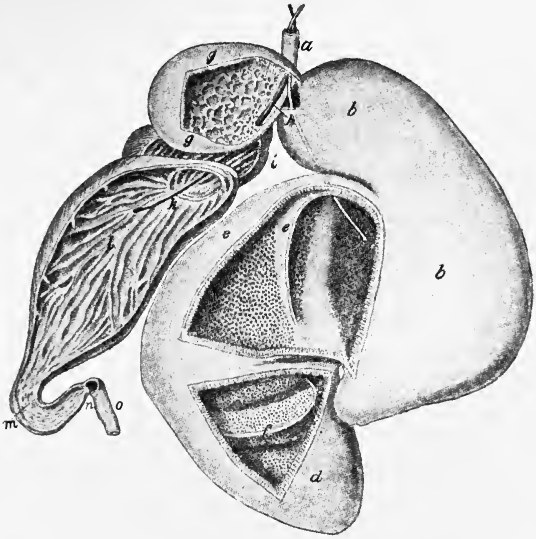
Section of the mucosa of the cardiac end of the stomach: *a*, gland mouth; *b*, cardiac gland-tube, "chief cells;" *c*, parietal cells; *d*, basement-membrane of connective tissue. This extends between the tubules and carries the vascular elements to these structures; *e*, interglandular connective tissue; *f*, general epithelial surface. (Bates.)

The fact that it is producible by the glands by direct stimulation during fasting seems to negate the theory that it is produced immediately from the sodium chloride of the food. It seems probable that much remains to be learned concerning the precise functions of the glands of the gastric antrum.

THE MOVEMENTS OF THE STOMACH have long been a fertile subject for description, but only recently, with the use of the much revealing

Röntgen rays, have we come to possess actual knowledge on this matter. The shape of the stomach depicted in the anatomies, an organ with an unbroken greater curvature extending from the pylorus to the left around the fundus and up to the cardia, exists only immediately after a large meal, when the viscus is distended with food and drink. One sees it so, in other words, only before the proper action and contraction of the organ has begun to make headway over the contained mass. Far from being a simple bag closable at its lower end by the pyloric valve, the stomach is essentially a double organ in the same sense that the stomach of the sheep has several chambers, although the omnivorous nature of man does not necessitate the elaborate mechanism needed for rumination. The human stomach is divided into parts, the fundus or left-hand distended portion, and the antrum, the active organ of digestion proper. This division is more obvious functionally than appears in the structure of the post-mortem organ. The parts are equally important, for, as we shall see, the mechanical functions of the stomach are at least as important as its uses in the way of chemical digestion.

Fig. 86

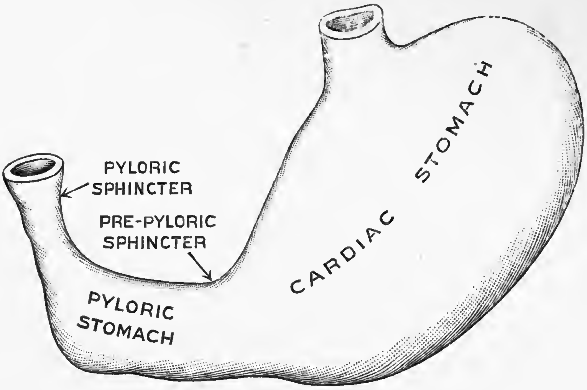


The stomach of a ruminant (sheep) partly laid open: *a*, esophagus; *g*, reticulum; *h*, channel for swallowed food; *i*, omasum, or psalterium; *l*, abomasum (rennet, or chemical stomach); *c*, *b*, rumen (reservoir-stomach). (Carus and Otto.)

The *fundus*, formerly called the cardiac end of the stomach, has movements which are gentle and slow compared with those of the antrum and of the small intestine. The fundus is largely a reservoir, and its motions correspond to such a use. They are of a gentle and slowly peristaltic nature just powerful enough to keep the antrum supplied with material for its solution into chyme. It appears from work by Austin and by

Cannon, the former working chemically and the latter with the Röntgen rays on cats, that the food as swallowed into the stomach may remain in the fundus an hour or more practically undisturbed. This allows amylolytic digestion by the ptyalin to continue, the contents for a time often not being mixed with the hydrochloric acid surrounding it in the stomach wall, and so remaining alkaline. The circular muscular fibers of the stomach's fundus make up the bulk of the musculature and by gradual tonic contraction combined with a slow peristalsis (occurring in the dog in waves three or five times per minute, according to Lommel) the size of the fundus is gradually reduced as its contents are passed through the sphincter of the antrum into the latter portion of the stomach. These gentle peristaltic waves probably are continuous with those descending the esophagus, and they pass from the cardiac end of the viscus to the pyloric valve. Combined with this there may be or not gentle swinging and tipping movements determined by the longitudinal and the oblique fibers of the gastric wall. It is brought about by the full final contraction of the circular fibers of the fundus that when the stomach is empty it has somewhat the shape of a boot (the antrum representing the foot), fixed above by the lower end of the esophagus. The stomach is seen to be an exceedingly adaptable organ so far as its shape is concerned, a faculty which the variety of direction of the muscular fibers makes possible. When nearly empty it is probable that the longitudinal fibers also contract somewhat, still further lessening the size of the viscus. It is thus that the food in the reservoir is gradually and entirely forced onward into the antrum, the walls apparently adjusting themselves perfectly to the volume of their contents.

Fig. 87

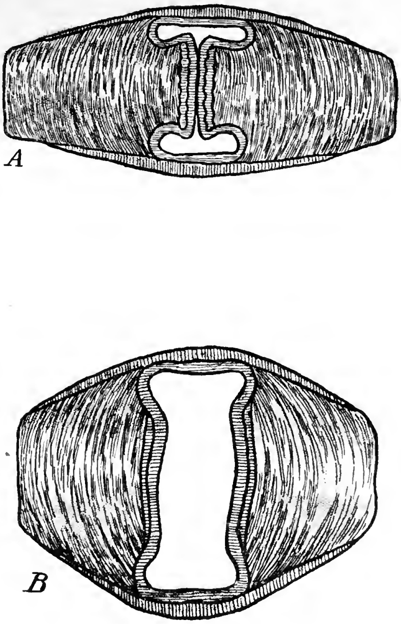


The human stomach, drawn (from a dissecting-room specimen) so as to make clear the two functional parts of the stomach. (Hutchison.)

The *antrum* within a few minutes after the ingestion of a meal begins to show slight annular contractions, rhythmic in character, near the pylorus, for some of the food taken into the now distended stomach went directly into this portion of the viscus, no dividing line between fundus and antrum being as yet present. Soon, however, the antrum begins to be shut off from the fundus by contraction of its sphincter, and it remains a distinct portion of the stomach until the viscus is quite emptied into the duodenum. This is a period which varies with the sort and amount of food eaten, from one to seven or even more hours. The movements of the antrum are rhythmically peristaltic, and they serve by their strong compression against the resisting pylorus to grind and squeeze whatever lumps of food may be present and are not too hard into a soft pultaceous mass. The contained pepsin, the hydrochloric acid, the mucus, and the heat of the organ materially aid in this process of chymification. The antrum contracts in the cat about once in ten seconds, according to Cannon, probably as a continuation of the peristalsis over the fundus, said by Lommel to occur in the dog somewhat less frequently. The small intestine is much more delicate and sensitive than is the stomach, and would be disturbed not a little by the reception of lumps or hard masses of solid food.

The pyloric valve opens periodically and in a rhythmic way. It is actuated by probably nervous influences sent out from the antrum's walls. It is stimulated to relaxation, that is, to open (according to Cannon), by strong acidity in the antrum, and it is closed by acidity in the duodenum beyond it. Thus, in cats fed on a proteid meal the forming chyme remains much longer in the antrum than when the food is carbohydrate. Protein does not absorb the free acid of the stomach as carbohydrate does, thus leaving the acid free to stimulate the pylorus to contraction. The carbohydrate takes large quantities of the acid early into the duodenum, and its presence there keeps the valve shut. The proteid has thus longer time for digestion in the antrum. To remain there would be useless in case of carbohydrates. Every two or three minutes, however, in the cat, the pyloric valve relaxes and allows part of the liquid portion of the chyme to escape into the intestine. The

Fig. 88



Gizzard of a bird: *A*, contracted state; *B*, relaxed state. (Jarrod.)

inspiratory contraction of the diaphragm probably aids somewhat in this squeezing work of the antrum, for it has been found that the antrum is moved by the descending diaphragm, but much less than is the cardiac portion of the stomach.

Vomiting is the process by which the stomach normally unloads itself of excessive or irritating food. Because of its close connection with the central nervous system it is also a frequent symptom of the onset of many diseases, especially in children. In young infants vomiting is a purely normal process very often, and allows of the easy unloading of a stomach into which too much has been put. In adults the process is usually preceded by the most unpleasant and complex feeling of nausea, the most conspicuous outward signs of which are usually a general peripheral vaso-constriction and a flow of saliva. Next comes retching, in which the feeling of nausea is intensified and the diaphragm makes powerful inspiratory contraction, the glottis being closed. Then the fauces open wide, the tongue takes the form of a rounded trough, the abdominal muscles vigorously contract, and simultaneously the diaphragm. Thus the stomach is strongly squeezed between two approaching resistances—below the mass of the intestines, etc., and above the rigid diaphragm. Under this gastric pressure the cardiac valve, recently closed, bursts open and the stomach-contents pour upward through the now wide-open glottis, pharynx, and mouth. The nasal passages are shut off (save in very violent emesis) by the closure of the soft palate, etc., in the same manner as in swallowing. In children's vomiting the muscular coats of the stomach appear to be much more active than in adults.

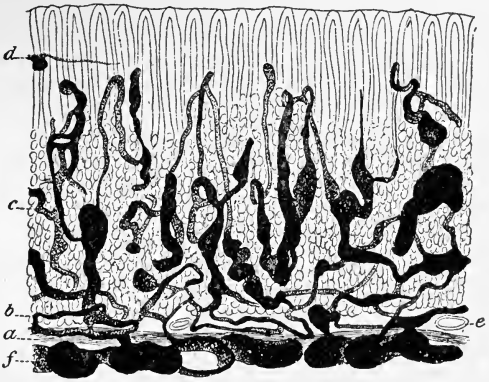
It is supposed that there is a center which coördinates the numerous muscular and glandular tissues of nausea and vomiting. This is probably in the medulla near the respiratory center and the center of deglutition. The nerves chiefly concerned are the tenth, the ninth, the phrenics, and the other spinal nerves, the tenth bearing apparently the greater part of the afferent impulses.

Emetics, substances causing emesis or vomiting, are of interest because they suggest the various ways in which this reflex act may be instigated. It may also be started mechanically, for example, by tickling the fauces with the finger or with a feather. *General emetics* are substances (for example apomorphin) which stimulate the vomiting-center in the medulla; just how they do so is unknown. Injection into the circulation is the most direct way of using this sort of emetic. *Local emetics* irritate the nerves and muscles of the stomach directly and thus reflexly cause vomiting. Mustard is a common example of these. Some emetics act in both of these ways, for example, tartar emetic. Anti-emetics are drugs which quiet the tendency to vomit. They also may act locally or generally, for example, morphine, which quiets at once the vomiting-center and the neuromuscular mechanism in the stomach-walls.

THE GASTRIC JUICE is the product of glandular activity in the stomach. It is a clear, nearly colorless liquid of a specific gravity of about 1003, but variable, a sour taste, and an odor peculiar to itself.

One of its characteristics is its permanence in the air, putrefaction never occurring. The average daily quantity is hard to determine, but in a man is very likely from two to five liters. In various animals its strength is very different. In the dog, for example, it is about three times as strong as in man, so that this animal can afford to bolt its food. In composition gastric juice probably varies greatly at different times according to the digestive habits of the individual. Schmidt's analyses are quoted as often as any, and it is interesting to compare his determinations of the gastric juice from an omnivorous animal (man), from a carnivorous animal (dog), and from an herbivorous animal (sheep). It is likely that the strength accorded to man's gastric juice is weaker than the average, especially in hydrochloric acid, which may be often 1 or even 2 per cent.

Fig. 89



Human gastric mucosa, peptic region, vertical section: *a*, muscularis mucosæ; *b*, subglandular lymph plexus; *c*, intraglandular lymph sinus; *d*, suggestion of an external plexus of lymph channels; *f*, submucous lymph plexus. (Loven.)

Composition of Gastric Juice (Schmidt).

Constituents.	Man.	Dog.	Sheep.
Water	994.404	973.062	986.143
Organic matter	3.195	17.127	4.055
HCl, free	+0.200	3.050	1.234
NaCl	1.465	2.507	4.369
KCl	0.550	1.125	1.518
$CaCl_2$	0.061	0.624	0.114
$Ca_32(PO_4)$		1.729	1.182
$Mg_32(PO_4)$	0.125	0.226	0.577
$FePO_4$		0.082	0.331
NH_4Cl	.....	0.468	0.473

The organic matter consists of pepsin, "rennin," lipase, and traces of a proteid and of mucin. Secretion of gastric juice apparently does not continue after the stomach becomes empty. It is readily induced, however, by the introduction of any solid substance into the organ, or by the sight, taste, smell, or even thought of food when the individual is hungry to some extent. For experimental purposes gastric juice is usually obtained from dogs in which a gastric fistula opening outward on the belly has been established. Sometimes an esophageal fistula opening on the exterior is also made and so arranged that food passes at the will of the observer either into the stomach or directly outside the body. To obtain a supply of gastric juice it is only necessary, then, to give the animal in this way a fictitious meal, whereupon reflex neural impulses cause a copious flow of the desired liquid, which is removed through the gastric fistula.

Fig. 90

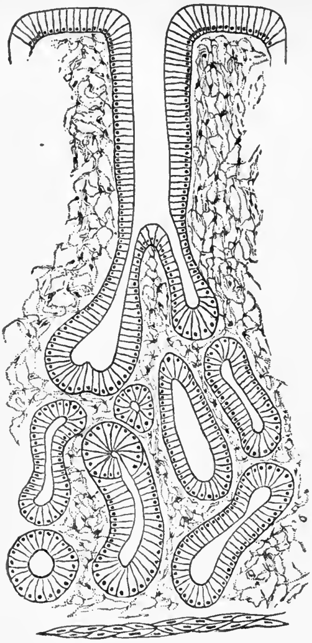
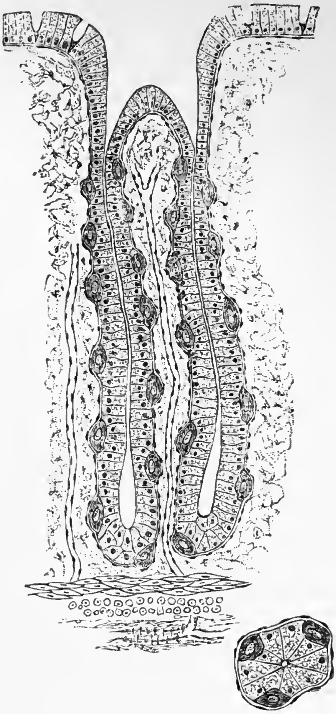


Fig. 91

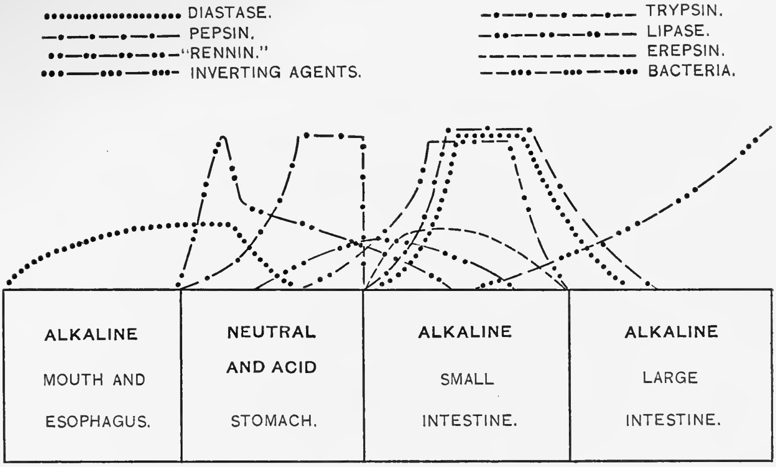


Two sorts of glands found in the gastric mucosa.

Digestion in the stomach is brought about chiefly by three enzymes or ferments—pepsin, rennin, and lipase—and by the hydrochloric acid. The action of the pytalin, too, secreted in the mouth, occurs also for the most part in the gastric fundus. We will next briefly examine into the chemical changes produced in various classes of foods by these still mysterious agents.

Ptyalin appears to have been first isolated from saliva by Mialke and in a somewhat purer state by Conheim; so far it has not been obtained free from admixture with protein and various metallic salts. It seems to be very similar to (according to Abderhalden identical with) the enzyme amylopsin secreted by the pancreas as one of its external secretions. It is, however, weaker than amylopsin, and does not under the normal conditions of digestion carry the zymolytic process so far—mainly the same difference which obtains between pepsin and trypsin. It acts in an alkaline, neutral, or even slightly acid medium, free acid, even 0.003 per cent., being, however, quickly destructive of its peculiar powers. In general it seems accurate to say that ptyalin acts best in a neutral medium, as Chittenden seems to have proved, such as may be supposed, indeed, to obtain in the mass of food as taken into and kept for a considerable while in the fundus of the stomach. The chemical composition of ptyalin cannot be stated with any degree of certainty at present, a statement equally true of all other enzymes.

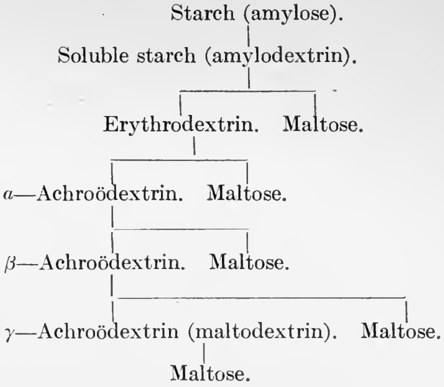
Fig. 92



This diagram shows, after the manner of the graphic method, the various chemical digestive agents and their respective times of action. In the complexity of interactions in the alimentary canal it must be pre-supposed, however, that the conditions are more variable than any diagram could indicate. (Modernized from Krukenberg.)

We consider the action of ptyalin, secreted in the mouth, under the heading of the stomach because its chief action is performed in that viscus and not in the mouth, as has already been suggested. The food remains in the stomach liable to diastatic digestion an hour for every minute, often for every second, that it remains in the mouth.

Ptyalin brings about the conversion of starch and of glycogen into sugar, the form of sugar produced by this ferment being finally maltose. The method of this change is hydrolysis: the absorption of water followed by a splitting of the amylodextrin or soluble starch so produced into molecules of maltose and probably, at first, also of dextrin. Because we are still ignorant of the exact molecule of starch (knowing only that it is some multiple of $(C_6H_{10}O_5)$ perhaps $(C_6H_{10}O_5)_{20}$, the precise reaction cannot be given. Neumeister, recognizing erythrodextrin as the first splitting-product from the amylodextrin (so named because with iodine it gives a red coloration), supposes that at least three forms of dextrin are successively produced, which, because they give us color with iodine, have received the name achroödextrins. These he named, respectively, alpha-achroödextrin, beta-achroödextrin, and gamma-achroôdextrin. Neumeister's theory of this hydrolysis, therefore, may be represented in a table, thus:



Musculus and Gruber corroborated this supposition, but still the proof that the three achroödextrins named are proper substances, stable and constant in composition, is far from conclusive. Ptyalin, unlike the dilute mineral acids, is unable to continue the splitting-reaction of the maltose into glucose or grape-sugar. Maltose, however, is not absorbable through the intestinal wall, but is inverted into dextrose before absorption into the blood takes place. This result is produced by the hydrochloric acid of the stomach, and especially by the enzyme maltase (or glucase) of the succus entericus. Were we to represent the hydrolytic cleavage in the simplest possible equation, it would be

$$\underset{\text{Starch.}}{3(C_6H_{10}O_5)} + 2(H_2O) = \underset{\text{Dextrose.}}{C_6H_{10}O_5} + \underset{\text{Maltose.}}{C_{12}H_{22}O_{11}}.$$

But this is misleading in a sense, for the reaction is very much more complex than the equation would indicate, starch, for example, not being $C_6H_{10}O_5$ but some multiple of that. If, then, we take m, n, and p as the unknown co-efficients of the starch, water, and dextrin molecules concerned, respectively, we have (Moore):

$$(C_6H_{10}O_5)m + (H_2O)n = \frac{m}{2}\,(C_{12}H_{22}O_{11})\,(H_2O) + \frac{n-m}{p}\,(C_6H_{10}O_5)p$$

as the most precise formula of diastatic action at present obtainable, and this is much more descriptive of the process than the previous formula given.

Pepsin is a proteolytic enzyme, secreted by the central cells of the gastric mucous membrane, especially by those of the fundus. The cray-fish secretes its pepsin in the mouth just as men produce ptyalin there, but use it largely in the stomach's undisturbed fundus. Pepsin is present in the stomach of the child at birth, but in many animals, especially the carnivora, for example the cat and the dog (Moriggia), it makes its appearance only two weeks or so after birth. It differs from most enzymes in requiring an acid medium for its activity. In an alkaline or even in a neutral medium pepsin is rapidly destroyed. Indeed some have supposed that the really active proteolytic agent is pepsin-hydrochloric-acid or even the acid alone. There is no proof that this is a true compound, while Maly has shown that other acids may serve in place of the hydrochloric acid. Nitric acid is the best substitute, but lactic, phosphoric, and three or four other common acids also serve experimentally this function of giving pepsin its "required acid medium." Maly's work suggests that part of the action of the acid may be to swell up and soften the proteid, and those acids which are most active in this respect are those which are also most effective in combination with the pepsin. The most recent theory is that the pepsin acts solely as a coupler between the protein and the acid, the latter doing the hydrolyzing work. This enzyme acts most rapidly at a temperature 2° or 3° above the normal temperature of the body, but is destroyed at about 80° C. (dry at 100°), a degree of heat about 12° higher than that which destroys ptyalin. As the temperature falls action becomes slower and quite ceases at zero. The pepsin of commerce is a gastric extract, containing usually either lactose or starch.

The function of pepsin has long been said to be to hydrolyze proteids and albuminoids so that they may be absorbed into the circulation and thus feed the organism. Pepsin's solvent power over different forms of proteid varies exceedingly. Casein is perhaps the most easily hydrolyzed of all the proteids, raw meat more easily than cooked meat, beef more readily (Cummens and Chittenden) than fish, and animal proteids more easily than those of vegetal origin.

Pepsin hydrolyzes proteids into peptone, probably into polypeptids, and possibly further into the amido-acids even, as the final products of its action. The intermediate substances produced are variously named and as variously described by different chemists, and must be considered as yet uncertain. Even less is known about the molecular structure of proteids and albuminoids than about that of starch, and here even more than there are the way-products undetermined. Two of these way-products, however, are fairly well known, namely, the albuminate syntonin (acid-albumin) and proteose ("propeptone," albumose, globulose, vitellose, gelatinose, elastose, etc.). It is very possible that syntonin may not be formed from all the proteid undergoing digestion, but usually the proteid swells all through owing to the combined action of the acid and pepsin, the softened mass then dissolving. By hydrolysis (absorption of water and molecular cleavage) the syntonin then splits into soluble proteoses. The debated question is largely as to how many different sorts of proteoses follow this as successive cleavage-products before the mass becomes peptone or polypeptids. The polypeptids are as yet ill-defined component parts apparently of peptones. These have already been synthesized artificially from their constituents; perhaps proteids themselves will be made before long. (See below.) Kühne and Neumeister suppose that two proteoses intervene between the syntonin and peptone called primary and secondary proteoses respectively. Pick finds reason to believe that there are four of these. In the great uncertainty attending the details of peptic hydrolysis at present it is almost useless to study the often contradictory theories of the matter farther. It is almost enough to suppose that the pepsin and acid (or the latter alone?) produce successively syntonin, then two or more proteoses, then one or more peptones, and possibly even amido-acids, each substance having a simpler and probably smaller molecule than its immediate predecessor. In schematic and probably incomplete form:

Proteid.
|
Syntonin.
|
Proto-proteose.
|
Deutero-proteose.
|
Ampho-peptone.

In this schema the "ampho" of the peptone implies the probable presence of two sorts of peptone, sometimes called hemi-peptones and anti-peptones respectively. Simpler than the peptones are substances, polypeptids, found by Pfaundler, E. Fischer, Salaskin, etc., which are probably combinations of amido-acids—for example, leucinimide. The molecular weights of these and simpler decomposition-products of peptic hydrolysis are probably not over 5 per cent. of that of the proteid with which the digestive process started. These obviously are, therefore, much more suitable materials for tissue-building than more complex and unstable substances. For the body-protoplasm to try to build protoplasmic tissue out of proteids, or peptones even, were much as if a contractor should attempt to make a satisfactory brick house out of second-hand bricks which had not been taken apart and cleaned, but used rather in the large masses in which the former walls had fallen. In the case of digestion by acid and pepsin it is still in doubt just how complete the separation and renovation of the proteid-materials are. There is some evidence (Mann) that the peptic process is one of aiding the disintegrating powers of the hydrogen and hydroxyl ions in the epithelium.

"*Rennin*" is the second of the enzymes so far isolated from the secretion-product of the stomach. It may be but an aspect of pepsin. Its function if a separate enzyme is to coagulate milk and to do probably other things not yet determined, for it is secreted by the stomachs of both birds and fishes, to which of course milk is for the most part quite unknown. Like pepsin, rennin acts only in an acid medium. As has been noted already, rennin is secreted by the central cells of the gastric mucous glands coming apparently from different zymogenic granules in the same cells that produce pepsin, these needing only reaction with acid to produce pepsin and rennin respectively. Like pepsin, the fundic glands produce it in much larger proportion than do the glands of the antrum. Rennin has never been isolated; its optimum temperature is about 40° C., and its action ceases at somewhat above zero. It is destroyed by a lower degree of heat than are most enzymes, namely at 63° in acid medium and at 70° in a neutral medium. Rennet, the dried fourth stomach of the calf, has been used for many centuries to curdle milk for the purpose of making cheese. Why the caseinogen, the soluble proteid of milk, requires coagulating before being hydrolyzed by the proteolytic enzymes is quite unknown, and it is especially hard to understand because the acidity of the gastric juice is sufficient after a while to bring about this coagulation. Perhaps the coagulation is required promptly on the entrance of food into the stomach, more promptly than the acid could do it in the relatively undisturbed fundus. But it is more likely that the rennin in some undiscovered way actually starts the hydrolysis of the milk-proteid, and still more likely, as already has been noted, that rennin has important functions as yet quite unguessed. The coagulation of milk in the stomach may even be a defect produced by the pepsin, since Pawlow claims that all proteolytic enzymes coagulate caseinogen. As has been said, rennin is perhaps only some chemical aspect of pepsin. We may possibly be even mistaking rennin for what is really an anti-rennin (an opponent of coagulation) in process of evolution. In the present ignorance of proteids themselves and of their metabolism such numerous doubts in description and in theory are inevitable.

The mode of action of rennin in coagulating caseinogen to casein is partly homologous to the coagulation of blood and some other body-liquids by thrombin, but is not wholly similar. Caseinogen is the protein of milk, and is apparently a nucleo-proteid soluble in the normal fluid. On the addition of rennin to milk, calcium phosphate always being present, this nucleo-proteid is made to absorb water and to split up into paracaseinic acid and an albumin by the usual process of hydrolytic cleavage. At least two new proteins are produced by this splitting process. One of these, casein (calcium paracaseinate), being insoluble, falls as a precipitate, the curd. The other is a whey-globulin which remains in solution, possibly with a third, an albumose, in small amount. Whether the reaction in the case of human milk is quite like this or not is in some slight degree of doubt, as nearly all the literature on the subject relates to the curdling of cows' milk. If the calcium phosphate be removed from the milk entirely, casein is not thrown down. Some have thought that in this coagulating process the action of the calcium was not to help the first reaction, changing the caseinogen to casein, so much as to assist in the separation of the two cleavage-proteids, casein and whey-proteid. The details of the process are, indeed, as yet much in doubt, and here, as elsewhere, hypothesis is a poor substitute for facts. Milk is curdled also by an excess of acid, but that its normal coagulation is not due to the acid of the stomach, but to the rennin's activity, is readily presumed by the fact that neutral rennin promptly coagulates alkaline milk, no acid being concerned at any time, while rennin always is present in the human stomach from birth onward (Heintz). Bacteria cause the curdling of milk after a time, but indirectly, by bringing about the presence of lactic acid, which curdles the milk. (The peptic digestion of casein produces paranuclein, which gradually dissolves.)

Lipase (steapsin) has been found in the human stomach by Volhard. Aside from the fact that it acts only on emulsified fats (*e. g.*, that of milk), little is as yet known about its work in this organ.

Hydrochloric acid as found in the stomach undoubtedly exerts some slight hydrolyzing action on the disaccharides (cane-sugar, lactose, and maltose), bringing about thus their "inversion." A special enzyme exists in the succus entericus (page 207), for this purpose, called invertase, and most of the maltose, made by the hydrolysis of carbohydrates, is doubtless inverted through the agency of this ferment and not by acid. Lehmann found invert-sugar in the stomach of rabbits fed on beets, while Seegen invariably obtained it from the stomachs of dogs fed on saccharose. No enzyme with an inverting power has been found in the stomach.

$$\underset{\text{Maltose.}}{C_{12}H_{22}O_{11}} + \underset{\text{Water.}}{H_2O} = \underset{\text{Dextrose.}}{2(C_6H_{12}O_6)}$$

It is as dextrose that most of the hydrolyzed carbohydrate is absorbed through into the capillaries of the intestinal villi. This hydrolytic inversion performed in the stomach by the dilute hydrochloric acid is perhaps small in amount, but is of theoretic importance.

When the acid reaches the duodenum it reacts on the prosecretin from the gut-wall and produces secretin (see below).

Aside from its hydrolytic powers this acid is a powerful antiseptic, as are most other acids. The importance of this action we have no means of estimating, but it must be considerable, for the bacteria which enter the stomach with the food and drink are of numberless varieties and of vast number. Some of these unchecked would derange all normal digestion, while others would cause the illness or death of the individual. The tubercle bacilli is not destroyed by gastric juice, but the germs of anthrax and of cholera are quickly killed. Perhaps in the long run the antiseptic action of the hydrochloric acid against the organisms of ordinary putrefaction are more important to man than its destruction of the virulent germs of disease.

THE STOMACH'S FUNCTIONS.—It will serve to fix the status of the stomach in mind if its functions are arranged in a schematic list. Ten sorts of usefulness may be noted, varying much in importance, but all of benefit to the organism, the order in which they are given here being apparently, in a general way, that of their relative importance.

1. As perhaps first in consequence the stomach is a *reservoir* for food and drink. Were there no such dilatation in the alimentary canal the taking of ordinary food in meals would be impracticable, and man would be in a somewhat literal sense the servant and not the master of his digestive functions. Now that the stomach is occasionally removed because of otherwise fatal disease, there is opportunity to observe the value of the organ in this direction, for this function alone is unrepresented elsewhere in the alimentary canal. Stomachs vary much in size in different individals, and are liable to functional distention as well as to almost tubular contraction, as already has been noted. A fair estimate of the size of an average adult fundus in a filled condition is perhaps a liter. By the ever-compressing force of this fundic reservoir the antrum is kept supplied with material on which to act, somewhat as the auricles of the heart are mainly reservoirs for the prompt filling of the more active ventricles.

2. The second in importance of the functions is perhaps the *hydrolyzing of proteids and of albuminoids* to forms which are absorbable from the gut farther on. It seems probable that there is more difference between peptic and tryptic proteolysis than is now generally recognized. It is hard to define the relative importance of these two to the organism, yet the stomachless mammal probably thrives much better without pepsin than he could without trypsin.

3. Another function of the stomach, close or even equal to the last-mentioned in importance, is the *digestion of soluble carbohydrates* begun by the ptyalin in the mouth. The contents of the gastric fundus being sometimes undisturbed for hours even, the major part of amylolysis takes place sometimes at least in the stomach. Here the advancing neutrality of reaction and perhaps soon a slight degree of acidity furnishes the ptyalin its best medium for action on starches and on sugars. As we have seen, the greater the proportion of carbohydrates in the stomach, absorbing the free hydrochloric acid and so removing the pyloric valve's closing-stimulus, the shorter the time the food remains in the stomach.

4. Another gastric function (Volhard) is probably the saponification of emulsified fats. The importance of this activity is as yet unknown.

5. A fifth function of the organ is to *coagulate the caseinogen* of milk into casein and possibly to start it toward digestion by this change. The enzyme rennin does this and besides, as has been said, may give the stomach still other functions as yet unsuspected.

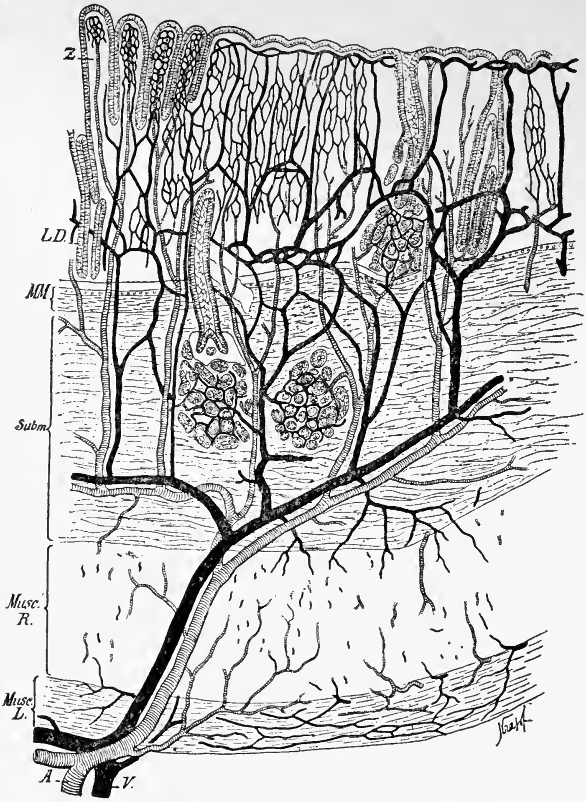
6. A sixth action in digestion is the *sterilization* of food containing bacteria, the free mineral-acid present in the gastric juice in amount of 1 per cent., more or less, being the chief agent in this direction.

7. The long-continuance of the food in the relatively insensitive stomach *adapts the chyme in temperature* for the best digestion and prevents injury or at least functional interference with the duodenal glands and muscles by chyme either too hot or too cold. This use depends directly on the first function noted—that the stomach is a reservoir. As

such it warms food too cold and cools food, usually liquids, taken too hot for the duodenum to bear well.

8. Another function similar to the last in its usefulness is the *liquefaction* of the food before its entrance to the gut proper, thus avoiding irritation and more or less injury. This process is a combination of chemical, mechanical, thermal, and secretory agencies.

Fig. 93



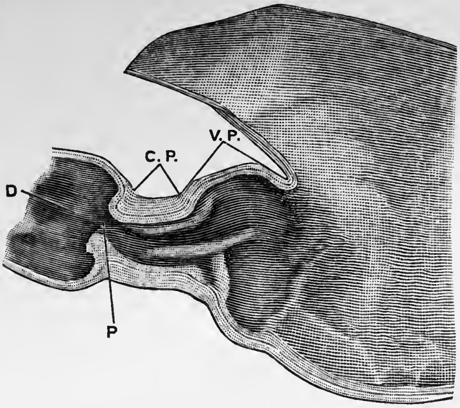
Section through the antrum-wall of the dog: *Z*, villi; *LD.*, Lieberkühn's glands (Brunner's glands are in the submucosa, *Subm.*); *MM*, muscularis mucosæ; *Musc. R.*, transverse, and *Musc. L.*, longitudinal section of the muscularis. The veins are shown black, the arteries cross-striated. $^{44}/_{1}$. (Mall.)

9. Another function is to *invert sugars* by means of its acid, whether the former are introduced into the stomach as such or are produced there by the hydrolysis of starch.

10. A tenth usefulness of the stomach is a *slight degree of absorption.* The materials absorbed are chiefly alcoholic solutions, alkaloids, salines, and possibly a very small amount of water and of hydrolyzed or soluble proteids.

Yet, with all these functions regularly performed by the normal stomach people live stomachless with a tolerable degree of comfort.

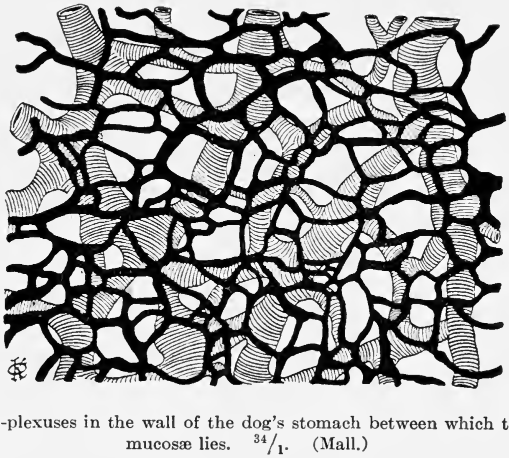
FIG. 94



Longitudinal section of the pyloric region: *P*, the pylorus; *D*, duodenum; *C.P.*, pyloric canal; *V.P.*, pyloric vestibule. (E. Müller.)

The Small Intestine.—The small intestine is a tube about 650 cm. long and somewhat larger at the upper end than at the lower. It has practically the same coats as the stomach. Exner and Bienenfeld suppose that the so-called muscularis mucosæ has for its function to prevent the puncture of the gut by bones and other sharp objects. The mucous membrane is made up of various secreting glands, of lymph-nodules, and of the villi which extend inward from it. One set of glands called the duodenal (or Brünner's glands) appear to the eye to be almost identical with those

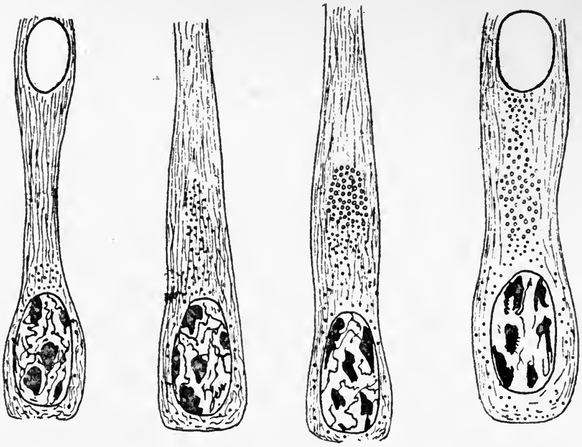
FIG. 95



The two lymph-plexuses in the wall of the dog's stomach between which the muscularis mucosæ lies. $^{34}/_{1}$. (Mall.)

in the fundus of stomach. Their function must be different, however, for no pepsin is formed in the duodenum; enterokinase, for example, is, however. These are largest in the upper part of the duodenum, but are not found below the first portion of the jejunum (simple follicles). The crypts of Lieberkühn are simple glands in the mucosa between the bases of the villi. Scattered among these are the goblet-cells, producing mucus; what else they secrete is still unknown. The valvulæ conniventes are prominent acute ridges running part way around the interior of the gut-wall. Their use is apparently to many times increase the secretive and absorptive surface of the intestine and also to retard the downward passage of the chyle. Some of these are nearly a centimeter in height. The villi are minute finger-like projections into the lumen of the small intestine. They are largest and most numerous in the duodenum and jejunum. Kräuse estimates their number at about 4,000,000, and they are from 0.5 to 3.0 mm. in length. From without inward a villus is composed of striped columnar epithelium, with goblet-cells scattered here and there through it. Beneath this is the membrane, then comes the reticular adenoid tissue, containing lymph-corpuscles, bloodvessels, and nerves in abundance. There are also numerous smooth muscle fibers, especially about the large lymphatic vessel in the middle of the villus. The lymph-nodules of the gut-wall are most numerous in the lower half of the ileum, where there are no valvulæ conniventes, especially in the ileum. These combine in masses to form Peyer's patches, which are from 1 to 10 cm. long.

Fig. 96

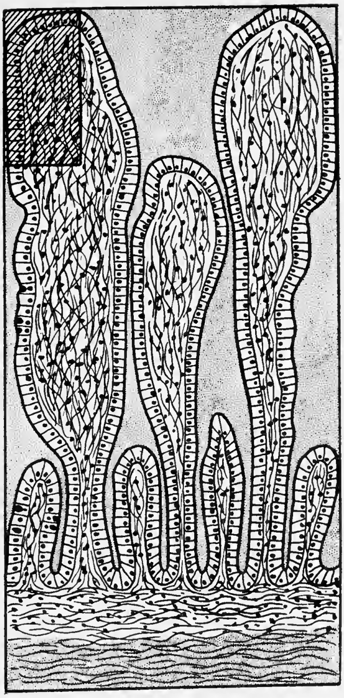


Goblet-cells from the gut of geotriton, to show the different functional conditions of this sort of epithelium. In the first, a secretory act has just ended and a second is beginning. In the second and third and fourth cells various stages of activity are shown, both in the cytoplasm and in the nucleus. (Galeotti.)

The nerve-supply of the small intestine comes from the spinal cord by way of the sympathetic chain, the great and small splanchnics, the solar and mesenteric plexuses, and especially from the vagus.

THE MOVEMENTS OF THE SMALL INTESTINE, for descriptive purposes only, may be analyzed into four varieties. These are peristalsis, longitudinal contractions, swinging movements, and, according to Cannon, "segmentation." The three first-mentioned are but aspects of one complex movement; the last is more or less separate, and as described by Cannon, only recently discovered.

FIG. 97



Magnification of the intestinal area by the villi. Were the villi not present the absorptive area of the gut would be only about one-nineteenth of what it is. This ratio is that of the smaller rectangle to the larger.

Intestinal *peristalsis,* like peristalsis elsewhere (esophagus, ureter, etc.), is a slow progressive contraction of the circular muscular fibers forming the major part of the musculature of the gut. This successive contraction of the rings of muscle causes a progressive narrowing of the lumen of the tube—a process well adapted to squeezing its contents slowly along. The progression is much aided by the automatic contraction of the fibers above a mass of food, while those below it are simultaneously relaxed (Bayliss and Starling). The rate of movement is slow. In one case a marble was pushed along only a trifle more than 1 cm. in a minute, but the normal propulsion of the chyle is doubtless often at a much greater rate. There is no direct evidence that antiperistalsis normally occurs in the small intestine, although it does occur in the large. It probably takes place, however, in certain abnormal conditions, and in the small crustacea (for example, Daphnia) antiperistalsis is the normal direction of the wave.

Lessening of the length of the gut by means of *contraction of the longitudinal fibers* is an almost indispensable part of the peristaltic movements, for by this means the intestinal tube is drawn over the contained mass, so leaving the latter, as it were, farther down the intestine than before. Thus, peristalsis and occasional shortening of a loop of the intestine together squeeze the contained mass slowly along. The speed of these movements is hastened several times when the intestines are exposed to the irritating air, as during an operation or a demonstration. Normally they are very slow—a gentle complex squirming movement hard to describe but easy to understand.

The *swinging* motions of the intestine depend on the manner in which loops of the gut are fastened posteriorly by the omentum. They are produced by contraction of both the circular and the longitudinal muscular fibers acting together, and occur every five or six seconds. They are not influenced by nerves, but they are by temperature (Ludwig).

FIG. 98

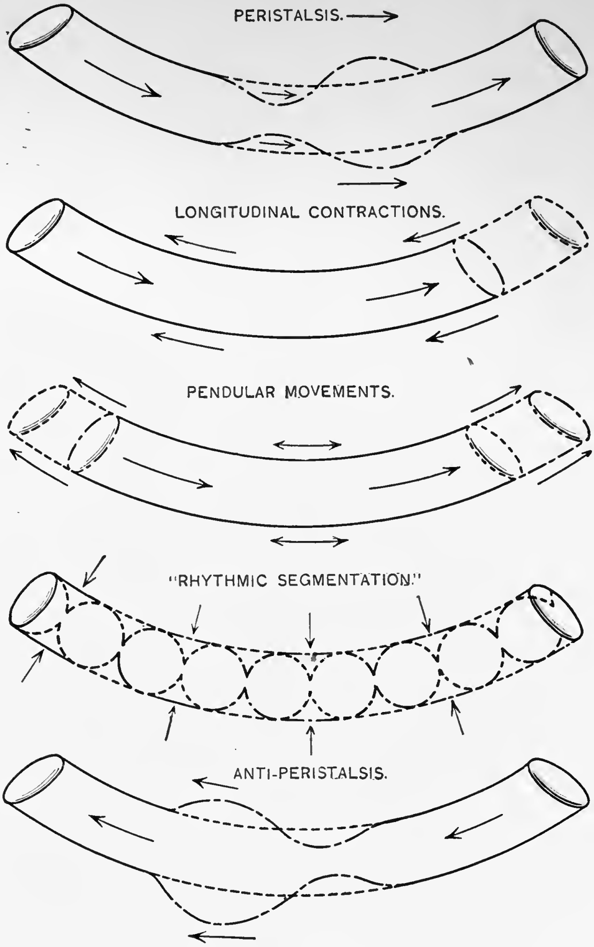


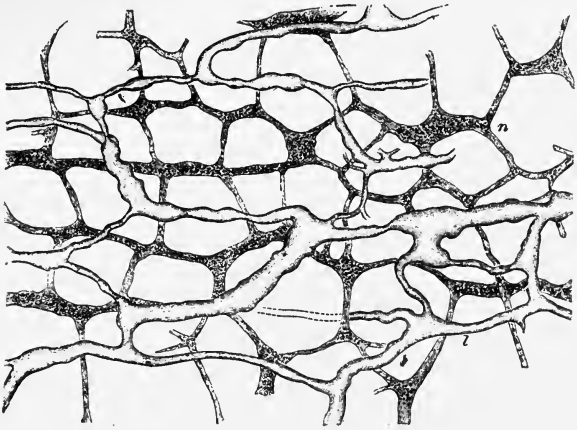
Diagram of the intestinal movements: the solid lines show one phase of the movement, and the dotted lines the other phase.

By the aid of this complex movement (a combination of peristalsis, shortening, and swinging), the first portion of an ordinary meal reaches the cecum in about three hours, on an average, and it is at least six hours more before the last part of such a meal passes through the ileocecal valve. Thus, a bit of food requires three hours to pass the
]

575 cm. or so of the small intestine, and an average meal remains within at least six hours and often twice as long if we include the stay in the stomach.

The process of "*rhythmic segmentation*" is well denoted by its name, due to Cannon, who described it from the shadows cast by the digesting intestine of the cat, dog, rat, and rabbit. Bismuth subnitrate having first been mixed with the animals' meals, the chyle was sufficiently opaque to the Röntgen rays, so that its position and condition as regards segmentation, etc., could be seen on the fluorescent screen. A cat contentedly digesting a meal could thus be studied and watched for hours under more or less normal conditions. Suppose a "string" of chyle 10 cm. long contained in a loop of the animal's intestine. Suddenly, by the simultaneous quick constriction of the gut in five or six places, this string-like mass of food is cut into as many separate pieces. Two seconds later (in the cat), by intestinal constrictions midway between those which occurred before, these five or six pieces are again divided each in the middle and the halves pushed aside and united again into five or six new pieces. Two seconds later constrictions occur where they occurred four seconds before, thus segmenting the food-mass once more as it was at that time. Thus, the alternate division and uniting and redivision and reuniting goes on thirty times a minute (in case of the cat), perhaps for half an hour or more. The string of chyle meanwhile does not advance along the cat's intestine, but remains to be chopped up by this process of the gut's circular muscular fibers. Wolff corroborates more or less fully these results obtained by Cannon. He thinks the gut's movements are not continuous with those of the antrum, but originate at a point farther down the intestine. In man, probably the rhythm, if it

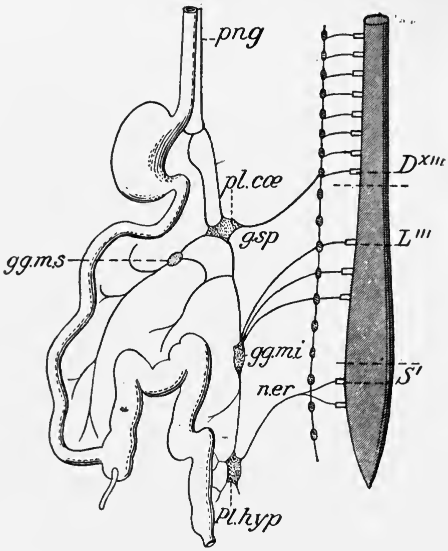
Fig. 99



Lymphatic and Auerbach's plexuses in the intestine's muscular coat: *n*, the nerve plexus; *l*, the lymphatic plexus. (Auerbach.)

occur at all, is much slower, for in the dog the movement is said to occur twenty times a minute only, while in the rat the segmentation takes place every second, rhythmic movements being generally more rapid the smaller the mammal. By this supposed rhythmic segmentation, occurring probably in many places in the gut at the same time, the food-mass may be thoroughly mixed with the juices of the intestine and any lumps remaining in it reduced. Moreover, by this means, if they obtain, the portion of the chyle which is hydrolyzed and ready for absorption is squeezed strongly against the absorbing organs, the villi thus furnishing a strong pressure inward several times a minute. This pumping-action would doubtless assist the capillary circulation of the villi and make them in general much more active in all their functions than else they could be. Further confirmation of this matter, however, is required before it is generally accepted as above described as a normal and universal fact in human digestion.

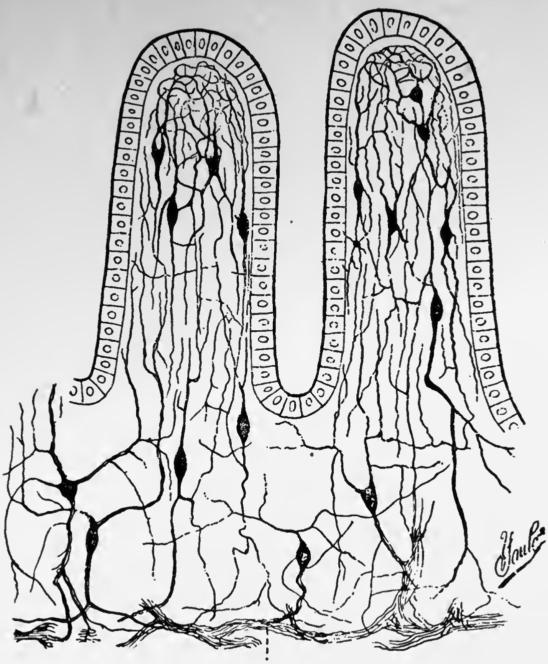
FIG. 100



The innervation of the gut (dog): *png*, vagus; *pl. cœ*, celiac plexus; *gg. m.s*, superior mesenteric ganglion; *gg. m.i*, inferior mesenteric ganglion; *Pl. hyp*, hypogastric plexus; *gsp*, great splanchnic; *n. er*, erector nerve; D^{XIII}, thirteenth dorsal pair; L^{III}, third lumbar pair; S^{I}, first sacral pair. (Morat.)

The *innervation* of the small intestine is still a matter of discussion so far as specific neural functions are concerned. Most observers deem the vagus the motor or actuating nerve of the gut. In the dog, at least, there is some evidence that the vagus contains also inhibitory fibers, perhaps, however, coming indirectly from a special place (Jacobi). Pflüger first claimed that the sympathetic was the inhibitory nerve of the intestine, and the opinion is being continually supported by researches. Mayer

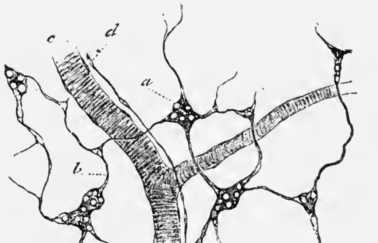
FIG. 101



The sympathetic nerve-fabric as seen in and below the intestinal villi. (Ramon y Cajal.)

and von Basch ascribe it, however, to the vaso-constrictor action of these nerves, but it has been shown that the action is inhibitory after the circulation has ceased. According to Ehrmann, the sympathetic (splanchnics) are inhibitory to the circular fibers, but motor to the longitudinal fibers of the intestinal muscle. Researches by Magnus indicate that Auerbach's plexus controls the movements of the circular muscular fibers and has nothing to do with the longitudinal movements. Removal of Meissner's plexus did not affect the peristalsis in an isolated loop of the gut. A center for the movements has been located by von Bechterew and Mislawski in the sigmoid gyrus, and this must be in close relation with the centers which are concerned

FIG. 102



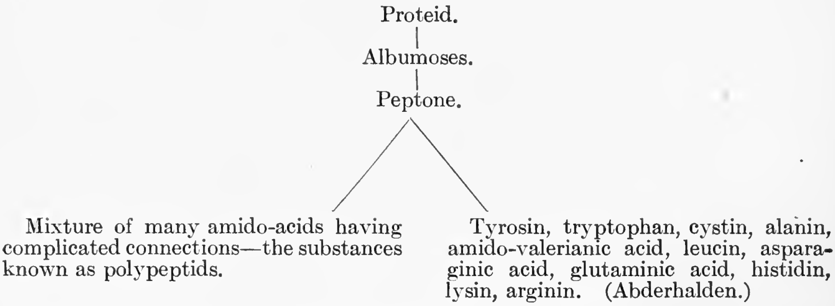
Meissner's plexus in the submucous layer of the gut: *a*, ganglia; *b*, cords of the plexus; *c*, small bloodvessel. (Cadiat.)

with the emotions, for the intestinal movements are easily disturbed. Other centers, actuating and inhibitory, probably are placed in the cord, the spinal ganglia, or in the great abdominal plexuses. Despite all these diverse facts, the probability is continually confirmed that the control of the whole alimentary canal is of the simplest sort through the nerve-net in its walls. Its neuro-muscular mechanism is doubtless a highly unified structure, whose details remain, however, to be described.

Pancreatic juice is poured out, mixed with the bile, into the upper portion of the duodenum; there it mixes with the intestinal juice proper, forming altogether a very complex digestive liquid. The external secretion of the pancreas is in different animals and at different times a very variable substance. From a dog's temporary fistula its specific gravity is about 1030; it is clear, but of a syrupy consistence, becoming still more viscid on cooling; at 75° or at 0° it coagulates. It is alkaline in reaction, due probably to salts of sodium. It is rich in proteid. A sample analyzed by C. Schmidt contained 900.8 parts water and 99.2 parts of solid material, of which 90.4 parts were organic matter and 8.8 parts ash. This ash was mostly sodium chloride, but contained also sodium oxide, potassium chloride, trisodic phosphate, lime, magnesia, earthy-phosphates, and iron. Its daily amount in man is perhaps 175 grams.

Pancreatic juice contains probably at least five enzymes: trypsinogen, hydrolyzing proteid; diastase (amylopsin), hydrolyzing carbohydrates; lipase (steapsin), saponifying and indirectly emulsifying fats; probably rennin, coagulating caseinogen; and perhaps lactase and invertase.

According to Bayliss and Starling, no trypsin is contained in fresh pancreatic juice, but the trypsinogen there found is changed to trypsin when it arrives in the intestine by the action of enterokinase (kinase), secreted by the upper end of the gut. By means of erepsin from the intestinal wall probably the peptone produced by hydrolysis is split still farther into the amido-acids.



Proteid.

Albumoses.

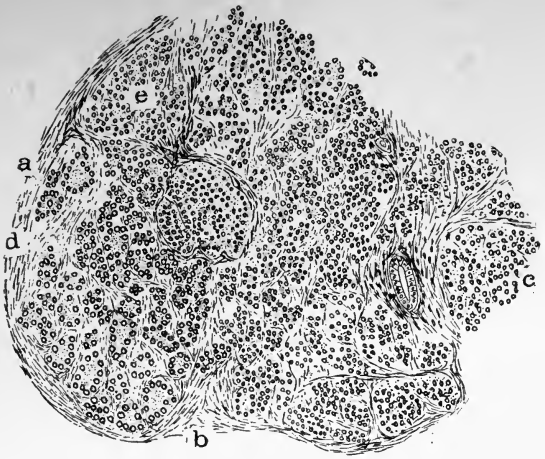
Peptone.

Mixture of many amido-acids having complicated connections—the substances known as polypeptids.

Tyrosin, tryptophan, cystin, alanin, amido-valerianic acid, leucin, asparaginic acid, glutaminic acid, histidin, lysin, arginin. (Abderhalden.)

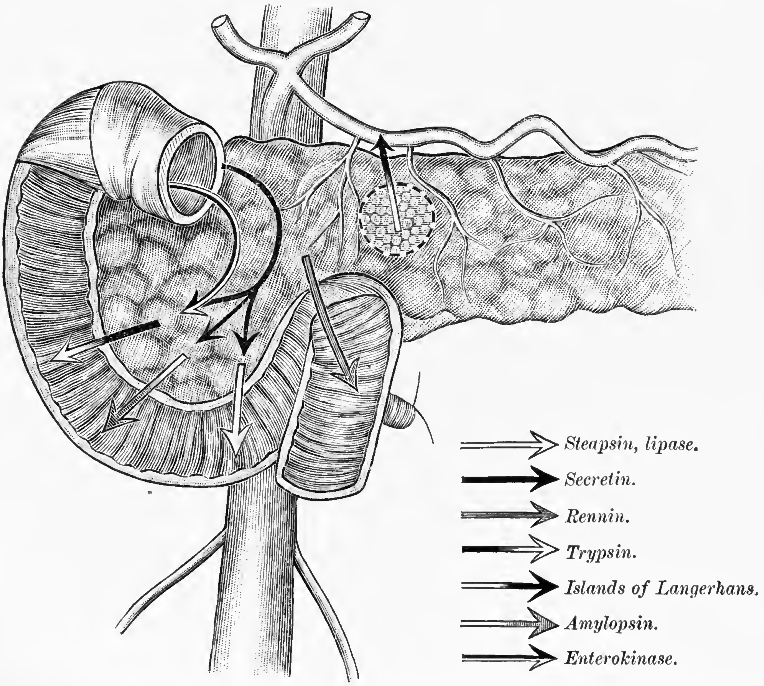
Inasmuch as Lowi, and others after him, have been able to keep dogs nourished by feeding them, for nitrogenous food, these amido-acid substances (leucin, tyrosin, arginin, aspartic acid, etc.), considered the end-products of tryptic proteolysis, it is now suspected by many that the albumoses and some albumins are synthetic products of the action of an

FIG. 103



Section of pancreas: *a*, alveolus; *b*, connective tissue; *c*, lobule; *d*, interlobular connective tissue; *e*, island of Langerhans. (Bates.)

FIG. 104



Functions of the pancreas. The arrows indicate the respective secretions of the organ, their origins and their destinations.

unknown substance secreted by the intestinal wall, the materials being these amido-acids. This synthesis may occur as the amido-bodies are absorbed through the protoplasm of the epithelium, or by other agency elsewhere. The theories of proteolysis have already been given in discussing the action of pepsin.

The action of the diastase (amylopsin) is not unlike that of ptyalin described above (page 188), but it is more vigorous, and it has the power of dissolving the cellulose covering of starch grains, thus allowing it to digest many uncooked vegetables and fruits more or less indigestible by saliva in its usual environment. It is doubtful if the diastatic amylopsin converts all the dextrin formed to maltose, this likely enough being in part a product of the synthesizing action of an enzyme in the absorptive mechanism of the gut-wall.

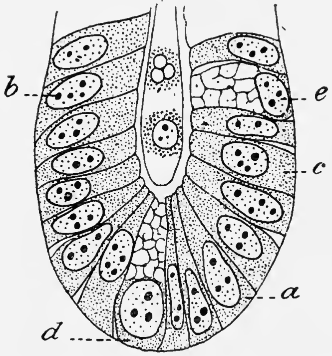
The action of pancreatic juice on fats by means of its lipase (steapsin) like some of its other functions, has probably a precedent in the stomach of perhaps much smaller importance. This enzyme is a very unstable one, and has not been isolated in even approximate purity. Loevenhart has recently claimed to have found evidence that lipase exists in all the tissues, especially in the liver, milk, blood, lymph, and intestinal juice, and he supposes that the tissue-fats (stearin, olein, and palmitin) are built up in the tissue-cells through its agency from free fatty acids circulating in the blood and lymph as soaps. In general, it has been presumed that the action of lipase was the usual one of hydrolysis followed immediately by cleavage into a glycerin and the fatty acid. Thus, in case of the triglyceride palmitin the reaction would be—

$$\underset{\text{Palmitin.}}{C_3H_5(OC_{15}H_{31}CO)_3} + \underset{\text{Water.}}{3H_2O} = \underset{\text{Palmitic acid.}}{3C_{15}H_{31}COOH} + \underset{\text{Glycerin.}}{C_3H_5(OH)_3}$$

the acid then uniting with potassium, sodium, or calcium either in the gut-wall or in the tissues to produce the corresponding soap. This in a nut-shell is the important process of *saponification* carried on by steapsin. In addition, the lipase indirectly *emulsifies* fats, this being a mechanical process (chemically performed by the fatty acids), while the other is a distinctly chemical process. The exact relation of these two processes has not even yet been well determined. Especially is it in doubt whether all the fat destined for food is saponified or whether some of it is emulsified only and directly absorbed. For the most part emulsification is probably due to the action of the fatty acids formed by saponification, so that very likely both processes go on side by side in the duodenum. In this process the bile, poured into the gut with the pancreatic juice, plays an important part. It probably aids saponification by means of its cholic acid. Furthermore, the action of lipase (steapsin) is at its best in the presence of bile plus hydrochloric acid, according to Rachford, so that the reagents on fat in the duodenum are very complex and the reactions correspondingly complicated. The actions of the supposed milk-curdling (rennin) and sugar-inverting enzymes (maltase, etc.) of the pancreatic external secretion need no special description; indeed, little that is definite and certain could be said about them.

INTESTINAL JUICE, or succus entericus, as it used to be called, is even less known than is pancreatic juice because it is secreted in very small quantity and becomes immediately mixed with the complex liquid compounded by the salivary glands, the stomach, the liver, and the pancreas. This juice is opalescent, straw-colored, strongly alkaline, with a specific gravity of about 1010, and contains much proteid, mucin, carbonate, and lactate. It is produced by the simple follicles, crypts of Lieberkühn of the small intestine, and perhaps in part also by Brunner's glands. The function of the intestinal juice appears to be to hydrolyze carbohydrates, to finish the hydrolysis of protein, and to invert sugars. It probably puts the finishing touches to the hydrolysis of carbohydrates preparatory to inverting them as they pass through the intestinal wall during absorption. As inverting enzymes, invertase (inverting saccharose to dextrose) and maltase (inverting maltose to dextrose) have been named. The proteolytic ferment present, according to Abderhalden, is erepsin.

FIG. 105



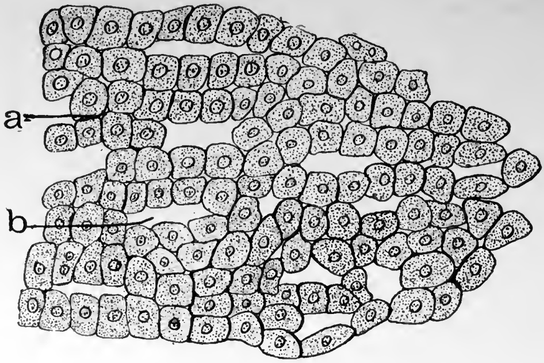
Section in the bottom end of a tubular gland of a dog's duodenum: *a*, *b*, *c*, "protoplasmic" cells; *d*, *e*, mucous cells. (Bizzozero.)

Whether the enzyme enterokinase, described by Bayliss and Starling as of such great importance for stimulating in union with secretin the pancreatic glands, is produced by the simple follicles or by Brunner's glands is undecided. Delezenne thinks it is secreted by the lymph-follicles, and Camus supposes that it is confined to the gut's lumen, while, on the other hand, the non-enzymic secretin may go directly into the blood-stream. In either event enterokinase would form a part of the intestinal juice, and in its supposed function of developing trypsinogen into trypsin would have considerable importance.

BILE has some proper influence on the intestinal digestion of fats as has been just suggested above, but the action, although perhaps important, is none too well understood.

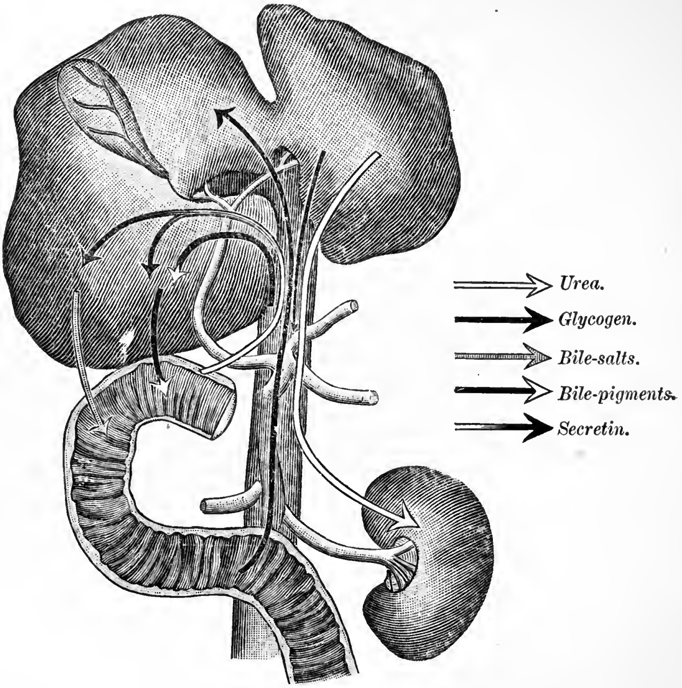
The Large Intestine.—The large intestine in structure is like the small intestine, but it is larger in diameter and shorter, being about 150 cm. long. The longitudinal muscular coat is much less complete than in the small intestine; in the rectum the circular coat is very thick. There

Fig. 106



Hepatic cell-cords: *a*, a cell; *b*, a lymph-space. (Bates.)

Fig. 107



Functions of the liver. The arrows indicate the respective secretions, internal and external, of this complex gland, their places of origin, and their destinations.

are no villi and no Brunner's glands, but the simple follicles (crypts of Lieberkühn) are both more numerous and larger than in the small intestine. Much mucus is secreted by the wall of this part of the intestine, but no enzymes have been isolated from its secretory product. The ileo-cecal valve guards the opening between the small and the large intestines. It consists of two folds of mucous membrane with muscular fibers, projecting into the large intestine. The mucosa of the rectum is thicker and more vascular than that of other parts of the gut. It has three or four large permanent folds of a semilunar shape. The lower portion of the rectum has two sphincters, made of tough bands of circular muscle-fibers, the former being supported by the levatores ani muscles. *The nerve-supply* of this part of the gut comes from two sources, from the upper lumbar roots (sympathetic), and from the lower mesenteric ganglion, the hypogastric plexus, the vagus, and the sacral

Fig. 108

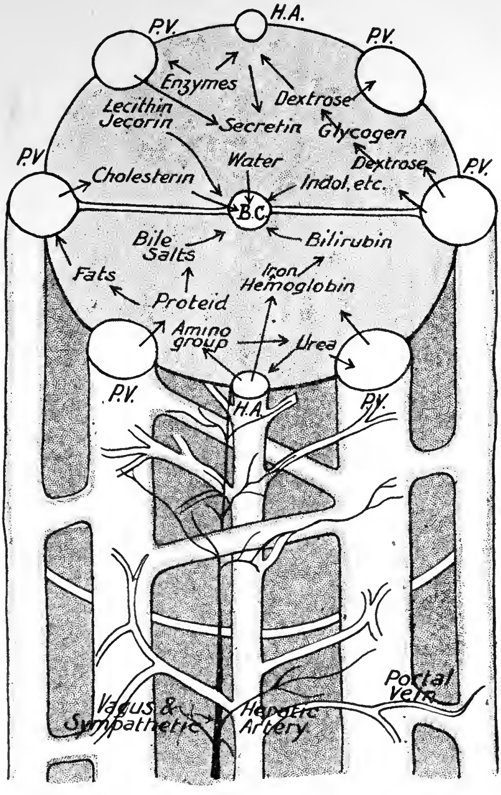
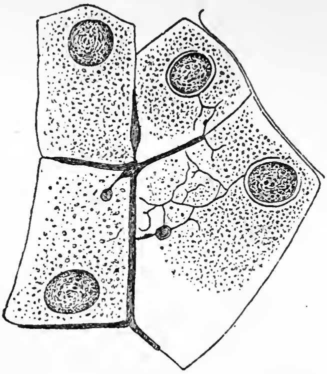


Diagram suggesting the functions of the liver. Parts of three hepatic cells are shown: *P.V.*, portal veins; *H.A.*, hepatic arteries; *B.C.*, bile capillary with its rootlets rising in the cytoplasm. The arrows suggest some of the relations and movements of the various substances.

roots. According to Fellner, the sacral nerves are motor for the rectal longitudinal muscle fibers, and inhibitory for the circular fibers, while the hypogastric influence is contractile for the circular fibers and relaxative to the longitudinal fibers (the so-called "crossed innervation"). Winkler claims that the hypogastric is the proper motor nerve of the whole large intestine. The vagus is probably both motor and inhibitory.

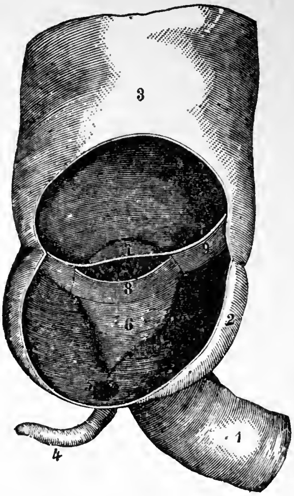
The movements of the large intestine are less complicated than are those of the small gut. According to Cannon, the chief movement of the descending colon is the very slow peristalsis produced by the progressive tonic contraction of the circular fibers. In the remainder of the large gut, in man the ascending and transverse colon and the cecum, the chief movement and themost common one is anti peristalsis.

Fig. 109



Cells of a frog's liver (injected with sodium sulphindigotate), to show how the bile-channels begin. (Kupffer.)

Fig. 110



The ileo-cecal valve as seen on cutting away a part of the cecum: 1, ileum; 2, cecum; 3, ascending colon; 4, vermiform appendix; 5, opening into the same; 6, inferior lip; 7, superior lip; 8, aperture of the valve; 9, its retinaculum. $^1/_2$. (Rauber.)

The result of this backward peristaltic movement is to keep the liquid chyle, coming continually into the colon from the ileum, a long time in the cecum and to prevent its being pushed onward into the rectum before absorption of its liquid has had time to take place. Each period of antiperistalsis (in the cat) lasts from two to eight minutes, and the periods recur at intervals of from ten to twenty minutes. Rhythmic pulsating or segmenting movements are of rare occurrence in the large gut of the cat, but were seen once or twice; tonic constrictions seem to occur at intervals along the colon when the latter is filled, and these tend to press the contents toward the rectum. Bayliss and Starling corroborate Cannon's observation that it is the distention of the colon with chyle that actuates the movements of the tube.

The *ileo-cecal valve* seems to be quite competent for preventing the backward passage of solid matters, that is, into the ileum, but it readily allows liquids to pass in this direction. It is possible then to inject nutrient enemata into the small intestine. Katz and Winkles find that stimulation of the vagus closes the valve, and that the splanchnics influence it to open; stimulation of the hypogastrics seemed to have no effect. (See Absorption, p. 216.)

Defecation is the process by which the useless residue of the chyle is periodically voided from the gut. In the human animal the process occurs usually once a day, most easily just after the first meal, the neural mechanism being then stimulated by the processes in the upper end of the alimentary canal. In many cases, however, defecation takes place twice daily, and in a much smaller proportion of persons only every other day. Defecation is a complicated reflex act voluntarily started and inhibitable at any stage. The outer, lower sphincter and the levatores ani muscles supporting the internal sphincter are made of cross-striated fibers. The internal sphincter and the strong circular fibers of the rectal wall and of the sigmoid flexure are of "unstriated" or smooth muscular tissue. It is probable, however, that the fibers of the external sphincter are made of neither typically skeletal nor smooth muscle, for they are unaffected by curare, and, as Goltz and Ewald have shown on dogs, destruction of the cord which causes atrophy of the skeletal muscles leaves the external sphincter unaffected.

The two sphincters are normally in a state of tonus dependent on their connection with the central nervous system, a tonus that is not destroyed by curare.

When defecation is to take place, the diaphragm is first made rigid in contraction, and the glottis is shut. The abdominal muscles then unite in forcible expiratory contraction, and, the perineal muscles and the sphincters being relaxed, feces are forced out of the sigmoid flexure (their habitual reservoir normally) into and through the rectum and out at the anus. Powerful contraction of the levatores ani serve, finally, to empty the lower end of the rectum between the two sphincters, which then at once recover their normal closure-tonus. The nerve-center coördinating the various movements of defecation is not as yet certainly known, although Frank-Hochwart has recently found much evidence that in dogs at least it is often to be demonstrated in the posterior end of the posterior central gyrus of the brain, in apes called "Sherrington's center." There are probably subsidiary centers in the lumbar cord or in the ganglia of the pelvis. Defecation is an excellent example of a process once wholly reflex (distention of the sigmoid flexure or irritation of upper end of rectum furnishing the afferent impulses), which has become more or less under the will's control in man and in some of the lower animals long associated with him. In infants and in most brutes the process is still wholly involuntary and largely reflex, as it is also in many conditions of nervous disease.

Digestion in the Large Intestine.—The chief function of the large intestine is undoubtedly absorption, especially of water, and as a reservoir for the ever-accumulating chyle. It is likely, however, that the uses of this part of the gut are more numerous than this, its hydrolysis of proteid, for example, being perhaps of consequence. It has long been known that in diseased conditions of the stomach, etc., a person may be kept alive a long time by enemata of, for example, a solution of the whites of eggs in water, and even when introduced in far too small amount to reach the ileum or jejunum. Berlatsky, working in Pawlow's laboratory, finds that the large intestine not only absorbs proteid, but that it digests it. Milk especially, he thinks, may be digested in this part of the intestine, the reaction there being regularly alkaline. Comparatively little research has been done on zymolysis in the colon.

Bacteria seem to have a part normally in digestive processes in the intestine, although their influence is possibly more helpful in absorption than in digestion proper. In the small intestine the bacteria are relatively few, but within a day after birth multitudes of them have developed in the colon and rectum, and they continue there through life. Their food is the various organic substances found in the feces (see page 252), especially the undigested bits of proteid and carbohydrate food and cellulose. The changes produced in the proteids by the bacteria are those of putrefaction; the end-products are the (odorous) substances indol, skatol, etc. The sugars and starches are promptly broken up, and cellulose with the liberation of methane (Moore), but in what manner is not well understood.

It is not obvious then what benefit the colonic bacteria are to their host, and it is possible that to be without them would be advantageous. Indeed, Arloing has shown that mucin and mucus are destructive of all microörganisms, even the most resistant if time enough be given. This then is probably the chief function of the mucus of the alimentary canal (especially abundant in the colon): to destroy the bacteria or some of them, or to lessen their activity. The well-known work of Nuttall and Thierfelder on guinea-pigs has shown that these young animals thrive for eight days after birth at least with no bacteria in them. Other researchers suppose, however, that this period is too short to be indicative, and that most animals at least do not grow to maturity without aid from the mysterious action of the bacteria in their intestines. Nevertheless, it is likely that there are many more bacteria in the colon than can be said to be normal. Those which are the most offensive decompose the proteids and produce thereby a large number of substances of an aromatic and almost alkaloidal nature. These are to a greater or less extent absorbed, and probably do harm, in ways little suspected as yet, before they are either decomposed or excreted bodily in the urine. Could the proteid food-fragments in the colon be lessened, much of this baterial growth would be checked. These fragments probably indicate the excessive ingestion of flesh-foods. Work by Fletcher and by Chittenden has shown a probable excess in meat-consumption by all but the poorest classes of society.

Could the amount eaten be reduced to the actual needs of tissue-repair (and in case of children, of tissue-growth), decided benefit might accrue to that large class of persons who take too little exercise and to that other large class whose nervous systems have become too unstable for normal "civilized" living. Persons of these sorts commonly suffer from intestinal atony, and the resulting too complete absorption of these putrefactive products may be the still unsuspected source of much disease.

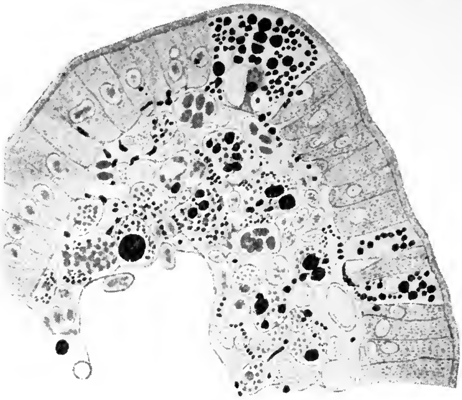
CHAPTER VI.

NUTRITION.

Having seen how the food is digested, we next naturally inquire as to the process by which the protoplasm of the organism is supplied with its nutritive material, and how and for what purposes this organized fuel is used by the body.

By nutrition we mean a complex of vital processes in part included under the term metabolism, but comprising also the two procedures, absorption and excretion. In this chapter then we shall take up the ultimate food-materials as they are left by the digestive juices of the gut and leave them only when they have been crudely traced through their changes in the body and excreted outside the organism again. These processes of nutrition in part form a link of this physiological chain—namely, that link which connects the digested food with the blood and tissues it supplies. So far as metabolism proper is concerned there are two sorts of processes, like two sides of an isosceles triangle (see Fig. 8), the apex of which between them is the normal composition of the blood and tissues. The up-going side is anabolism, constructive assimilation; the down-going side represents the katabolism, destructive dissimilation. Introductory to these two (metabolism) is absorption, while as a necessary consequence of them excretion must be considered. The former process introduces the nutriment actually into the blood and tissues;

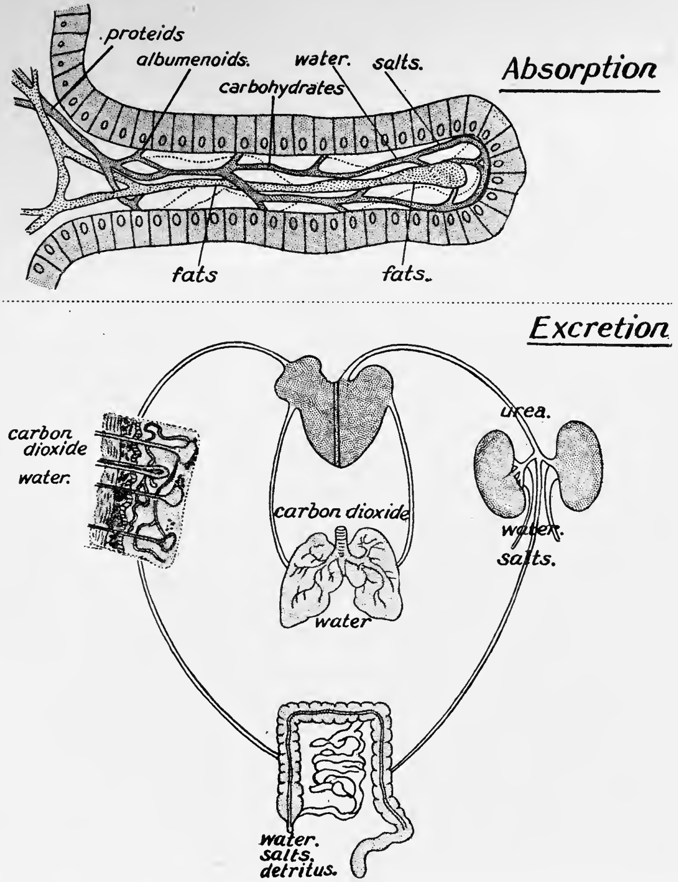
Fig. 111



The summit of the villus in the gut of a kitten, showing the absorption of fat by the various sorts of cells. (Heidenhain.)

while excretion, of necessity, removes the dead waste from these, lest it poison them. Nutrition then is more than metabolism, and constitutes a definite subject of great importance because at the basis of every vital process. Our discussions of protoplasm and of food are introductory to the descriptions of this chapter, yet do not infringe on its

Fig. 112



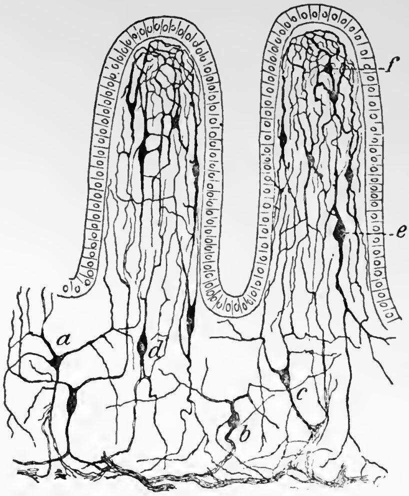
External nutrition. The upper picture suggests the places of absorption of the various proximate principles into the villus. The lower part of the figure indicates diagrammatically the various excretory organs and what chiefly passes out through each.

province of trying to explain how the food renews the ever-wasting body and supplies it with energy.

Nutrition, like respiration, is, for descriptive purposes, of two sorts, external and internal. External nutrition is that part of the total process by which, on the one hand, the blood receives its nutritious elements, and loses its excrementitious portions, on the other. The former enter it from the gut, while the latter leave it by way of the various excretory organs.

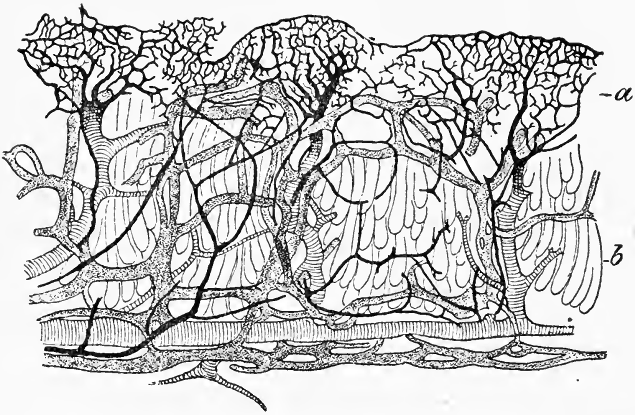
Internal nutrition is the portion of this general function that has to do with the passage of the blood's nutrients into the tissues and of the tissues' waste back into the blood. Both parts of each of these processes are indispensable to life. Of external nutrition the first process is absorption.

Fig. 113



The periglandular and the villous plexuses of nerves in the gut of the porpoise: *a*, *c*, *f*, triangular and stellate cells; *b*, *d*, *e*, fusiform cells. (Ramon y Cajal.)

Fig. 114

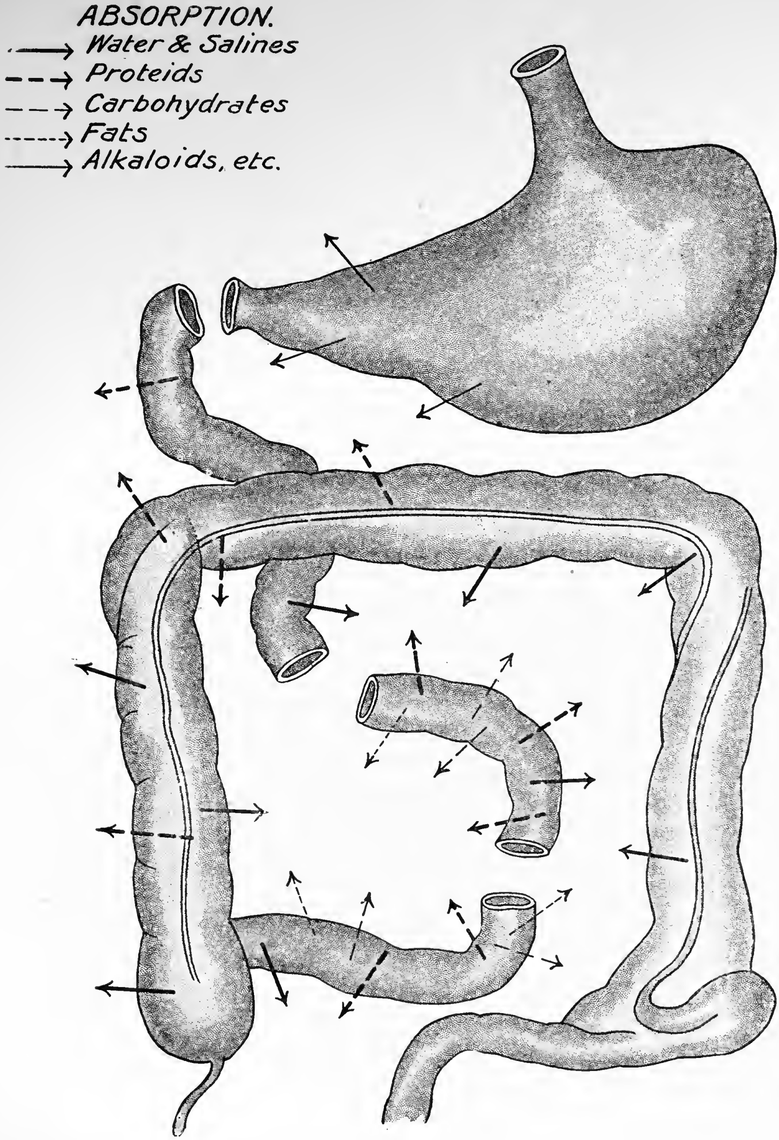


Section in the wall of the small gut of the eel-pout. The arteries are shown in black, the veins cross-striated, and the lymphatics granulated. (Melnikow.)

ABSORPTION.

Absorption is the process by which food is conveyed directly or indirectly into the circulating blood from the alimentary canal. From the mouth so little is absorbed that it may be disregarded as an absorbing organ. The small intestine is by far the most important site of absorption, the large intestine comes next, while the stomach is rated last in this respect.

Fig. 115



This diagram suggests in general the places where the various nutrient proximate principles are chiefly absorbed into the circulation.

Saline and other aqueous solutions are absorbed by the capillaries. The principles which underlie the absorption of these substances are doubtless those of the obscure physical chemistry of filtration, and especially of osmosis. The "selective power" of the epithelium plays an important part, but this selective power is probably only a matter of the complex physical aspects of chemism. While it is possible that the stomach absorbs some of the salines (as it does alkaloids and alcoholic extracts), both the small and large intestines are the chief sites of the absorption of these substances.

Fat is distinguished from all the other nutrient principles by being absorbed through the club-shaped lymphatics of the intestinal villi, and normally by no other route. It is likely that the lacteals of the jejunum and the ileum do most of this work. Much if not all of the fat absorbed is first split into fatty acids and glycerin, but these change back into neutral fat probably before leaving the epithelium of the gut on their way into the circulation. It is likely enough that the leukocytes of the villi have something to do with the transfer of fat-particles inward. During the digestion of a fatty meal the lymph of the great ducts may contain 15 or 20 per cent. of fat for hours. The capillaries also take up the fat-globules to some extent when the amount ingested is excessive. It has been supposed that the bile-salts assist in the absorption of the fat, but apparently they do so only indirectly through their emulsifying activities.

Carbohydrates are absorbed almost wholly as dextrose and levulose by the capillaries lining the intestines. Probably the intestinal epithelium changes the colloidal dextrin, cane-sugar, milk-sugar, and even starch to dextrose while they pass through it. Reach has shown that sugar is readily absorbed by the rectum, and this is a matter of some practical importance in therapeutics. Everything recently discovered goes to show that the intestinal epithelium is a very versatile tissue, acting by means of the potent enzymes as well as by those selective ("vital") powers afforded by its chemical and perhaps physical composition.

Protein and albuminoids (which may be discussed together so far as their absorption is concerned) also appear to be taken up wholly by the portal capillaries. In what exact chemical forms these complex substances enter the epithelium and in what shapes they leave it, is still under active discussion. The main question at issue discusses how far the food-proteids and albuminoids are broken down, and therefore as to the exact changes produced by the gut-epithelium before the proteins and albuminoids reach the circulation. The question cannot be exactly answered as yet. It is the capillaries of both the large and small intestines which absorb these substances.

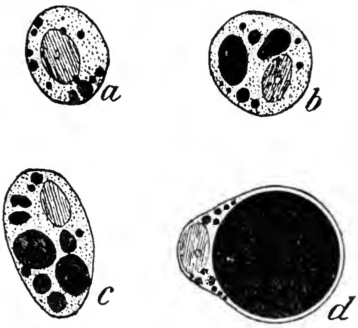
METABOLISM.

Metabolism consists of both the up-building process, anabolism, and the down-tearing process, katabolism. These terms apply especially to the chemical changes in the body-protoplasm rather than to food in the intestinal wall.

The anabolic processes of the organism are as yet too little known in their details to warrant even an attempt to describe them here. The reason for this lies in the fact that the chemistry of the anabolic processes is of unique complexity, besides being everywhere deeply hidden in the protoplasm of the intestinal walls or of the tissue-cells.

The katabolic processes of the body, in which the tissue-protoplasm is chemically simplified in its life-activities, are somewhat more accessible than the anabolic processes, and in consequence they have been better learned. In plants the opposite is true. The vital processes of the vegetable kingdom are essentially anabolic, while the phenomena of animal life depend on chemical reactions of a katabolic kind. It is by katabolism that an animal's body liberates the energy by which it lives. To be exact, life considered biologically *is* metabolism, especially in its katabolic phase.

Fig. 116



Fat cells from the subcutaneous connective tissue of an embryo calf of 45 cm. in length. In *a* the fat globules are few and small; in *b* some have coalesced; in *c* still more; while in *d* nearly the whole mass of the cell is fat. (Ranvier.)

Organic Growth and Repair in its histological aspects is not a subject germane to our present purpose, but it is necessary for completeness' sake to look briefly at the processes of anabolism in this respect. Until the adult stature is attained the body grows. Gaps made by wounds are filled in by new tissues, and lost blood, etc., are gradually regenerated. It is, of course, a prime characteristic of living matter to be, from use or degeneration, continually wasting, and this loss must be as continually replaced. These and the other wastes of animal tissue the food and the respiratory oxygen restore. As we have seen already in Chapter IV, only the proteids of food are capable of supplying adequately both tissue and energy to the animal organism, the other "proximate principles" having only special values in this direction. How then are the proteid anabolic processes conducted to this primary organic end of growth and repair?

Pflüger's hypothesis has much interest: "In the making of cell-substance, *i. e.*, of living proteid, out of the proteid of the food a change occurs in the latter, the nitrogen-atoms going into a relation with the carbon-atoms like that in cyanogen, with probably the absorption of much heat." This introduction of the cyanogen-radical into the vital molecule of the tissues introduces into it lively energy as motion, heat, etc., but also something which is of more immediate interest here—the power of spontaneously growing and of wasting. In a word, proteid anabolism means the power of spontaneous metabolism, of interchanging atoms or ions or lesser molecules (whichever it may be) within itself so that growth is possible. Conjectures as to the exact mode of this proteid-growth are well-nigh vain, so little do we know of the structure of the biomolecule or vital group, while of the proteid molecule itself we know but little more. One conjecture, however, seems reasonable—namely, that this protoplasmic unit or group (whatever in exact physical terms it may prove to be) increases in complexity by development and accretion up to a certain limit and then breaks up into daughter-units (each based on a cyanogen-root), which thereupon grow and split in turn. The developments which occur in this (protoplasmic) tissue-unit take place probably all through it and not on its periphery only. In other words, growth is real, inherent development and not mere accretion from without, for else the complexities of metabolism could not be accounted for (Hering). By some method the food that serves as the means of anabolism supplies particles of just the required composition, etc., to the tissue-units, and these thereupon grow and split up and so form a new particle of protoplasm. Finally, unknown multitudes of these biogenic particles become a tissue-cell, the morphological unit, with its organization of nucleoplasm and cytoplasm, familiar in every perfect cell.

It cannot be doubted that water, inorganic salts, fats, and carbohydrates take part simultaneously with proteid in the anabolic tissue-growth. It seems probable, however, that the fats and carbohydrates are not so intimately concerned in the formation of new protoplasmic units as are the proteid, the inorganic salts, and water. The proteid doubtless forms the core or basis of the unit, and either contains or carries the salts. The water is always inherent and basal in protoplasm. The fats and carbohydrates are perhaps related to this cyanogenic unit as necessary foodstuffs to lend it strength, thereby making its manifold metabolism and activity possible. Each sort of tissue-unit has the power of taking on from the lymph precisely those molecules of food which it needs, and each has the means of preventing the attachment of those it does not require. In this way it is self-perpetuating. At the same time, still more marvellously perhaps, every vital unit has the faculty of developing to meet those entirely novel requirements which new habits, new uses, and new environments are continually making essential in animal life. How else can we account for the molecular development of a scholar's brain, the cunning of the muscles of a human hand, or the adaptation to new needs of the organ of Corti in a musician's ear?

The remainder of this chapter deals with manifestations of metabolism more largely in its katabolic phase.

Secretion.—Between the process we have considered as growth and the other only less general phenomenon we shall now describe as secretion the differences are mainly arbitrary, but obviously with this exception: While in tissue-growth the new-formed substance becomes and remains for a time a part of the mother-tissue, in secretion the product must of necessity be removed with more or less promptness. In secretion, moreover, the product of the cell-metabolism is more unlike the secreting protoplasm than in the case of growth. The former process is more like manufacture, while the latter more resembles reproduction. A difference that is only apparent is that the product in growth is "solid" and in secretion usually liquid. Witness, however, the liquidity of the tissues generally and the solidity of the grains of glycogen in the liver-cells. So far as the metabolic changes occurring in the living unit are concerned, we can state no important differences between growth and secretion save that the former is largely anabolism and the latter mostly katabolism. As secretion is the chief function of all the epithelial and lymphoid tissue of the organism, it has an organ of its own, but growth is common to all the tissues.

Broadly speaking, however, secretion too is a function of all protoplasm, inasmuch as the process involves only the production of some material substance by an organic tissue. Thus, one sees amebæ (the individuals of which consist each of "only a drop of protoplasm") surrounding proteid food-particles, absorbing them intimately into the homogeneous colloidal matter of that part of the body that is by chance concerned, and then soon enclosing them by a food-vacuole filled with digestive juices secreted apparently from that part of the protoplasm that happens to be immediately about it.

It must not be imagined that even in man the tissues in general have lost their power of secretion. It appears, on the contrary, that every tissue produces certain particular enzymes that in part control its own special sort of metabolism. The substances needed widely or in large amounts or in certain organs are produced in special epithelia, but every true cell of the body seems to be the secretor of its own metabolic determinants, as ameba obviously is. The details of this matter, all new since knowledge of the internal secretions began to accumulate, are still unknown, and will largely remain so until at least the chemical nature of protoplasm is better learned. In this broad meaning of the term secretion there is included both absorption and excretion, and metabolism is evidently nearly its synonym.

Underlying all the secretory and absorptive functions of the body is the process which is known to physics as osmosis. The nature of this series of events must be somewhat understood as a basis for comprehending what goes on in the protoplasm of the general tissues.

Osmosis (from the Greek "pushing") is the passing or mixing of liquids through membranes immersed in them. Abbé Nollet first noticed the phenomenon in 1748. He observed that a bladder full of alcohol immersed in water soon became overdistended with the water that passed into it, the water pushing inward through the membrane faster than the alcohol moved outward. It has much more recently been shown by Pfeffer, working with plant-cells, that the pressure exerted by any solution whose molecules do not dissociate into ions is equal to the gaseous pressure which would be created by a like mass of the dissolved substance vaporized and confined in a space equal to that of the solution. As to how the dissolved salt exerts its pressure nothing is really known, although there are theories a-plenty. One observer supposes that the dissolved salt exists in the interstices between the molecules of the solvent in the state corresponding to a perfect gas, and hence that the stronger the solution the greater its pressure through a membrane toward a weaker solution. Another view (Poynting's) is that "the phenomenon known as osmotic pressure arises from the molecules of salt clinging to the molecules of water, and so diminishing the mobility and therefore the rate of diffusion of the latter," each molecule of salt completely impeding the movement of one molecule of water.

Ions, the parts into which the molecules of many crystalloids dissociate, act as regards the production of osmotic pressure just as would whole molecules. It is supposedly on this account that a solution of an inorganic acid or salt exerts more osmotic pressure than does an isotonic (equally pressing) solution of organic acids or salts, for many of the latter do not dissociate into ions. The solutions, then, whose molecules dissociate most will exert the greatest osmotic pressure. Moreover, as Arrhenius showed, when, for example, sodium chloride dissolves in water, some of its molecules dissociate into sodium ions and chlorine ions. The former are then bearers of positive "electrons" and the latter of negative "electrons." By means of these electrons the solution conducts electricity, and is called, therefore, an electrolyte. The greater the conductivity of an electrolyte the greater is its osmotic pressure. A solution of sodium chloride, therefore, injected into a mass of protoplasm that dissociates little tends to leave it, owing to its greater osmotic pressure, until a balance is found. It is on this principle, in part, that the tissues maintain their accustomed normal composition and perform some of their secretory functions.

Fig. 117

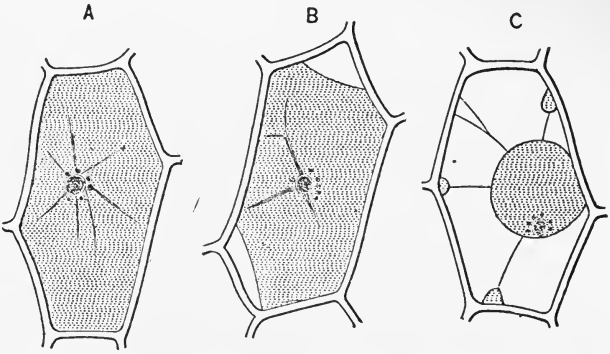


Diagram to show osmosis through the vital membranes (cells of the spiderwort, Tradescantia): *A*. When the cell is put in a dissociated solution (electrolyte) having the same pressure as that of the electrolytes of the cell biogen, no changes are apparent, and if in a less pressure solution the cellulose wall prevents the expansion which else would be obvious (more water passing in than electrolyte out). *B* and *C*. If immersed in a solution of stronger osmotic pressure, the opposite movement occurs and the biogen is retracted. (Jones.)

The reciprocal relation between dissociation, osmotic pressure, and the freezing-point of a solution presents a ready way of finding the osmotic pressure of any solution without testing it directly, and to determine its freezing-point is much simpler. The greater the dissociation, and so the more molecules a solution contains, the greater is its pressure and the lower its freezing-point. A gram-molecular solution is one containing as many grams dissolved as there are units in its molecular weight. Such a solution wherein no dissociation occurs has been found to lower the freezing-point 1.86° C. If, then, we find by means of an apparatus for the purpose how much lower than that of pure water is the freezing-point of the solution whose osmotic pressure is desired, we need only to divide the fraction of a degree of the lowering (expressed $\underline{\triangle}$) by the constant 1.86 to have the desired percentage of the lowering of the osmotic pressure. A gram-molecular solution of a non-electrolyte (no dissociation) exerts a pressure of 22+ atmospheres, and the percentage of lowering of the pressure found multiplied by this number gives the osmotic pressure desired in atmospheres. The pressure is proportionate to the concentration, a 2 per cent. solution of an electrolyte pressing twice as much as a 1 per cent. solution of the same substance.

By the freezing-point method we may, then, determine not only the osmotic pressure of any solution, whether an electrolyte or not, but also the degree of its electrolytic dissociation in case the solution be an electrolyte. This latter datum seems often to be of essential importance as regards the effects of saline electrolytes on protoplasm.

One of the most surprising things to the student of these matters at first is the great pressures exerted by solutions of this sort. Osmosis is clearly one of the great forces of organic nature, and it acts everywhere in plants and animals, and yet so quietly as to remain unsuspected save in its effects until the refinements of modern physical chemistry made it manifest.

"VITALISM."—This term is sometimes useful in biological discussions, but its meaning nowadays is much less significant than it was fifty years ago when the principles of physics and of chemistry had not as yet been applied to living processes. Indeed, the term vitalism then implied distinctly that organic reactions (absorption, secretion, etc.) were characteristic and unique, and essentially different in kind from those outside of living protoplasm. Today we know or at least think we know in what ways the vital processes are characteristic and different—namely, in their subtlety, complexity, and intricacy of interaction, and so far as we know only in these ways. Vitalism, then, today means only the sum total of the chemiphysical reactions of vital matter. Whether these will be known in detail sometime cannot be foretold. The important thing is that their nature is such that they might be known in detail were our methods refined enough, when without a doubt they would be found to be in kind like the rest of Nature.

THE PHENOMENA OF SECRETION are the secretory events so far as study of secreting and absorbing epithelia reveals them to us through the microscope or by chemical analysis. Obviously the active production of a new substance by the protoplasm of a secreting cell necessitates some degree of loss in that protoplasm, for the time being at least. On the basis of the degree of this destruction of the epithelial substance we may distinguish three types of secretion proper: In the first, the most common, the protoplasm is not obviously lessened, the preliminary product (zymogen) appearing as granules, etc., within the cell-body. In the second type the upper part of the cell-body becomes in a mass the secretory product; of this, milk-secretion is the best example. In the third sort of secretion the whole cell-body passes off as the product; mucous secretion is the type of this, and sebum the other chief instance. As hinted above, many substances are given out by epithelium that do not appear to view at all. These pass out of the protoplasm by osmosis or diffusion, and are crystalloids, gases, or, rarely perhaps liquids. About these invisible secretory phenomena, purely metabolic in nature, little is known as yet. The secretion-products with which we are now

Fig. 118

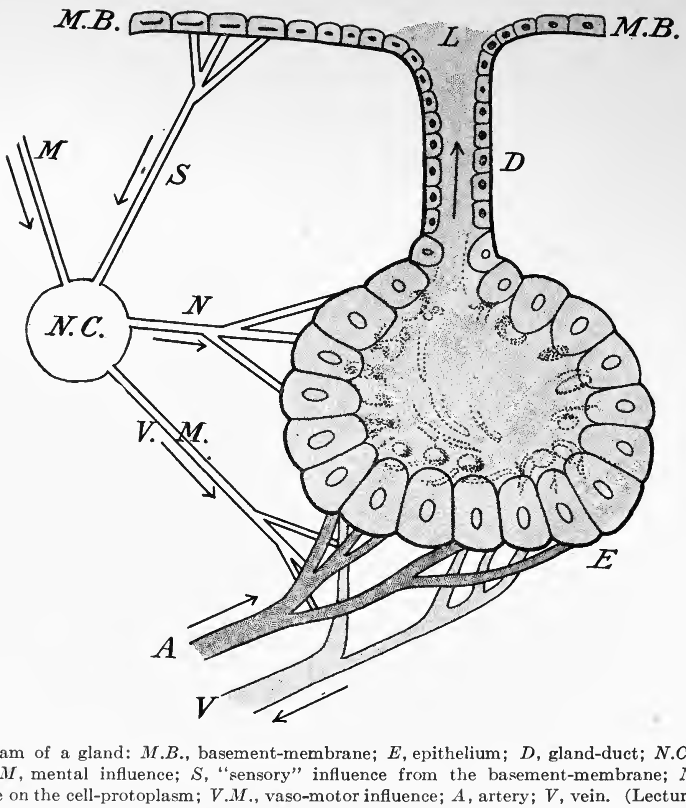
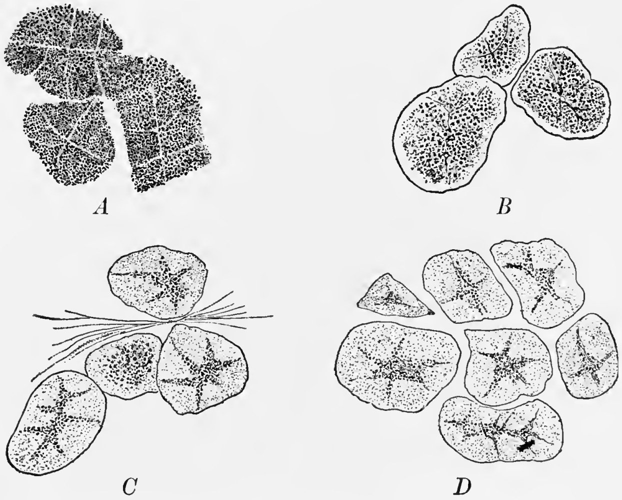


Diagram of a gland: *M.B.*, basement-membrane; *E*, epithelium; *D*, gland-duct; *N.C.*, nerve-center; *M*, mental influence; *S*, "sensory" influence from the basement-membrane; *N*, direct influence on the cell-protoplasm; *V.M.*, vaso-motor influence; *A*, artery; *V*, vein. (Lecture-chart.)

concerned, then, are for the most part colloids, which do not readily osmose. They therefore do not make their way out of the cell as fast as formed, like the others, but collect in the cytoplasm, and either osmose out of it slowly or pass off bodily in a mass. Among these substances are proteids, fats, glycogen, mucin, and numerous other products of anabolism, even less known than these, such as enzymes, pigments, and "extractives" of many sorts and uses. Many of these products probably have molecules so large and unstable (because complicated and loosely composed within) that they are broken up into parts before passing out of the cell. This is the case particularly with the granules which are conspicuous in secretory processes of the first type (*e. g.*, in salivary, pancreatic, hepatic cells). In case of mucus, not diffusible through membranes, the cell gives way bodily and allows the product to escape freely into the lumen of the gland.

Fig. 119

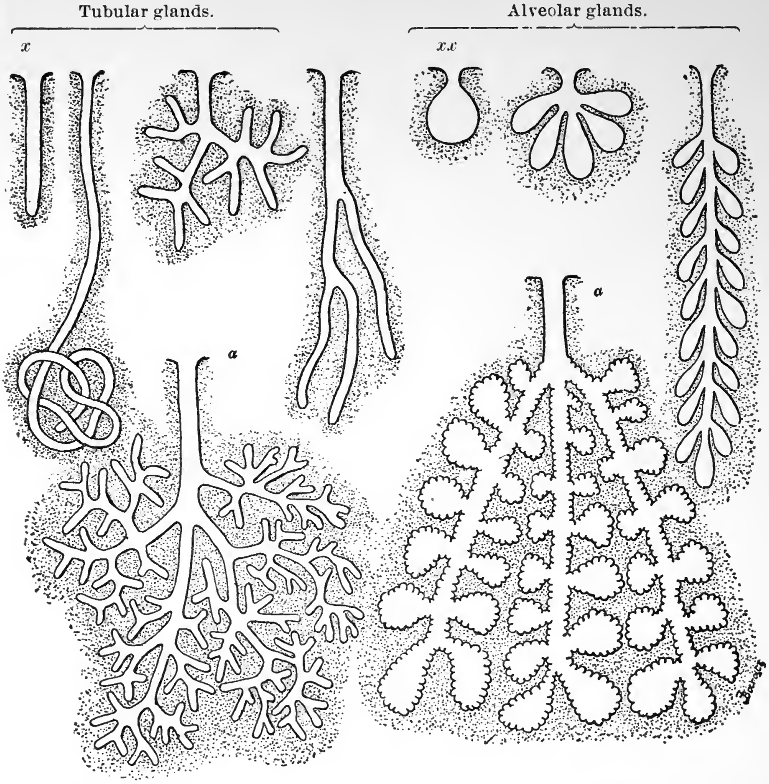


Secreting epithelium (parotid of a rabbit), to show the process, so far as to be seen under the microscope: *A*, resting, *B*, after action occasioned by pilocarpine; *C*, after more vigorous action occasioned by both pilocarpine and stimulation of the sympathetic; *D*, after long-continued action from stimulation of the sympathetic. (Langley.)

The internal secretions are poured into the blood instead of into the gut or on the skin. Among those of chief importance so far discovered are those produced by the pancreas, the duodenum, the liver, the thyroid, the thymus, the pituitary body, the adrenals, the kidneys, the spleen, the testes, and the ovaries. In addition to these, the coccygeals and the carotids produce internal secretions of unknown value, while all the lymphoid tissues secrete lymph. We can here mention only in a most summary way the uses of these various products secreted into the circulation. Little is as yet learned about them probably compared with what some day will be known.

It is generally supposed that the internal secretion of the "islands of Langerhans" of the *pancreas* has control over the oxidation or other destructive metabolism of the dextrose of the blood and tissues. Schültze finds evidence in addition that this product, like that of the pituitary body, regulates the blood-pressure of the vessels. The internal secretions of the *duodenum* have been already discussed in the chapter on Digestion. Among these are secretin and kinase (entero-kinase). Some claim that secretin is the product of all the tissues in the body as well as of the duodenal wall. The internal secretions of the *liver* are glycogen and an enzyme, sometimes called urease, which has the power of forming urea from some of the decomposition-products of proteid. Schäfer suggests that perhaps by means of an internal secretion the liver saves the iron from the breaking down red blood-corpuscles which otherwise would be lost to the body. The *thyroid,* either by means of a peculiar substance called colloid which collects in the alveoli (and is absorbed by the lymph), or by less obvious products which pass

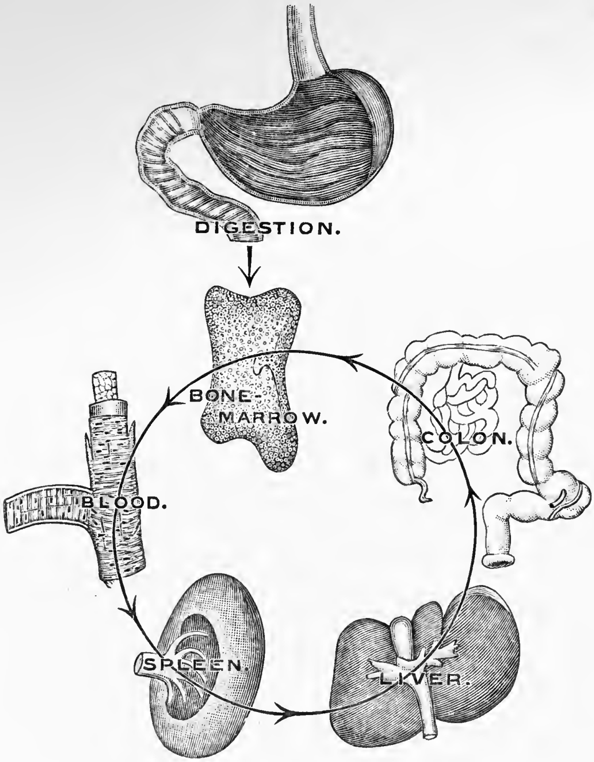
Fig. 120



A diagram of various typical forms of glands: *a*, duct; *x*, simple tubule; *xx*, simple alveolus. (Szymonowicz and MacCallum.)

it directly into the blood, or by both of these, exerts some essential influence over the processes of metabolism. Removal of the organ early in life creates the condition of peculiar idiocy known as cretinism. Extensive disease of this organ in adult years gives rise to a set of similar symptoms called myxedema. The symptoms of this disease may apparently be attributed to the disturbance in the nutrition of the nervous system and of the connective tissue. Kirshi's work indicated that the para-thyroids are embryonal tissue present in the body to serve as substitutes in case the thyroids are diseased. Injection of the extract of the thyroids of animals or even the successful implantation of their living thyroids into the abdominal cavity often cures these conditions of cretinism and myxedema.

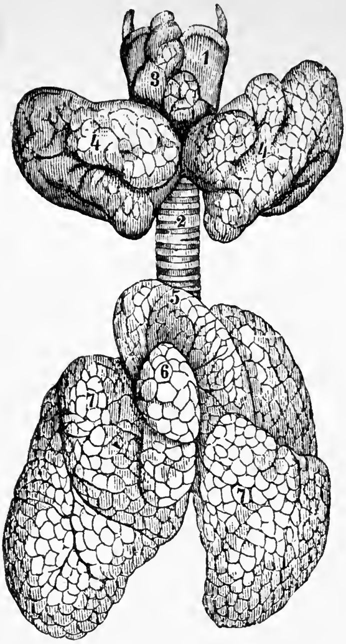
Fig. 121



The circulation of iron. It is possible at least that by some such route as this the iron liberated continually from the wearing-out erythrocytes is saved to the organism for re-use. Ingested in the food, it passes into the bone-marrow, is used as part of the hemoglobin in the circulation, is saved by the spleen, made into bile-pigments in the liver, absorbed by the colon, and then made over into hemoglobin.

The internal secretion of the *thymus*, which is especially prominent in the fetus and in childhood, appears to have something to do with fitting out the leukocytes for their numerous functions. It has been suggested that this organ in the fetus is the mother-tissue of all the lymphoid tissue of the adult. The *pituitary*, sometimes called the hypophysis cerebri, is a vascular mass situated at the base of the brain, and weighs only one-half gram. According to Schäfer and Vincent, extract of the pituitary body causes a rise or fall in the blood pressure, an effect which is probably brought about through the vagus. Its removal by disease or mechanically causes sometimes death and sometimes the symptoms of acromegaly, a condition characterized by the aberrant overgrowth of the bones of the face, skin, and extremities. The extract of the pituitary body is said to be thirty times stronger than that of the adrenals. The *adrenals*, formerly called the supra-renal capsules, secrete into the circulation a substance which when injected into a vein causes a powerful vaso-constriction in the arterioles and corresponding changes in the heart itself. Less than eight hundred-thousandths of a gram (0.00008 gm.) of adrenalin chloride are sufficient to affect the blood-vessels and heart of a man for a short time. Vincent has shown that the adrenals contain two sorts of glands, those of the rind and those of the interior. Of the function of the former nothing is known. The others are apparently concerned in maintaining the tone of the musculature, perhaps by controlling the oxidation of the tissues. The *kidneys* appear to have as their contribution to the agents of tissue-metabolism a proteolytic enzyme which when carried to the liver and perhaps to all the tissues of the body leads to the production of urea. The internal secretion of the *spleen* has been assigned many functions. All of these are complicated, but none of them are at all established, and we need not even mention them at this time. The *testes* and the *ovaries* apparently have substances secreted by their epithelium which have a tonic influence over the nervous system, especially in relation with the muscles. Injections of the extracts of these two organs increases nervous vigor and muscular tone, and semen exerts somewhat similar effects.

Fig. 122

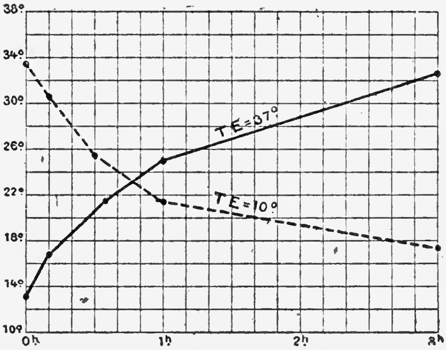


The thyroid and the inner thymus of a newborn child: 1, larynx; 2, trachea; 3, medial lobe; 4, lateral lobe; 5, apex of the thyroid; 6, medial lobe; 7, lateral lobe of the thymus. Natural size. (Rauber.)

Animal Heat.—The third of the manifestations of the general metabolism which we shall specify is animal- or body-heat. It is a process so largely derived from katabolic changes that we place it in that category.

In respect to their maintenance of bodily warmth, animals are divided into two classes, homotherms and poikilotherms, these terms corresponding to the older designations "warm-blooded" and "cold-blooded" animals, respectively. These phrases are scientifically misleading, for a so-called cold-blooded animal may in summer, even in the temperate zone, have a higher temperature than a "warm-blooded" animal in the same place. The terms homothermal and poikilothermal, on the contrary, well represent the physiological conditions. The former in the Greek means "of the same temperature," and indicates that such animals—namely, birds and mammals—maintain their heat at a relatively constant degree despite changing conditions, sometimes internal as well as external, The term poikilothermal means "of a varied temperature," thus implying that the temperature of such animals is not constant but variable (with the environment). As is usually the case in Nature, the dividing line between the two classes is not absolute, for several animals on the lower margin of mammalia, so to say, are only imperfect homotherms, while a number of other mammals become poikilotherms during their periods of hibernation. On the other hand, one or two of the reptiles, *e. g.*, the python, maintains its temperature 10° or 15° above that of the surrounding air, showing a tendency to homothermy. In general, however, the division practically holds that all animals save birds and mammals are poikilothermous. The difference of these two sorts of animals is sufficiently striking. Frogs, for example, are sometimes received in the laboratories in winter with their abdominal fluids obviously frozen, yet placed in tepid water for a few minutes the animals are as lively as ever. Six months later one of the same frogs might have a temperature

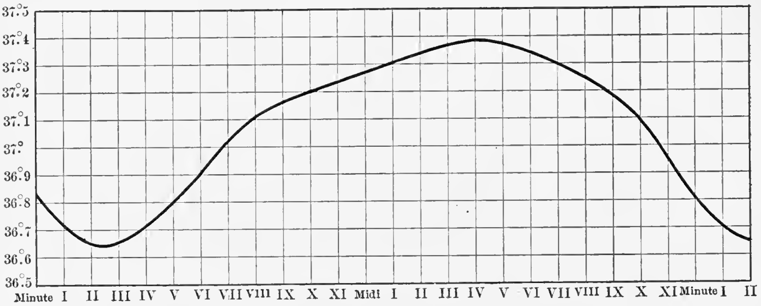
Fig. 123



The variation of a poikilotherm temperature with that of its environment (tortoise). With an initial temperature of 13°, placed in a temperature of 37°, in three hours there was a rise to nearly 33°. With an initial temperature of 33.5°, placed suddenly in environment at 10°, its temperature in three hours had fallen to about 17.5° (broken-line curve). (Richet.)

warmer by 35° C. Contrast with this the conditions in mammals. Many healthy persons, for example, go through life with a temperature-variation of less than 2° C., while we may be sure that the heat-range of the average individual is not over 4°, say from 36° to 40° C. (96.8° to 104° F.). (Unless otherwise stated, all temperatures in this book are in the Celsius (centigrade) scale.) Parry and Lyon observed that the temperature of an Arctic fox in a temperature of —35.6° was 38.3°, while Davy found the temperature of a trout in water at 4.4° to be 5.6°. Thus the temperature-range of the "cold-blooded" animal averages nearly ten times that of the warm-blooded bird or mammal. The reasons for this difference are mainly two: poikilotherms have a much less active metabolism than have homotherms, and they have no elaborate mechanism for maintaining a constant temperature such as is found in birds and mammals. Both this katabolism and this mechanism will be found described in their proper places.

Fig. 124



Hourly variation in the internal human temperature as given by Forel. On the left are the degrees of the Celsius scale, and at the bottom the hours of the day, beginning at midnight. The extreme variation is nearly 0.8° C.

Human Temperature is of much clinical importance, because it indicates better than any other one thing many conditions of illness and their progress, and no other artificial instrument is so indispensable to the physician as his clinical thermometer. As is the case with all biological data, average temperature or mean temperature is more or less misleading, for each patient is a unique individual, varying more or less from every average; none the less, averages and means have use. It is customary, therefore, to speak of the normal human temperature as about 37.1° (98.8° F. nearly). This is a few tenths of a degree too high for men and a few tenths too low for women, especially for female children. In the axilla, too, it is slightly less than this, and in the rectum or vagina or stream of urine nearly 1° more. Other normal causes of variation act on the principle that the more intense the body's metabolism the higher is the degree of heat produced. Thus, the temperature is somewhat higher after meals, in the day than in the night, at sunset than at sunrise, during muscular or mental or glandular work, in very young persons, and in small individuals, these conditions being examples of especially active katabolism. The normal diurnal variation, say between 5 A.M. and 5 P.M., is nearly 1°, in young children and nervous women often more—a fact often forgotten by physicians. The extreme range compatible with life is large. Reincke reported a rectal temperature of 24° in a drunkard exposed to cold and water, and he survived. Most of the persons who "freeze to death" are victims of alcohol rather than of cold. Teale saw an hysterical woman with a temperature of 50°, and Donkin recorded 44.2°, 44.5°, and 45°, recovery taking place; Richet collected degrees of heat, not fatal, even as high as 46°. But a temperature of 41.5° (106.7° F.) or even 41° continued for several hours in an adult is very dangerous. Halliburton has recently isolated from neural tissue a cell-globulin which coagulates at from 45° to 50°C. This is especially abundant in the nervous gray-matter, but probably occurs in most, if not in all, cells.

FIG. 125

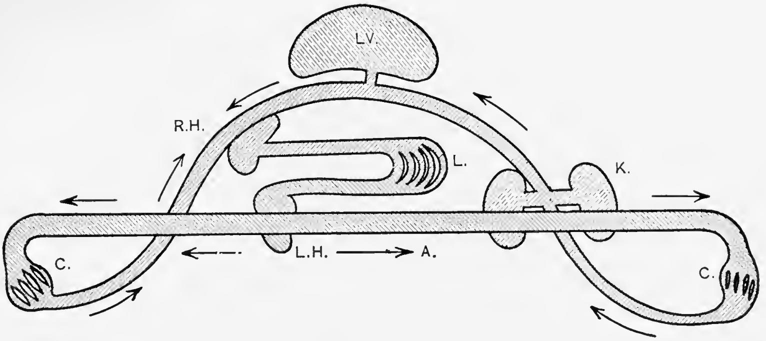


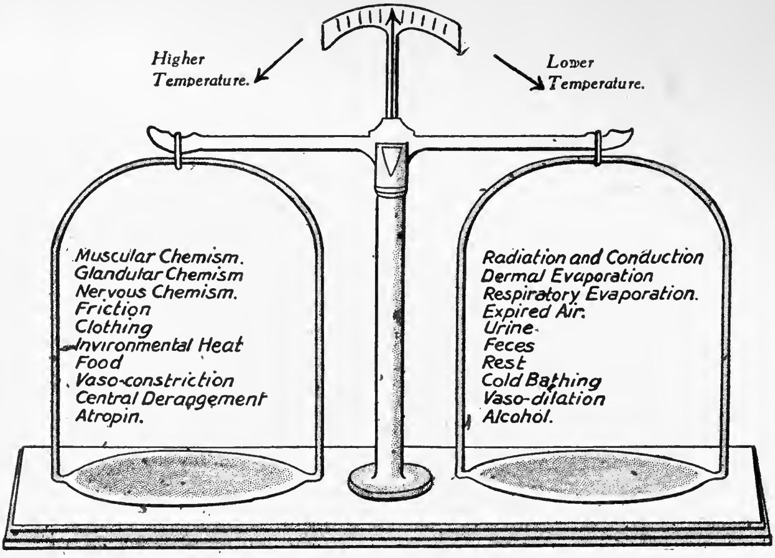
Diagram of the relative temperatures of the blood in various parts of the human body. The liver's temperature is highest and that of the systemic veinlets the lowest. (Langlois.)

A temperature of 47° leads to an instantaneous disappearance of the chromatophile granules of the nerve-cells, but 44° also brings this about after two hours. He supposes that the coagulation of this globulin, therefore, is the cause of death when the body-temperature stays at this point or passes much beyond it, that is, about 110° F. Insolation (sun-stroke), scarlet fever, influenza, and meningitis are perhaps the commonest causes of very high temperatures.

Depression of the degree of heat below the mean is comparatively infrequent. To the extent of 0.5° or so, however, it is not uncommon, the most frequent causes being alcohol and exposure to cold water. The temperature of animals other than man we need not consider here. In general those of poikilotherms are 1° or 2° above their environments, while those of homotherms range near that of man, usually within 1° or 2°, those of birds being especially high. The phenomena of hibernation will be considered later.

Thermotaxis.—The heat and other energy of the animal body are produced very largely by two sorts of processes. One of these is chemical—namely, metabolism (chemism), the other mechanical, friction. Besides these two and the heat afforded from without by warm air, water, and food, there are theoretically three other possible nutritional sources. These three are the condensation of air in the lungs, the liquefaction of gases, and the solidification of liquids. These produce so small an amount of body heat that they may be entirely neglected. Reichert estimates that of the two most important means of heating the body, the chemism provides about 90 per cent. of heat, and the friction only about 10 per cent.

Fig. 126

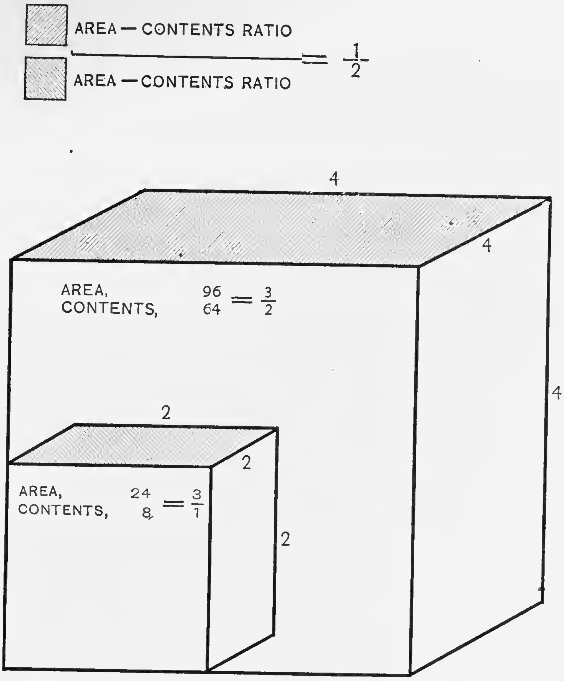


Human thermotaxis. The processes and conditions on the left hand make for greater heat-production or heat-conservation, while those on the right exert their influences toward less heat-production or for heat-loss.

Sources of heat from movement are the circulation, the lively and forcible churning of food-masses in the small intestine and by the antiperistalsis in the colon and rectum, the torsion of the costal cartilages in inspiration, and the rush of air up and down the bronchi and trachea. Everywhere, in short, that one bit of tissue or of liquid moves against another, heat from friction is liberated, and movement, both molar and molecular, is universal in the organism. All these many varied movements combined, however, furnish to the body only a small fraction of its internally derived heat (Fig. 126).

The means by which heat and energy are lost or expended in the body may be mentioned under seven heads, the most important coming first in the list: Radiation and conduction from the body; evaporation of water from the skin; evaporation of water from the nasal passages and the lungs; expiration of the warmed air; excretion of the warm urine and of the warm feces. Of these, radiation and conduction account for about 73 per cent. of the heat lost. In other words, about three-quarters of the heat made in the body is lost by warming its surroundings, air, water, bedclothes, clothing, chairs, etc. Evaporation from the skin loses probably about 15 per cent. of the total quantity of heat. Evaporation from the nasal passages and lungs expends not far from 7 per cent. of the total heat lost, while about 3 per cent. goes off in the expired air.

Fig. 127

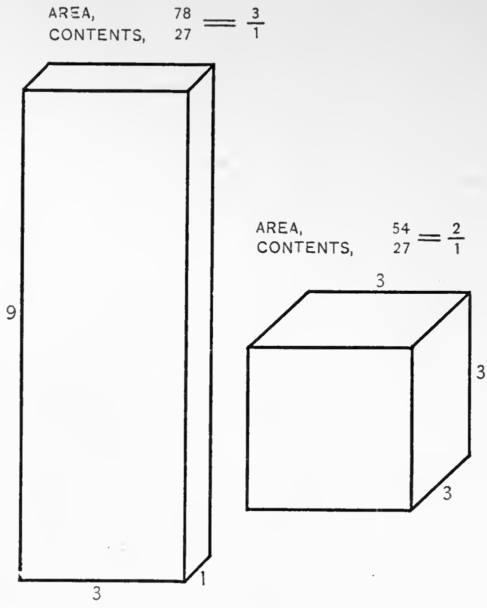


This diagram shows that in two animals of like shape the smaller may have twice as much surface-area (heat-loss) in proportion to its contents (heat-production) as the larger.

The term Thermotaxis, the regulation of body-heat, meaning literally "heat-arrangement," has already been met with in the chapter on Protoplasm (see page 43), and there indicates the reaction to heat of the entire body at once in case of certain small and simple organisms. As applied to man, etc., its meaning is somewhat different in that it indicates adjustment of parts of the organism to special thermic conditions. The arrangements in the human body by which these adjustments are brought about constitute one of the most elaborate mechanisms of the organism. By its means the temperature is kept constant despite the obvious wide variations in climate, food, dress, labor, etc.

There are two modes of regulating the amount and degree of heat in a homothermous animal—changing the production and altering the outgo of the heat. Since the actual temperature at any time throughout the body is the *balance* of these two phases, regulation consists in alteration of either or of both in the way circumstances at the time require. In practice both of these opposed processes are always in action at the same time. When the temperature tends to become too high, for example, not only is thermogenesis (heat-making) checked in one of various ways, but thermolysis (heat-loss) is increased. When body-heat trends unduly downward, the two processes work in just the opposite ways. In this way the balance is kept so perfectly that in health the temperature of the human body varies less than 2° from the adult mean of about 37°. One sees the immediate working of thermotaxis in the involuntary shivering which often ensues on exposure to cold, and Löwy has shown that this marked increase of rhythmic muscular contraction may even double the body's heat-producing metabolism. Another immediate proof of the presence of such a function in the body is seen in cold bathing, which, in a normally reacting organism raises the temperature. Again, one's appetite is normally somewhat less in a hot day of summer than on a cold winter day, metabolism and heat-production being thereby lessened. The arrangements for controlling body-heat consists, in

Fig. 128



This diagram shows that animal bodies of the same volume and mass (heat-production) may greatly differ in surface-area (heat-loss).

general terms, of various nerve-centers under the supreme dictation of one chief center, and of tissues and organs all over the body so coördinated that they bring about the result required. In infants (and in poikilotherms) the apparatus is not well developed.

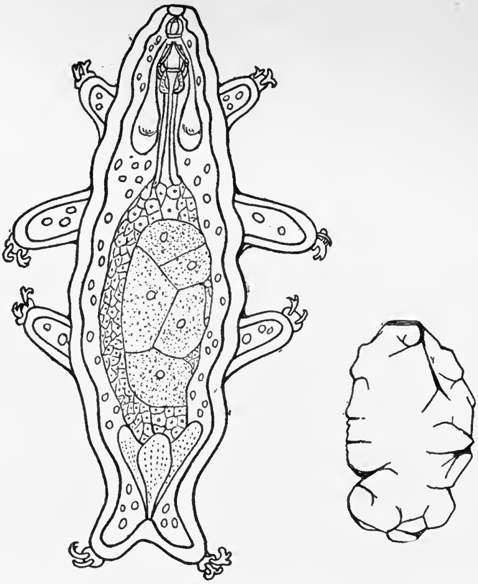
We can make the working of the heat-regulating mechanism clearer if we discuss its two phases (the control of heat-production and that of heat-expense) separately.

THE MEANS OF REGULATING HEAT-PRODUCTION are chiefly the increasing or decreasing of metabolism and of muscular activity; only in indirect ways can glandular activity be varied. In man these means are partly voluntary, although the "sensations" underlying the voluntary acts required are purely physiological. In cold weather animals "naturally," as we say, eat somewhat more food than on warm days. Moreover, the human appetite then tends to demand foods which are large producers of heat and energy—in winter beefsteak and potatoes and bacon and hot rich soups; in summer, on the other hand, salads, ices, fruits, and "plain living." These same tendencies are seen in whole racial diets. We find the dwellers of the far North eating much fat (combustion-equivalent, 9.3), while those of the Tropics live on fruits and cereals containing much liquid and waste cellulose. It is only from habit that perhaps most people eat nearly as much in warm weather as in cold, for the actual body-demand is much less. It is part of the heat-regulating arrangements (but how brought about is unknown), that fats are actually distasteful on a very warm day.

Besides tending to limit the general metabolism by thus decreasing its fuel, the organism automatically inclines to lessen that large percentage of heat and energy which the muscles give out. Exertion tends to be irksome in warm weather, partly it is true because the abundant sweat so occasioned is a source of much discomfort, but also because muscular exertion is unnatural in great heat and rest not only strongly desired but also based in physiological conditions which only the will can overcome. The same is true, but to a less extent, perhaps, in regard to mental labor, although the nervous system as compared with the muscles produces but little heat. Muscular contractions, however, always tend to be proportionate to mental activity. Sleep, as we shall see, tends to increase heat-loss as well as to limit heat-production, and there is a natural tendency to sleep when the temperature is high.

In the opposite direction corresponding influences are at work. These increase heat-production in cold surroundings or when heat-loss (thermolysis) is excessive. Under such circumstances one eats more and "heavier" food and takes less liquid than in the opposite condition of environment. Observing the diet of lumbermen in the northern woods in winter, one is almost surprised at the large amounts of bread, butter, baked-beans, bacon, salt-pork, and very hot tea that are consumed, and these diets often reach 6000 calories. Severe muscular exertion, cold, and wet combine to make the demand for fuel apparently excessive, the last two increasing the loss of heat to a high proportion, while the muscular labor keeps up the heat-production, and by urging a rapid flow of lymph all over the body, sustains the metabolic furnace at its limit of vigorous action. Contrast physiologically with these conditions those of the city business-man who rides from his home to his office in heated vehicles, takes no exercise, worries more or less, and who has in consequence a poor digestion. This man has no need of increasing heat-production by eating much, for his metabolic fire, low and dull as it is, supplies all needs. But physiologically speaking these are two distinct planes of living, if perfect metabolism be a just criterion. It is easy to increase heat-production, much easier than to lessen it, for the combustion in the tissues cannot be checked. If fuel, therefore, be not supplied them from without, they will consume themselves. As is well known, a rise of temperature usually increases chemical action, so that

Fig. 129



The common so-called bear-animalcule (Macrobiotus Hufelandi), a tartigrade, in its active and in its dried (hibernating) states. (Greef and Plate.) As seen under the microscope in the latter condition it is not to be distinguished from a speck of quartz. In this state the animal will remain months or even years, yet on addition of water, it will within an hour or two oftentimes resume its complex animal activities. This, then, is the extreme protoplasmic type of hibernation common to bears, hedgehogs, bats, gophers, woodchucks, etc., and voluntarily attained for purposes of gain by certain human fakirs of India. Eating no food, the temperature falls from 5° to 13° C., the heart slows and weakens its beat, respiration is greatly lessened, and the whole metabolism is reduced to a minimum. For the two to six months that hibernation lasts, the homotherm becomes practically a poikilotherm. In the case of mammals, actual drying of the protoplasm does not, of course, occur, but in both alike the two vital physical principles, heat and moisture, are lessened. These are the conditions of movement, and movement in turn is the physical basis of life. The bear of the forests and the bear-animalcule of the eaves-troughs of our houses alike, then, lower their metabolism for purposes of self-preservation during inevitable long periods of severe environmental stress which else would kill them.

if the body's heat increases from any cause whatever, metabolism is heightened. In addition to these modes of increasing heat-production there is apparently, in small animals in particular, an influence exerted by the nervous system directly on the heat-forming tissues. This acts especially on the muscles, and causes them to increase the body-temperature without actual (visible) contraction. This has been called "chemic tone," and in case of muscle differs little from muscular tone (see below, page 390), but when effected in other tissues, directly increasing metabolism, it is doubtless a portion of that little-understood system of trophic influences (see page 56). Various drugs, finally, increase metabolic heat, these being largely those like strychnine, *e. g.*, which increase muscular tone or muscular activity of a more obvious sort.

Muscular movements are instinctively employed by all animals, homotherms at least, for increasing their temperature. If one compares, for example, in this respect the people on the pavements in winter and in summer, the difference in their muscular activities is obvious. Shivering is a reflex action with considerable thermogenic powers.

The regulation of heat-loss is probably a more active function than is the control of thermogenesis. It is largely performed by means of vaso-motion (enlargement and narrowing of the arterioles) in connection with the secretion of sweat, both being under the direction of the nervous system. (See page 300.)

When the body-temperature tends to become unduly low from any cause, impulses are sent out from the medulla's vaso-constrictor centers to the arterioles and capillaries of the skin all over the body, and these thereupon become smaller in diameter. This drives much of the blood then on the surface into the body's interior. As will be recalled, about 88 per cent. of the total heat lost is expended from the skin, the amount depending on the quantity of warm blood the surface contains. By this peripheral vaso-constriction radiation and conduction are lessened as well as the production of "insensible" sweat, by whose evaporation much heat is lost. It is by a too sudden and too vigorous action of this vaso-constrictor mechanism that congestions of the nasal mucosa, lungs, kidneys, or ovaries are sometimes produced. Normally the process takes place gradually and the circulation adjusts itself so that no organ is harmfully over-charged with blood. By this means the latter, carrying so much vital heat with it in the course of a minute, is removed from the surface, whence that heat would be partly lost. Exposure to cold causes the skin to become blanched, but if it be excessive the nerves or muscles of the arterioles or both are paralyzed and the blood-vessels expand widely under the pressure from the heart, making the skin red. Chronic alcoholism, because of its continued surface vaso-dilating effect, has the same influence on the skin. Owing to the reciprocal action between the skin and the kidneys, the vaso-constriction in the former tends to increase the flow of urine. Only 1 or 2 per cent., however, of the body's heat is given off in the urine, so that this opposing effect counts but little in increasing thermolysis.

Voluntarily the loss of heat is decreased by man by wearing more clothing or furs, which besides being themselves non-conductors of heat, help to keep a layer of "dead," non-conducting air about the body. In the lower animals this fact is obvious, many animals having two suts of fur or of feathers of very different degrees of "warmth."

When the body-heat becomes or tends to become abnormally high, in general the opposite physiological movements occur. The dermal blood-vessels under the influence of the vaso-motor centers dilate, and much more blood being then forced into the skin, radiation and conduction increase and sweat is more freely poured out. The latter not only aids thermolysis by evaporation, but it makes conduction and radiation more active by increasing the conductivity of the skin. It acts, also, and more importantly, by pouring the water to be evaporated outside the oily and ill-conducting epidermis, it being the sebum and not the sweat which contains fat. This dermal vaso-dilatation is probably the most active means of heat-regulation, and it serves as a prompt and vigorous agent in expending surplus heat. Because of its failure in *fever,* owing to some disturbance in the medullary centers, the temperature rises; this increases metabolism, which in turn raises the heat still more. Many other influences at different times act in a similar way, chief among these being bacterial irritations from toxins. Sometimes during fever sweat is secreted, but it is exuded on a cool surface ("cold sweat") and usually under conditions which largely prevent its proper antipyretic effect. It is sweat-secretion of this purely "nervous origin," unaccompanied by dermal vaso-dilatation, which comes from some emotions, especially terror.

With the reflex vaso-dilatation in the skin may go the other more voluntary conditions, already noted, useful for the reduction of body-heat, such as frequent bathing and the removal of clothing. Any circumstance, in short, which will help to expose to a cooler environment (air or water) a larger amount of body-heat than before serves to cool the body, heat-production being at the same time reduced reflexly, instinctively, or voluntarily on a basis of instinct or of comfort.

THE THERMOTACTIC NERVES.—The neural mechanism of heat-regulation is as yet in its details not very well known. There is good functionary evidence that there is something like a reflex arc for this thermotactic purpose. The tissues have means of sending information concerning their thermic condition to the brain, which thereupon sets in motion the regulating mechanism in the direction required, either to stimulate the tissues (especially the muscles) to produce more heat or to stimulate the skin to lose more heat, or *vice versa.* As will be seen more fully in the chapter on the Sense Organs, there are minute spots scattered through the skin, some of which respond to stimulation by heat and some to simulation by cold. The presumption is allowable, at least, that besides affording the animal protection from external heat or cold, the nerve-end organs within these spots originate afferent impulses which actuate a thermotactic center, some knot of neurones which by its connection with the other centers of the brain controls all these various processes of heat-production and of heat-loss. No such action of the heat- and cold-spots has been actually demonstrated, however, so that this interesting matter must remain only a fair presumption until its truth has been actually proved. What evidence there is is in its favor.

About the heat-center or -centers there is more definite information. It is apparently located in the caudate nucleus of the corpus striatum. Puncture of this little area of the interior of the brain even with a fine needle causes in animals a marked rise of body-temperature. Ott found another and more likely thermogenic center in the tuber cinereum of the optic thalmus, and this has been corroborated. This latter region of the brain is closely connected with the vaso-motor apparatus, for puncture of its anterior part causes a marked fall of blood-pressure by vaso-dilatation. The increase of the heat-production which then follows is probably brought about by radiation of the nerve-influence into the adjacent motor paths. This would cause an innervation of the muscles and a rise in their trophic heat-production. Evidence of a probable thermolytic center is more vague.

Whatever the exact neural mechanism of thermotaxis, it does not reach its full development in the human animal until about the tenth year. We see evidence of this very often in the rapid rise of temperature in young children from causes so slight that they would not at all influence the adult temperature.

Other Forms of Energy-expense in which katabolism manifests itself are those other than growth and repair, secretion, and heat, which have now been discussed. They are mainly muscular and nervous force. Muscular power is discussed in a chapter by itself and nervous force with the functions of the nervous system. These need only mention in this place for the sake of systematic completeness.

There remains under the head of katobolism to briefly describe the excretory processes as such and the harmful substances to which these important processes give rise. This is comprised under the general term excretion, the latter phase of external nutrition.

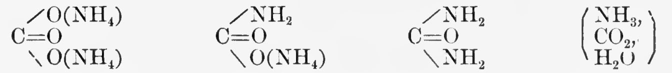
Excretion.—The excretion of substances of no further use to the organism is an indispensable part of nutrition. They are mostly of such a nature that they would poison the organism and promptly cause its destruction did they remain within it. The five familiar sorts of food-material (protein, fat, carbohydrate, salts, and water) partake more or less in the structure of the tissue-molecules, are sooner or later katabolized, and their elements at least sent out of the body either by the kidneys, the lungs, the rectum (including the liver's contribution), or the skin. Minute quantities, relatively, are also excreted by the reproductive and nasal organs, and as the dermal appendages, hair and nails, but these are negligible otherwise than in this mention. The most important of the actual end-products of katobolism excreted by man are urea, carbon dioxide, and water, these together representing the ultimate waste of the three basal "proximate principles," protein, fats, and carbohydrates (but not respectively). The salts and the water ingested are mostly excreted in unchanged condition. In our knowledge of the katabolism of proteids, fats, and carbohydrates there are as yet large gaps, and hence our description of this must be at present partly conjectural; indeed, in some of its aspects largely so. We shall do best, perhaps, by keeping out attention mainly on the nitrogen, the carbon-dioxide, and the water of katabolism. For practical convenience, however, we must describe this general katabolic excretion under the heads of the respective excreting organs: the kidneys excreting urine, the lungs carbon dioxide and water, the rectum feces, the liver bile, and the skin also water and carbon dioxide. Aside from the value of metabolic theory, these excretory menstrua have very large practical importance, and hence their respective compositions and modes of excretion from the body must be thoroughly understood.

The Urine.—The urine excretes about 94 per cent. of the nitrogen involved in proteid katabolism, 3 or 4 per cent. of the katabolic carbon, about one-half of the excreted water, and a large part of the inorganic salts used in the body. The nitrogen comes partly from the wasting tissues, but in varying proportions also from the circulating proteid. The carbon in the urine comes to a slight extent from the carbohydrates and fats of the tissues and the "food" still circulating in the blood, but mostly from the degenerating proteid molecules of the cells. The water is larely ingested as such, but about one-fourth part of it appears to be liberated or even compounded from the fats and carbohydrates katabolized in the body.

First, as to the nitrogen. As we saw above, the proteids absorbed from the intestine pass into the latter's epithelium as proteoses or peptones, or else (Bayliss and Starling) this epithelium constructs the peptones from the amido-acid products of tryptic zymolysis. These cells or the endothelium of the capillaries, or both, probably dehydrate the proteoses or peptones and change them over into the serum-albumin, serum-globulin, etc., of the blood. As such native proteids, then, the protein material from the gut passes through the portal vein on its way to the liver, first soaking through the spleen. There is no evidence that any of the circulating or food-proteid is stopped by the liver except when fat and carbohydrate are entirely lacking in the food. In this case, owing to the energetic demand of the body for these two proximate principles to furnish heat and power, some of the food-proteid from the intestine may be retained and changed into these substances along with urea. This urea-part of the suggested anabolism, however, would represent an unlikely waste of precious nitrogenous material, unless, indeed, the tissue-proteids and the circulating food-proteids are so closely allied that their separation is impossible. For this possible formation of fat, glycogen, and urea from protein in the liver, Dubois suggests the following equation, not as just what actually takes place, but as something similar perhaps to the reaction. (The proteid-formula is Lieberkühn's and also Loew's conjecture for albumin.)

$$\underset{\text{Proteid}}{4(C_{72}H_{112}N_{18}SO_{22})} + \underset{\text{Water}}{68H_2O} = \underset{\text{Fat}}{3(C_{55}H_{104}O_6)} + \underset{\text{Glycogen}}{12(C_6H_{10}O_5)} + \underset{\text{Urea}}{36(CON_2H_4)} + \underset{\text{Sulphurous acid}}{4(H_2SO_3)} + \underset{\text{Carbon dioxide.}}{15(CO_2)}$$

The food-derived or circulating proteid of the portal vein, unless excessive, probably goes through to the tissues sooner or later and largely to the muscles, where it is stored as part of the tissue in the way suggested vaguely below (page 383). Voit supposes, however, that this food-proteid does not become an intimate part of the tissue molecules in this simple way. The production of urea, made at the rate of thirty-two grams daily, cannot begin in the liver, as Schäfer shows, because sufficient oxidation to prepare its precursors does not occur in that organ, nor, indeed, elsewhere than in muscle, the chief tissue of bodily activity. Only a little urea, however, is produced in the muscles, the larger part of it by far being the product of the liver. If the ureagenic process starts in the muscles and is finished in the liver, what, then, are the intermediate steps, and especially in what form does it pass from the muscle to this great gland? Gaglio found lactic acid in the blood as a continual constituent, and sarco-lactic acid is known to be a product of muscular action. Schäfer supposes, therefore, that ammonium lactate is the form in which the product of proteid katabolism goes to the liver, there to be converted (perhaps by way of creatin as an intermediate stage) into urea, in which form the kidneys excrete it. Certain hexone bases and alloxuric bodies (*e. g.*, uric acid and the xanthins) may be other intermediate steps. As to the chemistry of this process, the hypothesis of Drechsel meets, perhaps, with most frequent acceptance. His supposition starts with ammonium carbonate. By losing one molecule of water this becomes ammonium carbamate, and the latter by giving up another water-molecule becomes urea.



$C{=}O\begin{cases}O(NH_4)\\O(NH_4)\end{cases}$ Ammonium carbonate. $C{=}O\begin{cases}NH_2\\O(NH_4)\end{cases}$ Ammonium carbamate. $C{=}O\begin{cases}NH_2\\NH_2\end{cases}$ Urea. $\left(\begin{matrix}NH_3,\\CO_2,\\H_2O\end{matrix}\right)$ Ultimate products.

The *urea*, CON_2H_4, as the bearer of about six-sevenths of the nitrogen excreted from the body and of part of the carbon, is of considerable importance in all metabolic work. From twenty to seventy grams, in round numbers, are excreted daily, the average amount on a mixed diet being thirty-two grams, which contain about fifteen grams of nitrogen. The two extremes given above are those of a bread-diet and an abundant lean-meat diet respectively. Urea (carbamide) is a diamide of carbonic acid, as was indicated above. It is freely soluble in water, but insoluble in ether, has a bitterish, cooling taste, and forms in slender, four-sided prisms with shiny surfaces and pyramidal ends. Heated with water it gives off ammonia and becomes converted into ammonium carbonate. Mammalian muscle contains 1 or 2 per cent. of urea. Its amount in urine is commonly determined by the method of Knop and Hüfner, which consists of decomposing it with sodium hypobromite in the presence of caustic alkali; the latter absorbs the carbonic dioxide and the nitrogen is collected in a graduated tube. From the amount of this nitrogen the quantity of the urea decomposed is calculated, every gram of urea giving 37.1 cubic centimeters of nitrogen by this method. The nitrate and oxalate of urea have importance in examinations for urea.

The non-nitrogenous portion of the product of the katabolic process in proteid is ultimately oxidized, like other such substances, to carbon dioxide and water, perhaps by way of glycogen or dextrose. The sulphur probably goes into the sulphates of the urine and of the feces. Such are the hypotheses which at present seem rather more probable than others to many biochemists and physiologists.

The water of the urine varies in amount largely at different times, but on the average perhaps runs within 200 c.c. of 1½ liters daily. It is derived from several sources. Part (perhaps two-fifths) is ingested directly as cold or warm drinks; part, about two-fifths, is ingested mixed chemically or mechanically with the food; the other fifth is produced anew by the body-katabolism. (The water excreted by the kidneys is only about half that excreted by the body, most of the remainder going out through the skin, and half a liter or less through the respiratory tubes.) The ingested water so far as known is not altered, unless it be mechanically, for there is no evidence that any of it is broken up, nor that it combines chemically with any element of protoplasm. If it did so, however, we could not know it, and the possibilities of its chemical reactions in the metabolism are very many. The water actually produced in the body is made by the oxidation of hydrogen. The fats especially are productive water-formers, for they contain much more hydrogen than is necessary to satisfy their oxygen, and are therefore fuel of the best type. The empirical formula of stearin, for example, is $C_{57}H_{110}O_6$, which shows at a glance the large amount of hydrogen with a maximum combustion-value available for oxidation, the oxygen for which respiration supplies. The carbohydrates and the proteids likewise contribute to the water-making, the former much more largely than the latter. The water is produced largely in the muscles from the combustion of glycogen and dextrose, but also wherever carbohydrate and fatty food or tissue is katabolized with the absorption of oxygen. The oxidative process probably occurs to some extent everywhere in the site of the former molecules. The katabolism precedes the oxidation rather than vice versa, for oxygen has no power to break down the protoplasmic molecule; it has however, great chemical affinity for simple combustibles which are free to combine with it.

The composition of the urine is a matter of much importance theoretically and practically, for it is this liquid which offers the best chance to learn what goes on chemically at different times under a multitude of various conditions, dietetic, metabolic, and pathologic, within the hidden tissues. The urine is able still to teach the physiologist much more even than it has taught him about metabolism, and the physician very much about the condition of his patient.

A complete list of all the substances found regularly in normal urine would be very long, but among them are the following dissolved in the water: Urea, uric acid, hippuric acid, creatinin, urochrome, urobilin, uroërythrin, hematoporphyrin, chromagens, dextrose, isomaltose, volatile fatty acids, xanthin, heteroxanthin, paraxanthin, hypoxanthin, guanin, adenin, amido-acids, phenol-sulphuric acid, cresol-sulphuric acid, etc., inosit, glycuronic acid, acetone, cholesterin, lecithin, sulphates and acid-sulphates of sodium and potassium, phosphates of sodium, potassium, calcium, and magnesium, chlorides of sodium, calcium, and potassium, sulphocyanide of potassium, lactic acid, iron, hydrogen peroxide, carbon dioxide, ammonia, and enzymes. Most of these would be reported in chemical analyses as traces merely. The important and measurable constituents are given in the following table:

Average Composition in Grams of a Day's Urine.

Important constituents.		Mixed diet.	Flesh diet.	Bread diet.
Total amounts (c.c.)		1500	1672	1920
Organic	Urea, CON_2H_4	33.18	67.200	20.600
	Uric acid, etc. (xanthins)	0.55	1.398	0.253
	Creatinin, $C_4ON_3H_7$	0.91	2.163	0.961
	Pigment, etc.	10.00	.....	.....
	Ammonia, NH_3	0.77	0.900	0.400
	Hippuric acid, C_9O_3,NH_9	0.40	.....	.....
Inorganic	K_2O	*2.50	3.308	1.314
	Na_2O	*11.09	3.991	3.923
	CaO	*0.26	0.328	0.339
	MgO	*0.21	0.294	0.139
	Cl	7.50	3.817	4.996
	SO_3	2.01	4.674	1.265
	P_2O	3.16	3.437	1.658

* Calculated as the metal and not as the oxide.

The above table (altered from one by MacLeod after analyses given by Parkes and Bunge) shows how wide is the variation in the composition of the urine with different diets. The urea, for example, in 1920 c.c. of urine excreted on a bread-diet was little more than 30 per cent. of its amount when all the food was meat, although in the latter case the amount of the urine was 248 c.c. less in quantity. This is a constant variation, for, other things equal, a meat-diet gives rise to a small amount of concentrated urine, the water-producing factors of the mixed and largely carbonaceous diets not being present. The average amount secreted is about 1500 c.c. (ranging from 1200 to 1700 c.c.), or about 1 c.c. each hour for every kilo of body weight. Women excrete about 200 c.c. less than men daily and children per kilo of weight 70 per cent. more. The amount is increased by drinking liquids or eating a large amount of proteid, by lack of respiratory oxygen, rise of renal blood-pressure, ingestion of a large amount of "extractives," vaso-constriction in the skin, various drugs, diabetes, and by some nervous derangements.

Urine is a yellowish clear liquid of a specific gravity of from 1017 to 1020, acid in reaction, with a bitter saline taste and a characteristic odor. For short times during the day, especially after meals, the reaction may be slightly alkaline, but the normal mixed urine of the twenty-four hours appears to be always somewhat acid due to the acid phosphates of sodium, calcium, and potassium. The specific gravity is normally in general inverse proportion to the quantity; to find approximately the number of grams of dissolved solids, multiply the last two figures of the specific-gravity number by 2.3 (Trapp). In fever, because usually little liquid and food are taken and because in consequence the tissues katabolize themselves, the urine is scanty, highly colored, and of high specific-gravity. The yellowness of urine is due to urochrome and to a slight extent to urobilin, especially in disease, while other pigments are present in small amounts under certain conditions: uroërythrin, hematoporphyrin, and certain chromogens. The odor of urine is due to the contained aromatics (phenol-skatoxyl, kresol, etc.), combined with

Fig. 130

The circulation about the convoluted tubules. Observe the contrast between the straight and large arterioles and the tortuous veinlets. (Bates.)

about 0.8 gram per liter of dissolved ammonia. The taste is largely that of sodium chloride plus a bitterness whose source is complicated.

THE EXCRETION OF URINE from the renal epithelium to the distal end of the urethra involves both the secretory function of protoplasm and a complicated series of muscular and recoiling movements; the latter part of the process, the expulsion of the urine from the bladder, is specified as micturition.

FIG. 131

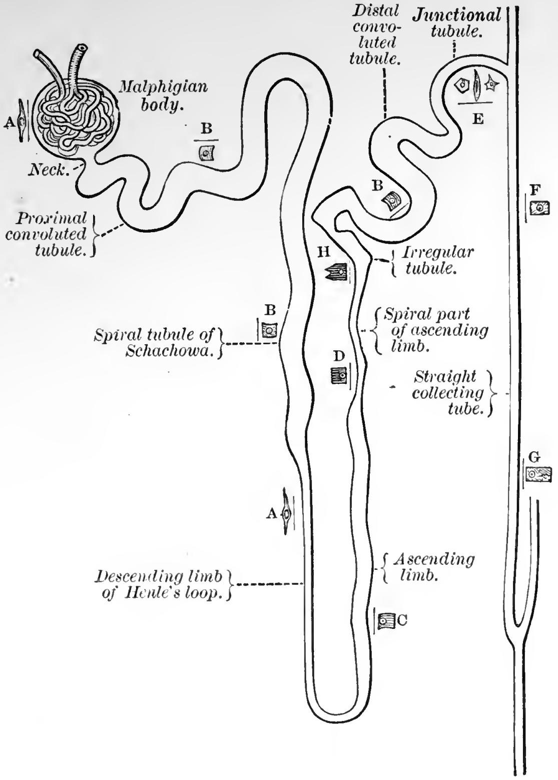
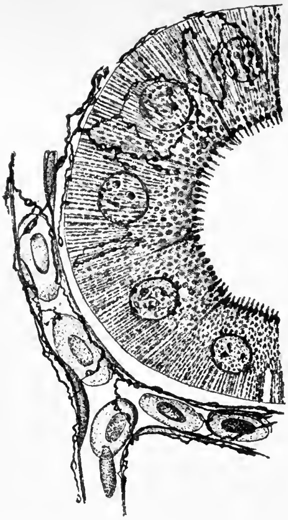


Diagram of a uriniferous tubule, suggesting vaguely the varieties of epithelium composing it: *A*, flattened cells with oval nuclei; *B*, polyhedral, striated cells; *C*, polyhedral, striated cells, but with their nuclei near the lumen of the tubule; *D*, polyhedral cells striated only in the outer part and with flattened and angular nuclei; *E*, variable cells: polyhedral, columnar, angular with short processes, and fusiform; *F* and *G*, columnar and variable cells; *H*, angular cells with conspicuous rodded striations. (Gray.)

The first matter to be examined into, then, is the manner in which some of the numerous complex substances recently enumerated are taken from the blood-stream and collected, dissolved in water, in the receiving hilum of the kidney. Not until all the secrets of protoplasmic secretion are unravelled will the details of these versatile chemical reactions be known, and here as elsewhere in discussing secretion it is only the gross processes and the general results which can be described. The illustration shows the various parts and twists of the uriniferous tubule, but it fails to describe their respective functions and what each of the several varieties of epithelium making up the tubule contributes to the urine's complex composition.

Few subjects in physiology have been more actively discussed than this, the matter resting on two basal presumptions, nearly opposite in theory, concerning renal secretion. These presumptions are still known as the theories of Bowman and of Ludwig respectively. Bowman supposed that the protoplasm of the capsule named for him, largely by virtue of its own secretory powers, took from the capillary blood the salts and the water of the urine; and that the varied epithelium of the different tubular parts farther down added the organic constituents, the urea, hippuric and uric acids, and the rest; Heidenhain has added much support to this theory. Ludwig's hypothesis was more mechanical so far as the working of the glomeruli are concerned, for he maintained that these tiny organs are little more than organized filters which by physical means take the urine in a dilute form out of the stream of blood to be condensed later by the absorption from it of water in the epithelial walls of the devious tubules. The research of Cushny and others makes them suppose with Ludwig that the water, salts, and urea pass from the glomeruli into the tubules, but that part of the salts and of the water pass from the latter again into the circulation. (See the figure opposite diagramming these three theories.) A compromise which recent work impels makes it likely that urinary excretion is accomplished by both mechanical filtration and by vital secretory action in the glomerulus, but that the epithelium of the tubules contributes perhaps numerous unknown substances to the urine. Here, as in the other cases, we may safely say that there is mechanical filtration surely enough, but that the filter is *alive* and selects what it shall let pass and passes nothing else so long as it is normal. The trend of recent work has been to prove directly that the "rodded" or striped epithelium of the tubules secretes products (such for example as uric acid) into them; urea also may be seen to collect in vacuoles in the epithelial cells, the former "bursting" after a while. The glomerulus acts in a manner and, occasionally at least, under

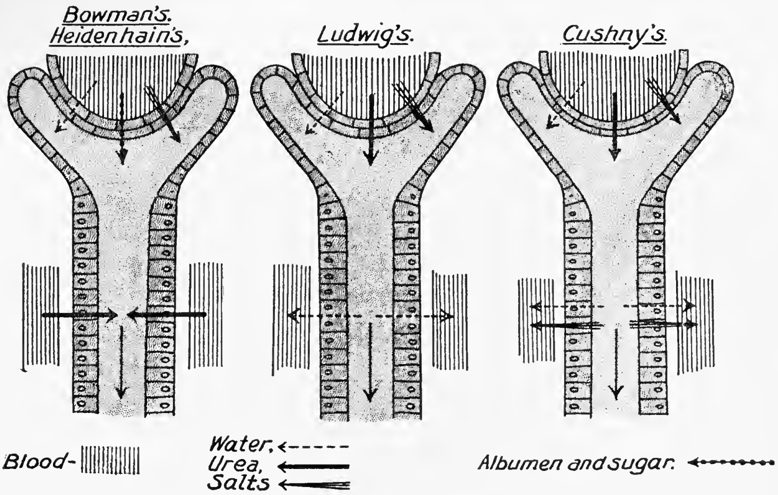
Fig. 132



The relation of the blood-capillaries to the convoluted tubule in the frog's kidney. The erythrocytes in the capillary close to the outer side of the tubular epithelium and the nerve fibers supplying the two last are obvious. (Smirnow.)

conditions in which no mere passive filter could do the work. Sometimes, for example, the glomerulus continues its excretion when the blood's pressure is below that in the tubules, while the osmotic pressure of the secreted urine is several times that of the blood, the current of urine none the less passing in the normal direction against this great balance of resistances. There is nothing present but the epithelium to supply this large amount of energy. In what way the varieties of epithelium up and down the tubules correspond, if at all, to the various constituents of the urine, we do not at all know. It is likely that the "salts" and much of the water enter the apparatus through the glomerulus, and that the organic constituents are added from the blood under much lower pressure by the protoplasm farther down. The mechanical phases of the process (and they may be of considerable importance) proceed undoubtedly in the Malpighian body.

Fig. 133



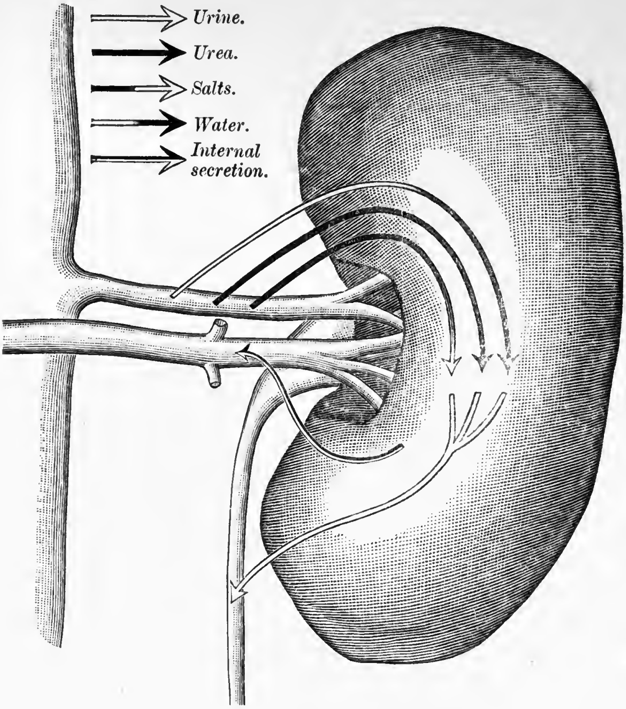
Theories of urinary secretion.

Which of the cells supply the kidney's supposed internal secretion (see page 228) is not known. It may serve not only to direct in some way whatever proteid katabolism goes on in the renal epithelium, but also to adjust the blood-pressure of the organ in the directions local needs require, acting in this perhaps in connection with the vasomotor centers.

The amount of urine excreted varies with the amount of blood passing through the renal capillaries as well as on the pressure of this blood. Heidenhain showed this by ligating the renal vein. This stopped altogether the secretion of urine, although the glomerular blood-pressure was much increased. Diuretics act in various ways: Digitalis increases the heart's work and so forces more blood through the renal vessels. Exposure of the skin to cold acts partly in the same way as digitalis, the increase of the general blood-pressure, owing to peripheral vaso-constriction, being, however, more conspicuous. Some diuretics, such as caffeine, seem to act on the renal epithelium. Others act directly on the renal vessels, increasing the blood-pressure locally.

THE DISCHARGE OF URINE.—The urine collects in the hilum of the kidney under a pressure (in the dog) of 60 mm. of mercury. The ducts of Bellini enter through the pyramids very obliquely in such a way that the greater the pressure within the hilum the more tightly are their orifices closed. This arrangement acts as a perfect automatic valve to prevent regurgitation of the urine upward into the collecting-tubes and consequent interference with the secretory process of the tubules in cases of impacted calculus, etc. From the hilum the urine passes in a continuous trickle through the pelvis of the kidney into the ureter. This tube, composed of fibrous, muscular, and mucous coats, is about 43 cm. long and 4 or 5 mm. in diameter, and connects the kidney with the urinary bladder. The muscle is of the smooth variety, the fibers running both longitudinally and circularly. It is supplied with sensory and motor nerves. The former are useful perhaps in adapting the vigor of the peristalsis to the resistance the latter has to ovecome, as, *e. g.*, in passing calculi through it. In man three sorts of forces seem to help in the passage of urine through the ureters: the secretory pushing "force from

FIG. 134



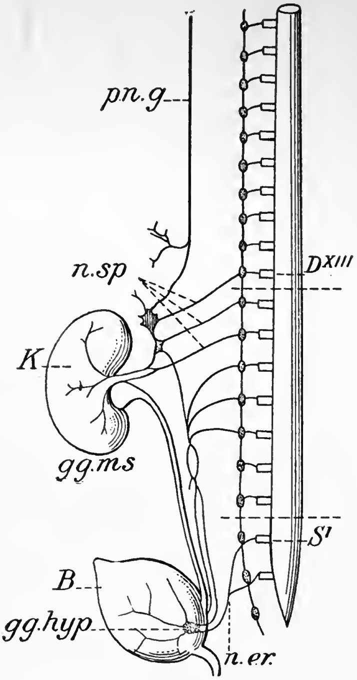
behind," peristalsis, and gravity. To Engelmann we owe our knowledge of the muscular movements of the ureter. He found that true peristaltic waves pass from the kidney to the bladder every half-minute on the average at the rate of 2 or 3 cm. per second (the muscle thus resting half or two-thirds of the time). Cases of non-closure of the bladder-walls during development (ectopia) show that the urine spirts into the bladder at about half-minute intervals. The activity (frequency and power) of these movements is increased by additional resistance in the tube. The musculature of the ureter is classed by the myogenists as "automatic," as if dependent largely on food-supply rather than on immediate and continuous nervous actuation. In this respect the ureter is like the heart, intestine, etc., each ureter being practically one continuous muscle-fiber. On the neurogenic theory, resident nerve-cells control all these activities.

The bladder serves the double function of a reservoir and an expelling viscus. The adult male bladder holds normally about 600 c.c., but it may contain well enough three times that quantity. This distention cannot, however, be said to be quite normal, being more or less harmful. The bladder might, but injuriously, accommodate, therefore, a whole day's urine, but it is ordinarily emptied when containing 400 or even 300 c.c. It performs its expelling-function by means of the elastic and muscular tissues of its walls, aided by abdominal pressure. The ureters enter very obliquely under the mucosa, somewhat as in the kidney, so that the greater the pressure within the viscus the less likely is the urine to return up the ureters. The smooth muscular fibers of the bladder are roughly arranged in three layers, which, however, are much intermixed. A thickened portion of the musculature at the bladder's outlet constitutes the sphincter, which is usually in tonic contraction. Nerves with ganglia in their course pass both to the mucosa and to the muscle-tissue. The bladder is thus supplied with sensory, motor, and vasomotor functions.

Micturition, the voidance of urine from the bladder, consists of a coordinated series of muscular contractions of the bladder, the abdomen, and the urethra. In children up to about the eighth month the process is purely reflex, for voluntary inhibition of the efferent nervous impulses has not then been acquired, probably because of the undeveloped state of the neurones. In adults, on the other hand, voluntary inhibition may be continued until the bladder's contractile mechanism has become temporarily paralyzed by the pressure, which over-stretches it. The normal retention of urine is the result of a functional balance between this pressure and the tonus of the retaining sphincter. Gradually the musculature accommodates itself to the incoming urine, there being no cavity in the bladder immediately after micturition. Nothing is felt of this increasing pressure until 300 or 400 cm. of urine have collected; then, unless the attention is fixed on some absorbing pursuit, the person becomes aware of a desire to micturate, especially if by mechanical joggling a drop of urine is pushed through the sphincter into the very sensitive beginning of the urethra. If micturition be then inconvenient, it may be postponed, but by irritation of the nerves in its walls the ever-distending viscus gradually increases the sense of discomfort until it perhaps becomes actual pain.

The forces acting in micturition are the contraction of the bladder's muscular walls, the passive elasticity of the viscus, the weight and pressure of the viscera above it, and the weight of the urine in the bladder. The first two of these tend continually to lessen the size of the organ much as is the case with the stomach. These four forces combined, and aided in cases of haste by voluntary contraction of the rectus abdominis, etc., quickly overcome the cohesion of the urethra's walls and the urine passes out, under a pressure of about 100 mm. of mercury or more. The urine left in the male urethra is then expelled by the bulbocavernosus and the levator ani muscles.

Fig. 135



The innervation of the kidney and of the bladder: *K*, kidney; *B*, bladder; DXIII, thirteenth dorsal root (dog); *pn.g*, vagus; *n.sp*, splanchnics (great and small); *gg.ms*, superior mesenteric ganglion; *gg.hyp*, hypogastric ganglion or plexus; *n.er.*, erector nerve. (Morat.)

The nerves concerned seem to come from the second, third, fourth, and fifth lumbar vertebral segments, but the sensory (afferent) and the inhibitory (efferent) impulses pass up and down the cord's lateral columns to the cortex cerebri, while some may go by way of the sympathetic. The inhibitory influence relaxes the sphincter. The mechanism may act quite independently of the central nervous system, directed probably by influences from local ganglia or a nervous reticulum. Friedman places a supposed micturition-center in the upper third of the posterior central convolution just behind the center for the arm's action. The bladder's contractions are rhythmic in nature, following each other at intervals averaging about fifty seconds (Sherrington), in a way somewhat similar to the contractions of the uterus and the spleen. The difference between the neural mechanism in the adult and that in the infant may very well be largely functional, and consist in a development of voluntary control over the smooth muscle of the bladder. This is seen frequently in almost all the smooth muscles of the body, and is not very rare even in case of the heart. The bladder is one of the most sensitive of the organs to nervous excitement and influences of many sorts, chemical as well as nervous.

Thus, mental agitation, emotions, and also slight irritations at the distal end of the urethra cause frequently a desire to micturate.

It remains to suggest the ways in which the katabolic waste is excreted through the lungs, the skin, and the rectum.

The Expired Air excretes waste matter next in importance to that of the urine, this matter consisting almost wholly of carbon dioxide and of water. The katabolism which produces these two substances has been already more or less described in our chapter on respiration and above in this chapter. A very large part of the carbon dioxide and about one-sixth of the water passes off through the respiratory organs. The sources of the water we have already seen (page 240).

The carbon dioxide comes from the oxidation of all the products of katabolism that contain carbon. Some of that arising from proteid passes out through the kidneys in the form of urea. Most of the carbon dioxide excreted, therefore, comes from the carbohydrates and fats of the tissues (and the blood?). The carbon from these is oxidized to carbon dioxide. There is evidence (obtained by Stoklasa) that the tissue-cells generally produce an anaërobic enzyme which occasions the fermentations of sugar to carbon dioxide and water; it is found also in milk and in blood. This evidence Borrino has confirmed. The chief seats of this oxidation are the muscles; then come the glands and the nervous system, the other tissues being far behind these as sites of oxidation. The muscles furnish about three-quarters of all the carbon dioxide excreted by these means combined.

Suppositions as to the exact mode of *oxidation* have been various; the real way or ways are unknown. Hoppe-Seyler considered it possible that nascent hydrogen, set free by certain decompositions, caused the diatomic molecule of oxygen to split, the atoms of oxygen thus becoming very active, making possible a vigorous attack on substances already in process of katabolism. Again, Spitzer supposes iron may play an important part in causing the absorption of oxygen into the breaking-down cell-protoplasm. This always contains iron in the nucleus, and ferrous iron may act as a carrier between the oxygen and the molecule, alternately taking on and losing an atom of oxygen (Herter). Probably (Traube) there are enzymes which cause the primary katabolism of the fats and the carbohydrates, or even the absorption of oxygen into the products of this katabolism. The pancreas may furnish such an enzyme to sugar—a ferment called an oxidase. Again, as Herter suggests, the hydroxyl (HO) ions of the alkaline salines of protoplasm may be the ultimate cause of oxidation, perhaps by dissolving the katabolic carbon dioxide and so removing it from the tissues, perhaps by liberating nascent oxygen to attack the tissue-molecules, water being simultaneously formed.

Regardless of hypotheses, it is certain that oxidation is inherent in protoplasm and that without it life cannot continue. The nucleus in case of the tissues is apparently the agent or at least the director of the process. There is no reason why there should be only one way in which the many various substances of the food and tissues are oxidized, so general is the process and chemism so various.

The fats and the carbohydrates from which water and carbon dioxide (by oxidation of their carbon) largely come have already been sufficiently described, as have also the means by which these excreta are transported from the tissues and given out by the lungs and nasal passages through the nostrils. (See the descriptions of katabolism above and the discussion of respiration in a preceding chapter.)

The Sweat is the next most important of the means of excreting some of the waste-products of katabolism. These are especially water, urea, ammonia, kreatinin, sodium chloride, and phosphate, the inorganic and ethereal sulphates, fats (Reid), and the inorganic salts, largely sodium chloride. The amount of water excreted through the skin it is hard to estimate from the discordant results obtained by experiment, for it greatly varies not only at different times and under different internal and external conditions, but also on different parts of the skin. The "insensible" sweat is the more important in studying normal excretion, yet every known means of measurement at once increases its output many times. On the whole the average daily quantity is probably not far from 1500 grams, the same as that of the urine, as will be recalled. So far, then, as excreting water is concerned, these two means are equivalent and the balance of their well-known and important reciprocal action (one decreasing in amount as the other increases) is rendered more perfect.

The Feces, although consisting daily of several hundred grams of waste material, excrete but a very small proportion of strictly katabolic product, for they are in large part merely the refuse of the digestive apparatus. It is here, however, that the systematic description of the feces properly belongs.

The quantity of the feces defecated daily by an adult living on an ordinary mixed diet is about 160 grams, but on a vegetal diet the amount may be three times as great, the difference being largely due, directly or indirectly, to cellulose. The percentage of water is from 60 to more than 80; the latter proportion belongs to the feces from a vegetal diet, because peristalsis is then much more active and less time is allowed for the water's absorption into the lymph- or blood-vessels of the colon. The fecal color varies from light yellow to black, depending on the amount of bile-pigments (stercobilin), iron salts, and sulphuretted hydrogen present. The odor is due largely to skatol, but sulphuretted hydrogen, fatty acids, and indol take part. The chemical reaction of feces may be either acid or alkaline.

The composition of the feces is of course exceedingly variable, for it depends directly on the food ingested and not absorbed. Water makes about three-quarters of its weight, and much of the solid material is undigested and indigestible bits of food and dried digestive juices. The undigested part of the food consists of bits of meat, fat-globules, and carbohydrate; the indigestible fragments are of bone, ligaments, keratin, cellulose, and vegetal gums. Then there are residues from the bile: stercobilin (similar to or identical with urobilin and hydrobilirubin), the product of the unabsorbed bile-pigments, and bile-salts likewise for some reason unabsorbed from the colon. Cholesterin is always present, as the refuse of the hepatic metabolism, as well as lecithin. The antiseptic mucin from the goblet-cells of the colon and detritus from the whole length of the alimentary canal's mucosa are never absent. Bacterial putrefaction, active despite the antiseptic powers of the colon's mucus, contributes the tyrosin and its derivatives (skatol, etc.) already noted, besides various complex organic and fatty acids and insoluble soaps. Then there is a substance unfortunately named secretin whose empirical formula is said to be $C_{20}H_{36}O$, and which has not been found outside of human feces. (This has nothing to do with the secretin internally secreted by the duodenal wall.) There are also many soluble and insoluble salts of the chief organic metals, calcium, sodium, potassium, magnesium, and iron.

Of the above fecal components, water, stercobilin, the bile-salts, cholesterin, lecithin, mucin, and most likely secretin represent in one way and place or other the katabolism of the tissues, but largely in a manner chemistry cannot at present explain in detail. Of the total three liters or so of water daily excreted, about 150 c.c. (or more on vegetal diet) pass out in the feces; this is about 5 per cent. Stercobilin, the name of the reduced bilirubin of the rectum, represents the iron and the proteid katabolism in the liver, as do, and more especially, the bile-salts. These latter contain nitrogen and some of them also sulphur, but no iron. Both of these hepatic products (pigments and salts) probably have, to some extent at least, a "circulation," being absorbed from the colon into the blood, the pigment being then made over into the hematin of new erythrocytes and the bile-acids entering into anabolic process even less understood, thus saving much constructive energy and material. The cholesterin and lecithin are apparently universal katabolic waste from protoplasm. The mucin, as is well-known, consists of the actual bodies of broken-down epithelium, and represents, therefore, as found in the feces, but a minimum of katabolic change.

CHAPTER VII.

THE BLOOD AND THE LYMPH.

We have discussed already the ways in which the various nutrients (including oxygen) become incorporated in the organism to furnish it energy and the materials for replacing its ever-wasting tissues. The means by which the oxygen and the absorbed food products are *distributed* to the myriad tissue-cells, some very remote, and by which the waste of these cells is *removed*, remain to be described. These means are, of course, the blood and lymph. Combined, these constitute one of the most essential of bodily tissues. Blood requires two modes of description, one of its chemical composition and the other of its morphological structure.

Physically human blood consists of a liquid bearing within it two sorts of corpuscles and little masses known as platelets not properly classed as corpuscles. The liquid is called plasma and the three kinds of bodies are the erythrocytes, or red corpuscles, the leukocytes, or white corpuscles, and the thrombocytes, or platelets. In chemical composition blood is exceedingly complex, theoretically more so even than the varied tissues, for it contains not only the materials on which the tissues live, but also the multifarious end-products of tissue-katabolism. Lymph is so nearly like blood-plasma in its composition that they are properly studied together.

The Chemical Composition of the Blood and Lymph has been more or less described, indirectly, in the preceding chapters, but requires to be set forth systematically. We shall then all the better appreciate in how literal a sense the circulation is but a means of distributing the food, oxygen, and heat, and of collecting the waste, of the body. Because these two processes comprise one of the largest functions of life, nutrition, a good knowledge of the blood is of unexcelled importance, for this complex "liquid" is indeed "life-blood." When it stops moving in its devious way among the cells life departs and death more or less gradually comes on. Mammalian blood, as we have seen, consists of plasma containing erythrocytes, leukocytes, and thrombocytes. Each of these, as well as lymph and serum, has functions and in consequence a chemical composition peculiar to itself which must be outlined each in its turn. The functions and the physical composition of the whole blood will be then the better understood.

The following substances appear to be regular constituents of human blood in its normal circulating condition. There are doubtless many others in mere traces and perhaps still others of importance not yet isolated. Water (80 per cent.), serum albumin, paraglobulin, nucleoproteid, fibrinogen, jecorin, hemoglobin, thrombin, dextrose, glycogen, fats, lecithin, serum lutein, oxygen, nitrogen, sodium chloride, sodium carbonate, sodium phosphate, potassium chloride, potassium phosphate, potassium sulphate, calcium phosphate, magnesium phosphate, various enzymes; lactic acid, kreatin, kreatinin, urea (trace only), uric acid, xanthin, cholesterin, and carbon dioxide. This list of substances, representing potentially all that goes on chemically in the body one way or another, will be found useful for future reference. Those to be used in the body are given first. The last eight are products more or less of katabolism, and are therefore mostly outward bound from the system.

THE CHEMICAL COMPONENTS OF THE PLASMA AND LYMPH may be described together, for these two are practically alike save that the lymph contains leukocytes and more water than the plasma. Plasma is whole blood as it circulates in the arteries and veins minus the three sorts of corpuscles. Lymph is found almost everywhere outside of the tubes of the circulation, and everywhere, too, within the closed system of the lymphatics, which are almost universal in the body. In the portal veins (bearing the products of absorption from the gut) just after a meal this lymph is white, being an emulsion, especially if the latter contain much fat. It is there and then called chyle, as is also the contents of the small intestine.

Hammarsten found the *plasma* of horse's blood to have the following composition:

PLASMA'S CHEMICAL COMPOSITION.

Water	917.6
Fibrin (from fibrinogen)	6.5
Paraglobulin	38.4
Serum albumin	24.6
Salts, fats, dextrose, kreatinin, etc. ("extractives")	12.9
	1000.0

Human plasma has a somewhat smaller proportion of paraglobulin and a larger proportion of serum-albumin. When an animal fasts the former increases and the latter decreases. The fats are tristearin, tripalmitin, and triolein, while the carbohydrates are dextrose and glycogen and perhaps animal-gum. The salts are the chloride, carbonate, sulphate, and phosphate of sodium, etc., as given in the list above. The katabolic nitrogenous substances are especially urea (0.016 per cent.), kreatin, lactic acid (possibly carbonic acid and sarcolactic acid). Carbon dioxide is present dissolved in the plasma as well as in the sodium carbonate and leukocytes.

In some *lymph*, perhaps rather thinner than the average, taken from a fistula in a man's leg, Hensen and Dähnhardt found the following proportions, nearly:

CHEMICAL COMPOSITION OF LYMPH.

Water	986.3
Fibrin	1.1
Albumin	1.4
Alkali-albuminate	0.9
Urea and leucin	1.0
Other extractives	0.5
Salts	8.8
	1000.0

A mixture of lymph and of chyle taken from the thoracic duct Rees found to contain 9.5 per cent. of solids, of which 7.8 per cent. were proteids and 1 per cent. each extractives and fatty materials. This might be termed digestion-lymph. Note that as compared with plasma, tissue-lymph contains much more water, much less fibrin, and less salts, fats, and sugars. The lymph is also much more variable than is plasma, since it depends more or less for its composition on the metabolism of the tissue where it is found. A sample of pericardial fluid (lymph) was found to be richer in solids, while cerebro-spinal fluid (lymph) Hoppe-Seyler found very little different from that reported above from the man's leg. *Chyle* is richer in fats and in proteids than lymph, but it is otherwise similar. *Synovia* (of the joints) contains much the same solids as lymph but more of them, and in addition a mucin-like substance (Salkowski).

THE CHEMICAL COMPONENTS OF THE ERYTHROCYTES or red corpuscles. These little bodies consist largely of water, hemoglobin, nucleo-proteid, lecithin, cholesterin, and salts of potassium and of phosphoric acid. The solids are one-third, or a little more, of the whole mass of moist corpuscles. The proteid stroma of the red corpuscles appears to be a globulin. It is noteworthy that while sodium salts much exceed in amount the potassium salts in the plasma, in the erythrocytes the reverse is true.

Hemoglobin is a variable histone-like globulin called globin combined with about 4 per cent. of a non-albuminous, iron-containing pigment of constant composition called hematin. It is theoretically interesting that hemoglobin is probably nearly or quite identical with the pigment of chlorophyll or plant-green so nearly universal in the vegetable kingdom. It is by means of this substance that the plant breathes and in the sunlight is able to construct carbohydrates out of purely inorganic materials, and through the agency of the hemoglobin in animals their tissues are supplied with the metabolic and life-giving oxygen. When combined with the latter gas, hemoglobin is called oxy-hemoglobin, and when this oxygen has been removed it is called reduced hemoglobin. The empirical formula of the hemoglobin of the dog is about $C_{758}H_{1253}N_{195}S_3FeO_{218}$, while Gamgee calculates that the hemoglobin of the ox has the formula $C_{759}H_{1208}N_{210}S_2FeO_{204}$, giving a molecular weight of 16,669. Although crystalline, oxy-hemoglobin is quite indiffusible, perhaps because of this large size of its molecule. It may be this quality which prevents its osmosis out of the capillaries into the tissue-spaces. As Bunge suggests, this large molecule with its relatively great momentum would more easily transport the very heavy atoms of iron than would a small molecule. Its great size and complexity helps undoubtedly in its instability, and this is a very important quality for the performance of its functions. Dry hemoglobin contains nearly 0.5 per cent. of its weight of iron, and it is doubtless on this metal that its quick alternate oxidation and reduction depend. Oxy-hemoglobin is, then, the form of the substance present in the arterial blood and reduced hemoglobin that of venous blood. It is of practical importance that hemoglobin readily forms more or less stable unions with gases other than oxygen, notably carbon dioxide, nitric oxide, and the fatal carbon monoxide. Because of the chemical affinity for the last of these three, coal gas and impure water gas cause many deaths annually, the carbon monoxide replacing and excluding the respiratory oxygen from the erythrocytes.

Since the development of hematology in the progressive division of medical labor, discussion of the various spectra of the blood, comparison of solutions of hemoglobin, etc., have become less and less a part of the science of physiology proper. Suffice it here to say, then, that each of the different compounds and pigment-derivatives of hemoglobin has an absorption-spectrum peculiar to itself, and that by this means blood may be readily recognized even in very old stains. Much may be learned from the blood by this method and others as to certain pathological conditions.

THE CHEMICAL COMPONENTS OF THE LEUKOCYTES, or white corpuscles, has so far not been directly determined, except that of pus-cells. These are dead protoplasm, however, whereas the leukocytes are alive, and there is as much difference chemically doubtless as otherwise. Halliburton quotes an analysis of lymphoid tissue made by Wooldridge which the former considers similar to that of leukocytes. This is as follows:

PROBABLE COMPOSITION OF LEUKOCYTES.

Water		885.1
Solids		114.9
		1000.0
Nuclein	68.78%	
Proteid	1.76	
Histon	8.67	
Lecithin	7.51	
Fat	4.02	
Cholesterin	4.40	
Glycogen	0.80	
Total nitrogen		150.3
Total phosphorus		30.1

Among the proteids are alkali-albumin, a myosin-like albumin, paraglobulin, and peptone. There is, moreover, probably "thrombin" in small amount.

The chemical components of the thrombocytes, or platelets, because of the smallness and fewness of these floating particles, is not definitely known. They consist perhaps chiefly of nucleo-proteid, or of globulin. Bürker has recently shown by quantitative and gravimetric methods that, whatever their composition, the fibrin of coagulation probably comes from them (see discussion of coagulation on page 260).

Whole blood, or, more simply, blood, is a "tissue" of the body in which the morphological "matrix" is a liquid with important functions, the contained cells being the three sorts already noted. It constitutes about 7 per cent. by weight of the human body. Its *specific gravity* is from 1050 to 1062, that of women and children ranging from the lower number to 1055, and man's from 1057 to 1062. The specific gravity of the corpuscles is about 1105, and of the plasma not far from 1030. In *chemical reaction* blood is always alkaline because of its plasma's sodium phosphate and carbonate. The mean alkalinity of the blood is about equal to that of 0.4 per cent. solution of sodium hydrate. It is lowest in the morning and highest at night. Owing to the passage into the circulation of lactic acid (from the decomposition of the muscle's proteid), bodily exercise decreases the blood's alkalinity. In *color* blood varies from the dull scarlet of the pulmonary vein, leading from the air in the lungs, to the purplish red of the pulmonary artery, leading from the oxygen-reducing tissues. The tinge then depends on the proportion of oxygen in the erythrocytes. The color-difference in health is much less than is generally supposed by those who use anatomical text-books with colored plates. It is in mass only that blood is red. No redness is perceptible in the capillaries, and the file of erythrocytes there is of a light straw-yellow color; yet it is from masses of these corpuscles that the redness of blood comes. In *taste* blood is saline, this being due largely to the sodium chloride of the plasma. The *odor* of blood is characteristic, and is largely caused by the various volatile fatty acids and the traces of excretory products present. The *viscidity* of blood is due to its composition and, soon after shedding, to commencing coagulation. Blood is markedly *opaque*, as is inevitable in a colored liquid containing so many opaque bodies in suspension. The *temperature* of the circulating blood varies more than a degree in different bodily parts. It is highest where the blood is coming from the actively metabolic liver, the largest single heat-producer in the organism. The blood constitutes one-twelfth or one-thirteenth of a man's body *weight*, a man of average size having then about five liters of blood in his body. The loss of one of these liters would ordinarily kill him, but a woman might lose proportionally somewhat more and survive. The blood's *distribution* in general is about as follows (Ranke): One-fourth of it is in the circulation including the lungs, another fourth in the skeletal muscles, another in the liver, and the remaining quarter is apportioned among the other parts of the body. During *inanition* the blood sometimes becomes more concentrated, the proportion of erythrocytes somewhat greater, the number of leukocytes decreased by 90 per cent., but the alkalinity is not lessened, and the sugar-content remains the same.

Few aspects of the chemical composition of the blood are more important than that of its electrolytic conductivity by means of ions, for on the relative number of its molecules and its ions depends probably much of the osmotic force everywhere exerted by the blood and lymph. On every hand we have seen the importance of osmosis and diffusion in bodily functions, and few of the physiological processes are independent of these physical processes. It has been found that so far as determining osmotic pressure is concerned, an ion acts exactly like a complete molecule. Hence the relative degree of dissociation into ions which the body-liquids exhibit under various conditions determines very largely most of the functions of the organism. According to the recently suggested electrical theory of organic functioning, the more dilute an electrolyte, for example the blood, is, the more ions does it contain and the better it conducts the supposed complicated electric currents of the body's action. Because of their membranous nature, the blood-corpuscles impede the passage of the ions which bear the electricity, while the plasma is an excellent electrical conductor. The fewer the corpuscles in blood proportional to the plasma, then, the better the blood's conductivity. Again, the more ions or molecules a solution contains the greater is its osmotic pressure through the animal-membranes (the capillary walls, cell-walls, Bowman's capsule, etc.) of the organism. The corpuscles of the blood are in this category, so that interchanges are continually taking place between them and the plasma as the degree of dissociation of their ions and the concentration of the electrolytes determine. It is not only the "inorganic" salts of the blood that furnish the ions, but the colloidal proteids and "extractives" as well. Because, however, of the large molecules of the proteids and of some of the extractives, the osmotic pressure exerted by these substances is small compared with that of the "inorganic" salts. On the other hand, the saline solutions osmose very readily and quickly and by this action largely control the passage of the blood's nutrients and of the tissue-waste in and out of the circulation and the tissues. It is on these principles (here only rudely outlined) that the composition of the blood in these ionic respects is of the largest importance. This composition has control not only over metabolism by chemical means, but also in other ways which chemophysics will doubtless soon make more clear.

WHOLE BLOOD'S COMPOSITION (Schmidt).

Water	788.71
Proteids and extractives	191.78
Fibrin (from fibrinogen)	3.93
Hematin (and iron)	7.70
Salts	7.88
	1000.00

The above analysis of the blood of a man shows the relative general amounts of the blood's components. In woman the salts and the water are in somewhat larger proportion. Under the head of proteids were included serum-albumin, paraglobulin, nucleo-proteid, jecorin, and thrombin, while the "extractives" were such various substances as dextrose, glycogen, fats, lecithin, lutein, lactic acid, kreatin, kreatinin, urea, uric acid, xanthin, and cholesterin. The salts may be noted from the preliminary complete list of the blood's constituents on page 255. They are chiefly chlorides, phosphates, carbonates, and sulphates of the common tissue-metals.

Coagulation of the blood is a function essential to the continuance of life, for without it any wound, however small, in the tissues would cause death by hemorrhage. This fact is all too often illustrated in the victims of hemophilia, commonly called "bleeders." Something is lacking congenitally in their blood so that it does not coagulate. In consequence of this defect they almost always die before maturity by hemorrhage from an open tooth-socket, the nose, or from some minor wound of the skin.

Given a multitude of soft corpuscles floating in a thin liquid: the evolutionary problem was to contrive a way of uniting them quickly into a solid mass dense enough to obstruct the blood-stream flowing swiftly and under considerable pressure through an injured vessel. For this purpose nothing could be better than a mesh of fine but tough and elastic fibers quickly formed in the blood when suddenly needed but by no means until then nor in any other place than at the seat of injury. Such indeed is the *fibrin* which forms in extravasated blood or in the blood-vessels whose walls have been badly injured, and thus made dangerous to the organism. How is this fibrin net-work formed and from which of the blood's components? It is not quite certain as yet.

As the name of the thrombocytes (given by Dekhuysen to the platelets) implies, it is perhaps this third sort of blood-particles which have most to do with coagulation. In 1904 Bürker studied them in great detail. He found that when a drop of blood was placed on a polished bit of clean paraffin in a moist-chamber, in half-an-hour or less the thrombocytes rose to the top of the drop, being lighter than the plasma, and with no dependence on the leukocytes. Under these excellent microscopic conditions the coagulation of the drop of blood could be accurately studied. It was seen that the coagulation-time depended directly on the relative number of thrombocytes present in the drop, and that those substances which inhibit coagulation (for example leech-extract) do so by preventing the decomposition of the thrombocytes. On the other hand, those agencies which hastened coagulation killed the platelets. Just before clotting was apparent in the blood (of man, cats, dogs, hens, frogs, etc., at least), the thrombocytes were observed by Ducceschi to agglutinate in white masses a quarter or a half of a millimeter in diameter on the sides of the containing vessel, and this occurred from forty to one-hundred-and-twenty seconds before any fibrin had formed.

Soon after, threads of fibrin shot outward from all these little masses and soon the contained erythrocytes and leukocytes were firmly enmeshed in this net, made of the finest of fine threads. These immediately began to contract upon the corpuscles, so making firmer the clot. Of this latter, however, not more than 0.2 per cent. is fibrin. Cray-fish blood contains particles which are like large thrombocytes and on the blood's shedding these break up with extreme quickness, with the result that cray-fish blood coagulates much more promptly than that of most animals.

In human blood coagulation begins as an increasing viscosity immediately and by the end of from three to ten minutes (depending on external conditions partly), the blood has formed into a jelly from which on overturning no liquid escapes. This mass, the *clot*, is gradually concentrated by the contraction of the fibrin, and lessening in size for a day or two leaves around it a yellowish limpid liquid called *serum*. Various agents vary the rapidity of coagulation. The more foreign matter there is scattered through and around the blood and the more the latter is agitated the quicker it clots. A few degrees of heat above the body-temperature, and injury to the endothelium of the containing blood-vessels act in a similar direction. So does the addition of calcium salts (for example, the lactate), to the circulation of the animal previously, or of the xanthins, uric acid, etc., to the shed blood. Acids and alkalies, glycerin, oxalates, magnesium sulphate, peptone, egg-albumin, and considerable cold are some of the agents which inhibit coagulation. It has long been a mystery why the blood fails to coagulate in the uninjured blood-vessels, even when they are excised and hung up, but it is now likely that the normal endothelium secretes some enzyme or other form of substance which prevents the clotting. When blood does clot in the vessels the process begins in the center and not about the walls where the inhibiting influence would be the stronger. Bürker found that the coagulation-time was constant for each individual. He also learned that the shortest time is late in the afternoon, and that independently of the outside temperature at the hour. Although cold is in our list of inhibiting influences, it is often used in medicine to check hemorrhage because sometimes, as in the vagina, its contracting-power over the bleeding blood-vessels more than counteracts its influence over the coagulating process. In hemophilia thyroid extract is said to be effective, but in what way is unknown; adrenalin acts by vaso-constriction.

The chemistry of blood-coagulation has not been as yet made out with certainty, but many things imply that the general reactions are somewhat as follows: Under the negative influence of the removal of the inhibiting substance secreted by the endothelium, or under the stimulus of some sort coming from contact with foreign bodies, or both, the thrombocytes of the shed blood (or leukocyte- or erythrocyte-nuclei) exude a nucleoproteid which unites with the calcium salts of the plasma to form a coagulating ferment called thrombin. This enzyme acts on the fibrinogen (perhaps a globulin) of the plasma and converts it into two substances.

One of these is the insoluble fibrin, while the other is a globulin called fibrin-globulin. This latter is a mere by-product, so far as known, of this reaction, whose sole purpose is to construct the fibrin-mesh. This is substantially the doctrine developed especially by Schmidt, Pekalharing, and Hammarsten. More lately evidences of a precursor of the thrombin have been discovered which is perhaps also an enzyme. Thus Morawitz supposes that a substance called prothrombin or thrombogen (occurring only in blood and lymph) under the influence of thrombokinase (an enzyme occurring in all tissues), unites with the calcium salts to form the ferment thrombin (this "thrombogen" being the nucleoproteid spoken of above). Besides the thrombocytes, the leukocytes may take part in the reaction by furnishing part of the nucleo-proteid. It is very doubtful, however, if this substance exists in solution in the plasma, because some of the body-fluids, such as hydrocele fluid, containing no platelets or leukocytes, fail to coagulate, although rich in fibrinogen. The precise reaction of the calcium in coagulation has not yet been demonstrated; it is not strictly indispensable to coagulation, for barium or strontium may be made artificially to replace it. These act much less well than calcium, however, and do not occur in appreciable amount in the blood or the tissues. It is possible that it may be the ionic values of these three melats which are the determining factors in their still mysterious function. Whatever be the mode of action, in normal coagulation calcium salts of some kind are necessary. They seem to be antagonized in this function by sodium and potasium, a fact of possible importance in explaining the inhibitory influence of the endothelial protoplasm. The relations of the gross elements entering into coagulation are almost graphically represented thus:

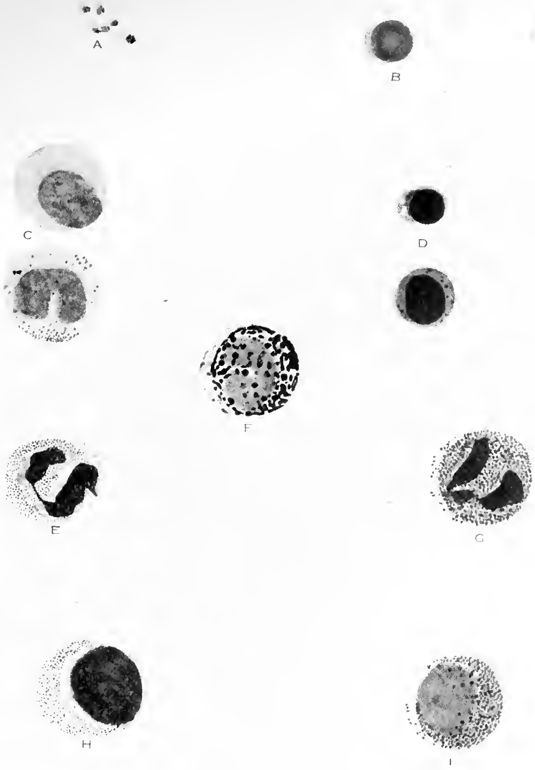
$$\text{Blood}\left\{\begin{array}{l}\text{Plasma}\ .\ \left\{\begin{array}{l}\text{Serum}\\ \text{Fibrin}\end{array}\right.\\ \text{Corpuscles}\quad .\quad .\end{array}\right.\left.\begin{array}{l}\\ \\ \end{array}\right\}\text{Clot.}$$

The plasma with the corpuscles constitutes blood, and in coagulation divides into serum and fibrin, which with the corpuscles forms the clot.

Besides blood, lymph, muscle-plasma, and milk normally coagulate. The lymph clots in much the same way as does blood, but with a less solid coagulum because of its lack of erythrocytes, and somewhat more slowly. Muscle-plasma coagulates in a similar way, the clot being called myosin. Milk coagulates in the stomach and duodenum by about the same sort of reaction as obtains in the case of blood; rennin is the active agent instead of thrombin, but calcium is similarly necessary. The aqueous humor of the eye and the pericardial fluid contain no thrombin, but having all the other essentials for coagulation, clot on the addition of this ferment. (See Plate V.)

The Physical Constitution of the Blood and Lymph.—The morphology of the blood and lymph embraces mainly the description and the functions of the corpuscles contained in them and the mechanical relations of these corpuscles to the circulating liquids. We have already seen how com-

PLATE V



Typical Blood-corpuscles, Stained. (R. C. Larrabee.)

A, thrombocytes or platelets; *B*, erythrocyte, red corpuscle: *C*, large mononuclear leukocytes, basophiles; *D*, small mononuclear leukocytes, lymphocytes, basophiles; *E*, polymorphonuclear leukocyte, neutrophile; *F*, polymorphonuclear leukocyte, mast-cell, basophile; *G*, polymorphonuclear leukocyte, eosinophile; *H*, myelocyte; *I*, eosinophilic myelocyte.

Fig. I

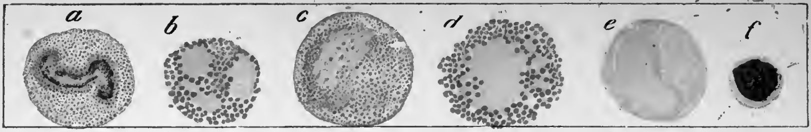


Fig II.

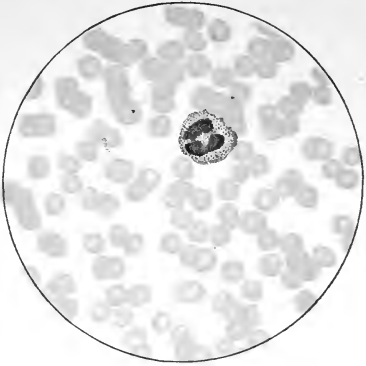


Fig. III

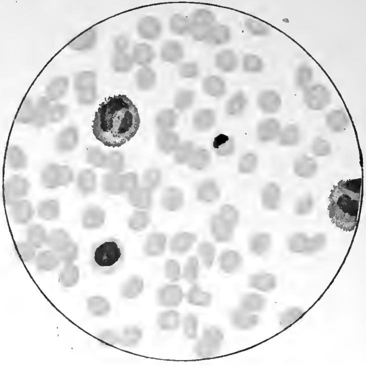


Fig IV.

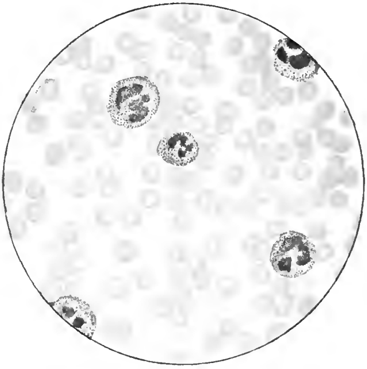


Fig. V.

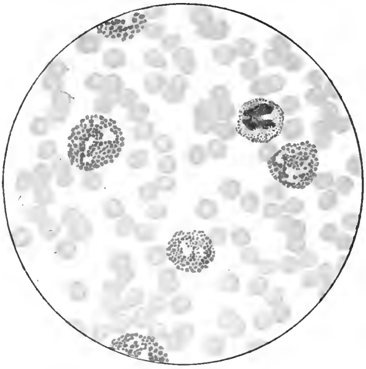


Fig VI.

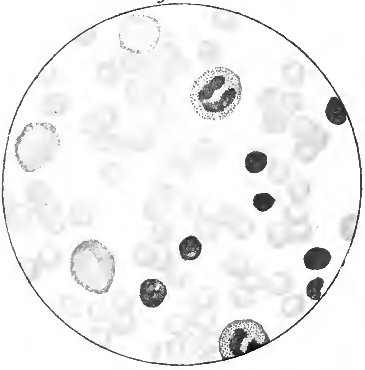


Fig. VII.

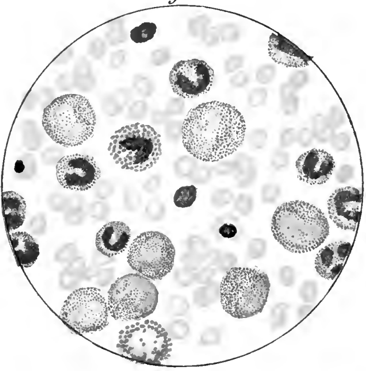
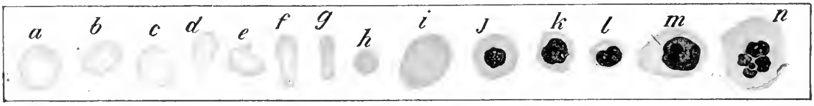


Fig. VIII.



DRAWN BY J.N.Z. CHASE

PLATE VI

BLOOD.

(Ehrlich triple stain.)

(Prepared by Dr. I. P. Lyon.)

Fig. I. TYPES OF LEUCOCYTES.

a. Polymorphonuclear Neutrophile. *b.* Polymorphonuclear Eosinophile. *c.* Myelocyte (Neutrophilic). *d.* Eosinophilic Myelocyte. *e.* Large Lymphocyte (large Mononuclear). *f.* Small Lymphocyte (small Mononuclear).

Fig. II. NORMAL BLOOD.

Field contains one neutrophile. Reds are normal.

Fig. III. ANÆMIA, POST-OPERATIVE (secondary).

The reds are fewer than normal, and are deficient in hæmoglobin and somewhat irregular in form. One normoblast is seen in the field, and two neutrophiles and one small lymphocyte, showing a marked post-hæmorrhagic anæmia, with leucocytosis.

Fig. IV. LEUCOCYTOSIS, INFLAMMATORY.

The reds are normal. A marked leucocytosis is shown, with five neutrophiles and one small lymphocyte. This illustration may also serve the purpose of showing the leucocytosis of malignant tumor

Fig. V. TRICHINOSIS.

A marked leucocytosis is shown, consisting of an eosinophilia.

Fig. VI. LYMPHATIC LEUKÆMIA.

Slight anæmia. A large relative and absolute increase of the lymphocytes (chiefly the small lymphocytes) is shown.

Fig. VII. SPLENO-MYELOGENOUS LEUKÆMIA.

The reds show a secondary anæmia. Two normoblasts are shown. The leucocytosis is massive. Twenty leucocytes are shown, consisting of nine neutrophiles, seven myelocytes, two small lymphocytes, one eosinophile (polymorphonuclear) and one eosinophilic myelocyte. Note the polymorphous condition of the leucocytes, *i.e.*, their variations from the typical in size and form.

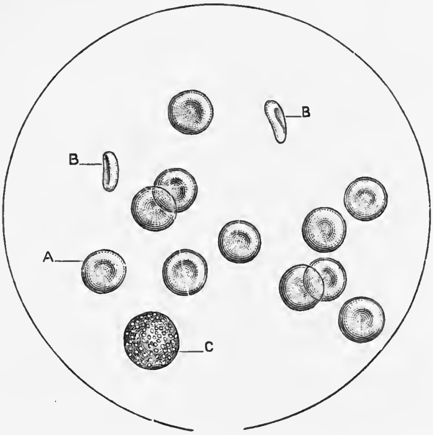
Fig. VIII. VARIETIES OF RED CORPUSCLES.

a. Normal Red Corpuscle (normocyte). *b, c.* Anæmic Red Corpuscles. *d-g.* Poikilocytes. *h.* Microcyte. *i.* Megalocyte. *j-n.* Nucleated Red Corpuscles. *j, k.* Normoblasts. *l.* Microblast. *m, n.* Megaloblasts.

plicated chemically these whole fluids are; we shall now see that their physical structure is not less complex and admirable.

Of whole blood about 45 per cent. by weight are corpuscles and 55 per cent. plasma. There are probably three sorts of corpuscles at least in the blood and lymph, one of which three kinds may possibly consist really of several varieties. The life-histories of the corpuscles is not yet fully known with certainty. The functions of the various corpuscles are somewhat more definitely understood, but probably the leukocytes and the thrombocytes at least have other uses in the economy than those we can describe at present. These two are more or less ameboid, and exhibit the versatility usual to little-differentiated (?) protoplasm. All the corpuscles have been the subject of a very large amount of research, but the two colorless sorts, owing partly perhaps to their easy destructibility and to their relative fewness, have largely escaped hitherto that direct observation which alone could give adequate knowledge of their functions.

Fig. 136

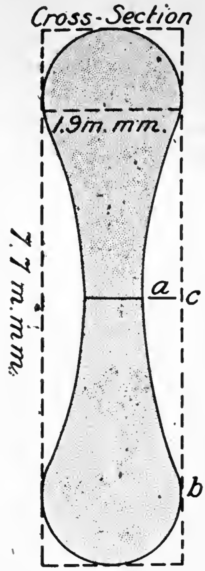


Microscopic view of some erythrocytes: *A*, on flat; *B*, on edge. (Dalton.)

The erythrocytes, the colored plastids or corpuscles, are frequently called red corpuscles because they give the blood its color. When seen singly, or in single rouleaux, however, no redness is apparent, but, if anything, besides a pale, straw-yellowness, a tinge of green. To the histologists the term erythrocyte indicates still the embryonic nucleated form of these corpuscles. The erythrocytes constitute about 40 per cent. of the weight of the whole blood. (See Plate VI.)

In their *structure* only three elements have been made out: a very delicate frame-work of transparent nucleo-proteid (globulin?) called the stroma; 90 per cent. of hemoglobin, already described; and a clear, glassy envelope of some gelatinous material, very thin and flexible (Deetjen). The erythrocytes originate most likely by the division of erythroblasts in the bones' red marrow and at first have nuclei. As no nucleus can be made out in the completed corpuscle it is usually supposed that none exists. Fehrsen always found nucleated red corpuscles up to the third hour after birth. It is barely possible, however, that the erythrocyte has a nucleus in a finely divided, scattered, granular condition, such as Gruber has called attention to in the unicellular rhizopod Pelomyxa. The abundance of nuclein present in the corpuscle and the closeness of its union with the hemoglobin (see page 256), tend to make this supposition at least possible and it has at present some support from observers. On general biological principles it is more or less probable, but inasmuch as reproduction of the erythrocytes themselves or any suggestion of it has seldom or never been observed, if perfect cells structurally they have become highly enough differentiated to lose one of the most basal of cellular functions. The so-called Poggis' corpuscles may prove to have some explanatory value in this respect.

FIG. 137

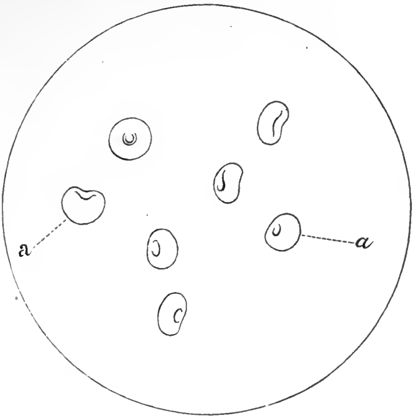


An erythrocyte in cross-section. The triangle *a*, *b*, *c*, suggests how the surface-area of the corpuscle is increased by the concavity with a less amount of material.

In *shape* the erythrocytes are biconcave disks with a diameter four times the greatest thickness. This is their shape when lying flat or free from restraint, but they are very flexible and elastic and are readily bent nearly double and distorted in various ways by the pressure of the circulation in the capillaries, etc. This biconcave-disk shape is perfectly adapted to best serve their function, for it makes them at once very flexible and very resilient, and these are important properties, as may be seen in a moment's observation of the circulation in a frog's foot or mesentery. It also places at its maximum the surface-area which they expose to the tissue-cells and to the alveoli of the lungs, thus making more rapid the diffusion and absorption of oxygen and perhaps of carbon dioxide, which are their sole known functions. Their combined surface-area in an adult of average size is not far from thirty-two hundred square meters, an almost astounding figure explained, despite the extreme smallness of each corpuscle, by the fact that the five liters of a man's blood contains about twenty-five million million (25,000,000,000,000) of these tiny masses of oxygen-bearing hemoglobin. Their shape, moreover, is that which exposes a maximum of surface in using a minimum of hemoglobin. Various physical agents, for example, heat and electricity, cause the erythrocytes to become distorted into many curious shapes, the most common of which is the crenated form, seen also as the dry under the microscope. Weidenreich (following Leeuwenhoek of two hundred years ago) has recently claimed that the erythrocytes are normally cup-shaped or even spherical, collapsing quickly when shed. This shape may be readily seen when the corpuscles are drawn from the animal into an excess of Senkler's fluid. It is more likely that this shape is a distortion caused by the powerful reagents in a manner not unlike the action of heat already noted. One of the unexplained peculiarities of the red corpuscles is their strong tendency when shed to collect in rouleaux like rolls of coin, as if the rims of these minute biconcave disks had some sort of attraction for each other.

The *size* of the human erythrocyte is of considerable medico-legal importance. On the average a red corpuscle is about seven and seven-tenths micromillimeters (7.7 microns) in diameter (a micromillimeter or micron being the thousandth part of a millimeter), and one-quarter as thick. The normal variation in diameter ranges between about 6.5 and 9.5 microns. When the blood is more watery than usual the corpuscles swell, while fever and inanition are said to occasion their shrinkage. (Further important details of much diagnostic importance, concerning the number, size, and shapes of the red corpuscles, are to be had from text-books on hematology.)

Fig. 138



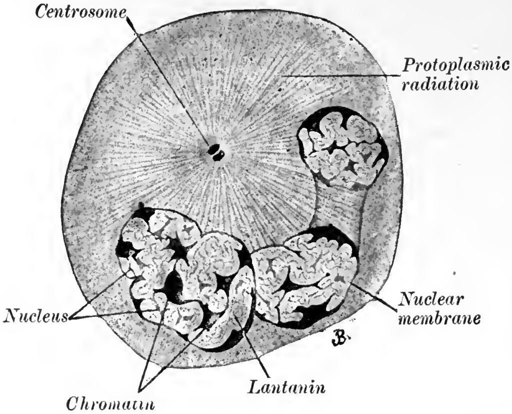
Erythrocytes as seen under certain conditions. This appearance is the basis of the recent claims that the normal functioning corpuscles are spherical.

The *number* of the erythrocytes varies in many different conditions of health as well as of disease, but there is for each sex an important normal average from which as a standard clinical blood-counts are made. Males have about five million erythrocytes to every cubic millimeter of their blood and adult females about four-and-a-half millions of them. Thus every cubic centimeter of a man's blood contains five thousand million erythrocytes.

The places of origin of the red corpuscles in the fetus seem to be in the spleen, the liver, the bone-marrow, by division of the nucleated corpuscles which are then present in the blood, and perhaps also in the lymphatic tissue. After birth it is probable that most, if not all of the erythrocytes are formed in the red marrow of the bones, especially in that of the skull, the trunk, and the ends of the long bones. After a severe hemorrhage, it is likely that the yellow marrow also gives rise to this sort of blood-corpuscles. The life-period of the erythrocytes has not been definitely determined,. but it may be perhaps some weeks or months.

It is unlikely that there is any place of destruction of these corpuscles for they probably wear out and gradually disintegrate into the circulation. Nevertheless, the liver undoubtedly takes from the worn-out corpuscles the portions containing iron and uses parts of the hemoglobin in the formation of its bile-pigment, bilirubin. The spleen also probably takes some of the iron out of these decomposing corpuscles, and this process may rapidly disintegrate them.

FIG. 139



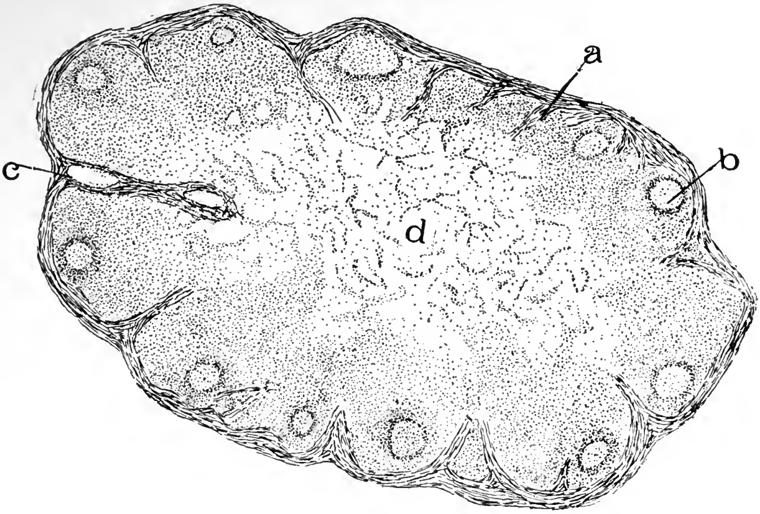
A leukocyte from the spleen of Proteus. Note the elaborate nucleus and the centrosome. (Siedlocki via Szymonowicz and McCallum.)

THE LEUKOCYTES or white corpuscles of the blood and lymph, unlike the red plastids, are perfect cells, for they have nuclei as well as cytoplasm.

The leukocyte, in general, is a minute more or less globular mass of uncolored granular protoplasm. There is to be found in them all the elements of a cell noted in the first chapter. They have, but in a very restricted degree, the same movements even which we described as characteristic of the ameba. In size leukocytes vary from three to fourteen one-thousandths of a millimeter in diameter. A fair average is ten or twelve microns; they are larger, then, than the red corpuscles.

It is convenient at the present time to describe four varieties of the leukocytes; small mononuclears (lymphocytes), large mononuclears, polymorphonuclears (myelocytes), and mast-cells. The *lymphocytes* or small mononuclear leukocytes, as their name implies, are the variety found largely in the lymphatic vessels and lymph-nodes. They are spherical, small cells each with only a thin layer of cytoplasm about the large nucleus. They ordinarily show little spontaneous movement, but Wlasson and Sepp found that by heating them to 44° or by treating them with placental tissue, peptone, or farina, they began to creep with ameboid movements as do the other sorts of leukocytes. About one-quarter of all the leukocytes to be found in the normal blood are (Ehrlich) of this simple variety. These originate in adenoid tissue—lymph-nodes, spleen, etc. The *large mononuclear leukocyte* is similar to the preceding sort, except that the cytoplasm is abundant instead of scanty, while the nucleus shows more irregularity in form and structure. These may come from the bone-marrow or if not probably they are endothelial cells loosened and floating in the blood. The *polymorphonuclear leukocytes* are well described by their name, for they have nuclei of very various shapes, that of a sausage or horseshoe being perhaps the most common. In these the different parts of the nucleus may be connected only by slender bands or even threads of nucleoplasm. The cytoplasm is large and contains fine granules. These are largely neutrophilic in their stain-affinity, but some of them are the "eosinophiles." These are the bone-marrow's specific cells. The basophilic leukocytes are the *mast-cells*. These are much like the preceding, but some of them have several small nuclei instead of one large and segmented nucleus. They also probably originate in the bone-marrow.

Fig. 140



Section of a lymph-node: *a*, fibrous coat which penetrates the organ in the form of trabeculæ; *b*, lymph-corpuscle; *c*, trabeculæ containing blood-vessels; *d*, is placed in the medulla of the organ in which will be seen numerous lymph-cords. (Bates.)

The last two sorts of leukocytes together constitute rather more than two-thirds of all the leukocytes, abut 70 per cent., the mast-cells being only relatively few. They are the most active in their spontaneous ameboid movement. From 1 to 4 per cent. of the polymorphonuclear leukocytes contain very coarse granules of some material which has a strong affinity for acid stains. Because eosin is the most used acid dye, these leukocytes are called eosinophiles or "lovers of eosin." About 68 per cent. of all leukocytes have finer granules which greedily absorb mixtures of acid and alkaline stains, and they are accordingly sometimes, especially by pathologists, termed neutrophiles. Of all the white corpuscles, from 0.5 to 1 per cent. absorb alkaline or basic stains into their coarse, irregular granules; these are the basophiles or mast-cells. Wolff maintains that the lymphocytes and the large mononuclears generally contain ephemeral basophilic granules, normally of much smaller size than the others. As regards nuclear shape and size there are many sorts of leukocytes intermediate between these named kinds. This fact suggests a development from the small, round-nuclear lymphocyte (fresh from the lymph node?) to the polynuclear sort, the nucleus elongating, bending, and gradually breaking apart into several separate nuclei. There is excellent evidence, however, for the truth of their different origins as stated above. The "salivary corpuscles" and "colostrum corpuscles" are probably only the remains of emigrated leukocytes which have become vacuolated and divided.

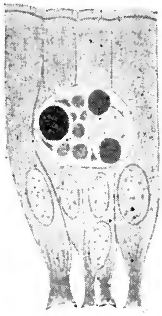
The number of the leukocytes, like most facts concerning them, varies very widely under different conditions and at various times. It is commonly said that there is one leukocyte to every five hundred erythrocytes on the average under ordinary conditions, which would make about ten thousand (10,000) in every cubic millimeter of a man's blood. During fasting the ratio lowers to about one in seven hundred; after a meal it becomes about one to three-hundred-and-fifty, and during pregnancy, according to one set of accounts, it is one to two-hundred-and-eighty. In the blood of the splenic vein there are many times more leukocytes than in that of the splenic artery, and generally more in veins than in arteries. In various conditions of disease the number of the leukocytes varies very widely; for example, in leukemia there is such an increase of leukocytes accompanied by a decrease of erythrocytes that the ratio of the two may be as high as one to five. The same tendency is seen in most acute fevers and in some inflammatory conditions, a fact which is taken advantage of for the early diagnosis of many abnormal conditions.

The functions of the leukocytes are not yet well known. We may mention several, however, which appear to be fairly certain. The most important of these perhaps is that of scavenger. In this work they serve as protectors of the organism's tissues from numerous poisons, organized and unorganized, and are then termed phagocytes ("devouring cells"). Scattered about the tissues and the circulation in such enormous numbers, and with spontaneous movements, they are admirably adapted to serve as agents for the destruction of any foreign bodies, dead or alive, to which they have access. Some of these they devour as if taking them as food, while others are chemically destroyed. It is possible at least that they have much to do with determining the opsonic index of the blood, this being in a word the power of the latter's resistance to invading bacteria and poisons through the presence in the plasma of substances of unknown nature termed opsonins.

A second function of the leukocytes is undoubtedly to aid in the absorption of fat and of proteid substances from the intestine. They help also to carry nutrition from the tissue-capillary to the tissue-cell. They may aid in the coagulation of the blood. Perhaps their proteids take part in maintaining the normal composition of the blood, and it is possible that they contribute carbohydrate and fat as well. In local inflammation, when tissue-cells are in danger of destruction, they crowd to the region in enormous numbers and do their best to destroy the invading bacteria, to restore to the endangered cells their normal constituents, and in general to help in the repair of the injured protoplasm. Another possible function which we may note is that of carrying katabolic products from the tissue-cells into the circulation on their way out of the body.

The life-history of the leukocytes cannot be written with any degree of completeness, but we know more about their places of origin than as to the way in which they disappear.

Fig. 141



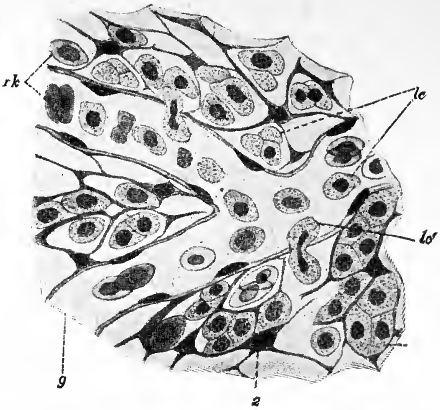
A phagocyte in the intestinal epithelium of a frog. (Heidenhain.)

The Thrombocytes or Platelets.—The physiological status of these minute particles of the blood is at present somewhat uncertain. They were discovered by Bizozero. They are colorless, jagged, or irregular masses of protoplasm, very variable in size, but averaging not far from three microns in diameter. Early in the summer of 1906 Wright published a report of observations which seem to prove beyond much doubt that the platelets are not complete cells, but that they may have ameboid movements. According to this observer, they come from the giant-cells (called by Howell megakaryocytes) common in the bone-marrow and in the spleen. These giant-cells are of spherical form mostly, but some of them "are of varied and irregular shape by reason of the distortion of their cytoplasm into processes and pseudopod-like prolongations of varying length, form, and width, so that they present all the varieties of form and outline shown by a motile ameba." (See Chapter I.) In some giant-cells nearly all the cytoplasm is extended thus as pseudopods, and the thrombocytes are these pseudopodia detached in the circulation. It is known that the giant-cells do lose their cytoplasm and the actual movements of their cytoplasm as well as that of the platelets may be seen. In other respects the supposition is strongly corroborated, and altogether it appears that the origin of the thrombocytes is now fairly well established.

Fine granules are to be seen in these corpuscles and indeed these form a conspicuous part of the platelet. The problem as to the meaning of these granules is an interesting one. What have they to do with coagulation? Is it possible that they represent a granular nucleus?

Because of their very rapid disintegration when blood is shed and of their abundant adherence to threads, etc., suspended in blood, it has long been suspected that the platelets were concerned in coagulation. Burker has now shown indeed that this process is dependent on their destruction or solution, as was described on page 260, and Ducceschi has corroborated part of this result. What other use they may have, if any, is unsuspected as yet.

FIG. 142



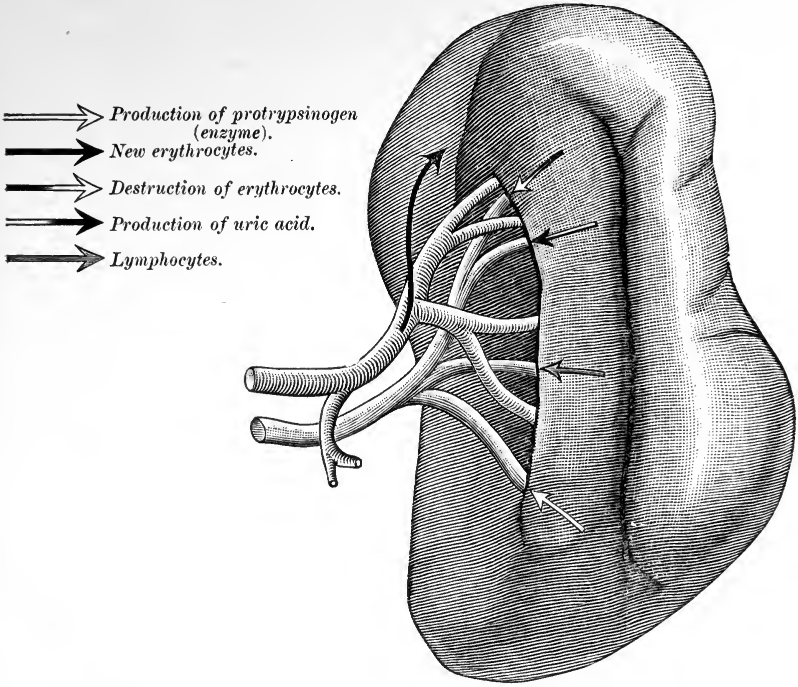
Highly magnified view in the spleen of a salamander: *g*, capillary; *z*, pulp; *lc*, *lc′*, leukocytes; *rk*, erythrocytes. (B. Haller.)

Besides these three sorts of relatively substantial structures floating in the blood, H. F. Muller discovered that there is another sort which he calls hemoconia or blood-atoms. They are much smaller than the platelets even. His claims have now been generally substantiated and it is an almost natural probability that the debris of the various corpuscles should persist a time in the blood. In particular the granules of the eosinophilic leukocytes have been thought of. What, if any, their function is no one as yet knows.

Lymph.—For the causes of the movement of the lymph see the next chapter; its chemical composition has already been given (page 256). Internal nutrition, the mutual interchanges between the tissues and the circulating blood, denotes in a single expression the function of the lymph. Lymph is in nearly all respects and all over the body the intermediary between the blood (the agent, in a sense, of external nutrition) and the cells. It thus bridges over, on one hand, the gap in the passage of the oxygen and nutrients *inward* from the blood-capillaries, and on the other hand that in the path of the carbon dioxide, water, sarcolactic acid, and other excreta *outward* from the varied tissue-protoplasm into the blood-capillaries.

The Formation of Lymph.—It is as important as it is difficult to fully realize how intimately related are the lymph and the blood. Indeed, as we have seen, the former is almost a diluted filtrate of the latter, a trifle richer in products of the tissues' waste, containing more water, only by accident any erythrocytes, and a much smaller proportion of proteids.

Fig. 143



Some theories as to the functions of the spleen. The arrows suggest five of the uses that have been proposed for this however still mysterious organ. Smooth muscle is present in the spleen, but what its motor purpose in the circulation is it would be at present hard to define.

It is, however, very variable (according to the metabolism) in all its components. Over and over again it has been shown experimentally that when crystalloids (freely osmosible, soluble substances) are injected into the circulation, the elapsed time before they appear in the lymph is inappreciable. In other words (and this cannot be too well understood), the whole body is largely liquid, and especially so is the endothelium of the blood-capillaries and lymphatics. The blood at a rapid rate circulates through almost every minute portion of the organism and makes a circuit so quickly and so often that, with the blood-capillaries so extremely permeable, the two-thirds-liquid tissues are made practically one, save as the selective powers of the endothelium and other protoplasm concerned alter the intake and the output to suit their own local demands. The blood rushing everywhere through the body, the ever-intervening lymph, and the living tissues form together a *unity* of semi-liquid protoplasm too perfect and too complicated in its interactions for us at present to understand it completely. In this unity and in these interactions of internal nutrition the lymph plays the very important part now sufficiently indicated. (See also below, p. 385.)

The forces which cause the passage back and forth out of and into the blood-capillaries, the lymph-spaces, and lymph-capillaries need not be gone over, for we have already seen practically the same process occurring in the lungs, in the gut-wall, in the kidneys, etc. It is apparently a complex event, partly filtration, diffusion, and osmosis, and partly a selective, physical sort of secretion. As we have said before, it is a sort of osmosis doubtless, but it is osmosis through an animal membrane which is *alive* and which selects what shall pass through it. This selection is probably determined more by the chemical composition of the liquids which pass back and forth than merely by hydraulic principles. Perhaps the ionic dissociation of the salines and of the organic crystalloids is especially important. We do not know to how great an extent by means of enzymes or ferments (oxidases, digestants, blood-pressure raisers, etc.), or other means the tissue-cells may determine what shall pass by way of the lymph into and out of them. It is surely not wholly a matter of selection by the endothelium, for the blood on one side of the "membrane" and the tissues on the other doubtless in a large measure direct the flow of lymph outward and inward. It is easy, however, to carry this "vitalistic" principle of lymph-formation too far and to leave out too completely the hydraulics of these lymph-movements. Some in this way have tried to convince their readers that lymph is not "transuded plasma" from the blood-capillaries slightly altered by the katabolism and needs of the tissue it goes to and comes from, but, rather that it is practically sewage from the tissues, bound outward into the excreting blood; from this aspect the blood-flow supplies the tissues with their food. In reality, it is only as a rude simile and then wholly in a mechanical sense and for one functional phase only that the lymph may be said to be like the sewerage-plant of a town. Rather is it like a combination, impossible outside an organism, of the water-supply and sewerage-system of a place, and then only in a mechanical, not at all in a chemical, sense.

Into the formation of lymph at least three processes enter, one being physical in nature, one chemical, and one probably having elements of both these others. The physical conditions of lymph-production are the pressure and the flow in the blood-capillaries; the chemical condition is the osmotic pressure of the lymph itself, dependent on molecular and ionic concentration; the mixed condition is the permeability of the blood- and lymph-capillary walls. The last is a matter of the constitution of protoplasm not at present definable, but without doubt chemophysical in nature. Heidenhain's experiments of obstructing the vena cava and the abdominal aorta respectively prove that capillary blood-pressure greatly influences the quantity of lymph produced. In the former case the lymph from the trunk was increased many times; in the latter case is was decreased in proportion to the obstruction in the capillary blood-flow. It is blood-pressure and blood-flow then that influence the filtrative and diffusive elements in the production of lymph.

How osmosis is determined by the molecular and ionic concentration of the plasma and the lymph has been discussed elsewhere (page 221). The conditions are, however, not those of dead animal membranes and of glass vessels, but of living endothelium and epithelium under intricate control. How far these differences alter the osmosis we do not know, but perhaps not much. The "membranes" in the organism are so minute and the forces in detail so slight that there is little probability of learning with present methods much more than is now known as to the details of the osmotic relations of these two similar liquids. Perhaps the unicellular or other simple animals may be made to tell us more than has yet been told in this direction, and here research is much demanded.

The blood-capillary wall's permeability is partly the same as the last condition, for the wall constitutes one of the membranes through which osmosis must take place, and its permeability in small part determines the osmosis. The main element, however, in the permeability is like secretive function in that the protoplasm of the membranes concerned may be altered, and so apparently that it can hasten or retard, or choose this or that, according to local or to organic needs. Thus, research by Galeotti shows that whereas the permeability of serous membranes is not influenced by their death, that of epithelium and endothelium is greatly altered when the protoplasm dies. Whether the nervous system brings about the normal condition is as yet undecided, but it may do so by the fibrils which some observers (*e. g.*, Sihler) have claimed surround the capillaries. The influence exerted by the tissue-metabolism and tissue-needs on lymph-production is direct and controlling, for it is to serve the tissues that the lymph exists.

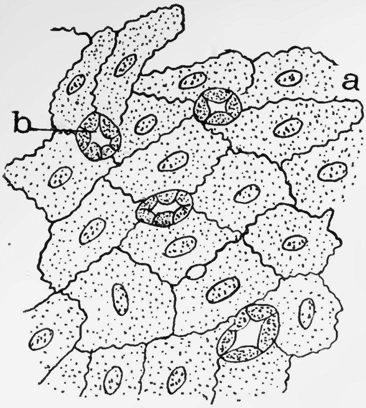
THE PHYSICAL CONSTITUTION OF LYMPH is simple, there being present a very variable plasma, analyses of which have been already given (on page 255), the lymphocytes (small mononuclear leukocytes) described on page 266, and the thrombocytes. The specific gravity of lymph varies widely, between 1020 and 1050 perhaps. In color it is watery, opalescent, or milky even after a fat-containing meal, the partial opacity being given by a varying proportion of emulsion composed of particles of fat much finer than those of milk even. In taste it is like blood-plasma, and in odor nearly so. Owing to the small amount of fibrin which forms in clotting lymph (0.05 per cent.) and to the practical absence of erythrocytes, its coagulum is much less firm than that of blood. Red corpuscles are usually found in lymph, sometimes enough to give it a pinkish tinge, but these must be considered as present by a physiological sort of accident only. The leukocytes in the lymph are present in very variable quantities but usually in numbers not very different from those of blood—namely eight to twelve thousand per cubic millimeter. The number of the thrombocytes has not been determined.

THE QUANTITY OF THE LYMPH produced and poured out of the two ducts into the subclavian veins is commonly stated to be every day one-thirteenth the body's weight. This is the same amount as that of the blood present on the average in the body, or nearly five liters. Like everything else lymphatic, this too is very variable, for it depends on the general blood-pressure, on the composition of the blood, on the capillary permeability, on the nature and degree of the metabolic activity in the tissues. Especially, as Hough has emphasized, does it depend on the activity of the skeletal muscles, on the amount of physical exercise. Lymph moves in a sort of circulation of its own. It is passed out of the direct blood-circulation, soaks through the tissues, and afterward enters again its system of "closed" lymph-vessels on its way again into the set of "closed" blood-tubes. Because of this soaking through the tissue-protoplasm and of the inexhaustible supply afforded by the circulating blood, anything which increases the metabolism of much tissue on the one hand, or which forces mechanically the onward lymph-flow on the other, will increase the quantity of lymph passed out of the thoracic ducts. The muscles constitute half the mass of the body and by their activity increase in both of the ways last mentioned the flow of lymph. Their heightened metabolism enlarges the demand for the food- and oxygen-supplying lymph and their contractions compress the lymphatic vessels and so crowd the lymph onward while the valves prevent its movement in the backward direction. Measurements have proved that an active muscle exudes five or six times as much lymph as the same muscle in a passive state. Active muscles then suck in as well as vigorously press out a large amount of lymph, and the draft thus produced cannot fail to increase the lymph-flow all over the body. This means in turn not only a better cleansing of the tissues of their excreta, but a largely increased food-supply for them, more oxygen, growth, vigor. This in part is doubtless the reason that physical exercise plays so large a part in sustaining or increasing the good health of all animals and of none no more than man, especially since his organism has been evolved on much more bodily exercise than the average man and woman of today provides it.

THE FUNCTIONS OF THE LYMPH scarcely need extended systematic description, for some of them have come out in the foregoing pages, namely the conveyance of food and of oxygen inward from the capillaries to the cells and the excretion into the capillary-blood of the tissues' waste. It supplies, then, the material from which the body-cells may feed themselves. There are, however, at least four other lymphatic functions which require mention: absorption of fat from the gut; the lubrication of the great serous surfaces; the maintenance in part of the blood's composition; and the filling of the cerebral ventricles.

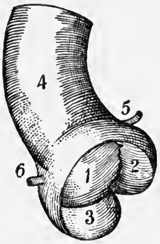
In the movements of the viscera on each other, the heart between the lungs, the lungs within the chest-walls, the diaphragm over the abdominal contents, the abdominal viscera on each other, the bones in the joints, etc., much friction would be caused were the intervening surfaces not well lubricated. Indeed, we cannot see how these organic movements could go on without this liquid supplied in just the right amounts between these opposed surfaces. In pleurisy, for example, a slight roughness is sometimes produced by the inflammatory exudation of fibrin on the pleura, and the accompanying pain and disturbance of function are severe. The lubricant of all these surfaces is lymph, and it is sometimes said that lymph "takes its origin" in part from the serous sacs. It does so in a certain sense, but it is better to consider that it lubricates these surfaces and then osmoses and drains away in the lymphatic vessels, the membranes constantly "secreting" their necessary supply from their blood-capillaries.

Fig. 144



The structure of the peritoneum: *a*, flat endothelial cells; *b*, stoma. A lining with such a structure is obviously ideally adapted to be a lubricating surface between the ever-moving abdominal viscera. Another function of the peritoneum is to shut off local inflammations, *e. g.*, appendicitis, from the fatal involvement of the whole abdominal cavity. (Bates.)

Fig. 145



The root of the aorta from in front, the valve being shut: 1, right; 2, left; and 3, posterior semilunar valve-flaps; 4, ascending aorta; 5 and 6, left and right coronaries, respectively. (Rauber.)

When almost any reasonable amount of harmless liquid (for example 0.06 per cent. aqueous solution of sodium chloride) is injected into the blood-vessels, it is very soon transuded into the lymph-spaces and into the gut and the blood has thereupon resumed its normal specific gravity. Thus, in surgical shock, where there is a dangerously low blood-pressure preventing metabolic exchange between circulation and tissues, the injection of Ringer's solution or of "normal saline" into the blood raises its pressure for only a few minutes, owing to this rapid transudation; the infusion soon has to be repeated. In respects other than that of the proportion of water the lymph may have much to do with maintaining the blood's composition, but how much cannot be stated. There is certainly a strong tendency for the blood to remain constant, often apparently at the expense of the lymph's inconstancy. Its percolation through the tissues and its mixture continually with the rapid circulation tend also to make it a means for maintaining the blood's constancy of composition. This is a matter of no little importance; the actuation of the coördinating nervous system is dependent on it, for example, as well as many other essential processes.

The ventricles of the cerebro-spinal axis are filled with lymph, but what exactly, except to regulate brain-pressure, is the function of these ventricles is uncertain. It is generally supposed that, in this process, the lymph preserves the requisite pressure perhaps partly by means of variation in its rate of transudation into and out of these cavities. The exact relation of the numerous lymphatics of the brain and cord to these reservoirs of lymph greatly needs working-out. (See also under the blood-supply in the chapter above on the nervous system, page 62; and the next chapter for further facts as to the relations of the lymph.)

CHAPTER VIII.

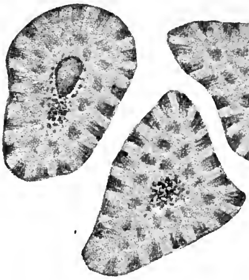
THE CIRCULATION.

We have now seen where the general combined body-liquid, the blood and lymph, comes from, and in general terms its composition. We must now try to get an idea of how and for what purpose it goes about the body. Few if any mechanisms with which we are familiar are more complicated than this, or do their work better. The precise mechanism of the human circulation is described by visceral and microscopic anatomy. The chief matters to be fully understood from these other text-books are the heart, the arteries, the capillaries, the lymphatics, and the veins, and the relations of the two sorts of capillaries to the tissue-cells. The heart in man is a double force- and suction-pump of four chambers and a complex system of valves which are marvels of hydraulic perfection. These valves are so constructed as to compel the circulation continually in one direction. There are distinct tubes for the blood and others for the lymph, and both of these sorts of conducting vessels ramify almost endlessly in every minute active portion of the body. It is now thought that the lymph-system is a set of tubes closed in the same sense that the blood capillaries are closed. It is only in a technical, anatomical sense, however, that either the blood-capillaries or the lymph-capillaries are said to be closed tubes. Their walls are so thin and so permeable to solutions or crystalloids (saline solutions) that the circulating fluid in them is in functional continuity with the liquid in the tissue-spaces. This almost complete unification of the circulating fluid with the more or less similar fluid everywhere between the tissue-cells is an important matter which must be well comprehended. For descriptive purposes these liquids are defined as different, but practically the blood soaks with the utmost freedom into the tissues and the lymph collects just as freely into the lymphatics. The exceedingly thin layer of protoplasm which forms the blood-capillaries and the lymph-capillaries is so permeable (through the processes called filtration and osmosis) that functionally under normal conditions it is almost as if it were not there.

Besides the blood- and lymph-vessels it is necessary to become thoroughly familiar with the elaborate system of nerves which control the heart and the caliber of the arteries (and possibly the permeability of the capillaries); but these cannot be described here. There are many things also in the histology of the arteries, veins, lymphatics, and capillaries which it is essential to have in mind as one studies their functions. Again, there are many principles and facts of physics connected with this elaborate hydraulic system which should be in mind before studying the physiology of the circulation. We are obliged, however, to confine ourselves here strictly to the human physiology, and therefore must omit more than this mere reference to the structural facts, however important, described by the correlated sciences.

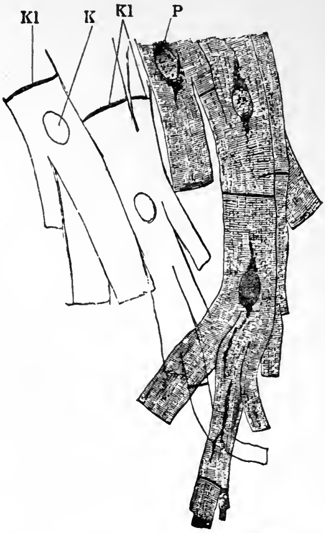
The Causes of the Circulation are at least five in number, namely: the contractile energy of the heart in systole (contraction), the elastic recoil of the arterial walls, the thoracic suction, the pressure of the body's muscles on the valve-supplied veins, and the suction of the auricles during diastole (relaxation). Of these, the first, chiefly ventricular contraction, unaided, is adequate to continue the circulation.

Fig. 146



Heart-cells of an adult in cross-section. (Minervini.)

Fig. 147



Fresh human heart-muscle: *K*, nucleus; *Kl*, cement-substance; *P*, pigment-masses. $^{224}/_{1}$. (Schiefferdecker and Kossel.)

The contraction of the heart (considered as a mere pump for the present), occurs on the average seventy-five times every minute. The comparatively long time of three-tenths of a second is required for he ventricles to contract. This is preceded by the auricular contraction which lasts one-tenth of a second. As already noted, the auricular beat merely fills the ventricles and for our present purpose need not be discussed. The ventricular systole (contraction) is essentially a constriction of the middle layer of muscle-fibers. This narrows the caliber of the chamber considered as a tube closed at the lower end by the other layers. The middle fibers furnish the chief motive power. The others, oblique, help to bring about the shortening of the ventricle, the forward up-rise of its apex against the chest-wall, and the partial descent of the heart's base as the whole heart twists, shortens, and becomes flatter antero-posteriorly. The exact meaning of all parts of the muscular structure is not yet well understood, for the whole process is one of great complexity, having in it the natures of both cross-striated and of smooth muscle. The former kind of muscle causes the beat and the latter the tonus of the heart. This tonus is as yet little known, but apparently is of no small use in adapting blood-pressure, etc., to the ever-varying organic needs. (See p. 300 et seq.)

The ventricles force into their respective outlet-tubes (against a pressure of about 150 millimeters of mercury in the aorta and of about 50 millimeters in the pulmonary artery) not far from 120 grams of blood at every contraction (Cowl), although some have claimed that the amount of blood is less. 150 millimeters of mercury exert about the same pressure as would 1.92 meters of blood, (taking the specific gravity of blood as 1055 and that of mercury as 13.5), so that the work done by the left ventricle at each systole equals that required to raise 60 grams of blood 1.92 meters against gravity, or 0.1152 kilogram-meters of work. With a pulse-rate of 75, there are 108,000 beats in twenty-four hours, and the left ventricle would do 12,441.6 kilogram-meters of work daily. If we estimate that done by the right ventricle as one-third that by the left and add it in, we have 16,588.8 kilogram-meters of work as that done by the ventricles daily. On the amount of energy then, used up by his heart's ventricles alone in one day, a man of average weight, say 70 kilos, could climb 237 meters up a mountain; it is equivalent to 36.7 kilocalories of energy. During severe muscular exertion this output by the heart may be as much as doubled (Zuntz). This increase is accomplished not only by a marked increase in the pulse-rate but through a large expansion of the heart's chambers by the mechanism which governs the tonus of the heart. Most of this large expenditure of energy by the heart is used in overcoming the *friction* of the blood-stream against the arterial walls.

The ventricular systole which forces 120 cubic centimeters or less of blood into the aorta already under an internal tension of about 150 millimeters of mercury, occurs rather suddenly (in 0.3 second) and the aortic blood is of necessity quickly displaced. This displacement occurs not only in the aorta but also in the pulmonary vein 75 times per minute, and with such a frequency even in rigid tubes there would be something approaching a continuous flow owing to the considerable friction. But the arteries are quite the opposite of rigid, for elasticity combined with strength is their most marked mechanical characteristic. (See the experiments with the circulation-schema described in the Appendix.)

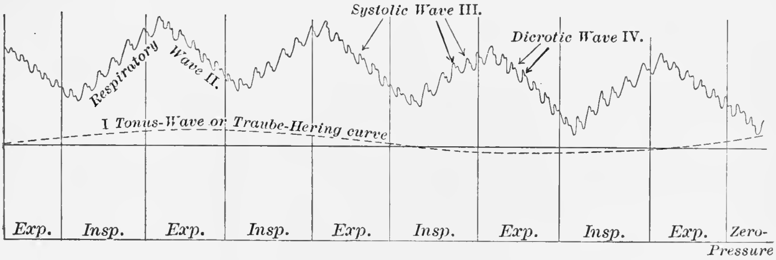
The recoil of the arterial walls, mentioned as the second most important cause of the circulation, depends immediately on this high elasticity, and must not be confused with the muscular vaso-motor contraction of the medial coat. The muscle-fibers present in the arterial wall increase somewhat the latter's elasticity, but this elasticity is mostly passive and the recoil is probably only the back-action of force put into the arterial wall by the systolic energy of the ventricles. The arteries being already full, the accession of blood at each beat in part pushes forward the blood already present and in part distends the arteries (this distention being the "pulse"). Compared with that of the aorta, the diameter of the single capillaries is insignificant, although the combined area of their cross-sections owing to their multitude is perhaps several hundred times that of the aorta. In small tubes, however, friction is enormous and the heart has this friction to overcome as a resistance. This raises the aortic blood-pressure to the 150 millimeters or more of mercury already noted. Thus, while the blood forced into the aorta at each beat pushes some of the contained blood onward into the smaller arteries, distending them in turn, some of the newly arrived blood distends the aorta directly. With a pulse-rate of 75 there is an interval of half-a-second between ventricular systoles. During this half-second the flow in the aorta would tend to slacken and that in the arterioles and capillaries to stop were it not for the energy put into the elastic arterial walls by their forcible distention, this distention in turn being dependent on the high resistance of the minute capillaries. But immediately the systole stops this energy of passive elastic recoil becomes kinetic and presses hard upon the sides of the cylinder of blood in the aorta, etc. Toward the heart the aortic valves (closed promptly after the ventricular systole ended by the back-pressure beyond them) shuts off absolutely the blood's escape, and the only way for the blood-mass to flow is toward the capillaries. Thus, while ventricular systole lasts 0.3 second, this strong recoil of the arterial wall pushes on the blood during the 0.5 second which elapses before another systole bursts open the aortic valves again and pushes out another ventricleful of blood to cause another pulse throughout the whole arterial system. (See the circulation-schema experiments in the Appendix.) It is to the high resistance in the capillaries and to the elasticity of the arteries that the constancy of the flow in the capillaries is due. When an artery is cut, intermittent spurting of blood is seen, for the taking up of the intermittence is not complete until the capillaries are reached. From veins, on the other hand, except in abnormal cases of overdilated capillaries, allowing the pulse to pass through them, the flow is uniform and gentle.

The muscle of the arterial wall is used to maintain the tonus of the circulation locally and to adapt the latter to the general systemic conditions. By its automatic or reflex contraction and relaxation the caliber of the artery is varied to suit the manifold conditions. It is not evident that its contraction ever occurs suddenly enough to make it an aid to the movement of the blood through its vessels. There is, however, no actual evidence that this sudden vaso-constriction does not occur, especially under abnormal conditions in the heart or the arteries. (See p. 298.)

THORACIC SUCTION, or the "aspiration of the thorax," is the most powerful of the three forces which act upon and assist the venous side of the circulation. The physical principles underlying this suction on the veins entering the boundaries of the chest have been gone over in our discussion of respiration (page 116).

The thorax is an adjustable box closed save for the trachea passing upward toward the nostrils and for the blood- and lymph-vessels extending from it both upward and downward. This box enlarges in every direction at each inspiration. Much of the increased space so made within the chest is filled by the tidal air. The same "suction" which causes the air to rush in through the trachea inevitably draws also upon the partly filled veins, which extend upward from the abdomen and downward from the neck, and, by tending to pull apart their flaccid walls, sucks inward their liquid contents toward the interior of the chest and the heart. The thoracic space being increased, fluids under pressure rush in to fill it up. This same influence is exerted on the heart itself, thereby assisting diastole of all its chambers, and also on the arteries which enter the thorax. Because, however, of their rigid, distended walls it would be nearly ineffective on the arteries, the balance of the suction thus favoring the circulation. The blood-pressure curve shows plainly that soon after the beginning of inspiration the general blood-pressure begins to rise, and that it reaches its maximum a short time after expiration begins. During inspiration the pulse-rate also tends to increase, this being effected by some nervous excitation, perhaps by an overcoming of the inhibitory influence exerted by the vagus as its augmentor fibers are stimulated in the expanding alveoli, but perhaps, too, in some other way.

FIG. 148



A typical blood-pressure tracing made from an artery. (Hall.)

COMPRESSION BY THE BODY-MUSCLES of the valve-supplied veins is another factor in causing the circulation. The veins are soft and easily compressed, being never normally distended with blood. The muscles when they contract thicken and harden, and not only thereby immediately compress the veins lying beneath, between, or within them, but they thus increase the pressure in the limb or in the vicinity and tend to cause a general compression of the veins of the region. Owing to the presence of valves within the veins, the displacement of the blood contained in these veins can occur only in one direction, and that always toward the heart. As we have seen already, this action is still more effective on the lymphatic system, and partly because the valves are there much more numerous. Of course, the contracting muscles tend to compress the arteries nearly as much as the veins, and so to impede the circulation; but here (as in the last-described cause of the circulation) the forcible distention and incompressibility of the arteries prevent any action and the balance of effect favors the circulation. In the hollow viscera having muscular movements of their own this influence on the veins must be marked—for example, because of the segmentation and the peristalsis of the intestine, and in the spleen and uterus.

THE SUCTION OF THE RELAXING AURICLES.—The last of our five causes of the circulation is the suction of the relaxing auricles. This is certainly the least important of the forces in action, for the diastole of the auricles is not a powerful movement, even the systole being relatively weak. But the diastole recurs very frequently and in itself is one of the constant causes of the circulation. Moreover, the auricular expansion is greatly aided by the respiratory enlargement of the thorax as described above. These agencies together are sufficient to produce in the vena cava and auricles of the dog a negative pressure equal to that of a few millimeters of mercury, as has often been shown by manometers connected with cannulæ in the vessels and auricles. Such a suction must have material influence in returning the blood to the heart from the flaccid veins (Fig. 65).

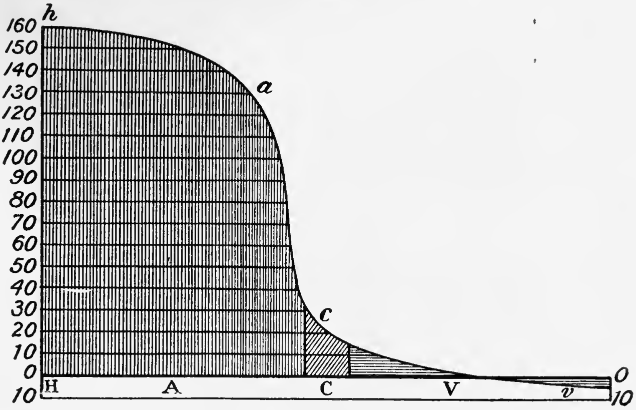
Agencies which tend to *retard* the circulation of the blood are easily appreciated from the foregoing facts as to the forces which promote it. Aside from function, these naturally are mostly pathological rather than normal. Growths on the heart's valves are probably the most frequent cause of disorder. The valves on this account being hindered from closing tightly, allow of regurgitation of the blood in the direction opposite to the proper circulation. In other cases the openings are narrowed by disease causing by this stenosis, as it is called, an incompleteness in the filling of the ventricles or in the distention of the great arteries. (See the experiments in the Appendix.) Sometimes the heart-muscle becomes weakened by a deposit of fat, or from too long-continued overwork, or from lack of normal metabolism due to worry perhaps. Often the arteries become hardened (sclerosed), so that they lose much of their essential elasticity. The capillaries may be far too permeable, allowing too much lymph to soak outward into the tissues, so forming edema (dropsy) when drainage back to the heart is poor. Sometimes by local pressure (as from a tumor) on a large vein, a condition of venous stasis is produced, and occasionally too much standing gives rise to a similar condition of chronic venous engorgement in the legs (varicose veins), man's organism not yet having become completely adapted, as it seems, to his recently assumed erect posture.

The Speed of the Blood-current has been studied mostly in the brutes, and yet we probably have a fair notion of it as it is in man. It varies widely in different places and at different times. The matter is more complex than appears at first glance, as the principles of hydraulics would suggest. All the considerations concerning speed are complicated by the ever-varying caliber of all the blood and lymph vessels except possibly the capillaries.

Perhaps a fair statement of the average arterial velocity in man is 150 mm. per second. It is much greater than this near the heart, and very much less near the capillaries, for the friction in a tube increases very greatly with decreasing diameter. In the aorta the speed may well enough be three times the average, while in the opposite direction the speed rapidly lessens perhaps to one three-hundredth of the average.

In the capillaries then it has been estimated that the blood's velocity is not over 0.5 mm. per second, which is about one mile in thirty-seven days. The capillaries average in length about 0.5 mm., so that the blood-flow through the capillaries requires about one second. In this 0.5 mm. alone and in this one second alone, the blood is in practical contact functionally with the tissues and performs promptly all its varied functions. If one compares this mile in thirty-seven days with the mile in three hours which the blood moves on the average in the arteries, one has somewhat of a rough measurement of the effects of the great friction in the capillaries, despite the exceedingly smooth surface of the endothelium in the tubes.

Fig. 149



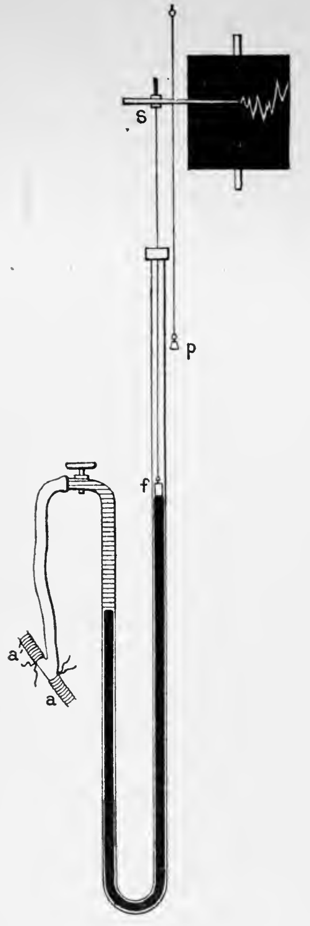
The blood's pressure as it varies in different regions of the circulation, indicated by the graphic method. Abscissa *o, o,* indicates the regions and zero pressure, while the ordinate *o, h,* suggests the blood-pressures in millimeters of mercury. The pressure then at the heart, *h*, is about 160 mm. Hg., falling at first slowly then rapidly in the arteries to about 35 mm.; ranging thither to about 15 mm. in the capillaries; while in the course of the veins the pressure falls to about 9 mm. Hg. less than zero, the suction of the heart in diastole. (Yeo.)

In the veins the velocity increases rapidly from the capillaries to the heart. Probably the average blood-speed here is less than that in the arteries.

The Circulation-time is the period in which a given erythrocyte, for example, if unimpeded, can go from the heart to the feet and back to the heart and thence around the pulmonary circulation. Hering's experiments showed that in a horse the time required for the pulmonary circulation plus the circulation through the head was twenty or thirty seconds, and Vierordt found the period in the dog to be about seventeen seconds. Stewart estimates that the total circulation-time in man is about one minute or a little more. These figures suggest vividly how active is the circulation and how completely unified by its means are the semi-fluid tissue-protoplasm and the circulating-liquid.

The Pulse-wave is a rapid impulse sent through the arteries by the ventricular contraction. It must be carefully distinguished from the current of blood whose velocity has just been mentioned. They have little in common, and yet they are sometimes at first confused. The wave is accompanied by a progressive distention of the arterial wall, and travels at a rate of from 7 to 9 m. per second. It is greater in the upper extremities than in the lower because the arteries there are more elastic than in the legs (Zermak). The pulse-wave is at least fifty times more rapid than the blood-current through the same blood-vessel. It is not to be found under ordinary conditions in the capillaries or in the veins because the extreme smallness of the former tubes prevents its passage through into the latter. The length of the pulse-wave is about 5 m. or would be were the arteries long enough to allow both crests of the wave to be distinguished at one time. (See the sphygmograms in the Appendix.)

Fig. 150

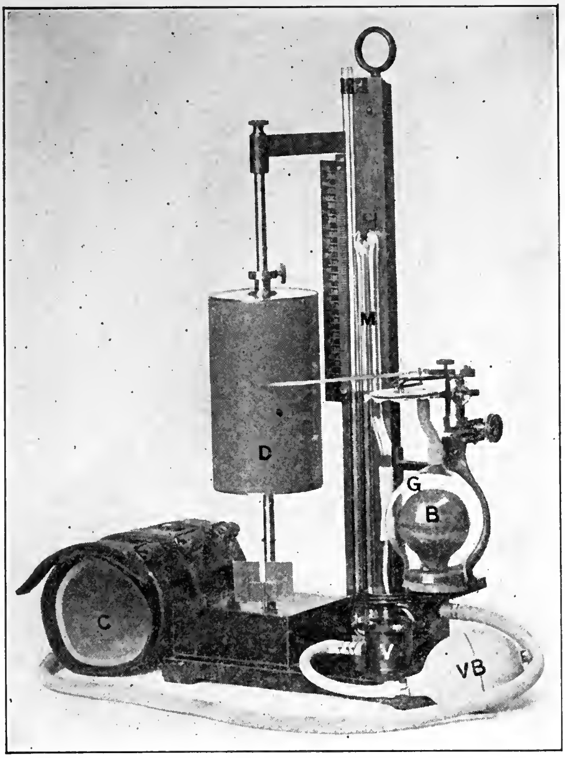


Ludwig's kymograph-manometer: *a*, *a'*, artery whose pulse and blood-pressure are being recorded on the smoked drum; the U-tube is filled with mercury, the tube between it and the artery with, say magnesium sulphate solution; *f* is a float, and *S*, the writing arm; *P* is a light pendulum resting against the arm to keep it in contact with the drum.

Blood-pressure has of late received much study from surgeons as well as from physiologists because of its practical importance, especially in relation to surgical shock. Blood-pressure is the very varying amount of force exerted laterally by the blood against the walls of the heart, arteries, capillaries, and veins enclosing it. Highest within the left ventricle at systole, the blood-pressure falls at first slowly through the arteries until the arterioles are reached, when it falls rapidly. Before entering the capillaries, 80 per cent. of the pressure has been taken up in friction and four-fifths of the total fall between the ventricle and the auricle again has occurred. Within the 0.5 mm. or so of the capillaries 10 per cent. more is lost and the blood enters the veins under a pressure of not more than 10 or 20 mm. of mercury. From here to the auricle the fall is more nearly uniform than elsewhere in the circulation. At some place within the veins (perhaps in the beginning of the vena cava) the blood loses all its positive pressure when compared with the atmospheric standard, and before it reaches the auricles, now expanding to receive it back, the pressure is a negative quantity, that is, a small degree of suction.

The instrument used to measure blood-pressure is called the sphygmometer, and of this apparatus there are many forms, some of which are practicable instruments of no little use in surgery. Their practical use to the surgeon is greatly lessened by the important fact that the blood-pressure in any one available artery is little indication of its degree in the more vital parts of the body. It is indeed a more variable and a more complicated matter than was suspected a few years ago. It is

Fig. 151

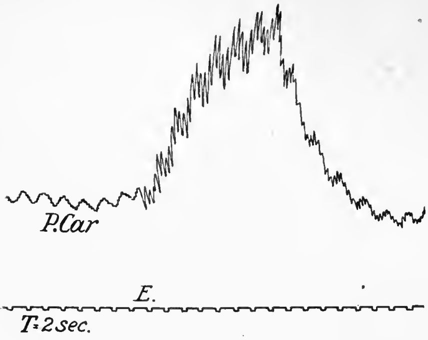


Erlanger's apparatus for determination of the blood-pressure in man. The apparatus is provided with a pneumatic cuff (*C*), which consists of an inside rubber bag and an outside leather band. The whole cuff can be buckled around the arm above the elbow. The air cavity within the rubber bag of the cuff communicates through a thick-walled rubber tube and a four-way connection, ${}^{2}\overset{3}{\underset{1}{=\!\!\!|\!\!\!=}}$ with the three other essential parts of the apparatus, namely: (1) *downward*, with the valved bulb (*V B*), by means of which air can be forced into the cuff and can thus be made to compress the arm; (2) *to the left*, with the mercury manometer (*M*), from which the amount of pressure applied to the arm can be read directly in *mm.* of *Hg.;* and (3) *upward*, with the distensible bag (*B*) inside the glass chamber (*G*). This bag, last mentioned, responds to fluctuations of pressure inside the rubber bag of the arm, which are due to vibrations of the arterial wall, and the tambour at the top records such vibrations on the drum (*D*).

one of the functions of the elaborate vasomotor apparatus always to adapt the pressure in a given part to the needs of that region at that time. The blood-pressure therefore is continually changing in all parts of the body as the needs of different areas require. Blood-pressure in general is one index of the quantity and activity of the blood-supply. Under certain conditions, however, the arteries and arterioles may be relaxed and ample blood be coming to the part, although under a low pressure.

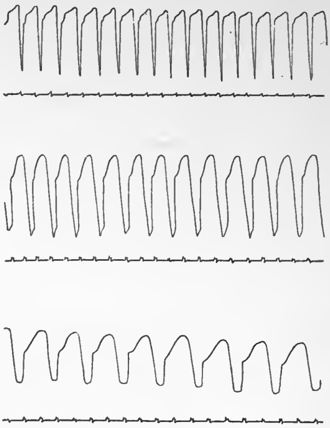
The average arterial pressure in young men appears to lie between 90 and 150 mm. of mercury. Mental excitement or fever, for example, promptly raises the blood-pressure, while pain lowers it. The actual blood-pressure in a vessel at any time is the result of an hydraulic balance between the caliber of the arteries and the work done by the heart. If the arteries are dilated and the heart is beating fast and vigorously the pressure in a given artery may be the same as it would be if the artery were constricted and the heart beating slowly and with less vigor. In the capillaries the blood-pressure is from 20 to perhaps 70 mm. of mercury. In the veins it is from 15 mm. or so to a negative quantity of from 3 to 7 mm. (See Fig. 149.)

FIG. 152



Tracing to show the rise of pressure in the carotid from excitation of an afferent nerve other than the depressor. The stimulus was applied at *E* and continued fourteen seconds. (Meyer.)

FIG. 153



Frog-cardiograms to show the relations of pulse-rate to the heart-muscle's temperature The top curve records the beat of the heart at 35° C., the middle line at 20°, and the bottom line at 5°. By the suspension-method. To be read from left to right. The time-line is in seconds. Reduced.

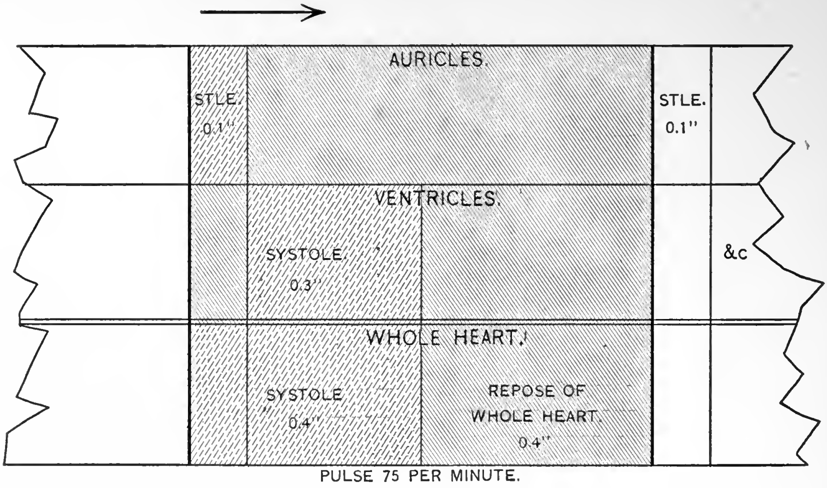
The Pulse-rate of the Heart is the number of times per minute that it beats; sometimes the term heart-rate is used. In the average man, the pulse-rate is about 72 per minute, and in the average woman not far from 78 or 80. As an average rate (like many other averages, seldom met with in fact), we may use 75, especially because then by chance the various movements of the heart occupy periods of time which may be stated exactly in whole tenths of a second. Personal variations of considerable degree from the average are common. Some individuals in perfect health exhibit a normal rate of 60, or even less, while the hearts of others contract year after year 90 times per minute. A rate of 20 has once or twice been recorded, and several times rates of much over 100. Napoleon exhibited his variation from the average of humanity by a pulse-rate of 40 not less than by so many other deviations.

Many sorts of influences effect the pulse-rate, most of which, at least, are dependent on the activity of tissue-metabolism or on the degree of excitement in the nervous system, or on both of these at once, although, in a sense, nervous excitement is reducible to the terms of tissue-metabolism. It is, then, not far wrong to say that any influence or condition which increases metabolism to a considerable degree increases the heart-rate. There are sixteen or seventeen of these conditions in man which may be noted. Most conspicuous, perhaps, of these is age, for in the embryo the heart beats 150 times or so per minute. The rate falls progressively to the normal adult figures given above and rises again slightly in old age. Sex is practically the next most important variant of the heart-rate. Females have higher rates than males of like age and temperament. One sees this difference not only as regards the number but as regards the variability of the female rate. Young girls especially are subject to very wide changes in the pulse-rate in a purely physiological way. Size influences pulse-rate, for it is higher in small than in large persons. Temperament is very effective, slow phlegmatic persons having a lower heart-rate than those with short reaction-times. Persons who are normally nervous have a wide range in their heart-rates. Bodily or atmospheric temperature causes a variation, a rise of temperature within or without the body producing an increase in the rapidity of the heart. Eating increases the rate for two hours or so, until the activity of metabolism has dropped back to its average. Being above the sea-level increases the pulse-rate because the necessary increase in respiration demands greater activity in the circulation. Increase of respirations from whatever cause tends to increase the activity of the heart, there being a tendency to keep a ratio of one to four. Sleep lessens the heart-rate. Muscular exercise increases the pulse-rate markedly, even up to 200 or more. Posture has considerable influence, the rate being higher when a person stands than when he sits and lowest when he is reclining. Mental excitement increases the frequency of the heart-rate, especially in females. Pain increases the pulse-rate in man, although in the rabbit, for example, it decreases it. Extreme bodily weakness is liable to show increase in the heart-rate. An increase in arterial blood-pressure raises it, the more rapid rate being necessary to compensate for the increased friction. And many drugs change the frequency of the heart-beat in one or the other direction.

These variants of the pulse-rate are of much practical importance. The more of them the physician takes into consideration in estimating any given patient's pulse, the more valuable will be his estimate as an index of the latter's condition. The trained physician and surgeon take practically all of these variants into consideration without realizing it perhaps, but they none the less on that account affect the estimate.

The Cardiac Sequence comprises the various contractile events in one complete beat of the heart and their time-relations. This "cycle" extends from the beginning of one auricular systole to that of the next. We will take the average rate of 75 beats per minute and see how the various parts of the heart are differently using these beat-periods. At this rate each beat occupies one seventy-fifth of sixty seconds or 0.8 second, and tenths of a second are also eighths of a beat-period, as it very conveniently happens. The systole of the auricle (or auricles, for the two contract almost exactly together, as do the two ventricles) occupies, at this pulse-rate, 0.1 second. Immediately begins the systole of the ventricles, and this requires 0.3 second, which, added to the 0.1 second, makes 0.4 second, or half of the 0.8 second which the beat requires. The other half of the 0.8 second, 0.4 second, is part of the whole heart's rest-time. During this period, as well as during the 0.1 second of the succeeding auricular systole, the ventricles are in restful diastole while being slowly filled with blood from the auricles and great veins. Thus, the ventricles work in each beat-period 0.3 second and rest the remainder of the beat-period, 0.5 second. The auricles work only 0.1 second (if we disregard the possibility of an active diastole), and rest during the remaining 0.7 second, while the ventricles are both contracting and resting. Thus the auricles work one-eighth of the time and rest seven-

FIG. 154



The cardiac sequence. One beat out of the continuous series. The lighter areas, contraction (systole); the darker areas, rest or relaxation (diastole).

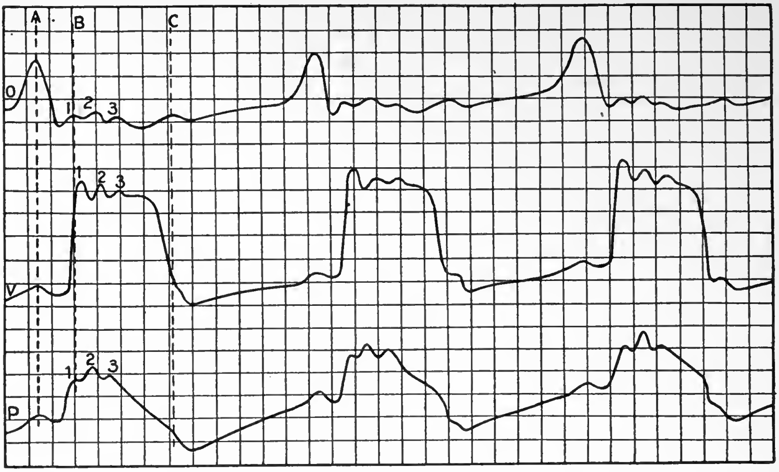
eighths of the time; the ventricles work three-eighths of the time and rest five-eighths. Averaging the rest-periods of the auricles and of the ventricles, we see that the heart, as a whole, may be said to rest six-eighths or three-quarters of every beat-period. We can no longer think, therefore, of the heart as "an organ which never rests"—it works, indeed, only six hours out of the twenty-four! When the rate increases, the rest-periods are shortened, and the time of the systoles is very little decreased.

It is not known exactly what proportions of the 0.7 second in the auricles and of 0.5 second in the ventricles (intervals between their respective systoles) are actually occupied in relaxation or diastole, but probably a large part of these periods is so occupied. In any event, practically all of it is a period of rest or anabolism for the muscle-protoplasm, unless (a possibility only) some of the muscle-cells of the auricles are meanwhile working to actively expand them.

The relations of the valves' actions to the movements of the chambers will be understood if we go over somewhat more in detail *the phenomena of the beat.* While the auricles are contracting the ventricles are having the last fifth of their rest; while the ventricles are contracting the auricles are expanding; after the contraction of the ventricles the whole heart at once rests until the auricles contract again. This latter contraction begins in the great veins, and extends with great rapidity over both auricles at once toward the auriculo-ventricular groove. This systole very suddenly (0.1 second) empties the auricles in the direction of the least resistance—namely, into the now expanded ventricles through the wide-open mitral and tricuspid valves. Upward there is more resistance than below, not so much because of the few valves between the auricles and the veins, as because the veins have previously contracted and so exert the resistance of a column of blood extending backward, against much pressure, even to the capillaries. It is likely that the passive relaxation of the very thick ventricular walls exerts a suction on the auricles of rather more than 23 mm. of mercury. The semilunar valves are meanwhile shut. The very sudden and quick systole of the auricles completely fills the ventricles, and the eddies formed by this sudden torrent pouring in among the thickly set papillary muscles, promptly float together the flaps of the auriculo-ventricular valves. The close apposition of the edges of the flaps is secured by contraction of the papillary muscles which begins (according to Chaveau) in the very brief interval between the two systoles. As the ventricles contract, the auriculo-ventricular openings lessen, also, thus tightening still more these valves for the pressure they are to withstand. Without appreciable pause, the ventricles begin to contract, but they occupy thrice as much time in their systole as do the auricles. Meanwhile, this strains the auriculo-ventricular valves and stretches tight the tendinous cords which prevents their flaps from being pushed upward into the auricles.

As the ventricles contract, the pressure within them rapidly rises and soon reaches such a degree that, despite the pressure in the great arteries holding the semilunar valves shut, these valves are forcibly burst open and the torrent of blood pours outward into the aorta and the pulmonary arteries. The opening of these valves could occur only when the pressure below them had come to exceed that in the arteries above them—namely, about 200 mm. of mercury. As the great arteries are distended with blood, the little pouches (sinuses of Valsalva) behind the cups of the semilunar valves become filled. At the instant when ventricular systole is complete and the pressure in the ventricles therefore stops rising, more blood is forced into these sinuses by the instantaneous passive recoil of the distended arterial walls, and thus the cups of these semilunar valves are pushed together. With the aid of the corpora Arantii they quite close their openings. The semilunar valves then are open only during the latter part of ventricular systole, say for 0.2 second, just long enough for the blood to be crowded through them into the already distended arteries. The auriculo-ventricular (mitral and tricuspid) valves are closed for a somewhat longer period—namely, during practically the whole of ventricular systole and for a brief interval afterward, for 0.4 second perhaps altogether. These two sets of valves are open alternately, but never at the same time save for a specious instant at the beginning of ventricular systole when the semilunars are already open, but the auriculo-ventriculars are not yet closed. This is a condition that in practice may or may not be present, depending on the pressure in the great arteries which determines the time of opening of the semilunars.

Fig. 155



Traces showing *O*, the auricular pressure; *V*, the ventricular pressure; and *P*, the beat of the heart, together with their time-relations, in the horse. (Chauveau and Marey.)

At once after ventricular systole, ventricular diastole begins and lasts about 0.5 second, until the conclusion of the auricular systole of the next sequence or beat. During nearly all this time the semilunar valves are shut and the mitral and tricuspid open. This allows the blood constantly returning to the heart by the veins to pour through the auricles directly, it is likely, into the ventricles. This flow is urged by the suction of the expanding auricles during ventricular systole, and then by the suction of the expanding ventricles themselves. In those beats which occur during inspiration, the enlargement of the thorax helps the expansion of all the heart's chambers, but the influence exerted on the thin-walled auricles is much greater than that on the ventricles whose walls are many times as thick. During expiration, on the contrary, when the highly elastic lungs, etc., are compressing the contents of the chest, the great veins and the auricles share in the compression, auricular systole being aided more than ventricular.

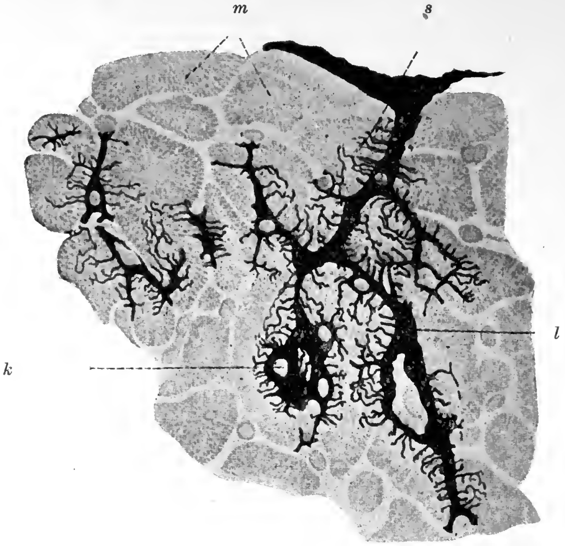
The various valves of the heart are marvels of mechanical perfection. We do not need to go into the functional details of these organs, however, for there is little about them, unless it be the exact mode of action of the tendinous cords, and papillary muscles, which their detailed anatomy does not at once suggest. When one remembers that these complicated valves act perfectly for the average individual more than a hundred thousand times every day, the wonder is that valvular heart-disease is not more common than it is, and sudden death not much more frequent from their laceration or obstruction.

The Sounds of the Heart may be heard plainly by the ear placed on any part of the thorax, but most clearly in front on either side of the sternum. In number these sounds are two, separated by a short pause, while a longer pause separates those of one beat from the first sound of the next. If we try to represent these sounds by letters, we may use *flūb* and *dŭp* better than any others perhaps (the vowel in the first being long and that in the second very short), while the interval between them is shorter even than the second sound.

The *first sound* has given rise to considerable discussion, especially as to its mechanical cause in the heart. With a pulse-rate of 75, this sound lasts about the same time as does the ventricular systole, 0.3 second, and coincides with it in time. Its cause, then, is doubtless, in part at least, the powerful contraction of the three layers of muscle composing the ventricles as they sharply slide over and compress one another and the mass of blood within them.

Within the ventricles are numerous muscular and tendinous structures extending nearly all through the cavity of the ventricles, and these are crowded together and by their vibrations produce sound as they squeeze the blood out from between them. Careful analysis of the sound with resonators has made obvious two elements: a sort of flapping and string-like tone of higher pitch, and beneath and subduing it a longer noise more like a rumble. The former part probably comes from the closure of the auriculo-ventricular valves, and especially from the vibration of the tendinous cords attached to them and stretched in both directions by the forced closure of the valve-flaps and the contraction of the papillary muscles and fleshy columns during the first portion of the systole. It cannot be doubted that the friction of the heart's apex against the chest-wall plays a part in producing this sound, and probably also the vibration of the columns of blood both within the ventricles and in the first part of the great arteries. When one considers the extreme and sudden vigor with which the ventricles contract, becoming very tense and hard, it is not difficult to understand how a sound is produced. The valves' closure has comparatively little to do with it, for when the valves are mechanically kept from closing, the gross sound is altered but little, and the main tone persists in its entirety. That many elements enter into the production of the first sound is certain, and of these probably the more important have now been described.

Fig. 156



Nutrition of the heart-muscle in the pig; Golgi's method: *l*, intermuscular spaces from which numerous nutrition-canals (*s*) pass into the muscle-fibers; *k*, blood-capillaries; *m*, sectioned muscle-fibers. (Nyström.)

The *second sound* follows the first after a very brief interval, perhaps 0.1 second, the gradual dying-away of the first sound including most of this period. There has been less discussion as to the cause of the second sound, for it is obviously the kind of noise made by the sudden closure of a valve at the end of a tube in which the pressure of a liquid is high. Furthermore, it occurs just at the time when the two semilunar valves are closing—namely, just after the end of ventricular systole. It is then undoubtedly made by the sudden closure of these valves. Did the pulmonary and the aortic valves close exactly at the same time, this sound would be still shorter and sharper than it is. Owing, however, probably to local variations in the pressures within the aorta and the pulmonary arteries sometimes, one valve may close a minute fraction of a second before the others. The sound is intensified and perhaps altered materially in tone by the vibration of the tense column of blood set in motion by the ventricular systole and by the slapping shut of the valves as the arterial walls passively (and hence almost instantly) recoil.

The Heart-beat as Muscular Action.—The physiology of the heart as a muscle is studied in the laboratory (see Expt. 69, etc., therefore, in the Appendix). Out of the large mass of facts learned about the complexities of the cardiac muscle, one of the most important perhaps is the rhythmicity apparently inherent in the heart. Whether the rhythmic heart-beat is produced by the action of the circulating salines (perhaps through the ions) on the heart muscle directly or is brought about by the rhythmic stimulation of nerve cells, as Dogiel has recently claimed so vigorously, it is the most striking fact in relation to the heart. Another fact about the heart muscle recently come into prominence is its duality of action; it has apparently the characteristics of both smooth muscle and of cross-striated muscle. The former kind of contractile tissue is represented in the heart's action by its tonic variations in size. These occur probably under the influence of the vasomotor apparatus and correlate its action with the caliber of the arteries. The cross-striated aspect of the heart-muscle is represented in its sharp, quick, and powerful beat. It is hoped that the years soon to come will clear up these matters concerning the heart, for they are of the utmost practical importance to diseased humanity and in a theoretical way to physiology, striving to arrive at the principles of organic things.

The Influence of Nerves on the Heart.—We do not yet know the exact relations between the nerves of the heart and its muscle-cells. One hypothesis, the neurogenic theory, maintains that the heart's rhythmic beat depends on rhythmic stimulation from the central nervous system or at least from nerve cells in the heart. The other supposition, the myogenic theory, maintains that, provided the heart-muscle be supplied with its nutritive fluid (the blood and the lymph) of the right temperature, etc., the heart tends to keep up its rhythmicity without continual influence from the nervous system. To the "myogenists," then, it seems that

FIG. 157

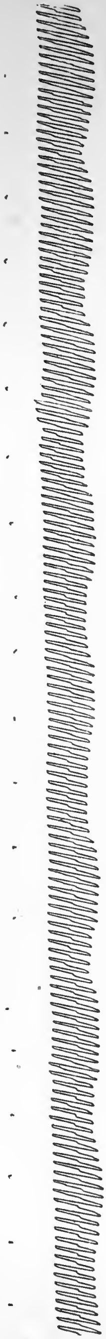


FIG. 157.—This tracing shows in an unusual degree the tonus in the frog's heart. Suspension-method. To be read from left to right. The dots are at about ten-second intervals. $^2/_3$.

the nervous system only *controls* its beat, coördinating it with the needs of the organism. The recent researches of Dogiel and his colleagues indicate very strongly that neurones centering in the various ganglia of the heart itself direct and perhaps initiate the actual contractions of the organ. These knots of short neurones are in the closest relation with the central nervous system, and it is with the latter and the nerves between it and the heart that we are chiefly concerned. (See the experiments in the Appendix, page 515.) On the other hand, the auriculo-ventricular muscle-bundle, which connects intimately and directly the inter-auricular septum with the musculature of the ventricles tends to complicate still further the question of heart-actuation. The large number of facts and suppositions which have been accumulated on each side of this far-reaching question of the relation of muscle and nerve remain to be unified into the certain truth.

In general terms the nervous impulses connected with the heart appear to be at least of three sorts. In the first place, there is probably a set of afferent nerve-paths (in the rabbit and dog called the depressor) which keep the central nervous system informed as to the nutritive and hydraulic conditions in the heart-muscle. There are influences always coming to the heart which tend to check its action—namely, the inhibitory influences. And there are impulses continually passing to the heart which cause it to augment its activity.

THE SYMPATHETIC INFLUENCE (to consider the last first) comes probably to the muscle-cells of the heart from a center in the medulla by a route now fairly well known in the dog, rabbit, and cat; it is doubtless similar in man. The fibers bearing these augmentor impulses leave the spinal cord by the anterior roots of the second and third, and perhaps fourth and fifth, thoracic nerves, pass, by means of the rami communicantes, to the ganglion stellatum (the first thoracic ganglion of the sympathetic), thence upward through the annulus of Vieussens (surrounding the subclavian artery) to the inferior cervical ganglion. Thence, and from the annulus as well, non-medullated fibers pass to the heart-muscle by way of nerve-cells. These fibers are post-ganglionic branches (axones) of cells in the stellate ganglion, which in turn are in close relation with the fine, medullated, preganglionic fibers coming from the cord. In man these post-ganglionic fibers pass from the inferior cervical ganglion and the annulus in three groups and enter the cardiac plexus, whence they pass to the muscle-cells.

Stimulation with electricity of these branches of the cervical ganglion causes in the dog an increase in the frequency of the pulse of even 75 per cent. of its normal rate, while the force of the contraction is also much increased. The conductivity of the heart-muscle is raised also, and a negative electric variation set up opposite in direction from that of inhibition. The sympathetic is therefore a truly augmentory nerve, its influence from the medulla oblongata probably not only hastening but increasing the force of the beat. It has no power, however, of starting a heart which has stopped all contraction as seen through a microscope.

The sympathetic exerts its augmentor effect very slowly, but it affects both ventricle and auricle (Gaskell).

The influence of the vagus on the heart is in general opposite to that of the sympathetic. The fine medullated efferent fibers of the vagus-trunk arise in the floor of the fourth ventricle of the brain in a cluster of nerve-cells near the tip of the calamus scriptorius—not far then from the respiratory centers with which they are obviously closely connected functionally. The course of the fibers between this center and the heart is still in doubt. It is, for example, not certainly known as yet what relations, if any, they have with the spinal accessory. It is apparent that the (preganglionic) fibers passing to the heart-muscle end in ganglion-cells situated mostly in the auricles, and that (postganglionic) fibers of the unmedullated sort pass from these cells, one perhaps from each to the muscle-tissue Here again there is difference in the experimental product of various researches, and the anatomy of the vagus from brain to heart-cells is obviously very incomplete.

The action of the vagus nerve on the heart is in the direction of a lessening of that organ's activity. In other words, it is inhibitory. Stimulation of the vagus produces inhibition in several respects (Gaskell). It lengthens the diastole of the heart and thus decreases the number of beats in a given time. It lessens the force of systole, making the auricles and ventricles contract less vigorously. It diminishes the tonus (size, etc.) of the organ. It decreases the conductivity of the contractile impulse to the muscle. It changes the electrical state of the heart-muscle, making it more positive.

The whole subject of *inhibition* is a mysterious one, but its great importance as a mode of animal functioning becomes continually clearer. In the heart one sees an excellent example of it, but how is it brought about? Gaskell's trophic theory is at present receiving more notice than any other hypothesis, and many things of different kinds point to its probable truth. This supposition is, in a word, that inhibition in the heart means a balance of the anabolic and the katabolic processes in the nutrition of its protoplasm. Action implies katabolism in the active cells, but an increase in constructive, anabolic process would tend to check these destructive katabolic changes, to rest the heart, and to increase its store of energy. In the frog's heart one sees in the secondary augmentation noted below evidence that the organ's energy rises during the period of inhibition, and in mammals the same tendency obtains. The anabolic (vagal) influence seems to interfere more with the katabolism than does the katabolic (sympathetic) influence with the anabolism of the muscle. Until more than is now known is learned about the metabolic processes of muscle in general little can be done to prove or to disprove this interesting theory. It appears at any rate to be a step toward the solution of the problem of trophic influence which the nervous system is supposed to exert, and it may be useful later on in helping out our knowledge of secretion. Just now it is the easiest way to explain(?) the inhibition of the heart and, by analogy, of the other viscera.

If the vagus be cut within the skull of an animal (amphibian or mammal), and the peripheral stump be stimulated with an induced electrical current, the result is inhibition, more or less, of the heart. The details of this effect depend not only on the strength of the stimulus, but on the condition, as well as the genus, of the animal. A latent period is first obvious, then there occurs a slowing of the beat (perhaps a stopping) and a decrease in the force of the contractions. If the stimulation last only a few seconds, the inhibition is continued meanwhile and for a longer or a shorter time after the former is stopped. Immediately afterward the heart gradually increases the force (extent) of its contractions until they may far exceed their amplitude and rate before the stimulation. If the excitation be long-continued, it is soon obvious that the vagus has lost control of the heart, for despite its influence the diastoles shorten, the contractions increase in force, and the heart is soon beating almost as if the vagus were not conducting inhibitory impulses to it. This last phenomenon is due perhaps to the rhythmicity which is almost part of the muscle-cells of the heart, and perhaps due to resident ganglia. It shows that nothing short of destruction of tissue can long impede the beating. The secondary augmentation of the beat (occurring after the inhibition) is much more conspicuous in the frog, etc., than in the mammal, and so far is the influence of the vagus over the ventricles. Indeed, in the mammal this latter effect is often quite inappreciable.

There is plenty of evidence that both of these sets of nerves are conducting regulating impulses to the heart continually and that the way the viscus works is in a measure the result of the balance between the two influences, augmentor and inhibitory. Removal of the inhibitory factor by the cutting of both vagi alone allows the augmentor to increase the rate of the heart-beat. On the contrary, cutting of both vagi and removal of the two ganglia in the course of the augmentor fibers from the cord to the heart (the stellate and the inferior cervical ganglia) make the organ work harder. Changes in the action of the heart occasioned reflexly by afferent (sensory) impulses from different parts of the body are sometimes in one direction and sometimes in the other, depending largely apparently on which of the two so-called centers receives the stronger impression. This may be partly due, however, to the fact that the inhibitor is much more dependent apparently than is the augmentor on the length and the strength of its stimulus. The latter is sometimes influenced by a stimulation so brief that it would affect the inhibitor little or not at all.

The nerves of the heart are in some sort of connection with the brain-cortex as a whole. In consequence, the heart may be readily influenced by impulses coming down the central nervous system from above as well as by afferent impulses passing upward. Thus, occasionally one meets a person who can voluntarily slow or even stop his heart-beat. It is possible, indeed, that the fakirs of India who put themselves into a state of artificial hibernation for long periods possess this dangerous faculty. This influence probably comes primarily from the cortex of the frontal lobes. On the other hand, many emotions and mental excitement in general hasten the heart, these impulses coming perhaps from the optic thalami, the possible centers of emotional expression. Depressive or asthenic emotions (for example, terror) may inhibit the heart at first even to complete and sometimes permanent stand-still, as one sees too often in practical jokes with "ghosts," etc., played on "nervous" people. (See Expts. 85, 86, and 87, in the Appendix.)

THE AFFERENT NERVE OF THE HEART in man runs its fibers in the vagus trunk, but in the rabbit it is a separate nerve. It is distributed over the ventricles, and centrally seems to be in close relation with the vasomotor centers located probably in the medulla. Stimulation of the peripheral stump after the nerve has been cut gives no effect appreciable, but stimulation of the central stump causes often a halving of the blood-pressure (due probably to general vaso-dilatation) and a diminution of the pulse-rate. Both of these effects are in the direction of reducing the labor of the heart, and this is apparently one of the most important functions of this nerve. The depressor seems to be in relation with the sensory centers of the brain, for when the central stump is stimulated in an animal not unconscious there are sometimes signs of pain. These afferent fibers of the vagus received their name "depressor" from the lowering of blood-pressure which its stimulation produces, but, as we shall soon see, the same effect may come in other ways which affect the vaso-motor (vaso-dilator?) centers.

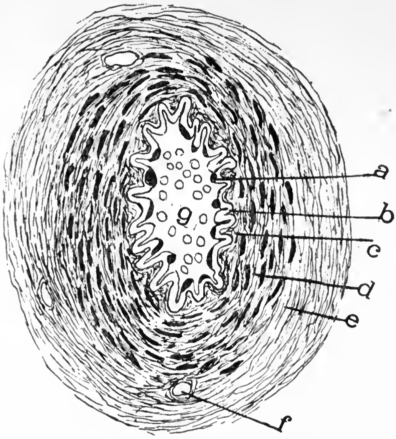
CARDIAC CENTERS.—As has been hinted already, it is probable that the medulla oblongata is the site of knots of fibers and of nerve-cells which jointly or severally control the impulses passing to the heart. They also connect these impulses and those coming from the heart with other "centers," especially with those which regulate the tonus of the blood-vessels. The former conception of a nerve-center has about gone by, leaving us in ignorance of how the fibrils of these various nerves are connected in the medulla. We may be confident, however, that each nerve does not have a localized and independent area of nerve-tissue from which messages are sent out as from one desk in a large telegraph office, quite independently of all the others. The obvious organic complexity makes unlikely any such simplicity in the control of the heart. One must think, then, of a center as an ordered system of fibers or of fibrils dominated in some way or ways by nerve-cells, trophically, and possibly but not probably as centers of force.

The Functions of the Blood- and Lymph-vessels.—These may well be described under the headings of the four sorts of vessels: arteries, capillaries, lymphatics, and veins. Each takes a somewhat different part in the circulation, although all of course are primarily the distributing tubes of the one circulation. Their differences depend on the respective uses of the vessels: the arteries distribute the blood in a complicated way; the capillaries are its somewhat loosely defined channels through the tissues; the lymphatics return the osmosed plasma to the blood-vessels proper; and the veins are passive completers of the circulation round to the heart after the blood's work is done.

The Physiology of the Arteries.—The structure of the blood-vessels will be found described in the text-books of anatomy and of histology. The structure of each sort of vessel is immediately dependent on its functions and vice versa. The arterial walls are very elastic and strong, and contractile by means of the thick layers of unstriated muscle-cells contained in them.

In discussing the causes of the circulation we have already seen in what way the passive elasticity of the arteries serves the distribution of blood. It acts as a propelling force during the five-eighths of the time when the ventricles are not contracting. The pressure is purely a passive recoil of elastic tissues and not an active muscular movement. The elasticity is of use furthermore in allowing of the distention of the arteries to accommodate the sudden influx of blood at each heart-beat. It is the uprise of the arterial wall during this influx which gives the pulse, long an important practical matter in medical art and science.

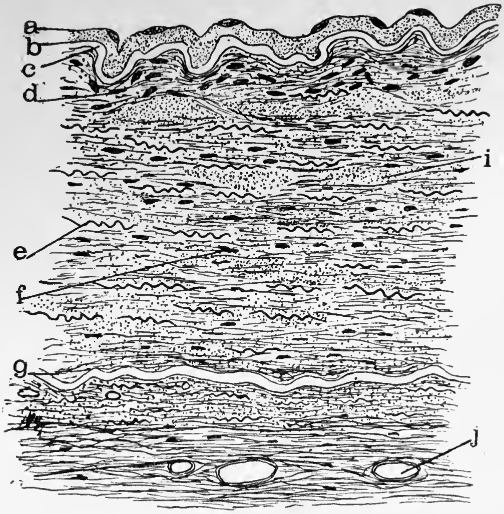
Fig. 158



Cross-section of medium sized artery: *a*, endothelium cells lining the lumen; *b*, internal elastic membrane; *c*, subendothelial connective tissue; *d*, muscle-cells of media; *e*, connective tissue of adventitia; *f*, vasa vasorum. (Bates.)

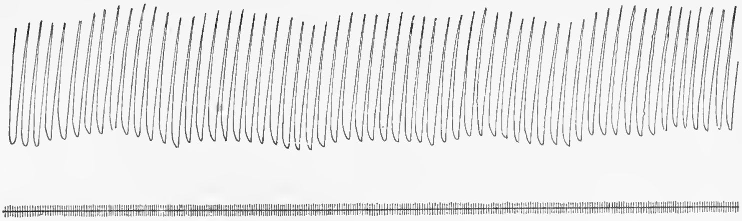
The pulse may be felt with the finger over any artery not too small or too deeply hidden in the body. The vessel most often employed for observation of the qualities of the pulse is the radial artery in the wrist, although the temporal is often used just anterior to the tragus of the ear, especially in case of children. The carotids at either side of and just below the larynx are sometimes convenient, but they indicate less than the others because of the soft tissues, rather than bone, behind them. Wherever it be felt, the essential element of the pulse is an uprise of the arterial wall toward the finger as the tube distends with the blood pushed onward from the ventricle. The trained finger readily distinguishes the gradual though quick hardening of the arterial cylinder and its more gradual softening again, at each heart-beat. The conditions are such that the pulse gives information not only concerning the vigor of the heart, the quickness of its systole, the pulse-rate, and whether the valves are working properly or not, but also to the trained observer the scarcely less important information as to the relative elasticity or rigidity of the arterial wall, the tonal size of the artery, and the resistance peripheral to it. These seven relations, and others of less practical importance, are all purely mechanical conditions dependent solely on the structure and workings of the cardiac pump and the tubes of the circulation. So much in the animal economy depends on the functions of the heart and on the relations of the blood-pressure that the pulse is of great practical and theoretical importance. The knowledge to be gained from it is somewhat lessened by the fact that what is felt is the resultant effect, the balance, of several combined influences, and it may be hard to accord this effect to its several true causes. Thus, for example, a low peripheral resistance from relaxed capillaries may give the same sort of

Fig. 159



Section through the wall of an artery: *a*, endothelial cells of intima; *b*, subendothelial connective-tissue; *c*, internal elastic membrane; *d*, elastic connective-tissue; *e*, elastic fibers in the substance of the media; *f*, nuclei of involuntary muscle fibers; *g*, external elastic membrane; *h*, adventitia; *i*, connective-tissue; *j*, vasa vasorum. (Bates.)

Fig. 160

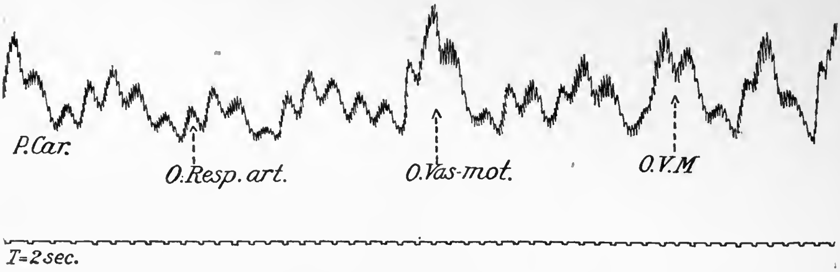


Tortoise cardiograms by the isolated suspension-method to show the tonus. The larger waves are the (vaso-motor?) variations in tone. To be read from left to right. The time-line is in seconds. (See also Fig. 157.)

pulse that would come from a low central resistance due, say, to an aortic-valve insufficiency. A hard "pulse" (artery) might come from a very vigorous systole with low capillary resistance or from a much weaker systole with narrowed capillaries; in either case, however, it represents a high arterial pressure, whatever the conditions giving rise to it. Again, a very quick sudden systole would be partly masked were the arteries somewhat inelastic from disease. The important elements of blood-pressure lie largely in the capillaries, for there its effects are exercised, but the conditions in the arteries must be well understood, because they supply the capillaries with blood.

Whether felt directly with the trained finger or observed indirectly in the tracing made by a mechanical appliance (sphygmograph), these several factors of the pulse produce effects which may be studied, measured, and compared, and especially in the permanent written trace, the sphygmogram.

Fig. 161



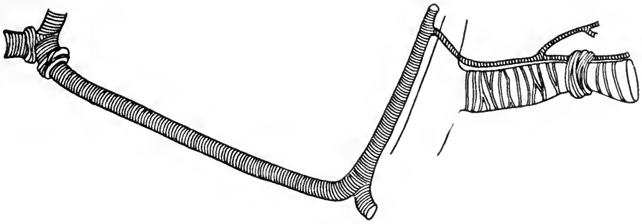
Sphygmogram from a curarized dog kept alive by artificial respiration to show especially the vaso-motor pressure-changes: *Resp. art.*, an artificial respiration making the pressure rise and fall; *Vas-mot.* and *V. M.*, rises and falls of pressure from vaso-motor changes. (The smallest waves are those of the pulse. Each division of the time-line is 2 seconds.) (Meyer.)

Vaso-motion is the narrowing and expanding of the arterial tubes by the contraction and relaxation respectively of the smooth muscle-fibers in their walls. It is then, so far at least as the constriction is concerned, purely an active process. The expansion of the arteries is also an active process in its nervous influences and probably also in the action of the muscle fibers themselves. Vaso-motion then has to do with the tonus of the arteries. It must be carefully distinguished from the purely passive enlargement caused by the heart-beat and from the perhaps equally passive narrowing of the arterial caliber by the elastic recoil of the walls distended at each pulse. These distinctions, though basal, are easily neglected, the result being mental confusion as regards the various important forces of the circulation and the blood-pressure. Vaso-motion is probably not in normal cases concerned with the circulation of the blood, but it directly determines in large part the blood-pressure. On the other hand, the arterial elasticity is an important cause of the circulation, as we have seen, and is also a factor in blood-pressure.

The exceedingly important functions of vaso-motion are those on which blood-supply and blood-pressure depend. When a part becomes active it requires more blood than while resting: the increase is supplied largely by vaso-dilatation. Heat-regulation, as we have seen, is chiefly accomplished by varying the amount of blood in the viscera and on the body's periphery as the case demands; this is one of the chief uses of vaso-motion. The nutrition of the tissues by the lymph depends largely on osmosis from the capillaries, and this in turn is dependent on the supply of blood at the spot and on its pressure in the vessels. The case is similar with glandular action. We see, therefore, that some of the most fundamental of organic functions depend sooner or later on the relative caliber of the arteries.

The mechanism of vaso-motion (discovered by Claude Bernard in 1851) is none too well known, but it is certain that there are (autonomic) nerves connected with the arterial muscle-cells which influence the latter to contract (the vaso-constrictors), and that there are others which somehow occasion the relaxation of the arteries (the vaso-dilators). Each of these sets of sympathetic nerves has moreover a center or centers in the central nervous system, while a general directing vaso-motor center is probably one of the numerous centers of the medulla oblongata. The muscle-fibers of the arterial walls are chiefly circular, and their contraction narrows the arterial caliber. It has not been demonstrated as yet how, if at all, nervous influence causes active relaxation of a muscle cell. The process appears to occur not only here but in the heart-muscle, the inhibitory influence of the vagus being perhaps essentially of this nature (see above, page 295). Starting, then, with an average tone (or degree of contraction) of the circular fibers, vaso-constrictor influence from the nerves on Gaskell's theory would increase their katabolism and their activity which is contraction. If, however, the influence be vaso-dilator, katabolism would be partly checked (whether replaced by anabolism or not) and the pressure of the blood from the heart would force open somewhat the now relaxed arterial walls. It is possible, too, that the arrangement of the muscular fibers in the arterial wall is such, (some being longitudinal and some of all degrees of obliquity), that a positive enlargement of the tube may be actively produced by their con-

Fig 162



An artery and a vein from the stomach of a frog to show the sphincters about them. $^{34}/_{1}$. (Mayer.)

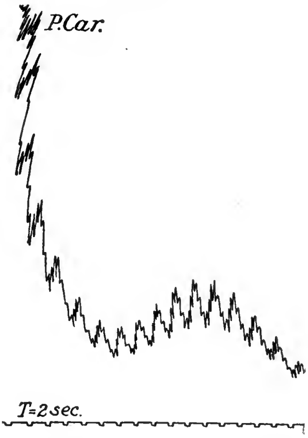
traction. Whatever be the vaso-motor mechanism in the artery, the two sorts of movement and the normal usual tonus which is the balance between them are facts easily observed. See Fig. 162 for a variant of ordinary vaso-motor apparatus found in an amphibian.

The *vaso-constrictor centers and nerves* have been known longer than the nervous apparatus of vaso-dilatation, but their exact courses are still not completely understood. There seems to be in the floor of the fourth ventricle of the brain and just above the point of the calamus scriptorius a nerve "center" whose severance from the cord by transverse incision of the medulla below it occasions vaso-dilatation. This is brought about evidently by removing from the arteries concerned the tonic and continued vaso-constrictor stimulus. This cluster of nerve-cells, double probably, part on each side, dominates vaso-motion. Its stimulation causes constriction. Influences from it pass downward to the grey horn and thence by spinal neurones to centers of more local influence situated mostly in the dorsal sympathetic ganglia; thence the influence passes outward in the post-ganglionic fibers of the sympathetic. As there is no good evidence of a general vaso-dilator center, this clump of cells and fibers in an area of the medulla a few millimeters square may be considered both the vaso-motor and the vaso-constrictor center, the latter term being preferable as somewhat more specific. Stimulation with electricity of this little region in the medulla or of the ends of fibers exposed by transverse section just below it causes a marked rise of blood-pressure which is due to general vaso-constricton. The nature of the normal stimulus is not understood, but it is probably in part chemical and resident in the blood flowing through it. Besides being influenced like the respiratory center by changes in the oxygen and carbon dioxide content of the blood, the vaso-constrictor center is promptly stimulated to action by a decrease in the amount of blood flowing through it. Its chief work is to keep the blood-supply up to the normal standard by increasing the blood-pressure when necessary. This is readily accomplished by vaso-constriction. On the other hand, when more blood than is normal is passing through this center its action of constriction lessens and the blood-pressure consequently falls. Besides these efferent neural means there is probably a more or less elaborate system of afferent fibers for regulating the blood-supply of the various parts of the body—depressors—acting reflexly on the constrictor center or on the sympathetic ganglia. By being thus affected by the amount and perhaps by the pressure of the blood flowing through them and through the arteries, the double center in the medulla and subsidiary centers in the cord below it are able to control the general blood-supply.

These assistant centers probably have specialized duties for maintaining the pressure in various areas, large or small, of the organism. The impulses connecting them with the main center seem to pass down the anterior lateral columns, some crossing over meanwhile. The precise locations of these subsidiary centers have not been determined, but they are probably in the anterior horns and perhaps in part in the cells of the lateral tracts. From them small medullated fibers pass outward as parts of the anterior roots and enter ganglla in the so-called thoracic sympathetic chain and perhaps elsewhere in the body. From these ganglia, probably of the nature of locally distributing centers, unmedullated preganglionic fibers convey the impulses to the smooth muscle-cells in the arteries, complex motor end-organs intervening between the fibers and the muscle-units.

The *"vaso-dilator centers" and nerves* have been less well located than the preceding, their functional antagonists. Impulses causing vaso-dilatation through a sort of inhibitory action seem to arise from various regions of the cord all the way from the medulla to the sacrum. As is the case with the vaso-constrictors, most of the dilator nerves come from the thoracic segments of the cord and from the first and second lumbar segments. No general vaso-dilator center is known. Coming from these regions the fibers pass outward to very many ganglia scattered in different parts of the body, especially of the trunk. Some of these ganglia are large and some are small; some control single organs and others considerable regions of the tissues generally. These fibers bearing vaso-motor impulses between the cord and their destination are not usually separate nerves. On the other hand, they generally form parts of the complex bundles of fibers making up "the nerves" of the body, for these are mostly bearers of very many different sorts of influences and messages. The sciatic nerve, for example, contains both kinds of vaso-motor fibers, and the vaso-motor effects of the artificial stimulation of the cut sciatic depends on the experimental conditions. The constrictor influence usually at first overpowers the dilator, but soon becomes fatigued in some way, leaving the dilator effect in control of the parts supplied. The dilators, however, as Bowditch and Warren showed, are more susceptible to weak and relatively infrequent stimuli than are the constrictor centers. Whether the constrictor and the dilator influences act continually, making the tonus of the arteries thus a balance of opposed forces, or whether (as is more likely) the constrictor centers by themselves control the tone, the dilatation being passive, is as yet uncertain. The dilator-influence on the latter supposition would be exerted only occasionally, when, for example, rapid or marked dilatation was necessary or when perhaps the blood-pressure was locally too low to promptly open the arteries. Local actions are probably elaborately provided for as regards both blood-pressure and vaso-motion. Indeed, so distinct is this local control that it might almost be said that normally

Fig. 163



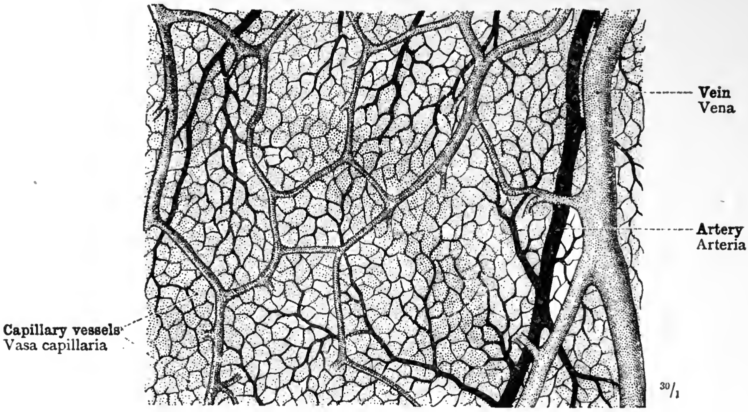
Tracing to show the fall of pressure in the carotid caused by vaso-dilatation. (Meyer.)

there is no such thing either as "general blood-pressure" or universal vaso-motion, so readily, so much, and so often do the local conditions vary. Each organ and each functional group of cells even, probably controls its own supply of blood either through enzymes or by the action of local nerve-ganglion. (See also Expt. 82 in the Appendix).

Concerning the precise relations of the tonal variation in the size of the heart (Figs. 157 and 160), to the arterial and capillary vaso-motion, nothing definite as yet, unfortunately, is known. There is probably some direct reciprocal relationship.

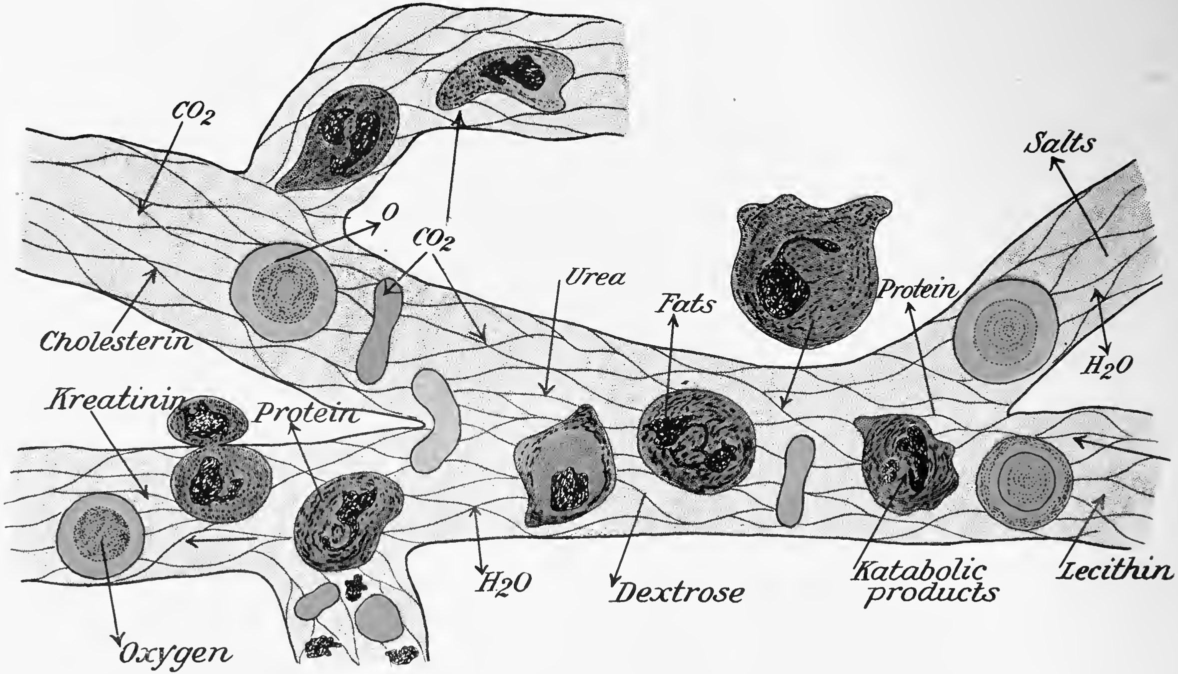
The Functions of the Blood Capillaries.—Inasmuch as practically the whole interchange between the blood and the tissues takes place through the capillary-walls, it is obvious that the functions of this part of the circulation should be thoroughly known. The details are as yet, however, largely unrevealed. The small size of these tubes (less than a millimeter long and from $\frac{2}{1000}$ to $\frac{2}{100}$ of a millimeter in diameter) together with the fact that their functions are largely based on molecular movements, are the recondite conditions which have kept the workings of the capillaries doubtful to us. Even their structure is not definitely known in all its details, especially whether a plexus of nerve-fibrils surrounds them, and what the nature is of the cement-substance joining together the edges of the cells. The protoplasm composing them is nearly transparent and of extreme thinness and apparent simplicity, yet either with or without the influence of the nervous system it probably determines more than almost any other one sort of tissue the metabolism of the body, for through it passes the means by which the body lives. For the sake of what goes on in the millimeter or half-millimeter of these billions of capillaries all the remainder of the mechanism of the circulation exists.

Fig. 164



The venous and arterial networks as seen in the corium of the gastric mucosa. $^{30}/_{1}$. (Toldt.)

PLATE VII



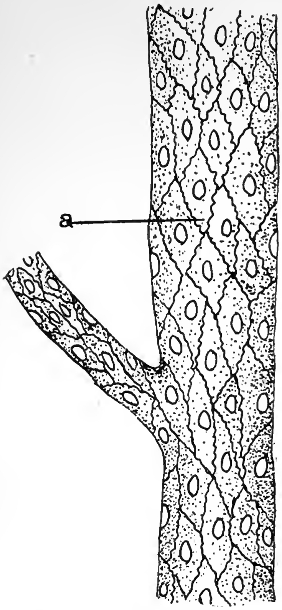
Functions of the Blood-capillaries.

Surrounding the capillaries everywhere, of course, is the metabolizing tissue-protoplasm.

It is only here that the blood performs its indispensable functions. The capillaries are the essential portion of the circulatory system—the arteries and veins are only subsidiary to them.

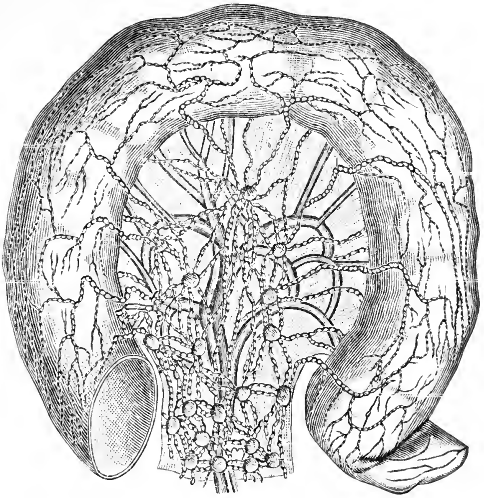
At least five sorts of processes take place in the capillaries and through its walls. These are: the out-flow through the walls of the nutrient blood plasma on the physical principle of osmosis, determined by its saline molecular density; the out-flow of oxygen by diffusion; the inflow of carbon dioxide also by diffusion; diapedesis or the passing through of the leukocytes; and a probable, but little known, vaso-motion. The first three of these have already been explained after a fashion in the chapters on nutrition and on respiration.

Fig. 165



Blood-capillary: *a*, one of the endothelial cells which entirely compose the tube (unless a plexus of nerve-fibrils is also present). (Bates.)

Fig. 166



Lymphatics of the small intestine. (Poirier and Charpy.)

The Lymphatic Portion of the Circulation.—As the blood circulates through the capillaries only part of it at each passage performs some specific function, the remainder flowing on to make itself useful to the tissues perhaps the next time it passes through capillaries. Meanwhile it is carrying back to the heart and lungs its share of carbon dioxide and bearing off for excretion into the kidneys its burden of dissolved tissue-waste. Of the capillary-blood a part osmoses through the thin endothelial plates forming the capillaries to serve the tissue-cells immediately outside in ways discussed in the latter part of the preceding chapter. It is this abstracted part of the plasma, splitting off from the circulation proper, which continually keeps up the lymph-flow. This is part, however, properly, of the hemolymph round from the ventricle to auricle again. Let us examine into the forces which cause the plasma to split away from the circulation proper and to pass as lymph so promptly and in such large amounts (five liters daily at least) out of the capillaries and into the veins by this indirect route of the tissue cell-spaces and the lymphatics.

Fig. 167

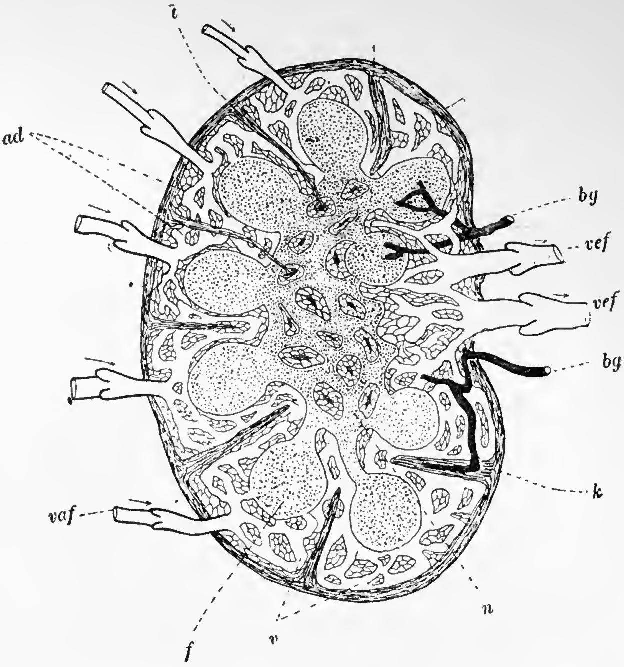
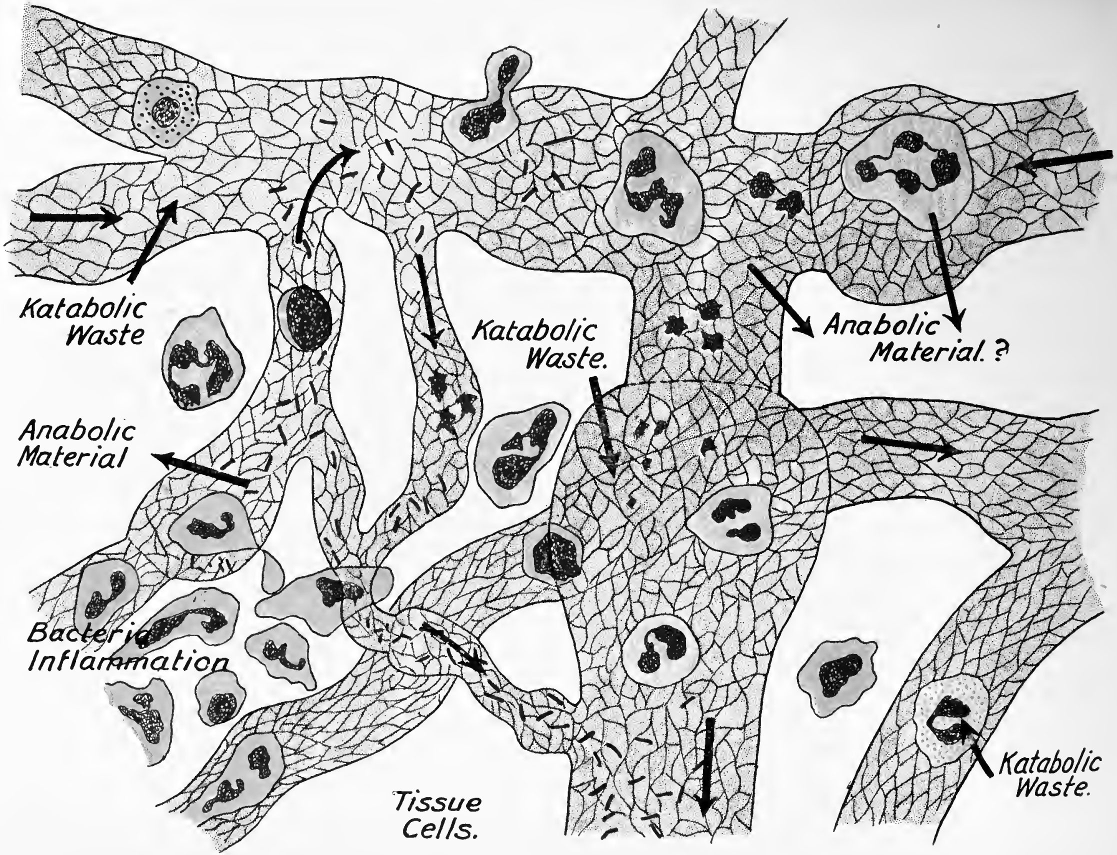


Diagram of a lymph-gland or -node as seen in section: *vef*, efferent lymphatics; *vaf*, afferent lymphatics; *bg*, blood-vessel; *k*, connective-tissue capsule; *t*, trabeculum; *ad*, adenoid tissue; *v*, lymph-spaces; *f*, follicle (the essential tissue of the lymph-gland); *n*, reticulum. (B. Haller.)

Causes of the Lymph-flow.—Four general causes of the lymph-flow are apparent, and we may speak of them by these names: the pressure from behind; the compression by muscles; the aspiration of the thorax; and the muscular constriction of the lymphatic walls. Which of these is the most important we do not know, and in the absence of this information we may consider them in the order named.

The cause of the immediate passage of blood-plasma out through the capillary-wall into the lymph-spaces is doubtless a complex of several forces, physical and physichemical. These we may denote as *blood-pressure* and *osmosis*.

PLATE VIII

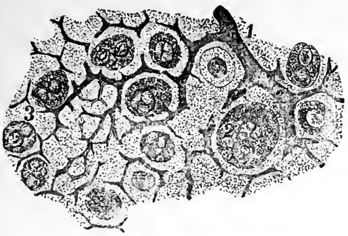


The Functions of the Lymph-capillaries.

Around these capillaries everywhere are the tissue-cells. The arrows show the direction of the currents. The phagocytic function of the leukocytes is shown in the lower left-hand corner, where there is an invasion of bacilli.

The pressure of the blood within the capillaries is sufficient to force some of the same through their walls. The capillary blood-pressure is said to average about 15 mm. of mercury (more at the arterial end of the capillary and surely less at the venous end), and if no other forces aided these there would doubtless be a slow and continual soakage outward into the tissues wherever a thoroughfare could be established. Between the endothelial plates, through them, or through the small rents which must continually occur in them some plasma would escape under this mechanical influence alone. This process would be filtration, at least in part. The nature of osmosis has been described, and nowhere does it occur more actively or more importantly than here. It is one of the most powerful factors of the lymph-flow, but whether more so than filtration cannot be determined. Its nature makes of it under certain conditions a force of enormous power, and it may exert a powerful influence on the plasma and lymph. It is dependent not on differences of hydraulic pressure, but on molecular conditions of solution still open both to study and to doubt. (See our brief consideration of osmosis on page 221 and those following.) It is to maintain the normal osmotic pressure in the capillaries, perhaps, as well as in the cells and elsewhere, that the salines of our food have a chief usefulness.

Fig. 168



The lymphatics of the outer skin, injected; black. $^{50}/_{1}$. (Rauber.)

Fig. 169

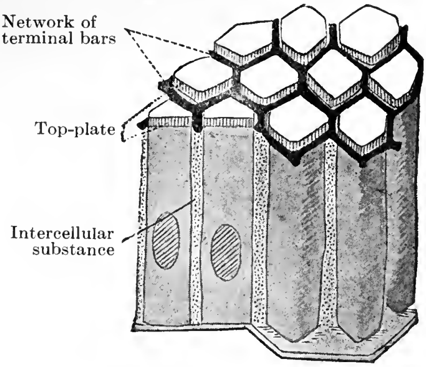


Diagram of some columnar epithelial cells to show how the intercellular spaces are shut off from the free surface of the gland by the "terminal bars." (Stöhr.)

Having passed through the capillary-wall, the plasma, now termed lymph, finds less resistance beyond than behind, and so soaks between the cells and out again. It then osmoses into freer channels and into the lymphatics. The osmosis and the filtration are continually going on, and they constitute the continual "force from behind" which crowds the lymph onward through the tissue-chinks. Perhaps this alone would be sufficient to continue the flow even into the subclavian veins, but more likely not, at least in that regularity, certainty, and promptness the metabolic processes require.

A second cause of the lymph-flow is the *compression of the lymphatics* by muscles. The system of the lymphatics ramifies everywhere throughout the body and is subject in very many places to compression by this means. This influence is especially strong probably wherever the vessels are crowded against bones, as, for example, in the arms, where contraction of the biceps, triceps, etc., compresses lymphatics of considerable size against the resistant humerus. In the legs and in the thorax the same conditions obtain. The powerful and rapid movements in the small intestine must compress the villi and serve to pump the lymph contained onward toward the lymphatic trunks. The reason for the almost constant succession of strong valves in the lymph-vessels becomes plain when one considers the effect which compression by the skeletal muscles would exert were they not present. The lymph in the vessels would be forced in that case as strongly backward as onward. By the action of these valves, however, all the influence exerted is in the right direction, for regurgitation cannot take place even to a small extent so close together are the valves. The muscles exerting this motive-power over the lymph are practically all those of the body, for even where no bones are near, contraction of muscular tissue increases the pressure considerably in the part where it occurs. Muscular activity (like muscle-tissue itself) is much more universal than is often appreciated, for all the muscles are continually in a state of varying tone when not more vigorously contracting.

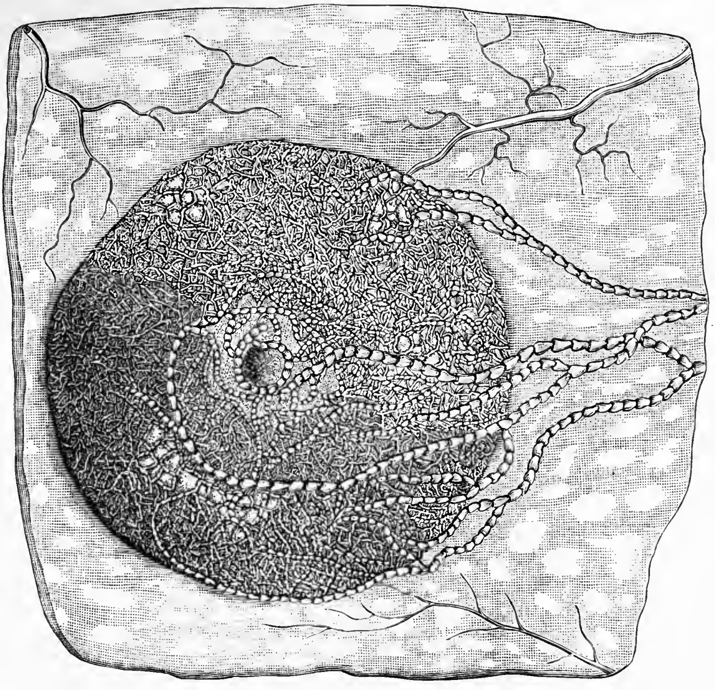
FIG. 170

The subcapillary lymphatics of the human conjunctiva. $^{30}/_{1}$. (Toldt.)

A third cause of the lymph's movement is the *aspiration of the thorax* as it is technically called. This is the suction exerted by the bellows-action of the chest at each respiration on every vessel entering it from without, especially through the diaphragm and from the neck. This matter has been already dwelt upon in considering the causes of the blood's circulation proper (see page 280) and needs no further description here, for the influence on the lymphatics is identical with that exerted on the veins. It probably is even more complete, however, owing to the greater abundance of valves in the lymphatics than in the veins.

The last force concerned in the production of the lymph-flow which we need consider is at present more or less problematical. It may be mentioned, however, as the slight constriction of the lymphatics themselves by *contraction of the circular muscular fibers* in their walls. The relative importance of this as a motive force it is not easy to estimate, but it undoubtedly exists. When, owing to abnormal conditions, the pressure in the lymphatics tends to rise too high, it may become an important means of restoring the onward flow. In many animals of simpler structure than man, frogs, for example, there are distinct pulsatile lymph-hearts (see Appendix, page 508), while in others (*e.g.*, guinea-pigs) the lymph-vessels themselves pulsate. Whether or not such action is of much account normally in man remains to be investigated. Perhaps it is, especially in the larger vessels.

Fig. 171



The vessels and lymphatics of the anterior face of the mammary glands. (Sappey.)

Under the combined influence of these forces blood-plasma oozes out of the capillaries, soaks in between the cells composing the body, collects by osmosis gradually in a myriad minute channels, and makes its way more or less rapidly into the subclavian veins at the base of the neck, where it becomes again part and parcel of the blood. The quickness with which the plasma osmoses and filters outward and inward again as lymph is surprising. The time varies with the nature of the liquid (colloids not passing out at all), but readily diffusible crystaloids injected into the blood-vessels appear in the lymph without any appreciable interval, as Colenstein showed and as is demonstrated frequently in the surgical procedure. A minute or two is perhaps an average time for the passage outward of salines from the capillaries. This shows in a striking manner how unified in composition at all times and under most circumstances are the tissue-fluids and the blood.

Edema is a pathological condition, but one which well illustrates certain principles in the physiology of the lymph. It consists essentially of a collection of lymph in the soft parts or in the great serous sacs of the body. It then has special names, such as ascites when the fluid is collected in the peritoneal cavity. The causes of edema are various and, first or last, mechanical. Thus anything which obstructs the flow of lymph out of the tissues into the veins occasions its collection among the cells, swelling the part and making it obviously more liquid in composition than normally. In valvular heart-disease, owing to defects in the pump which cripple a prompt circulation and so cause venous stasis, edema is a frequent symptom; thus people formerly were said to die of "the dropsy." Bright's disease of the kidneys shows a similar effect, but here, owing to the incomplete excretion of waste from the blood, the capillary walls probably become diseased, thus allowing of the too great escape of more or less abnormal plasma into the tissues. In the ankles and under the eyes the mechanical conditions are such that here the distention makes its first appearance.

Other matters concerning the lymph are discussed in the previous chapter where the composition and functions of the circulating liquids are described. The most important part of the truth about the lymph, namely, the exact chemical reactions which take place between it and the tissue-cells, still remains a blind secret. From this view-point the physiology of the lymph is almost the whole science of organic metabolism.

The Functions of the Veins, compared with those of the arteries and the capillaries, are simple and easily described. One might almost say that the veins have only one function, namely, to return the blood to the heart that it may be sent out again to perform its duties in the capillaries under the control of the arteries. The veins outside of this requirement have nearly negative qualities. The walls are *tough,* that they may stand when necessary much pressure. They are *lined with endothelium* to reduce the friction and to perform functions doubtless of a chemical nature on the blood. They are *thin-walled* partly because the low pressure within them does not require them to have the strength coming from greater thickness, and partly that they may collapse promptly when severed and thus prevent death from air sucked into the heart from wounds. They are *capacious* (two or three or even more times as spacious as the arteries), in order that the friction of the blood within them may be lessened and the speed therefore as great as possible. They are *situated oftentimes superficially,* because, from the teleological point of view at least, injury to them from without is much less dangerous than a similar wound of an artery would be, owing to the relatively small pressure within them. The veins are *furnished with valves* lest local conditions of muscular compression or pressure from other causes would interfere with the round of the blood in a prompt and complete manner. Whatever the source of external compression, when valves are present the circulation is not hindered but rather helped. Another use of the valves is seen especially in the legs: were they not present the veins of the feet would have to support a column of blood a meter or more high. This would not only fill them so full as to impede the movements of the blood by friction, but it would compel an unnecessary resistance for the heart and the other forces causing the circulation to overcome. As it is, no portion of the great leg-veins supports more than a very short column of blood even when the man is standing, for the support is divided among many valves.

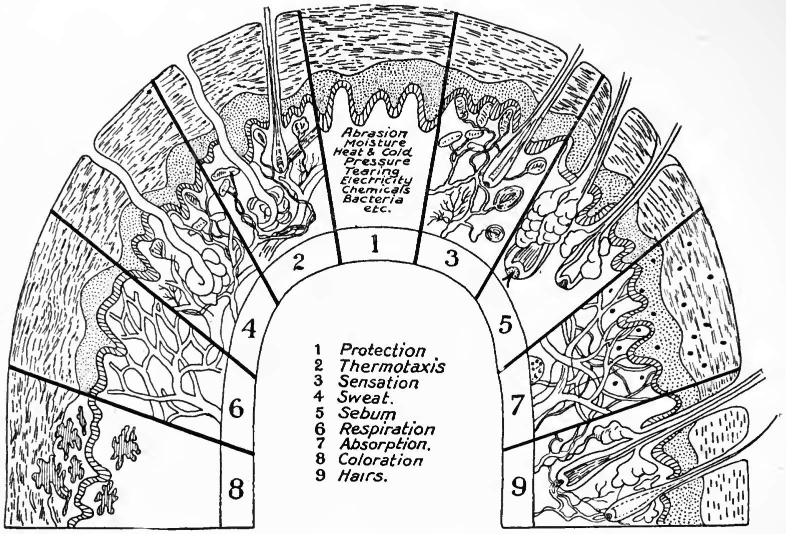
CHAPTER IX.

THE SKIN.

It is much easier to under-estimate than to over-estimate the importance of the functions of the human skin as an organ of the body. It is not merely a chance bounding layer of the organism, but truly a living organ as important as any of the viscera. Indeed, few organs have so many functions concerned with so many sorts of essential animal activity

Again we must refer the reader to the text-books of gross and microscopic anatomy, that he may acquire a knowledge of the structure of the skin before he tries to understand its functions.

Fig. 172

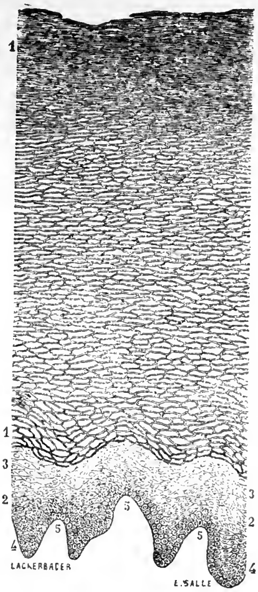


The functions of the skin. In each of the nine portions of this diagram there is represented those dermal structures chiefly concerned in that function.

The Functions of the Skin.—Among the many uses which the human skin might be said by an ingenious person to have, nine especially may be noted. These are of various degrees of importance to the organism, and only the first four or five are essential to its health. These nine uses of the skin, if we are to denote each of them by some one common expression, are protection, sensation, thermotaxis, excretion of sweat, secretion of sebum, respiration, absorption, coloration, and support of the nails and hairs. If it were reasonable to say of animal functions altogether composing one harmonious whole that "this function is more important than that one," we might consider the order given above as perhaps that of their relative consequence to the organism. (See the diagram, Fig. 172.)

Protection is well afforded by the skin through its structure, composition, and relations to the bodily parts it covers. It protects from physical and chemical stimuli which might injure the organism in two opposed directions—from mild stimuli by its sense-organs which warn the nervous system of their presence, and from severer stimuli by the horny layer which it exposes to them. It is with the latter only that we are just now concerned. The structure of the stratum corneum is peculiarly well adapted to its functions, for it consists of very many layers of dead or half dead squames or scales piled up in multitudes on each other but firmly connected so that they form a membrane, flexible, extensible, and soft.

Fig. 173



Vertical section of the epiderm of the hand's palm. × 100 diameters: 1, very thick, horny layer, composed of superimposed cells without their nuclei; 2, mucous layer of nucleated cells; 3, upper part of this layer separated from the rest by a wavy line; 4, interpapillary depressions; 5, papillary recesses. (Sappey.)

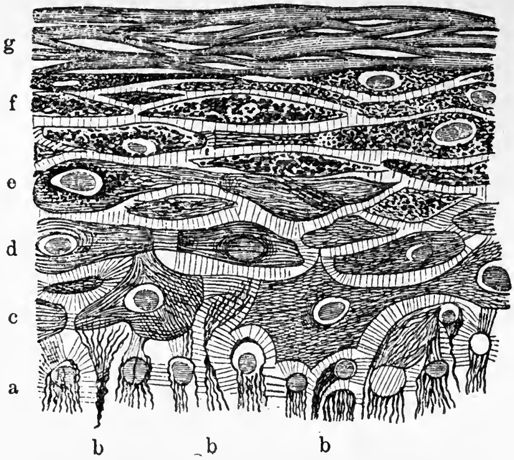
Because of the absence of nerves from the epidermis it has no sensibility and the individual is not irritated by contact with the air, water, and solid bodies, as he would be did the nerves ramify in the surface; of course life under the latter circumstances is almost inconceivable. The epidermal scarf-skin on this account is an ideal bounding surface of an animal body.

The epidermis because of its chief chemical component, keratin (an albuminoid), as also because of its scaly structure, is a fine non-conductor of heat. It thus shields the body from the sun to an extent and from excessive artificial heat. When pigment is developed in the skin (as in freckles, in "tanning" from sun- and wind-burn, and in the Negro race), it is biologically supposed to be deposited as a still further protection against excessive light and heat. The dead keratin of the skin's outer layers when dry is also a non-conductor of electricity, and this is a matter of some importance because of the electrical developments of recent years.

This same scaly structure makes the skin a relatively poor absorber of everything, as good protection requires. As we shall see before long, only fats and oils enter it readily. No substance passes through it, however, with anywhere near the readiness with which it would be absorbed by the average naked body-tissues served with an abundance of lymphatics and of capillaries. Water finds its way through the unctuous scaly epidermis only in minute amounts, this waterproofing of the skin being produced by the sebum, a fat poured out into the hair-follicles and on the surface (see below).

The skin is freely movable over the fatty subcutaneous tissues and is, moreover, very elastic. These two properties prevent the body's injury by contact with such heavy objects as press and move at the same time. In these cases the skin glides over the muscles, etc., beneath it and the surface of the body is not torn or bruised.

Fig. 174



The lower part of the epidermis of the hand-palm, as seen in schematic section: *a*, layer of cylinder cells; *b*, basal fibers; *c*, layer of cells whose fibers extend in all directions; *d*, layer of cells whose fibers are parallel to the skin's surface; *e*, layer of cells whose fibers are beginning to disappear in the cytoplasm; *f*, stratum granulosum; *g*, stratum corneum (a small part of it). (Kromayer.)

The two parts of the skin, the corium and epidermis, are both very elastic, the former by virtue of its network of elastic fibers and the latter because of its scaly structure, which allows of considerable stretching. It is essential that the covering of the different parts of the body should be extensible to a large degree, because many temporary conditions, normal and abnormal, increase the size of local portions of the organism. Thus when the biceps of the arm contracts vigorously the arm increases much in circumference around the center of the muscle. In pregnancy, if the skin were not elastic to a high degree it would be torn at times. Tumors superficially placed and ascites sometimes show a like need for dermal stretching.

In several places by the thickness of its epidermis the skin constitutes a pad which prevents frequent injury to the parts beneath it, for example, over the gluteus maximus and on parts of the palm of the hand. The subcutaneous fat helps in this matter. Under the heel the skin is very thick, especially the fat and the epidermis, and constitutes a cushion to relieve the jarring of the spine which else would occur, and with injurious effect, in walking. As is familiarly seen in the causation of corns and of calluses, especially on the hands, continued or oft-repeated pressure on a portion of the skin gradually causes a thickening of the epidermis. By this principle active manual occupations and sports soon lead to the development of defences to abrasion and inflammation at just the spots where they are needed.

In cases of injury to the external parts of the body which are much in contact, especially the fingers and the toes, the presence of the dead epidermis not liable to inflammation prevents the injured parts from growing together before they come into use again.

Because of its structure and the materials from which it is made, the skin is flexible and soft yet resistant to all but incisive blows. It has in short in a lesser degree the well-known and unique properties of leather, which of course is skin killed, hardened, and preserved.

Besides these physical agencies there are many solid, liquid, and gaseous chemical substances which come in contact with the skin occasionally. The epidermis, however, especially the superficial parts of it, is little more than a complicated network of keratin, which is one of the most insoluble substances entering into the organism. It is unaffected by most of the things which in a state of nature are apt to come in contact with it. Many of these (for example, the alcohols) would injure seriously the average living tissues, and alkalies and strong acids attack it still more readily. In general, however, it is a very resistant material and therefore one excellently adapted to intervene between an organism and its varied environment. (See further as to the chemical status of the albuminoids in the chapters on protoplasm, food, and nutrition.) (Fig. 173.)

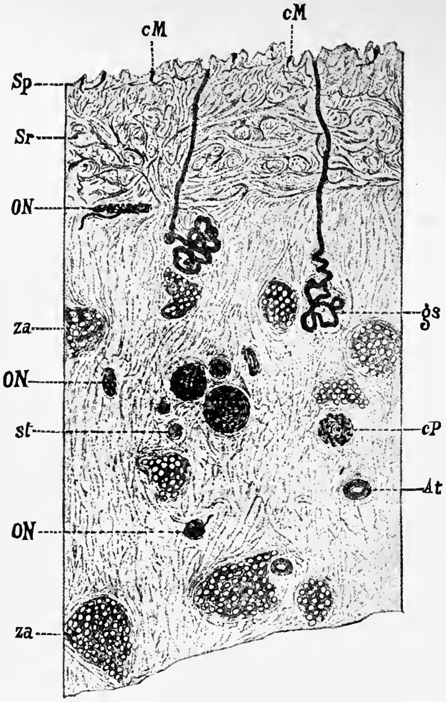
Light is one of the agencies, chemiphysical in action, against too much of which the pigment-cells of the epidermis protect the body-tissues.

In addition to furnishing protection to a degree against physical and chemical adversaries of its organism, the integument is a defence against parasites, including the pathogenic bacteria except such as dwell within its tissues. As long as the uncracked epidermis only is presented to bacteria there is relatively little danger of infection, for its mass of minute dead scales admirably serves as a filter against their passage, much as does cotton in the bacteriological laboratory. Contrast with this the prompt and vigorous invasion of mucous membranes by germs of disease. These former do not have the dry, cool, filtering mass of scales which make up the epidermis, but are living tissues rich in most of the conditions the development of microörganisms requires, such as moisture, warmth, and nutriment.

The continual exfoliation of the dead epidermal squames protects the body largely from the growth of parasites such as one sees sometimes on the shells of molluscs and the carapaces of turtles. The many parasitic diseases of the skin which are found, such as scabies, tricophytosis, etc., are due to rapidly growing organisms, and are liable to occur especially on skins in which, through infrequency of bathing (which is essentially maceration followed by exfoliation) the outer layers of the epidermis remain unduly long exposed to the environment.

Sensation or sensitivity is perhaps the next most important function of the human skin. If the term protection be used in a broad sense, much of the usefulness of the skin's sensitivity would come under it.

Fig. 175



Half-schematic section of the skin on the ball of the finger to show the locations of the sense-organs: *Sp*, layer of papillæ; *Sr*, reticular layer; *ON*, Ruffini corpuscles; *St*, nerve-trunk; *la*, fat globules; *cM*, Meissner corpuscle; *cP*, Vater-Pacinian corpuscle; *gs*, sweat-gland; *At*, artery. Gold-chloride. (Rauber.)

One of the chief functions of the dermal sense-organs is to warn the animal within of external injurious conditions such as heat, cold, and various sorts of contact with foreign bodies. Because the sense-organs have functions other than protection, however, we consider them as having uses of their own. The description of these afferent end-organs and of their functions is given in a later chapter (page 351, etc.), so that here we need only mention some of the general conditions of their activity.

One of the most basal of biological principles is that of the unity of the living world: each part is more or less dependent on every other part. Further than this every animal is at once the product of and dependent on its environment of natural energies and materials. By way of the stomach and the lungs these in great numbers enter more or less into the animal's metabolism or affect it in many ways through its nervous systems. Some of these latter influences enter by way of the sense-organs of the skin.

There are numerous minute "spots" in the skin sensitive to pressure (touch), pain, heat, and cold, respectively, and it is not difficult to stimulate these various points in such a way as to produce pure sensations of at least these four kinds. (See below, page 366, where some details are given.) When, for example, a touch-organ is stimulated separately, nothing whatever but a sensation of touch is experienced, no pain or cold or warmth. When a "pain-spot" is properly excited only pain is experienced—no suggestion of touch or of cold or of warmth. Besides the definite end-organs, there seem to be everywhere fibrils of nerve-tissue. Especially is this the case among the epithelial cells of the epidermis and of the mucous membranes, and in the cylinders of tissue encasing the lower ends of the almost universally distributed hairs. Mechanical irritation of these fibers or fibrils starts impulses in their afferent nerves, but how these differ in their mode of sensation-making from those set going from the various touch-corpuscles, etc., is at present not understood.

The considerable variety and immense number of the skin's sense-organs are the facts to be noted here. By them this organ is made practically a perfect coupler between the animal and its physical environment.

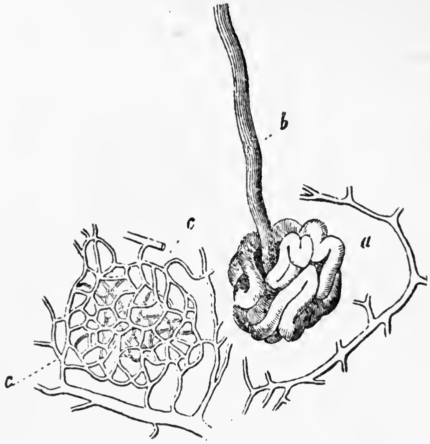
Thermotaxis, the regulation to body-temperature, is one of the important functions of the integument. By the reflex or voluntary action of various and certain elements within the skin's thickness, combined with the nervous system, the temperature is kept within the limits with which we are familiar, namely, one or two degrees above or below 37° centigrade. We have already discussed the methods of heat-production and of heat-loss and have seen that the arrangements for heat-regulation involve nearly all parts of the body. Of the organs thus concerned, none, it will be recalled, is more important than the skin. From it the very large part of the heat lost from the body is radiated or conducted. As we have seen, the proportional area of the skin to the metabolic tissue-mass producing heat within it is a chief factor in the conduct of thermolysis. Again, it is the skin which secretes the sweat, by whose evaporation largely the heat is lost from the body.

The Sweat.—Another function of the human skin, but partly involving the preceding, is the excretion of sweat. This substance is a liquid of very low specific gravity produced by certain closely coiled glands lying in the subcutaneous layer of tissue. Their product, however, is poured out on the skin's surface. Sweat is termed an "excretion" because it is waste matter. It is, however, of great use to the organism as it passes away from it. It is only because of its location on the body-surface that the skin rather than some internal organ excretes the sweat, for it passes off largely by evaporation, for the purpose just considered above.

The purely excretory aspects of the sweat have been briefly treated of especially in the chapter on Nutrition (see page 252). We have now to describe its composition, mode of production, and relations to the skin and to thermotaxis rather than to the removal of waste from the body. First, a few words as to its physical and chemical nature.

Human sweat is a somewhat opalescent colorless liquid with a specific gravity varying between 1003 and 1010 according to the conditions under which it is produced, but averaging perhaps 1005; it is, then, one of the most watery of the body-liquids. Three samples analyzed by Camerer had an average of 98.5 per cent. of water and 1.5 per cent. of "solids:" three-quarters of the ash was sodium chloride. In reaction sweat appears to be either alkaline or (later) acid, depending on the time it has been in contact with the epidermis. Camerer found the sweat poured out in a hot-air bath to be acid, that in the more sudorific vapor-bath, alkaline. There is some evidence that what one might call muscular-katabolic sweat tends to be more acid than that excreted by the glands during bodily rest, the more profuse the sweat the greater its liability to be neutral or alkaline. There are present small proportions of neutral fats, urea, uric acid, aromatic oxy-acids, sulphates of phenol, skatol, etc., kreatinin, formic and acetic acids, and traces of proteid (especially in alkaline sweat). Altogether about 0.15 per cent. of nitrogen are present, most of which are in the urea and uric acid. The universally excreted cholesterin does not fail to be present. There are contained

Fig. 176



A human sweat-gland: *a*, the knot of the gland surrounded by veinlets; *b*, excretory duct; *c*, basket-like capillary network about the gland. (Todd-Bowman.)

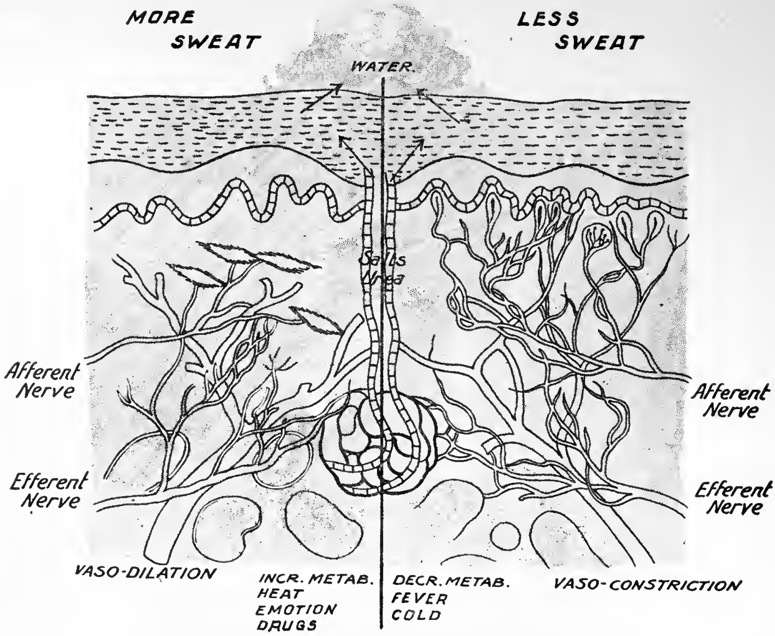
also at all times traces of sulphocyanides, and it is these, perhaps, in combination with proteid decomposition-products of unknown nature, that make the sweat toxic when ingested. The odor of sweat, especially if old, varies with the volatile fatty acids excreted at that place, for the latter differ somewhat in various localities. The sodium chloride present gives sweat a salty taste. Under the microscope sweat is seen to contain epidermal debris and an occasional waste-product from the tissues in and about the sweat-glands. The urea present at all times more or less may be of great importance during incapacitating disease of the kidneys. Ordinarily it constitutes about one part in a thousand of sweat, but when the excretion of urine is suppressed it may be in quantity sufficient to be seen in crystals on the skin, and to materially aid in the life-saving excretion of nitrogen.

The nervous system superintends the secretion of sweat. Its influences pass out in the neuraxones of the sympathetic by way of the anterior roots of the cord. Centrally the fibers of the sweat-nerves probably pass upward in the cord to a center or centers in the medulla probably, but as yet not exactly located. Function indicates their very close relation both with the vasomotor and with the thermogenic centers. The unilateral sweating seen occasionally in nerve-clinics suggests very strongly that there is a center on each side of the medulla.

Sweat is excreted continually and when in quantities too small to be seen on the skin is termed invisible or "insensible" sweat. Its quantity is continually changing as the regulation of body-heat requires, but may average 1500 c.c. daily. Under certain normal conditions, all of which involve an increase of body-katabolism or at least of body-heat, the sweat is so much augmented that it is no longer evaporated as fast as excreted, and it then collects on the surface. It is then termed "sensible" or visible perspiration. As we have seen, these two sorts may differ somewhat in composition, but not much; the more abundant the sweat, however, the larger the proportion of water and the more likely it is to be alkaline instead of acid. Besides the normal conditions mentioned below, sweat may be augmented by pathological causes not involving metabolism, for example certain drugs (as pilocarpine and nicotine), and by some sort of derangement of the sympathetic sweat-nerves or -centers in certain nervous diseases. This is called by dermatologists a condition of hyperidrosis. Its etiology is often obscure, but is usually some derangement of the sympathetic.

Among the physiological conditions determining an increase of sweat are these six: An increase in the temperature of the blood; vaso-dilatation in the skin; a high external temperature; an increase in the proportion of water in the blood (hydremia); venosity of the blood; and direct cerebral stimulation of the sweat-centers in emotional conditions, for example fear. Physical and even mental exercise (the former being perhaps the most common cause of the appearance of sweat on the skin) produce the effect by heating the blood thus stimulating the centers and perhaps also the glands directly, at the same time causing peripheral vaso-dilatation which in turn increases the flow of sweat. The enlarged amount of proteid-katabolism in muscular exercise has little to do with the increase of the sweat, for the kidneys are the glands arranged to take these nitrogenous excreta from the blood. The excretion of the water produced, however, is shared between the two. It is only when the epithelium of the kidneys is thrown out of action or destroyed (as in Bright's disease) that the sweat-glands vicariously take on the excretion of considerable amounts of nitrogen in urea, this then soon degenerating to ammonia.

Fig. 177



Mechanism of sweat-secretion? On the left side of the picture are represented the mechanism and some of the conditions of an increased production of sweat, and on the right side those of less sweat. In the middle is a diagrammatic sweat-gland delivering its product into the epidermis.

A high temperature of the skin's environment stimulates the flow of sweat reflexly, and probably through the agency of the minute automatic thermostats (heat-corpuscles) scattered throughout the integument. (See Chapter X.) Sweat runs by the liter from the workmen in foundries, glass-works, and rolling-mills, for they sometimes work in temperatures which would be promptly fatal were the air very moist instead of dry and were the skin deprived of its active sweating by any other cause. Excessive heat, internal or external, as well as cold, checks the secretion, and by methods the reader can doubtless readily explain.

Of the six conditions mentioned as more or less normal states showing an increase of sweat-secretion, five most likely act largely or wholly on the centers in the medulla and the cord. The least normal, a watery state of the blood, probably produces its effect directly on the epithelium of the sweat-glands, much as does the same sort of action in the kidneys. In just what manner the presence of too much carbon dioxide in the blood works is not at present understood. Many sorts of reflex stimulation of the spinal cord and brain cause an increased flow of sweat, whether the stimuli come from the sensory nerves or from deeply lying parts of the brain such as the optic thalami, the centers of emotional expression. The sweat-glands are not readily stimulated directly by warming the skin containing them, but easily and from many different directions by first stimulating the controlling centers in the central nervous system.

We have already considered above in two different places the two general functions of the sweat, namely, to excrete water (and many other things in small amounts) and, largely by this latter means, to regulate the loss of body-heat. These statements need not be renewed here. As a means of excreting water from the organism the sweat-glands seem to be just about on a parity with the kidneys. As regulator of heat-loss the sweat is paramount.

The Secretion of Sebum is a dermal function more or less closely concerned in the skin's protection of the body. Because largely useful, sebum is classed as a secretion rather than as an excretion. Sebum is of many different varieties according to its precise function on different parts of the body. It varies in the hair-follicles, in the external auditory meatus, on the edges of the eye-lids, on the lips and in corners of the mouth, in the cervix, corona glandis, foreskin, labia minora, etc. Vernix caseosa, the sebum covering the body at birth, is still unlike all the others.

Wherever it occurs, the essence of sebum's *composition* is fat, largely olein and palmitin. These make the excretion liquid when secreted and allow it to harden more or less on exposure to the cool air. Soaps are present in considerable proportion, and glycerin, and a casein-like nucleo-proteid. It contains earthy and alkaline phosphates and chlorides of sodium and potassium. Cholesterin is always to be found. In appearance also sebum varies largely with the place where it is secreted; so does its odor as well, smegma, for example, having in the brutes an odor with much biological value.

The *sebaceous glands* are attached to the follicles of the hairs and pour their product into them, whence it is distributed throughout the epidermis by the movements of the skin. Just within the hair-sheath is the membrana propria, continuous with a similar layer in the follicle. Within this in turn are several strata of gland-cells proper, the outer two or three being like those of the external root-sheath of the hairs. The inner strata of epithelial cells are different, containing fat-globules in quantities sufficient to give the cytoplasm a reticulated appearance, while the nuclei are compressed. These fat-globules constitute the product of the secretion, for the innermost cells containing them are continually breaking down in a mass, thus becoming sebum. These are as continually replaced by the basilar cells below them, which in turn develop sebum-granules and press toward the lumen of the alveoli. This process is in essential respects like that of the goblet-cells secreting mucin. Sometimes the cell does not go to pieces in situ but only after being extruded from the gland. The excretory ducts are wide and ordinarily empty into the upper third of the hair-follicle; their walls also secrete sebum.

The *functions* of sebum are not hard to understand when its general fatty, emollient nature and the place of its excretion are kept in mind. It is essentially and primarily an oily softener of the epidermis and of the hairs found nearly everywhere over the body. Without it the epidermal scales and the scaly hair would become hard and brittle and unfit to perform their protective functions. One of the most common features of the body's environment is water or watery vapor. The fat which the sebum supplies to the epidermis serves to make the latter tough and impervious to water, which else sometimes would be absorbed by the capillaries and derange the organism more or less. The hairs especially are dependent on an abundance of oil for their normal suppleness and strength. In general over the body then the sebum keeps the skin's outer layer soft and pliable, and prevents the maceration of the epidermis which water would else be sure to cause. There are no sebaceous glands on the palms of the hands or on the soles of the feet, nor in two or three other narrow localities.

In special locations, mostly mentioned above, the sebum has special functions in addition to its general uses just described: In the eyelids, the secretion of the sebaceous (Meibomian) glands has the function of preventing the cohesion of the lids when they are closed, as during sleep. One sees its use in conjunctivitis of various sorts, for then the secretory process is often exaggerated and the lids cannot be opened in the morning until the adhesive sebum is softened and removed.

In the inner part of the external ear, the external meatus, the sebum is termed cerumen or ear-wax. There it lubricates the membrana. It serves also the purpose of partly preventing the entrance of insects and even of small particles of lifeless foreign matter, the stiff hairs also often present aiding in this. For the purpose of making the cavity still more inhospitable to insects, the cerumen has an intensely bitter taste, thus the better preventing small insects from coming in contact with the membrana tympani.

On the lips and corners of the mouth the sebum is necessary to prevent the cracking of the integument, for these are places where the skin is thin and liable to be broken or slightly torn.

The vernix caseosa which covers the infant at birth is evidently a lubricant facilitating the passage outward of the child and preventing abrasion both of the latter's very delicate skin and of the birth-canal of the mother. Pigeons' milk is a form of sebum on which the young birds are fed at first; it comes from temporary sebaceous glands developed in the crops of both parents. The sebum of sheep is called lanolin, and serves to keep the wool soft, pliable, and water-proof. When the amount of the sebum is generally excessive in quantity the condition is known in dermatology as seborrhea and popularly as dandruff. Sometimes the secretory product is along with its over-abundance abnormally oily (seborrhea oleosa), while at other and more frequent times the excessive sebum is thicker in consistence than usual (seborrhea sicca). The cause of this hyper-secretion is not known, but it seems to be related to some lowered tone of the nervous system or the blood. It is most abundant in those regions where the sebaceous glands are most common.

Respiration is another subsidiary function of the skin. It appears that under normal conditions about one-half of one per cent. of the body's total respiration is carried on directly through the epidermis. When the lungs are thrown out of function in large part the respiratory action of the skin may be largely increased, although not to an extent which makes it ever life-saving to the human organism. The subject has already been discussed in the chapter on respiration (see page 129).

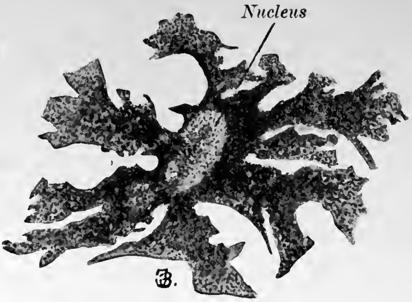
Absorption of certain substances through the skin takes place under the necessary conditions. The process is more important therapeutically, by artificial means, than as a spontaneous physiological process. It is not apparent that naturally any substance save perhaps oxygen in very small amounts passes inward through the intact epidermis, so perfect is the protective structure and function of the integument.

When the body is immersed in water, especially if the latter be warm, it is likely that a very small amount finds its way into the circulation. Thus, ship-wrecked persons have often relieved themselves, somewhat, of the feeling of thirst by immersing their bodies even in the salty ocean-water. This, however, is no proof that any valuable amount of the water enters the body, for in the first place, no one has ever saved himself from dying of thirst (that is from loss of water from the blood and body-tissues) by thus surrounding the body with water. This loss of water normally occurs half at least by evaporation from the skin, and immersion in water would check this evaporation and so give relief to some extent.

The sort of substances which may be made artificially to pass into and through the normal skin (including the epidermis) are mostly such as are already there, namely fats. These even when only placed upon the epidermis are absorbed, and unlimited amounts may be made to pass inward by inunction. Naturally also substances soluble in fats likewise readily enter the organism. This fact is taken advantage of in medicating not only the skin itself, but the entire organism. Thus, a person is readily salivated by the inunction of mercurial ointments. Similarly, alcoholic extracts and ethereal solutions, being soluble in the sebum and body-fats, may be readily made to enter the unbroken skin.

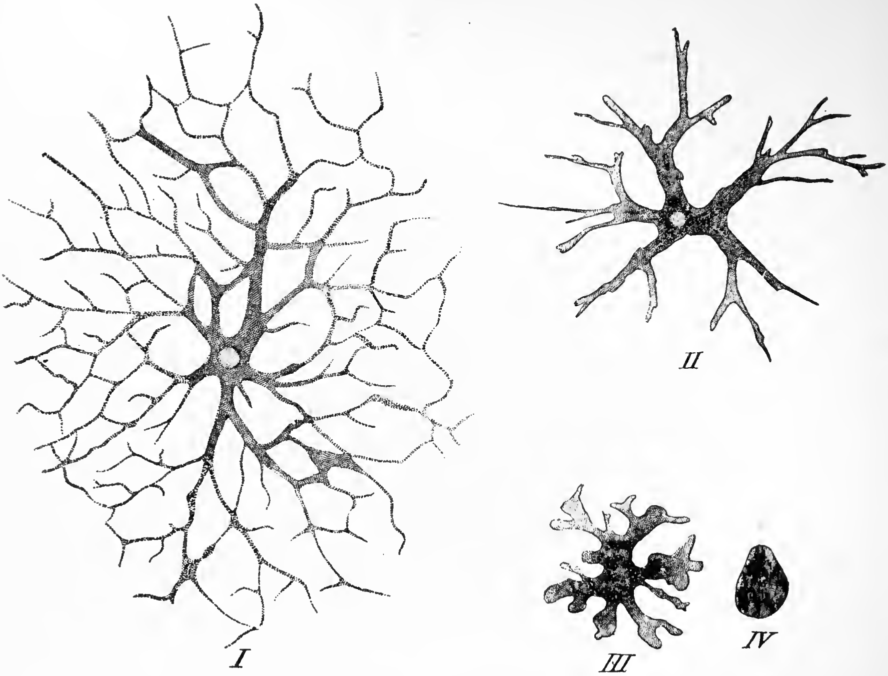
It is the oiled epidermis which prevents the passage inward of most substances, for the mucous membranes and the naked tissue-protoplasm readily absorb a large variety of materials. The subject of absorption through the skin has not nearly the importance or popularity now that it had formerly when it was supposed by many that the organism received much benefit by absorbing the substances, for example, dissolved in various sorts of natural springs. The benefits from such bathing is now known to be much more indirect: hygienic and mental rather than chemical.

Fig. 178



Pigment-cell from a young salamander's skin. $^{100}/_{1}$. (Szymonowicz and MacCallum.)

Fig. 179

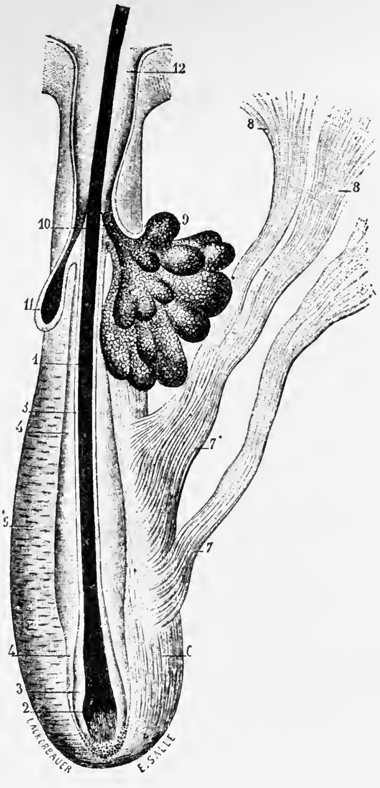


Pigment cells from the skin of the frog: *I*, extended; *II*, and *III*, degrees of contraction; *IV*, wholly contracted. (Verworn.)

Coloration.—This dermal function is served by pigment-cells of various colors and in many various locations on the body's surface. We need not discuss the chemistry of the different pigments found in protoplasm, for the coloring-matters are complex, and besides their relation to the tissue-metabolism is not yet well understood.

The pigments are the secretory products of certain cells of the connective-tissue class, but differentiated further for this special purpose. In some of the "lower" animals these cells have distinct ameboid retraction-and-expansion movements described somewhat in the chapter on Protoplasm. A tendency to this perhaps is seen in the going and coming of freckles and tan and especially in the quick blanching of the hair of the head (*e. g.*, Henry M. Stanley in the African forest of the Pigmies) under the emotion of terror or from the more chronic emotional condition of worry and trouble.

Fig. 180



Hair-follicle showing its unstriated muscles and the sebaceous gland: 1, the hair-root; 2, its bulb embracing the papilla of the hair-follicle; 3, internal sheath of the root, and 4, external sheath; 5, tunic of transverse fibers of the follicle; 6, tunic of longitudinal fibers; 7, unstriated muscles inserted in the latter layer; 8, their free ends, losing themselves in the superficial strata of the skin; 9, multilobular sebaceous gland; 10, excretory duct of same; 11, simple sebaceous gland; 12, mouth of the hair-follicle. (Sappey.)

At least two biological functions are served by surface-pigmentation in man, namely, to make the body more beautiful and to protect its protoplasm from excessive sun-light.

Biologically the former function, that of ornamenting the body, is a secondary sexual adaptation. It is intended to make the sexes mutually more attractive, and this tends to draw them together reproductively. But human beauty has other reasons for existence than this, is indeed "its own excuse for being." To this virtue the various pigments of the skin and its appendages, especially the hair, distinctly minister, for they help materially to increase the beauty of the human form.

As protectors of the sensitive body-protoplasm from excessive sunlight the status of the pigmentation is more in doubt. It is not easy in particular to decide whether the secretion of brown or black pigment which occurs after long exposure to bright sunlight is a sort of degenerative reaction or a protective process. In the iris it has evidently the latter function; in the hair of the scalp blackness, on the other hand, would tend to make the brain warmer than were the hairs white. Ornamental pigmentation tends to occur on the body in places not especially exposed to light, for example on the scrotum.

In general the whole subject of dermal pigmentation needs more careful working-out in its chemical as well as its histological aspects.

The Hairs and the Nails are properly parts of the skin or appendages to it.

Hairs are found nearly all over the body, the palms and soles being marked exceptions. In various places the hairs differ greatly in size and rigidity. In its adult stage, the hair consists of medulla, cortical fibers, and cuticle. The pigment-granules are scattered in the cortical layer. An inner and an outer-root sheath surround the growing hair, the latter being an invagination from part of the epidermis. In the center of the base of the hair when in the follicle is the very vascular papilla. Attached to each follicle is a bundle of smooth muscle-fibers so placed that its contraction pulls the hair into an erect position, as happens in terror. Each follicle receives one nerve-fiber which enters the former just below the duct of the sebaceous gland. Here it divides into two non-medullated fibers which surround the hair-follicle and from this partial or complete ring many varicose fibers extend upward and terminate outside the so-called glassy layer, in some of the brutes in special end-organs (Retzius). The muscles of the hairs are supplied from the gray rami communicantes of the sympathetic (Huber).

From what we know of the structure and the nature of the hairs three functions at least may be noted: protection in various ways, especially from cold and heat; as sense-organs of touch; and ornamentation.

The *nails* scarcely need discussion. They are keratinous coverings of the ends of the fingers and toes, extending from the epidermis and continually pushing out at a slow rate by growth at their matrix. They serve to protect the ends of the fingers and toes from injury and render these organs, especially the latter, useful for many purposes which else they could not serve.

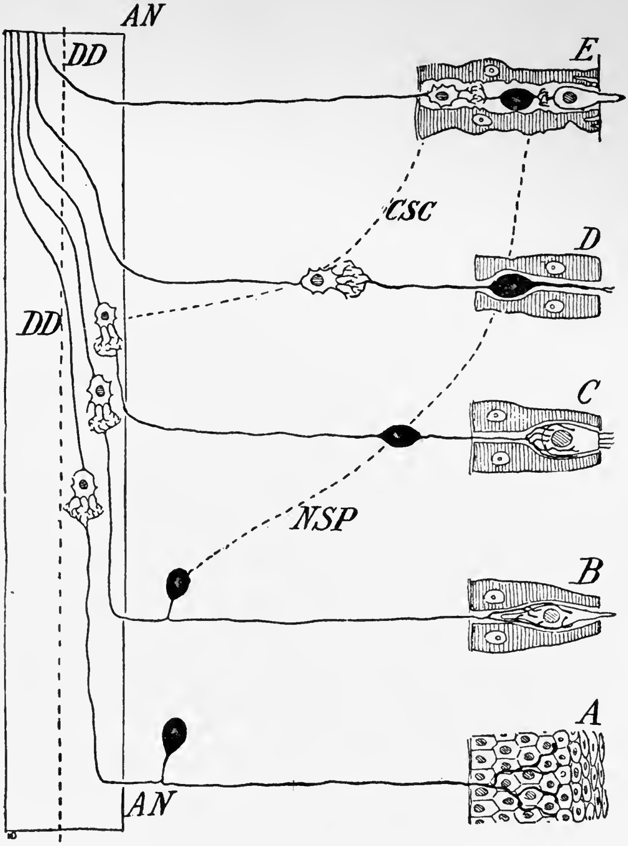
CHAPTER X.

THE SENSES.

We have already learned that one of the chief functions of the nervous system is to correlate the parts of the organism into a unity, and the organism as a whole with its varied and changeful environment. The animal is no independent entity, but rather part and parcel of its environment to an extent not often realized. Just as the whole animal has an environment scarcely ever twice alike, so also has each of the organism's parts, large or small. It is the main function then of the sense-organs, so called, to help this double adaptation. The sense-organs are the peripherally terminal portions of the afferent nervous system, the means by which the latter connects itself with its local environment. Homologous to the sense-organs at the periphery of the afferent nerves are the muscles and the glands at the periphery of the efferent set of nerves. The former receive for transmission the messages from the "environment" as already defined; the latter perform in the environment, within or without the organism, the bidding of the animal's will whether "reflexly" or "voluntarily" performed. All of these from one point of view are but parts of the nervous system; functionally, however, every bodily part is sovereign and none the servant of any other. Just as in this chapter we consider the receptive organs in the periphery of the afferent nervous system, so in the next chapter the muscles are discussed—the two homologous agents of the individual as expressed through his neural fabric.

These are the afferent nerve-endings or, less correctly, the sense-organs. The term "sense-organ" is an old and accepted one. From the modern view-point as to the relations of body and mind it is somewhat misleading, however, since it implies that whenever a sense-organ acts it represents a conscious sensation. It is likely, indeed, that this is so, that each one of the millions of afferent fibrils in the nervous system, centripetally transmitting some impulse, contributes to the mass of consciousness. This is the basis of the notion of consciousness to be found stated below (see page 405). If, however, we always think of the impulses passing inward through the sense-organ gates as *afferent* rather than as "sensory" we shall be making no hypotheses and be sure we are thinking rightly. This is the more important because it is becoming more and more apparent that it is the organism which is conscious, rather than the mere nerve-cells, and that at any rate to prove that the efferent impulses are not accompanied by "sensation" is quite impossible. Whichever theory of the mental process is taken as the basis, in the majority of the actions of sense-organs (including of course the cutaneous and tendo-muscular end-organs), no *separable* conscious impression is represented by the separate afferent organs. Each impulse, however, going inward more or less, probably does or tends to *do* something in the organism. Each is useful in its degree and probably also conscious in its degree, but each is not necessarily directive of the attention of the individual so as to make him fully conscious of any sensation.

FIG. 181



Plan of the afferent paths from the sense-organs, showing their morphological differences. (Peripheral neurone-cell in back; central neurone-cell in white.) *A*, "general sensibility;" *B*, taste; *C*, hearing; *D*, smell; *E*, vision; *AN*, spinal cord; *DD*, decussation of the neuraxones of the central neurones. (Morat.)

Another matter needs an introductory word for clearness' sake. It is the province of anatomy to describe the structure of the sense-organs. It is just as surely the duty of psychology to describe their function which partly is consciousness. But physiology in this case ordinarily does something of both, for the mode of working of these often complicated organs is sometimes quite blind without a general notion of the way they are built, while their "function" sometimes is indistinguishable from sensation, even if much more often not. Thus, while we divide the chapter into kinesthesia, vision, hearing, and so forth (functions), our chief concern will be with the organs serving these functions and especially with the ways in which they serve them.

The senses are special and general. The former have end-organs, nerves, and cerebral centers somewhere or other, probably. The latter arise, in ways unknown at present, more or less throughout the body.

The order of consideration of the different senses is intended to be that of their probable importance in the conduct of the organism's life, although the positions in the latter part of the list are confessedly arbitrary. We shall discuss kinesthesia, vision, hearing, touch and pressure, taste, smell, the temperature-senses, pain, pleasure, and the general senses, fatigue, thirst, hunger, nausea, and vertigo.

With these introductory explanations (necessarily different from the preceding parts of the physiology but indispensable as a basis of departure), we shall be in a better position to appreciate the importance of especially the great multitude of afferent organs other than the eyes and ears and taste-buds and smell-cells on which the organism is basally dependent for its activities.

KINESTHESIA.

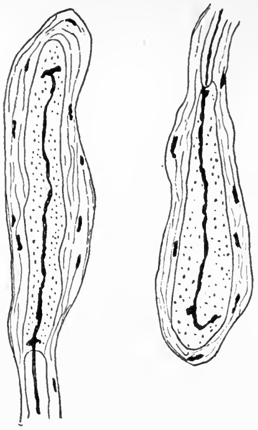
The etymology of this word indicates "the feeling of movement." It includes then the afferent impulses of the organism which are actuated by its movements. These movements are largely produced in the muscles, the tendons, and the joints. We shall discuss first the sense-organs in these parts, because it is becoming yearly more apparent that they have more to do with directing the immediate life of the animal than have any other of the afferent nerve-organs. Their mode of action in connection with the nerve-centers we saw in the chapter on the nervous system and we shall discuss the matter further in relation to the muscles in the next chapter.

Compared with the great sense-organs of vision and of hearing, these sensory nerve-endings in the muscles, tendons, and joints are simple structures. This may be seen from the accompanying figures. They are, as Huber calls them, the "peripheral teleodendria of dendrites of peripheral sensory neurones." The forms of the nerve-endings already described by histologists are various and consists of two general varieties free and encapsulated. The free endings have not been discovered in muscles or tendons, but they occur in mucosæ and in epithelium.

Afferent Endings in Muscle.—These are of several forms whose shapes more or less merge into each other. They are probably all actuated by mechanical pressure.

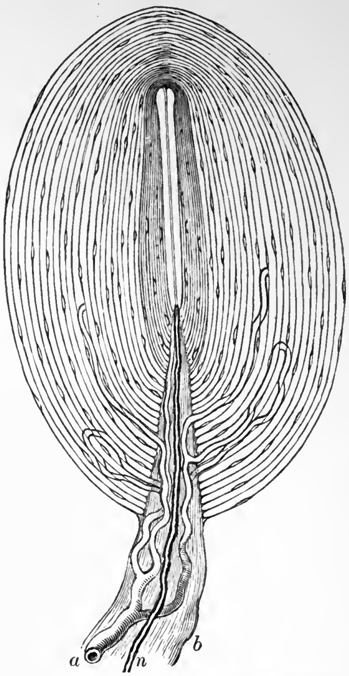
Fig. 182 shows well the cylindric end-bulb of Krause. This is found in cross-striated muscle and in tendon as well as in the skin and mucous membranes. It consists of a thin nucleated capsule investing a semi-fluid core containing the nerve-fiber. It is obvious that such an instrument among the fibers of muscle or tendon will be stimulated when the muscle hardens in contraction or when the fibrous bundles of the tendon are drawn together as the tendon is put on stretch. The Vater-Pacinian corpuscle is built on the same plan as the preceding, but it is on a larger scale and more elaborate. They are sometimes 3 mm. long and 1 or 2 broad and have as many as 60 fibrous lamellæ, each of which according to Schwalbe is covered on both surfaces by a layer of endothelial plates. These end-organs are of many varieties and are found in many kinds of places. They are in the skin especially of the foot and the hand near the joints and particularly on the flexor sides of the latter, in the periosteum of the bones, in the tendons of intermuscular septa, in the muscles themselves, and in the coverings of the viscera and of the nerves (Figs. 183, 184, and 208). Of a different nature (and function who can doubt?) are the neuro-muscular and neuro-tendinous end-organs described by Sherrington and Golgi. Instead of being compact and rounded organs, these apparently

Fig. 182



The cylindric end-bulbs of Krause. The same structure is seen as in the Vater-Pacinian corpuscles, but this sense-organ is better adapted to its position between muscle-fibers. These are perhaps the more passive end-organs of kinesthesia.

Fig. 183



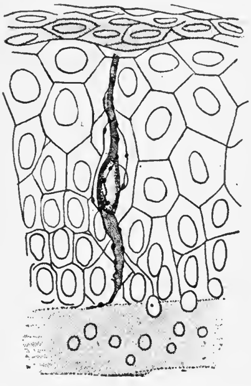
A Pacinian corpuscle from a cat's mesentery. (Von Frey.)

are the means by which the nerve ends freely among the muscular and tendinous fibers. These are the so-called muscle-spindles of Kühne and Sherrington. To each of these end-organs go two, three, or four large medullated nerve-fibers, which, after dividing, end in fibrils wound about the fibers of the muscle or else in irregular disks. They are found in nearly all cross-striated muscle save the intrinsic eye-muscles and those of the tongue and larynx. They are especially abundant in the delicate muscles of the hand and the foot. Kerschner supposes that these are stimulated by the electrical action-current of the muscle rather than by compression. It is suggestive that these are found only in cross-striated voluntary muscle. Perhaps they represent, therefore, the active contraction of the muscle rather than its passive movement (Fig. 186).

Fig. 184

Two Pacinian-Vater-Herbst corpuscles. The nerve-fibers (neuraxones) are seen to divide inside the connective-tissue organ in various ways, each division ending in a knoblet. (Dogiel.) There are many forms of this general afferent nerve-instrument variously known by the three names given above. These are concerned, perhaps passively, in muscular control.

Fig. 185

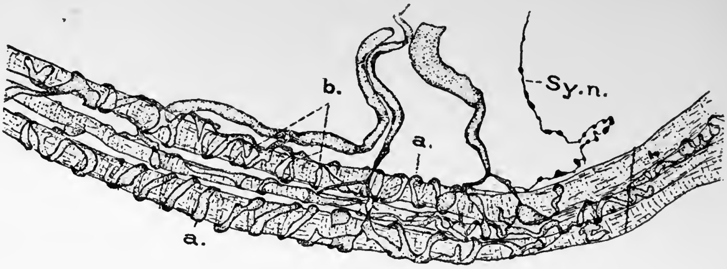


A sense-cell in the upper vocal cord of a dog, showing the nerve-net about it. (Ploschko.)

Afferent Endings in Tendons.—The neuro-tendinous nerve end-organs ("the Golgi organs" of Sherrington) are constructed on a similar general plan. These are found only in tendons and they too are especially numerous in connection with the small muscles of the hand and foot (Fig. 187).

The Afferent Endings in the Joints, etc.—Less is known about these than about the end-organs of the muscles and tendons. Kölliker has described the sensory nerves of bone. In the periosteum nerves are also found, but they are smaller and less numerous. There are in the joints the so-called articular end-bulbs which are in connection with the Pacinian corpuscles already described. The four articular regions (bone, periosteum, synovial membrane, and skin over the joints) probably combine to send to the brain important knowledge of the movements of the limb at a joint.

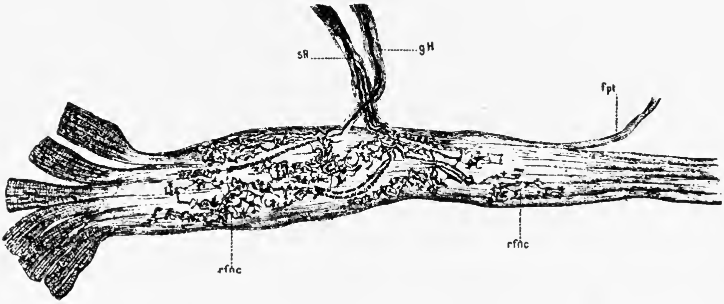
Fig. 186



A muscle-spindle from a cross-striated muscle of a dog: *a* and *b* are coils of the nerve fiber making up the "spindle," while *sy.n.*, is a sympathetic vasomotor fiber. (This may be the organ through which cross-striated muscle is actively and delicately controlled.) (Gluber and De Witt.)

Kinesthetic Function.—Such are the most important of the known afferent organs serving the kinesthetic sense. The general purpose of all these afferent impulses is to furnish the person information as to the postures and relative activity of his limbs and other bodily muscular parts. More essential than these ideas of posture ordinarily are the impressions we receive from these end-organs concerning the movements of our limbs and muscles, active or passive, of which the active are the

Fig. 187



A neurotendinous end-organ from the tendo-Achillis of man: *sR* and *gH*, two nerve fibers; *fpt*, a primitive fibrillary bundle of the tendon; *rfnc*, the ultimate ribbon-shaped branches of the nerve-fibers. (Ciacio via Barker.)

more important. Muscular action, reflex or voluntary, depends for its usefulness in nearly all cases upon its guiding coördination from the central nervous system. In the complex voluntary actions of life especially one sees the essential importance of these myo-tendo-articular impulses or sensations, for skill, culture, and even civilization itself in part depend on the fine adjustment of voluntary muscles in ever new and more delicate ways. Imagine a "laborer" accustomed only to the rough use of the pick and shovel in a trench, attempting to engrave a delicate monogram on a small seal-ring. The inability in such a case might be due wholly to the lack of this complex sense of delicate voluntary movement. These conditions are present everywhere and always in our motor activities. Take for another example the act of walking. This is almost a reflex action in the person more than three years old. (See the description of the process, page 392.) As one walks, continuous streams of impulses are passing upward into the gray matter of several segments of the cord and into the cerebellum and probably into the posterior and anterior central cortex cerebri. These come from every part of every muscle and tendon of the legs and from many of those of the trunk and neck engaged in the body's equilibrium. From all the joints concerned (hip-joints, knees, ankles, feet, spine, etc.) other sets of impulses pass similarly, and from the skin, especially over the joints and wherever it comes in contact with our garments. Moreover, we are kept dimly aware of the nature of the path we walk, whether hard or soft or rough or smooth, by these same sets of impulses. These too help reflexly to direct the spinal and other centers in their complex task of control over these multifarious walking-parts. One may similarly trace the same process in speaking, swallowing, chewing, and numerous other movements, as well as in thousands of purely voluntary actions known to the many trades, occupations, and amusements. It is, in short, only on the information furnished by these numberless incoming messages that the centers directing movement can do their work. When we make voluntary movements, especially with the arms and hands, the eyes usually follow the movements and we are apt to think that it is by vision that they are directed. They, however, can be made even better in many cases after some practice, without any use of the eyes whatever. Unless there were sent into the kinesthetic centers information of an exact nature concerning the relative degree of contraction of each muscle-fiber, these central motor cells could not properly actuate the muscles. A partly contracted fiber, for example, would need a different degree of stimulus from one contracted fully. Not only must a number of different muscles be made to contract, but each one often in a particular way, hard enough but not too hard and each at exactly the right time and for exactly the right period. In short, a maze of relations exists which would make of a movement not thus minutely directed by afferent messages a mere jerk or convulsion. Never would we have the wonderfully adapted, perfect, and certain action we are familiar with. The concertos of de Pachmann differ from the drumming of our fair but misguided neighbor in the next house chiefly because in de Pachmann this sense we are considering is developed to its human limit, while in her apparently it is not.

Another use of the muscular nerve-impulses combined with those from the tendons, joints, etc., is the direction of the power of contraction needful to overcome a required resistance, as, for example, that of gravity in lifting a weight. This estimate is made by the intellectual "centers" of the brain, but only from repeated experiences given through the afferent muscular and other senses. The effort is expended under the guidance of impulses coming from the contracting muscle.

Fig. 188

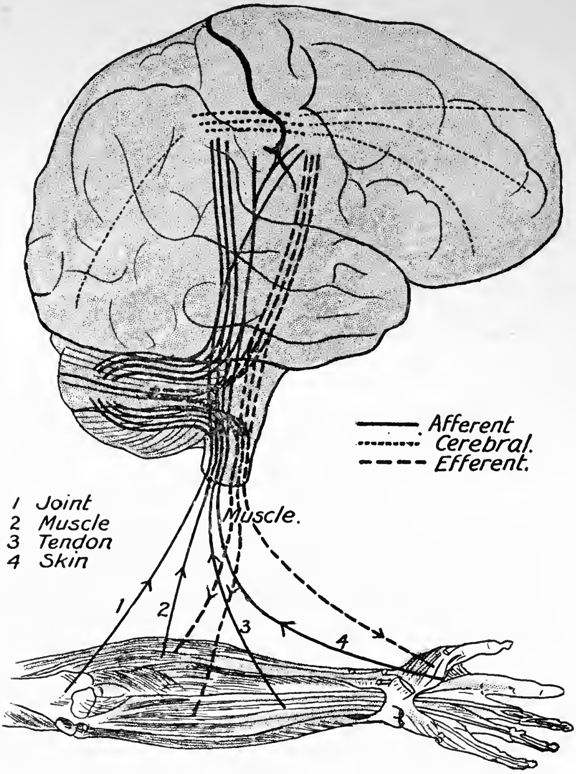


Diagram of the chief kinesthetic nerve-impulses. From the joints, muscles, tendons, and skin nervous influences pass inward and upward to the "motor centers" of the cord and brain, making general connection with the cerebellum on the way. Numerous "central" impulses connect these incoming messages with other parts of the brain, motor and sensory, and especially with the regions which control the efferent influences to muscle and to epithelium. The impulses passing down and out likewise have much to do with the cerebellum. This whole apparatus together—end-organs, afferent influences, centers, central impulses, efferent influences, and muscles—constitutes the neuro-muscular mechanism.

That kinesthesia has separate centers somewhere in the brain, or else separate paths up the cord, is made evident by the occasional cases in which this sense alone is lost, those of the skin, for example, remaining unharmed. On the other hand the skin's sensations are sometimes lost without disturbance of the kinesthetic sense. The location of these centers is still in doubt, but evidence is accumulating that it is in the posterior central convolutions, and possibly also in front of the Rolandic fissure on the cortex cerebri.

One would expect these centers, moreover, to be very closely allied with the centers of voluntary movement. These impulses probably pass up in the long paths of the dorsal columns and in the direct cerebellar tracts.

(For further facts as to muscular control see Chapter XII.)

Partial loss of the kinesthetic sense produces a greater or less degree of ataxia or imperfect muscular adjustment and coördination such as is seen, *e.g.*, in ataxic aphasia, in locomotor ataxia, and in paralytic dementia ("paresis"). The spinal afferent fibers are disturbed or destroyed in these conditions. A heightening of this sense beyond its normal state is produced by small doses of alcohol, and is felt more normally whenever, because of a lack of muscular exercise, the irritability of the muscles and their tonic balancing back and forth is increased. This condition is all too familiar to persons of sedentary habit. They feel "fidgety," and yet nothing is necessary to relieve the unpleasant feeling but vigorous muscular exercise with its accompanying aëration of the tissues and the removal of accumulated metabolic substances from the muscles and the nerve-centers. It is one of the functions of these essential afferent end-organs then to incite the individual to a normal amount of physical exercise. Thus, indirectly, one maintains the normal metabolism in the muscles (about half the mass of the body) and, by increasing the flow of lymph, invigorates and stimulates all the essential organs of the body.

VISION.

Markedly in contrast in some respects with the kinesthetic sense is the queenly sense of vision, of experiencing the flooding light of day. The organs of the muscle-sense and its congeners are minute, simple, and hidden. They send inward a host, one may almost say figuratively a mass, of impulses, most of them singly quite "unfelt," to direct the body's motions. The eyes, on the contrary, are large and complicated end-organs, stars of "the human face divine" which somehow (we can never imagine how) set going into the brain nerve-impulses which give rise to that flooding and overwhelming sensation we call *light*. Vision at first seems easily "queen of the senses," and, by its very nature, to many the larger part of consciousness.

The organ of vision, the eye, is too elaborate an instrument for detailed description here, and consequently we shall run over the structure of only those portions of the organ which are immediately essential to its various functions as the end-organs of certain afferent nerves and brain-centers. For adequate knowledge as to the detailed structure of the eye, one of the most complicated parts of the wondrous animal body, the reader is referred to text-books of anatomy and histology. Study of such an organic mechanism always much more than repays the time and labor which may be put on it, and in this case is entirely indispensable for any proper understanding of the visual function. Here we are concerned only with the way in which its most essential parts enable us to

FIG. 189

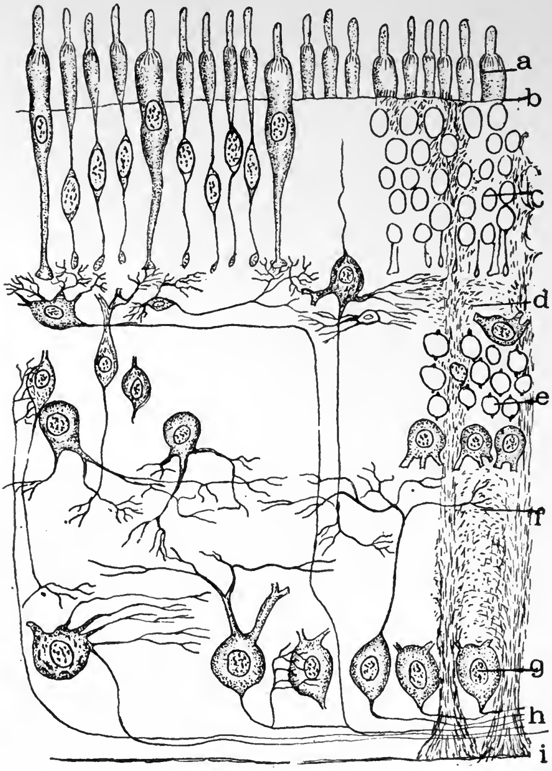


Diagram of the retina: *a*, rod- and cone-layer; *b*, external limiting membrane; *c*, external granular layer; *d*, external reticular layer; *e*, internal granular layer; *f*, internal reticular layer; *g*, ganglion-cell layer; *h*, nerve-fiber layer; *i*, internal limiting membrane. The pigment-layer is not represented. (Bates.)

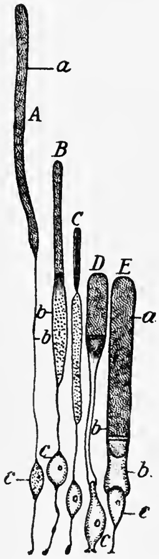
see the world's infinite variety of form and color, to somehow perceive objects by waves of light sent into the periphery of the nervous system.

The eye, then, is essentially a photographic optical instrument for impressing on the extended peripheral termination of the second cranial nerve an image of whatever is placed before it. The nerve then conveys the nature of this image to the brain, and vision results. In order that this image on the retina may be always clear, the eye has lenses and means of accommodating its function not only to the light's brightness, but to the distance or size of the object. Vibrations in the hypothetical "ether" of space occurring between 392,000,000,000,000 and 757,000,000,000,000 times per second give the eyes their proper stimulus. Vibrations outside this narrow range we do not perceive as light, but as heat, electricity, or other manifestations of vibratile energy. The tendency now is to think of this ether as attenuated matter streaming in radiations from the sun.

(The common refractive defects of human vision and their remedies with lenses will be found described with sufficient detail for our purpose in the Appendix, page 526, etc.)

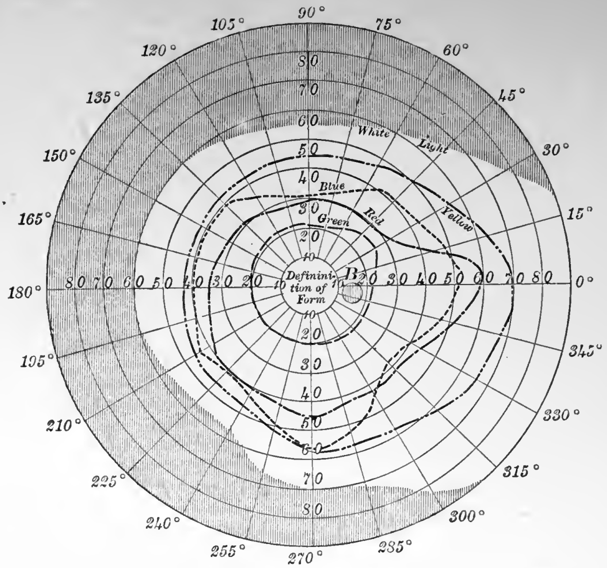
The Receptive Apparatus of the Eye (as distinct from the transmitting mechanism) consists of the retina and the optic nerve and tracts and the centers behind them. Of all the complex structures of the retina (not yet much understood), the visual cells are the essential portions. These are the rods and the cones. Each *rod-cell* consists of a rod and a rod-fiber with its nucleus. The rod, averaging 45 microns long, is made up of two segments, the outer of which (doubly refracting) consists of numerous transverse disks, while the inner segment is striated longitudinally. The rod-fibers extend downward to the outer nuclear layer (see Fig. 190) where they end in tiny bulbs. The rods contain in their outer parts the essential pigment called visual purple or rhodopsin, and granules in their inner ends. The *cone-cells* consist each of a cone and a nucleated cone-fiber. The cone averages 20 microns long, and its fiber, like that of the rod, extends inward to the outer nuclear layer of the retina where it ends in a branched basal plate. The proportion of rods to cones varies much in the different retinal regions. In the macula lutea, the sole region of sharply focused vision, there are no rods, but in other parts an average of fourteen rods to one cone are found, but fewer cones the farther away from the macula a region lies. It is noteworthy that the cones contain no visual purple. The rods and cones are the only ocular elements capable of reacting to the minute vibrations of the luminiferous ether, but how they do so is quite unknown—evidently, however, by a transformation of force, the light waves becoming waves of nervous impulse. About seven cones, a hundred rods, and seven of the pig-

Fig. 190



Different shapes of retinal rods: *A*, that of the perch; *B*, man; *C*, pig; *D*, green rod of the frog; *E*, red rod of the frog; *a*, external segment; *b*, internal segment; *c*, cellular body. (Greeff.)

Fig. 191



A perimeter chart with records for a right eye: *B*, blind spot. The unshaded portion is the field of clear vision for white light. The fields for yellow, blue, red, and green light respectively are indicated by the variously broken lines. It is only within the inner circle of the chart that vision is direct and perfect. (Krapart.)

Fig. 192

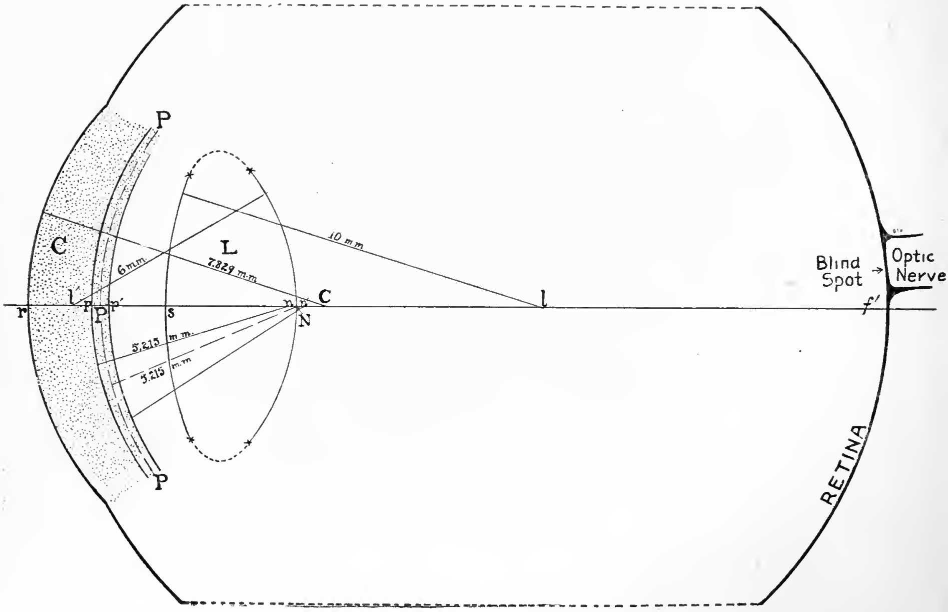


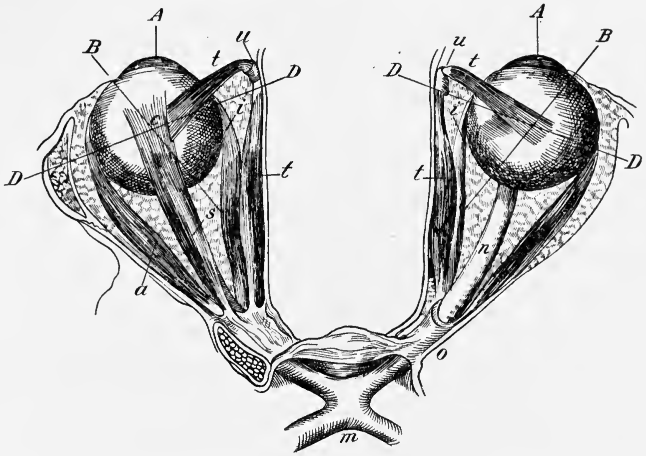
Diagram showing relative positions of the eye's refractive media and the reduced refracting medium (*PPP*). Drawn to scale and five times the natural size. (Hall.)

mented cells are connected with each of the half-million or more fibers of each optic nerve. Many details of the structure of the rods and the cones are known, for knowledge of which the reader is referred to the special literature. At present, however, these facts of structure throw little or no light on the real nature of vision. We can see the rods and cones and the neurones beneath them, but as to their actions we know nothing.

The fovea centralis is the center of the macula lutea, and is the spot on which the visual image has to be focused whenever the object is to be clearly seen. This focusing is accomplished by several sorts of complex movements.

The Various Adjustments of the Eyes.—As has been just suggested, the fovea centralis, a spot only a few millimeters in diameter at the inner end of the visual axis (not of the optical axis) of each eye, is the only part of the whole retina at which vision is quite distinct. In other words, the eyes must be continually so directed toward any point of an object which is to be clearly seen that the rays of light therefrom shall fall exactly on this narrow spot, the fovea. There must therefore be some adequate arrangement for quickly and reflexly directing the eyes in exactly the right direction if vision is to be useful. Moreover, the intensity of the light entering the eyes and the distance of the objects looked at vary greatly and there is required some means of adjustment to these conditions also. The former sort of adjustments are made by movements of the head and of the eyes within the head, and the latter kind by means of the accommodating mechanism proper (the iris, ciliary muscle, etc.), assisted sometimes by the muscles of the eyelid.

Fig. 193



The extrinsic eye-muscles, and the eye-balls' axes of rotation. (Gariel.)

Head-movements for visual purposes scarcely need detailed description. The possible movements of the head upon the axis at the top of the vertebral column are very numerous and in all directions. It is enough to know that for the most part the muscles producing these movements are small and therefore perfectly adapted for any desired movement. They are controlled by what is practically reflex action. The afferent impulses come especially from the retinæ, but also from the voluntary cortex and from many other places under the influences of many different sorts of stimuli, for example from the ears.

Eye-movements have been the subject of a large amount of careful and ingenious study, especially by the psychologists. For example, Delabarre attached to his cornea a minute concave mirror with a hole in its center and studied the directions taken by a ray of light reflected from it on to a photographic plate. The movements, however, occur so often, so quickly, so unconsciously, and are often of such small extent, that real progress in the subject has been slow. Knowledge of these movements is of great importance in many theoretical and practical problems, for example the ideal mode of composing printed matter for being read.

Fig. 194

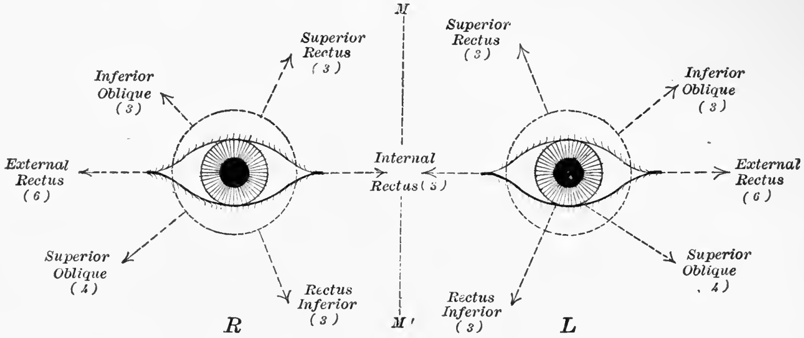


Diagram of the actions of the external muscles of the eye-ball. The figures in parentheses indicate the nerves which supply the muscles. (Waller.)

Fig. 194 shows well the gross movements as produced by the six extrinsic eye-muscles. The nearly spherical globe of the eye is set in a soft bed of fat and of vascular tissue and rotates with great readiness under the influence of the muscles (the superior, inferior, internal, and external recti, and the superior and inferior obliques) attached to it. Thus, the internal and external recti rotate the eye in the directions their names indicate; the superior rectus rotates it upward and inward, and the inferior rectus downward and inward; the superior oblique rotates it downward and outward, and the inferior oblique upward and outward. In the majority of cases, if not in all, the muscles work in combination, and are always in such a state of balancing tonus as to hold the eye functionally, but not actually, still. The muscles of the two eyes always move together, but their contractions become less effective in old age. All movements normally take place about the rotation-point, 11 mm.

behind the front of the cornea, and about any one of three axes, the visual, transverse, and vertical.

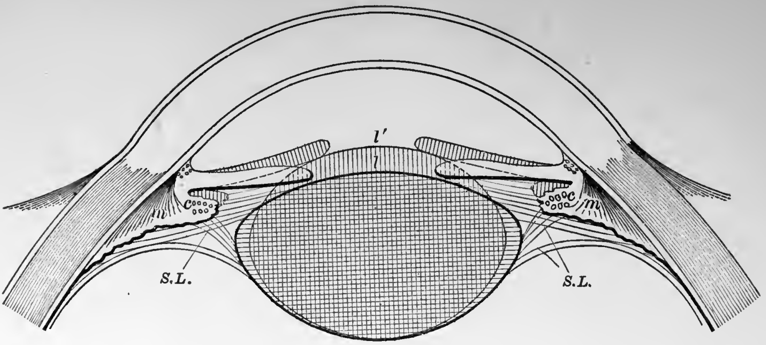
Besides the larger movements produced by the extrinsic muscles and apparent both from within and, to others, without, there are numerous minute unconscious and entirely involuntary movements of extreme quickness and jerky in nature, whose full purpose is yet by no means quite clear. They are discernible only by delicate means, and most readily when the eye is made to fixate rigidly a point or to trace carefully along a given line. It is likely that these movements are intended to avoid the tiring of the sensitive rod or rods and cones of the retina by distributing the stimulus over a larger number than else would be innervated. Another and perhaps a more important function of these minute movements, of which the seer is always entirely unconsciousness, may be to help the synthesis of disparate visual impressions into a "field of vision," a homogeneous general impression. The synthesis of actual vision is not wholly the work of the visual centers or of "the mind," but in part at least of the afferent end-organ (retina) as well. Experts in these matters are at present discussing the rather primary question as to whether the individual sees during these quick, short, intermittent eye-movements or during the very short periods of rest between them. Woodworth's contention for the former seems well-grounded both in theory and in facts.

Accommodation is the reflex adjustment of the refracting mechanism of the eyes to the ever-changing conditions in the intensity and distance of the object. The mechanism concerned includes the ciliary muscle, the lens, the suspensory ligament, and the iris.

The chief need of accommodation lies in the optical fact that rays coming from an object near the eyes, and therefore directed in more divergent directions, require a stronger (convexer) lens to converge them upon the fixed retina than do more nearly parallel rays coming from a distance. In a camera or in a compound microscope this focusing is brought about by moving the lenses away from their screen or object, but in the living eye it is more convenient to change the refracting power of the lens itself. This change is easily brought about because of the softness of the lens-protoplasm, especially in its interior. The anterior capsule of the lens is thick and some of its lamellæ are directly continuous with the fibers of the suspensory ligament.

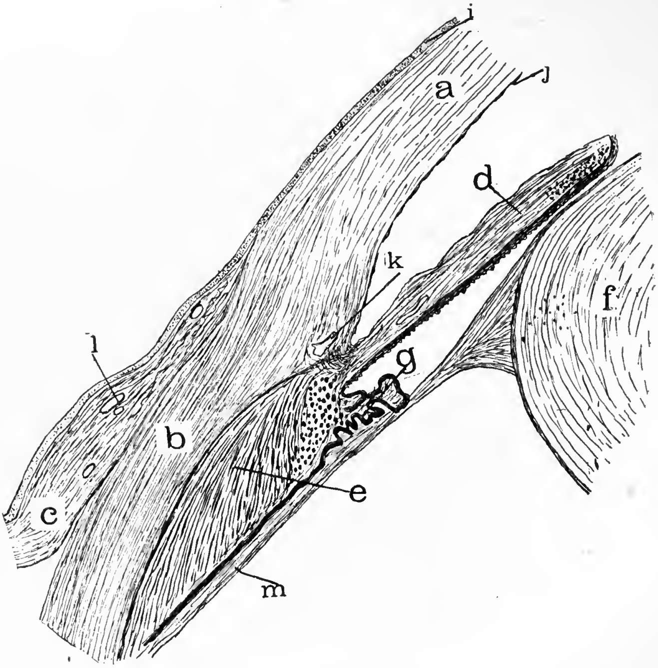
The theory of accommodation originating with the great Helmholtz is still held (in a condition somewhat modified by Hess, Smith, and Einthoven) by the great majority of physiologists. The accompanying illustration (Fig. 195), devised by Schoen to show how the lens changes shape (on a theory opposed to that of Helmholtz), gives a good notion of what appears to take place in accommodation to near-vision. The anterior surface of the lens bulges into the shape shown in the figure (although in a degree much less marked of course than that shown). This is the tendency of the lens itself, because of its structure, whenever the restraint of the suspensory ligament and the ciliary muscle exerted

FIG. 195



Visual accommodation: *m*, meridional muscle; *c*, circular muscle; *S.L.*, suspensory ligament. The position of the lens and iris as shown by the vertical shading is the position when accommodated to a near-point. (Landolt.)

FIG. 196



Section of the front of the eye: *a*, cornea; *b*, sclera; *c*, conjunctiva; *d*, iris; *e*, ciliary body; *f*, crystalline lens; *g*, ciliary processes; *i*, stratified epithelial covering to the outside of the cornea; *j*, endothelial lining of the inside of the cornea forming the outer wall of the anterior chamber; *k*, canal of Schlemm. It will be seen that the sclera projects forward to form the cornea, while the iris comes off from the ciliary body. This in turn is a forward projection of the choroid. The dark line which covers the inner side of the ciliary processes and the iris is the pigment layer of the retina. *l*, bloodvessel in the conjunctiva; *m*, suspensory ligament which holds the lens. (Bates.)

about its edge is relaxed. According to this view, then, the chief activity of the ciliary muscle is to relax the centrifugal support of the suspensory ligament, thus allowing the lens to bulge somewhat in the manner shown.

The notion of Tscherning and of Schoen is that the ciliary muscle in contracting stretches the ligament instead of relaxing it, and that it is this centripetal pressure on the edge and sides of the lens which causes its soft substance to become more convex in accommodation to a near-point. The discovery of Hess, that when the ciliary muscle is made to contract strongly by eserin the lens wobbles back and forth within the suspensory ligament, seems to dispose of this supposition.

With the increase in the convexity of the lens in accommodating to near objects (amounting at its maximum to an increase in strength of 14 diopters up to 34 diopters) occur two other adjustments of the eyes. One of these is the convergence of the eyes necessary to place a near object on both fovea. This is produced by contraction of the internal recti muscles, the degree of convergence depending on the nearness of the object seen. The internal recti are relatively strong muscles because used so much, and when the eyes are quite at rest (as in sleep) tend to converge the eyes mechanically so that the visual axes would meet if prolonged 40 cm. from the eyes. One sees this atonal condition often, also, when persons are in a "brown study," one of those lapses of consciousness which occur at times, and which are really just the opposite in nature from study.

The other adjustment which is properly part of the process of accommodation is contraction of the iris (pupil). This shuts out the peripheral rays from the eye, prevents spherical aberration and so makes the definition of the object's retinal image sharper. The iris has movements other than those associated with accommodation. It serves as a diaphragm for adjusting the eye to differences in the intensity of light. Its movements are closely watched in conditions of anesthesia out of many a serious condition involving the central nervous system. Its size is affected furthermore by many drugs, contracting to opium, nicotine, and muscarine, and dilating to atropine. (See the experiments in the Appendix, p. 521.)

Visual Theories.—When one has summarized thus briefly some of the most essential structures of the eye and some few of the principles on which these structures work he has had suggested to him many interesting phenomena, but he has still left, quite unconsidered, the essential part of vision, namely, how and in what different ways the eyes see. In other words, we would have explained to us, if we might, exactly what takes place in the minute retinal rods and cones when the rays of light, thus carefully admitted to them, stimulate them and cause them to send to the visual centers of the brain the several different sorts of vision that most of us experience. For example, if our eyes, etc., are normal we see light, the forms and colors of objects, and the spatiality of objects. We can see in the dazzle of noonday and form, at least, in the quasi-darkness of night. We experience after-images and our eyes are prone to be deceived in numberless illusions. We suspect that chemical processes take place in the retina when light falls on it. What then exactly are these processes in terms of modern chemistry? Why are there no rods in the fovea? Why do different zones of the retina see particular colors only? Why do we not experience a hole in our monocular landscape where the blind-spot is? Is color-blindness a defect of the retina or of the brain? Questions of which these are only important examples beset us everywhere while observing the immensely complex facts of vision. Their explanation, however, in statements to which all must agree, are quite beyond us as yet.

THE PERCEPTION OF LIGHT depends in some way on the chemical changes produced in some substance found in the rods or the cones or in both by the vibrations of the "ether" entering the eye. This is probably some chemical change, but just what is by no means certain as yet. It appears to be in the nature of a bleaching of a pigment. In addition the etheric vibrations cause the outer parts of the rods to increase in diameter and the inner parts to thicken and shorten; on the other hand, the lower parts of the cones contract. These movements, like those of the pigment, depend much on the nervous system. The bleaching of the visual purple is not at all so influenced. It is obvious how inadequate such statements are. Such chemical reactions and other movements, whatever they are, could do practically nothing toward explaining the wonderful experience we call light, but they would have great interest for the physiology of the nervous system.

THEORIES OF COLOR-VISION.—These have been numerous, those of Young, Helmholtz, Hering, Wundt, and Mrs. Franklin being perhaps the most conspicuous. Out of these theoretical complexities we need discuss, even briefly, no more than the last-mentioned.

Mrs. Franklin's theory of color-vision takes account of various facts recently learned which give it much weight and promise, perhaps more than any other. It is likely that the child for many weeks, perhaps months, after birth lacks the color-sense. This theory supposes, then, that the visual substance present at birth in the retina is affected at first only by light ranging in tone from white to black through the grays, but that the substance decomposes through this kind of photic influence and so stimulates the optic nerve-fibers. In the first or second years of life some of this gray-perceiving retinal substance develops into two other retinal pigments, one for blue-perception and one for yellow. A little later, part of the yellow-seeing substance in turn differentiates into a green-perceiving substance and a red-perceiving substance. All of these pigments except the gray-perceiving, congenital one, develop in the *cones*. This theory, then, supposes that it is the cones of the adult retina that represent color, while the rods react only to light-waves of the black-white sort. Each color-sensation corresponds to one combination of ether wave-lengths striking the retina, every anabolic and katabolic color-process being dependent for its stimulation on certain vibration-numbers in the ether. There is no end to the number of combinations of physical rays which may occur, and consequently no theoretical limit can be set to the color-tones perceptible by the human eye. (In practice about 150 tones of color can be distinguished, and 700 degrees of brightness; the total number of elementary chromatic sensations is in the neighborhood of 30,000.) Whenever the combination of wave-lengths in a beam of compound light is such that each sort of pigment is stimulated equally at the same time, the sensation of whiteness is produced.

COLOR-BLINDNESS is a technical defect of much practical and theoretical importance in which a person lacks the power to perceive certain colors. About one in twenty of all males are more or less color-blind, but not more than one in four hundred of females. It is often hereditary. The most common form is that in which a confusion of red and green occurs. One of the points in favor of Mrs. Franklin's theory is that it explains the various sorts of color-blindness apparently better than any other hypothesis, for it is necessary only to suppose a partial or complete non-evolution of the color-pigments of the cones.

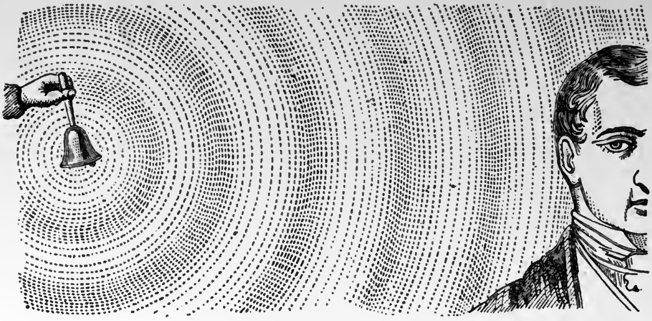
SPACE-PERCEPTION.—It is probable that the human eye does not at first perceive the third dimension of space, that is depth away from the eye. To the infant just born most likely the objects of the room appear as if they were differently colored spaces on a screen hung before its eyes. It is only when a child begins to use his muscles that the idea of space in three dimensions begins to grow up in the mind. The sensations which come from the muscles of the arms and of the legs in action are probably assisted in this matter by the accommodative movements of the eye-muscles. This in a word is the so-called empiric theory of space-perception. The nativistic theory, on the contrary, supposes that the perception of space is directly given visually from the moment the eyes are first opened.

HEARING.

Only less informing than vision as to occurrences in the environment is the experience called sound. Its nature we cannot discuss here any more than we can that of light, for that is the province of philosophy. It is enough to say that what comes to our afferent nervous end-organs (ears) out of the environment is not sound but physical vibrations, usually in the air. We and other animals make the sound and the light, in some way, out of these.

These sonorous vibrations of the environment are given out by all rapidly vibrating elastic bodies: huge masses of gaseous matter in the clouds disturbed by lightning, the air in a great organ-pipe, the head of a drum, the string of a violin, or the cords in a singer's or speaker's larynx. These and thousands of other natural and artificial objects moving rhythmically, or otherwise, fast or slowly, make waves in the ear's environment which the individual perceives as sound, whether noise or music. These waves given out by moving objects, like hollow spheres, radiate outward in all directions (in air at the rate of 332 meters (1093 feet) per second), and consist in alternate rarefactions and compressions of the air. The vibrations move back and forth in the line of advance, (while in case of light, the vibrations are at right angles to the line of advance). For the range of the human ear these waves vary in length, that is from crest to crest, from about 1.5 cm. to more than 12 m.; their number varies from about 16 to 35,000 (even 50,000?) per second. In case of noises, all sounds which have not the qualities of musical tones, the conditions are more complex and various and in fact little understood. It is supposed that the vibrations producing them are irregular in many ways, while those making tones are essentially rhythmic however complex the rhythm. It is presumed by many that it is the ampullæ of the semicircular that represent noise, these being homologous to the hearing-organs of many of the molluscs and other simple animals. (See Figs. 221 and 222.)

Fig. 197



A suggestion as to the nature of sound-vibrations as distinct from those producing light (which are vertical to the ray's direction). Moreover, the sonorous vibrations are those of material particles of air, while those of light are of the ether, perhaps not of a material nature.

Fig. 198

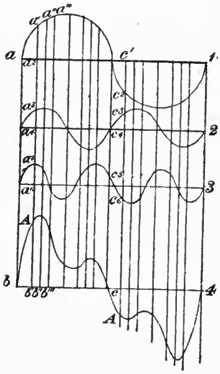


Diagram to suggest the compounding of sound-waves out of simpler forms. In this case the bottom curve (4) represents the combination of the other three curves, these beating in the ratio of 1, 2, and 3. (McGregor Robinson.)

As in case of vision, we may divide the ear for descriptive physiological purposes into a transmitting part and a receiving part. The conditions are relatively simple until we come to the essential nerve end-organ of Corti. Even this we can sketch in merest outline only, for this structure, minute as it is, makes the ear perhaps the most complicated of all known mechanisms. At any rate it has a complexity, even that which is known, far beyond the power of man at present to understand.

THE TRANSMITTING APPARATUS AND FUNCTIONS OF THE EAR include the pinna and the external auditory meatus (making up the outer ear),

FIG. 199

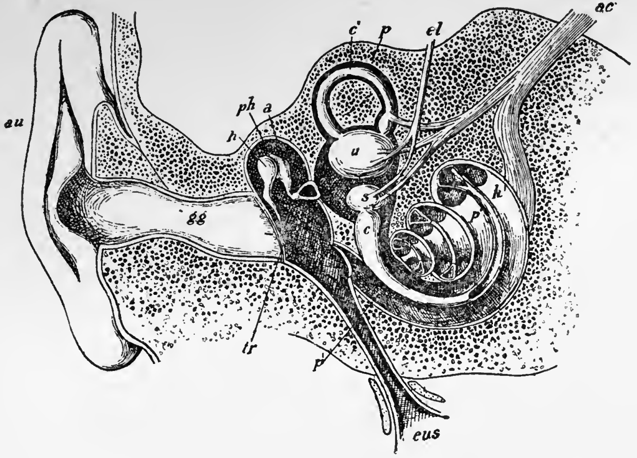


Diagram of the grosser mechanism of the ear: *au*, auricle or pinna; *gg*, external auditory meatus; *tr*, membrana tympani; *h*, malleus; *a*, incus, attached to the head of the stapes whose foot is in the foramen ovale of the labyrinth; *h'*, *p*, *p'*, perilymphatic space of the labyrinth; *c*, membranous labyrinth; *c'*, one of the three semicircular canals; *u*, utricle; *s*, saccule; *ph*, drum or middle-ear cavity; *eus*, Eustachian tube extending to the posterior nares; *el*, endolymphatic duct extending to a blind bulbous ending between layers of dura mater above; *ac*, eighth cranial or auditory nerve shows its two parts, cochlear and vestibular. (Czermak.)

FIG. 200

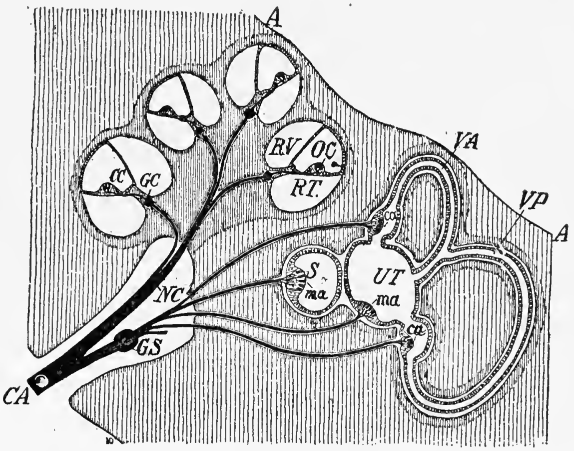


Diagram of the internal ear: *RT*, scala tympani; *RV*, scala vestibuli; *CC*, canalis cochlearis; *OC*, Corti's organ; *GC*, Corti's ganglion; *S*, sacculus; *UT*, utriculus; *VA* and *VP*, two of the three semicircular canals; *ma*, auditory maculæ; *ca*, auditory crests of the ampullæ; *GS*, Scarpa's ganglion. (Duval.)

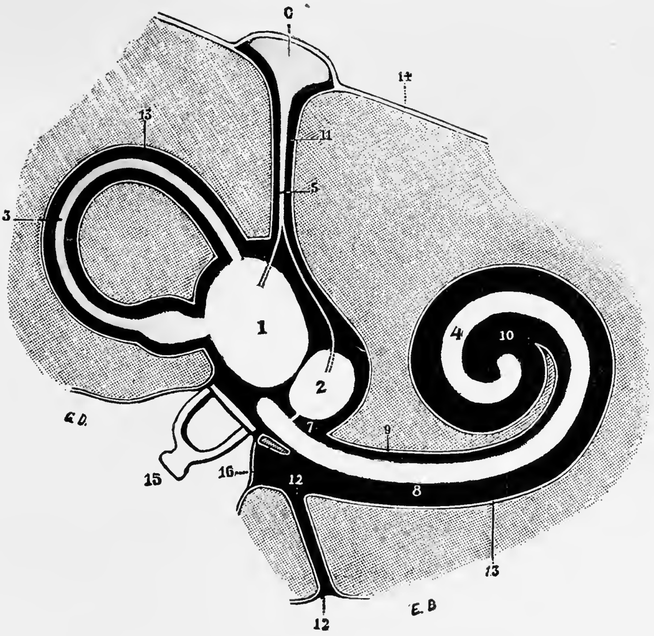
the membrana tympani, the interesting structures within the middle ear, the Eustachian tube leading from the latter to the pharynx, and the endolymph of the inner ear. Here, as elsewhere, the reader is referred to adequate descriptions of these mechanisms to be found in anatomical works. (Plate IX.)

THE ORGAN OF CORTI is the proper afferent end-organ of the auditory nerve, all the rest of the ear being but a mechanical means of securing the proper stimulation of this minute and obscurely intricate structure. We shall note here only a few of the very numerous details of this organ—those which seem most important. Erected on the membrana basilaris (which extends the length of the spiral of the cochlea) are two rows of chitinous pillars called the rods of Corti. These are connected above, while the tunnel of Corti runs between them below. The inner row is made up of about 7000 of these pillars; the outer has about 4600 of them. From the summit of this arch extends inward and outward a thin membrane (also of chitinous material), the membrana reticularis, and through minute holes in this net extend the numerous bristle-like filaments of long cylindrical epithelial cells beneath. These cells recline more or less on the outer sides of the pillars of Corti, and are called respectively the inner and outer auditory cells or hair-cells. Each has several unique structures within it whose significance is quite unknown. There are about 18,000 of these cells; one row of the inner cells and three or four rows of the outer. Between the hair-cells are scattered certain supporting-cells, named for Deiters. The fibrils of the auditory nerve pass from the ganglion spirale within the lamina spiralis to the bases of the hair-cells, and the filaments on the summits of these cells are apparently, the nerve being afferent, the beginnings of the cochlear branch of the auditory nerve. Above the filaments extends outward from the lamina spiralis at the base of Reissner's membrane (separating the scala media from the scala vestibuli above it) the soft membrana tectoria, striated and cuticular, and apparently free in the endolymph of the scala media.

The membrana basilaris, on which as it curves about in the spiral of the cochlea Corti's organ is placed, is made up of transverse fibers, about 24,000 in number. Were this membrane uncoiled and spread out it would suggest in its structure and shape a xylophone. Contrary to what one might expect, the longest fibers are at the apex of the cochlear spiral and the shortest at its base. The extreme lengths of these fibers are 0.05 mm. long and 0.45 mm. It is hard not to suppose on the principle of analogy that the respective lengths of these fibers of the membrana basilaris do not correspond in some way and degree to the differences in pitch of sounds, but this is by no means sure.

HOW DOES THE ORGAN OF CORTI ACT?—To this question many have replied, but all differently. A notion of its mode of working perhaps more common than others is that which follows, little altered in all the busy years since the master of sonology, Helmholtz, suggested it: When, started by a vibrating body, an air-wave strikes against the membrana tympani, through the agency of the elaborate bony levers of the middle

PLATE IX



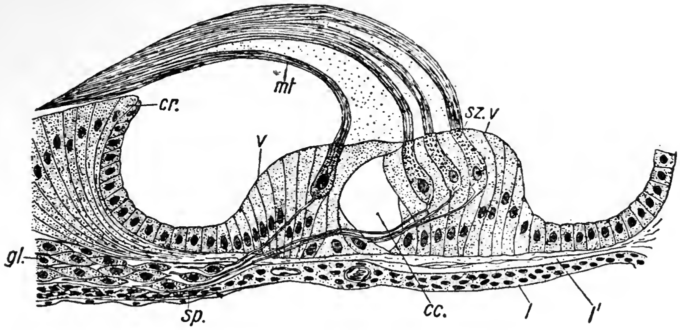
Plan of the Endolymphatic and the Perilymphatic Spaces.
(Testut.)

1, utricle; 2, saccule; 3, semicircular canal; 4, canalis cochlearis; 5, ductus endolymphaticus; 6, saccus endolymphaticus; 7, canalis reuniens (Hensen's); 8, scala tympani; 9, scala vestibuli; 10, helicotrema; 11, aqueductus vestibuli; 12, aqueductus cochlearis; 13, periosteum; 14, dura mater; 15, stapes with its base in the foramen ovalis; 16, membrane in the fenestra rotundum.

ear, the stapes is slightly but powerfully pressed into the perilymph of the scala vestibula through the fenestra ovalis. The pressure is almost instantly communicated to the very thin and elastic Reissner's membrane and passes into the endolymph of the scala media (containing Corti's organ), through it, and into the perilymph of the scala tympani below. As it passes through the membrana basilaris (bearing the organ of Corti), it causes to vibrate that particular transverse fiber of this continuous membrane which corresponds by its length most exactly to the vibration-number of the original producer of the sound. This fiber of the membrana basilaris (more or less accompanied by several fibers on either side), rises slightly and with it rise the pillars of Corti and the hair-cells attached to them above.

As to what happens further than this there is a still greater disagreement of opinion. Perhaps these cells are pressed against the membrana tectoria, the latter then either damping the vibrations of their filaments or pressing them downward against the nerve-fibrils below. Perhaps the membrana tectoria is the vibrating part of the organ. Perhaps it is the filaments only of the hair-cells which vibrate, or even the rods only. One or two experts have claimed that the ligamentum spirale (by which the membrana basilaris is attached to the outer wall of the cochlea) contains muscle-cells, and that therefore it probably serves to tighten the transverse fibers of that membrane. Much of importance remains to be learned about the auditory hair-cells especially, not only as to their filaments but as to their very complicated internal structure. About the function of the pillars of Corti and the tunnel between them information is also sorely needed before any satisfactory theory of the organ of Corti can be suggested. In all these parts (and in many others we have not even named here) there is a mechanism whose

Fig. 201



Organ of Corti: *gl*, ganglion; *SP*, nerve-fibers; *CC*, Corti's canal; *l*, *l'*, laminæ basilares; *SZ.V*, hearing cells; *V*, supporting cells; *mt*, membrana tectoria; *cr*, cresta spiralis. (B. Haller.) The membrana reticularis (just over the hair-cells) is not shown. This diagram represents one out of several theories of the organ's structure and action. One chief doubt is as to whether the hairs of the hair-cells (*SZ*) are continuous with the fibers of the membrana tectoria, *mt*.

intricacy in some measure corresponds with the mathematical complexity of the air-waves producing the sensations of tone and of noise which we continually experience.

Certain Qualities of Sounds.—All sounds, practically speaking (that from a tuning-fork is sometimes excepted), have within them elements both of tone and of noise. "No player of the violin avoids all noise of scraping from the bow; no stroke of a workman's hammer or slamming of a door that does not start and catch up into itself some trace of musical sound." But noises for the most part remain unstudied and their relation to the ears is almost unknown. They constitute, however, especially in cities, no inconsiderable portion of the sounds with which the ear has to do.

Tones or musical sounds have three basal characteristics: intensity, pitch, and quality (timbre). The *intensity* of a tone, depends wholly upon the amplitude of the air-vibrations which move the membrana tympani. This amplitude must not be confused with the frequency of the vibrations, for it has nothing to do with it.

The *pitch* of musical sounds (noises lack especially this quality) depends wholly, so far as we know, on the number of vibrations per second produced in the organ of Corti by the sonorous body. The discrimination of differences in pitch varies very widely in different persons. Some cannot distinguish between two contiguous whole tones, while in some parts of the scale many musicians can distinguish differences dependent on one-third of a single vibration-number, a variation of about 0.00066 per cent.

This faculty of discriminating pitch-differences is in most persons capable of a great degree of development, but by what parts of the ear this improvement is accomplished is not known. The fact of its possibility would seem to imply that the various muscles of the ear (perhaps fibers in the ligamentum spirale among the rest) have much to do with auditory adjustments, because the muscles are, to say the least, much more fully under voluntary control than other sorts of tissue in the organism. Many of the lower animals (*e. g.*, cats and numerous sorts of insects) can hear sounds far too high for the human ear, while others are very sensitive to jars we should not notice. Recent highly valuable writings of Helen Kellar (learned and capable, although deaf and blind) reveal how much the jars and unsonorous vibrations of things of our environment may teach us when they have a chance. They were partly represented in the auditory nerve, although largely it appears by the kinesthetic sense-organs in the joints and muscles.

The *quality* of tones, technically called timbre, depends on many various conditions, part of which are unknown. The difference in the quality of tones is illustrated in the uniqueness of each human voice and by the variations in the same note when sounded, for instance, on a violin, a cornet, a piano, an organ, and a harp. Another sort of qualitative difference is expressed by the word *volume*, illustrated by the difference between the sound of a vocal solo and that of a chorus, or between that of a small and a large orchestra, when the intensity does not differ. How all these differences are represented by the mechanisms of the ear is quite unknown.

The *direction* from which sounds come, biologically often of great importance, is given the individual by his comparison of the respective intensities of the sensation in the two ears. When these are equal it is considered that the sound is originated either directly in front or directly behind the middle of the head.

The Perception of Obstructions.—Another experience given us by the ears is that of perceiving without aid from the eyes an obstruction, such as a wall or even a book held broadside close by. There is in this a feeling of being shut in. This sensation probably comes from inappreciable sound reflected from the object into the ear or ears. It is experienceable, however, when no sounds are audible as such, and when all air-currents are excluded. It probably corresponds to some special adjustment of the apparatus in the middle ear (William James).

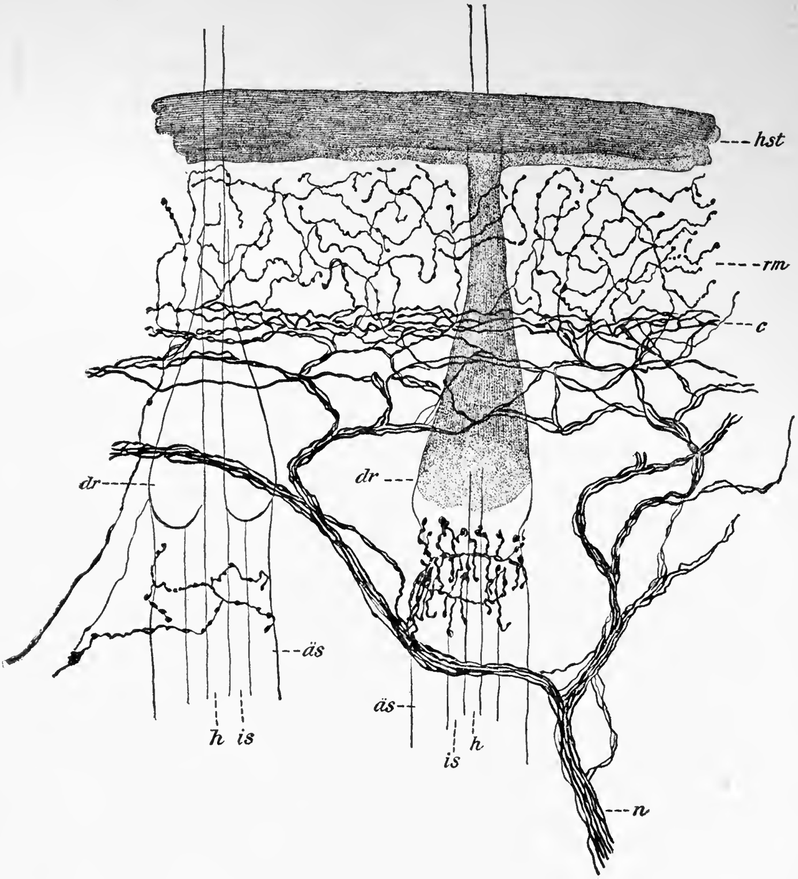
TOUCH, PRESSURE, AND LOCATION.

These senses are probably only aspects of but one sensory experience. When the stimulus is of weak intensity and of short duration we perceive "touch," and when it is strong enough to bend the skin downward we fell it as "pressure," but in every case there is inherent in the sensation, we know not how, awareness also of the location on or in our bodies of the stimulus (its "local sign"). In general, then, it will be understood in what follows that the two last-mentioned aspects of the sensation are always involved, although we may use only the term touch. Included also in a list of the various afferent end-organs of this sense of location should be included those of the joints and muscles in some cases perhaps, but these have already been described under kinesthesia.

Organs and Functions.—At various times and by different observers there have been described at least seven sorts of afferent nerve-endings which probably are concerned with tactile sensibility. It is possible that some of these are concerned with the temperature-senses, or with pain, etc., but for this there is at present no direct evidence. The seven or eight probable tactile end-organs are as follows: Meissner's corpuscles, the spheric end-bulbs of Krause, the Vater-Pacinian corpuscles (including the Golgi and Mazzoni and other variants), the elastic-tissue spindles of Ruffini, the nerve-rings of Bonnet, and the tactile menisci. Two of these, the cylindrical end-bulbs and the Vater-Pacinian corpuscles, are found also in muscle and in tendon, and have been described already. We find in these various organs none of the mechanical or chemical intricacy so discouraging in trying to understand Corti's organ and the retina, but we do find much uncertainty about their specific functions. The presence of these afferent nerve-endings in so large a variety suggests once more in a striking way the complexity of the means by which the functions of the nervous system are controlled, and in part also the constitution of consciousness. The analysis of both of these aspects, the neural and the mental, await the fruitful attention of modern research.

Meissner's corpuscles consist essentially of a spiral or twisted plexus of the fibrils of from one to five medullated nerve-fibers enclosed in a thin lamellated connective-tissue capsule. These are found in the tactile papillæ of the true skin. Rows of them make up the concentric lines to be seen on the distal phalanges of the fingers. Every fourth papilla is tactile and contains one or sometimes two corpuscles of Meissner. There appear to be in this region about twenty-one in every square milli-

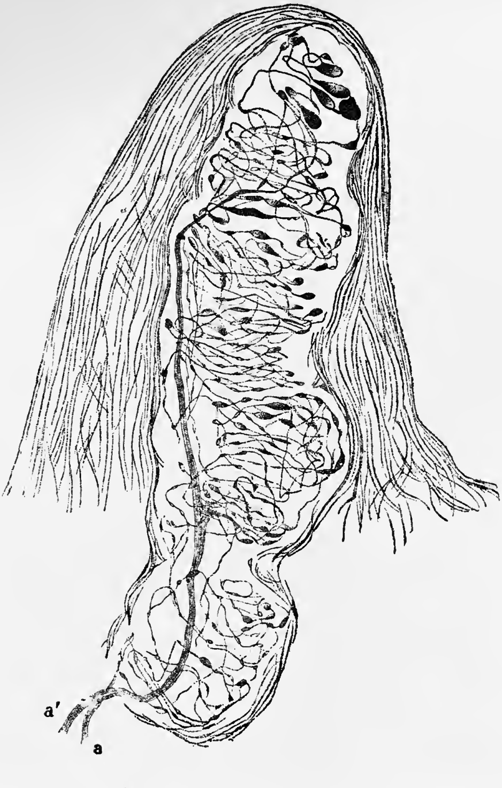
FIG. 202



Nerves and their endings in the human skin: *hst*, epidermis; *rm*, germinative layer (Malpighii); *c*, superficial plexus of nerve-fibrils; *n*, cutaneous nervelet; *h*, *as*, *is*, a hair and its sheaths; *dr*, sebaceous glands. (Retzius.)

meter of skin, while in the middle of the foot-sole there are about two in this unit of area. The spherical end-bulbs of Kräuse are of a similar general structure to the preceding. (See Fig. 215.) They are, however, shaped somewhat differently, being spherical, oval, or pear-shaped. They are located more deeply than the preceding sort of end-organ. The cylindrical end-bulbs of Kräuse were described on page 330, which see. The Pacinian corpuscles, of which there are many varieties, have also been described under the head of muscle-sense organs. (See page 330.) These are apparently the most elaborate of the tactile organs, and are often large enough to be seen with the naked eye. The Vater-Pacinian corpuscle, the corpuscle of Herbst, and the Golgi-Mazzoni corpuscle are various forms of these last, and differ chiefly in the structure of the core and in the relative thickness of the transmitting mechanism around it. The elastic-tissue spindles (Ruffini) are found in the corium and

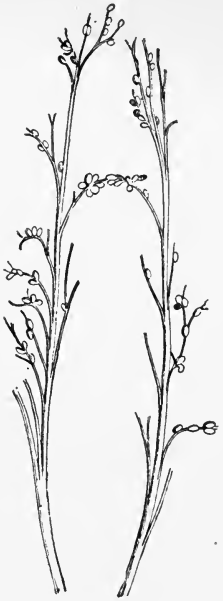
Fig. 203



A Meissner corpuscle: *a* and *a'*, are nerve-fibers which break up above into a complicated system of loops and knoblets. The whole is surrounded by connective-tissue lamellæ, inside the papillæ. Rows of these make up the lines on the finger-ends, etc. (Probably the end-organ of gross touch.)

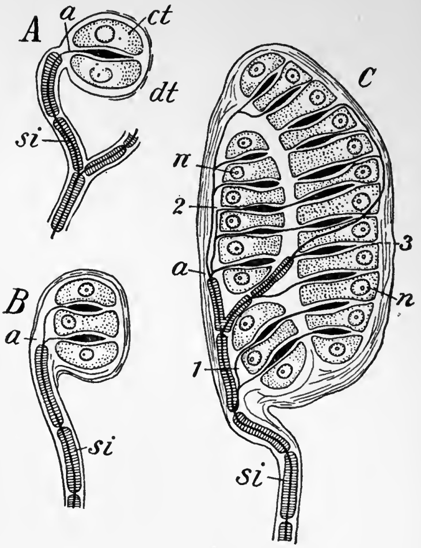
often closely associated with the Pacinian corpuscles. They consist of a connective-tissue frame-work on which a plexus of teleodendria is arranged about the elastic fibers. Another organ bearing Ruffini's name is the plume-organ so-called. This von Frey suggests may be the end-organ of heat. Nerve-rings of the hair-follicles (Bonnet) (Fig. 206) have been recently described. These for the first time suggest a useful function of the lanugo hairs found on nearly all parts of the body, the hand-palms and the foot-soles being marked exceptions. These end-organs consist essentially of a ring of nerve-fibrils forming a narrow cylindrical plexus in the wall of the hair-follicle just below the ducts of the sebaceous glands. When the hair is bent, as by a touch on the skin, its shaft acts as a lever and compresses on one side this ring of nerve-fibrils. The tactile menisci or disks are the most superficial of the cutaneous sense-organs of touch. They each consist of an epithelial cell placed upon a delicate meniscus, each disk being connected below with a nerve-fiber (Fig. 207). These are placed in the lowest portions of the epidermis. In addition to the foregoing, it is likely enough that a certain free nerve-ending in the cornea (Fig. 219) and possibly also an encapsulated end-organ figured by Longworth represent touch.

Fig. 204



The afferent nerves and Pacinian corpuscles of the third finger. (Henle and Kölliker.)

Fig. 205

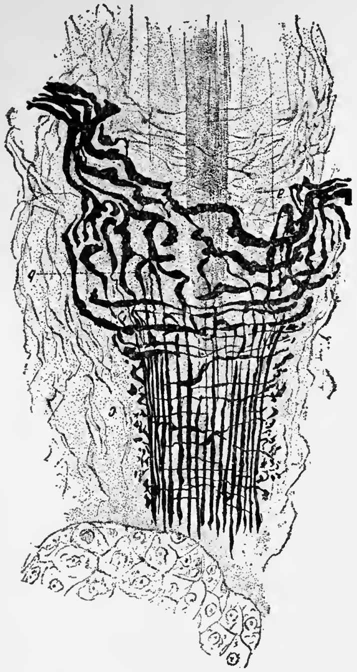


Tactile corpuscles of three degrees of complexity (diagrammatic): *A*, corpuscle of Grandry with one tactile disk, *dt*, and two tactile cells, *ct; B*, corpuscle with two disks and three cells; *C*, Meissner's corpuscle; 1, 2, 3, its component parts (Grandry's corpuscles); *n*, nuclei of the tactile cells; *a*, nerve-fiber; *si*, interannular segment. (Duval via Morat.)

Some of these are found in the body's interior, but in small numbers. Many regions of the viscera are quite devoid of touch-sensation.

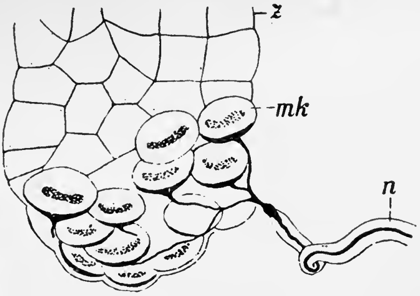
All these kinds of end-organs are probably connected by special nerve-fibrils to the cord. The impulses pass up by columns and to centers already described, and may stop in the posterior frontal convolutions, but it is unlikely that these kinds of sensation have any sharply defined areas of cerebral representation.

Fig. 206



The nerve-ring (of Bonnet) about a large hair of a dog: *a* and *b*, begin to ascend the longitudinal fibrils, while at *c* the circular fibrils may be seen. (Probably the most sensitive of the touch end-organs). (Bonnet.)

Fig. 207

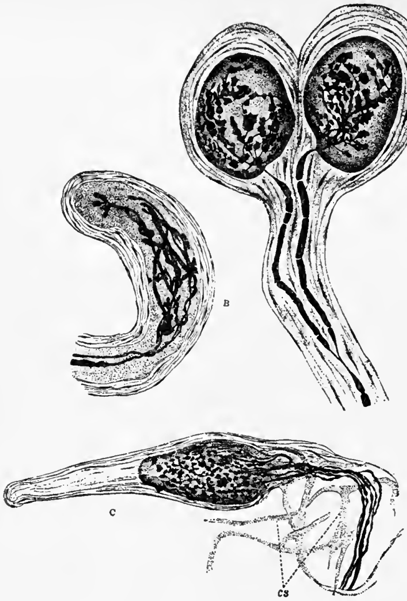


Tactile disks from the epithelium of the pig's snout: *mk*, the tactile disks; *z*, epithelial wall; *n*, nerve. (Tretjakoff.)

Touch-spots.—Goldscheider in 1884 showed that the skin is dotted with minute areas each of which possesses a sort of sensation peculiar to itself—touch, heat, cold, or pain (see below). There is still more or less disagreement as to the arrangement of these "spots," but as later study shows that these areas may be reduced to mere spots, each is undoubtedly some one of the end-organs just described. On running a needle ground especially fine into one of these spots no suggestion of pain (nor of warmth nor of cold) is felt, but a strong, sharply localized sensation of pressure unaccompanied by any other sensation than that of its relative location on or in the body. Almost always there are one or more touch-spots close to a hair, usually on the side from which the hair slopes, and they also are apt to be arranged in certain regions in short lines radiating from the hair-follicles. Where no hairs exist the arrangement of the spots is the same.

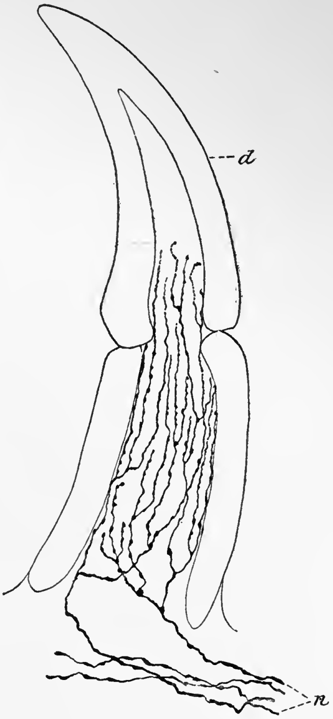
Certain Tactual Qualities.—It is plain that the large variety of the touch-pressure-location end-organs noted above suggest a like number of qualities to these sensations. These qualities, however, are unknown. Sensations being known if anything is, this is tantamount to saying either that some of these described afferent end-organs transmit inward to the cord, etc., impulses which give rise to no analyzable portions of consciousness, or that some of these organs, either directly or through nerve-fibrils connected with them, represent other sensations subserved by the skin: of heat, cold, pain, tickling, electricity, pleasure, or what-not.

Fig. 208



"Golgi-Mazzoni corpuscles" found by Ruffini in the subcutaneous connective-tissue of the ball of the finger.

Fig. 209



Nerve-terminations in a tooth of the fish Gobius: *d*, dentine; *n*, nerve-fibers. (Retzius.)

At present, in short, the specific duties of some of these end-organs described by good observers as tactual in function cannot be told any more than can their relations to each other, to the touch-pressure spots, and to the brain.

Landois showed that the finger recognizes as separate the vibrations of a string occurring 1552 times per second, while induced electrical currents of 130 per second are felt as disparate. The latent period and the subsidence-period of touch-organs are then both very brief.

The *threshold-stimulus* for the different parts of the body-surface varies widely. In general the sensitivity of a tactile region is roughly proportional to the amount of its use in touching or being pressed upon. Von Frey, using Hensen's method of stimulating with glass-wool fibers ranging in surface from 0.002 to 0.06 sq. mm., found the following thresholds for various regions.

	Grams per square millimeter.
Tongue and nose	2.0
Lips	2.5
Finger-tip and forehead	3.0
Back of finger	5.0
Palm, arm, thigh	7.0
Forearm	8.0
Back of hand	12.0
Calf, shoulder	16.0
Back of upper arm Abdomen Outside of thigh	26.0
Shin and sole	28.0
Back of forearm	33.0
Loins	48.0

When it is remembered that sometimes these stimulating fibers were not more than $\frac{2}{1000}$ sq. mm. in area, the great sensitivity of the tongue and nose, for example, is readily seen. In some cases even 0.001 gram actual pressure is readily felt. On the forehead, tongue, etc. (Eutenberg), an increase of pressure of 3 or 4 per cent. was found to be perceptible.

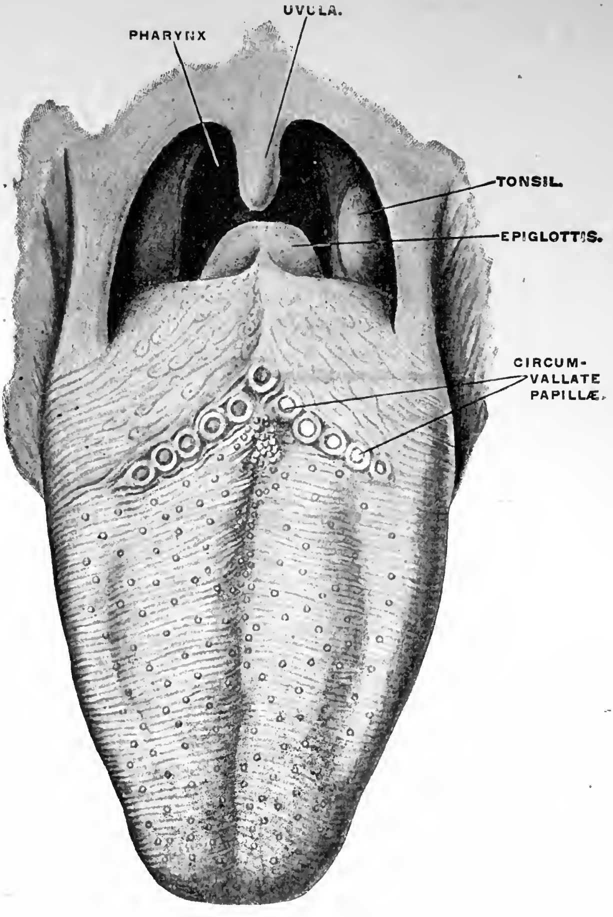
Two points at the skin-temperature are felt as two (rather than as one) when only 1.1 mm. apart on the tongue-tip of a man, but on the middle of the back and on the thigh when 67 mm. apart they are felt as one.

How the sense of *location* is served by these organs is a complete mystery. Every spot we can touch on the skin has a "local sign" (Lotze) by which the individual knows just where on his body that particular spot is located. However produced, and whether native (congenital) or acquired by infinite touches in combination with vision, muscle-sense, etc., it is a strong argument for the theory of "the specific energy of nerves" in its newer form that the central nervous system represents somehow in its cells and fibers the whole body.

TASTE.

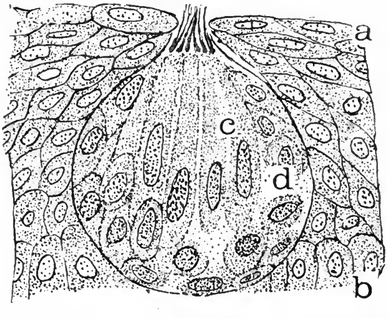
The sense of taste furnishes us most of the pleasure derived from eating, which in turn assures us the full complement of the food required by the organism. Its end-organs help reflexly to cause the secretion of the digestive juices. Lastly, it serves sometimes as a means of discriminating between the beneficial and the harmful among eatable substances, for most proper foods are pleasant to the average palate.

Fig. 210



Upper surface of the tongue.

Fig. 211

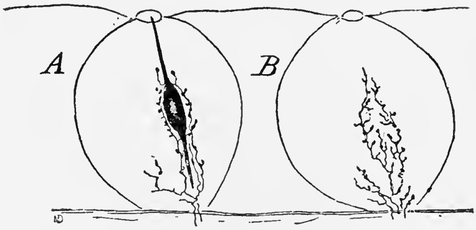


A taste-bud from the circumvallate papillæ of the tongue: *a*, surface stratified epithelium; *b*, lower layers of the same; *c*, sensory cells surmounted by delicate hair-like processes; *d*, supporting cells. (Bates.)

The Gustatory Apparatus consists chiefly of certain afferent nerve end-organs called taste-buds, of certain afferent nerves, and of the central regions to which they transmit their impulses.

THE TASTE-BUDS (Schwalbe) are minute flask-shaped organs composed of four sorts of elongated fusiform cells, of which three are perhaps sustentacular in function and only one gustatory. The buds average about 0.075 mm. deep by perhaps 0.040 mm. in diameter (see Fig. 211). The gustatory cells proper, neuro-epithelial, are elongated and fusiform with the nucleus in the thickest part of the cell, and have stiff slender filaments projecting above them into the open taste-pore. They are encircled by nerve-fibrils. This pore is often 0.01 mm. deep and is filled with the liquid of the mucous membrane around. From one to ten of the taste-cells are found in each bud. The buds are found on the back, edges, and root of the tongue, on the soft palate, the uvula, the pillars of the fauces, the under surface of the epiglottis (Nicholson) and posteriorly in small numbers, in the larynx, and in the olfactory region of the nose. Thousands of them are found in two of the three sorts of papillæ which beset the tongue's dorsum, namely, in many of the fungiform papillæ scattered over the surface of the tongue, and especially in the sides of the circumvallate papillæ of the back of that organ. They are not present apparently in the filiform papillæ, but are present in the level mucous membrane.

FIG. 212



The nerve-filaments about the taste-cells. In *A* the taste-cell is indicated also; in *B* not. (Duval.)

THE NERVES OF THE SENSE OF TASTE are still not certain. There is, however, excellent evidence that the ninth cranial (glosso-pharyngeal) nerve is one of them, supplying the rear third of the tongue. The pars intermedia of Wrisberg, running in the trunk of the seventh (facial), is another taste-nerve, supplying the soft palate and the rest of the tongue. The doubt now lies chiefly as to whether the superior laryngeal branch of the tenth (vagus) nerve carries taste-impulses or not, the strong probability at present being (Zwaardemaker) that it supplies taste to the region of the central circumvallate papilla (foramen cecum), to the epiglottis, and to the inside of the larynx. The trigeminal (fifth cranial) nerve supplies without doubt the taste-buds recently found in the olfactory region of the nasal mucosa called the Schneiderian membrane.

The *cerebral center* of the gustatory nerve-fibers, it is likely, will be shown to be low down on the mesial surface of the cortex of the temporal lobe, just below one of the probable centers of smell. Von Bechterew thinks he has located the center for bitter and salt in the anterior Sylvian gyrus and for sour and sweet in the anterior ectosylvian gyrus (in apes), in the region of the operculum.

Some Characteristics of Taste.—A substance in order to have a taste must be at least slightly soluble in the alkaline fluid of the mouth. Thus, while iron gives a taste, sulphur does not. But not all substances soluble in the mouth's secretions have tastes, and what it is that determines whether or not a substance is to have a taste is quite unknown. There is evidence that the taste-cells can be mechanically and electrically stimulated to give gustatory sensations. This is an indication that the taste of objects, like the "light" of the ether and the "sound" of vibrating objects, is subjective, that is, resident in or the production of the perceiving animal. Still sapid substances must have qualities of some sort which determine their tastes. In this direction Haycraft finds reasons to suppose that the compound chemical radicle $COOH$ occasions the acrid taste and CH_2OH the sweet taste.

No classification of the taste acceptable to all has yet been made. In the nature of the sensations none is possible, perhaps. Some classification may one day be made on the basis of the sensory cells. There is, however, fairly good agreement that four classes of tastes are properly described, namely sweet, bitter, salt, and sour. Seemingly a fifth taste, metallic, should be added and perhaps a sixth, alkaline, although more properly perhaps this is a variety of salt tastes. It is probable that all the tastes are represented in every portion of the gustatory areas above defined, but some parts give one taste more readily or more strongly than another. Kiesow found the following threshold-values, the numbers being percentages of the substances in distilled water; about half a cubic centimeter of the solution was used in each case.

Substance.	Tip of the tongue.	Edge of the tongue.	Base of the tongue.
Sodium chloride	0.25	0.24 to 0.25	0.28
Cane sugar	0.49	0.76 to 0.72	0.79
Hydrochloric acid	0.01	0.007 to 0.006	0.016
Quinine sulphate	0.003	0.0002	0.00005

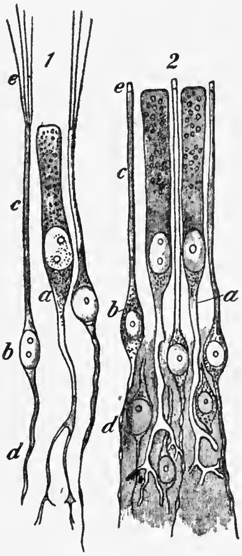
Perhaps one bud or even one taste-cell has to do with only one sort of taste. Experimentation is difficult and more or less uncertain because when the papillæ are with difficulty made dry they are abnormal, but when they are moist the liquid carries the sapid substances used as stimuli to more than one end-organ.

The reaction-time of the taste-buds differs with different substances: salt is tasted most promptly and bitter least so. There are after-images of taste as there are of vision and of the other senses. Various contrast-effects also are observed here as in the other senses. Some drugs abolish the senses of taste in various ways; thus, for example, cocaine abolishes the bitter taste first.

SMELL.

This sense, as already suggested, is far less important in the conduct of life in man than it is in many of the lower animals. Dogs, for instance, apparently obtain more information through their sense of smell than even by vision. In man it serves, much as does taste, to furnish both pleasure and protection and to incite to fulness of function. In this, respiration is chiefly served, for in the flowery fields of summer or the spruce forests it impels the organism to inhale deeply the pure air, while in places where the air would harm instead of benefit, it causes us to reduce as far as possible its intake and to escape from it at once. Moreover, when the air is sweet it incites respiration through the nose, its proper organ, rather than by the mouth. As a further protection it warns us away from putrid food unfit to be eaten and from water too full of vegetable matter to be proper drink. Its sexual relation, very important in most of the brutes, is nearly obsolete in civilized man except in the feminine use of perfumes. To a less extent than taste, smell serves as the sense by which go inward the impulses which reflexly start the secretion of the digestive juices. Thus, the odor of roasting meat makes a hungry man's mouth "water" and, as we have already seen, his stomach as well. Helen Kellar emphasizes how useful the sense of smell is to her, each acquaintance, for example, having a unique odor appreciable at some distance.

Fig. 213



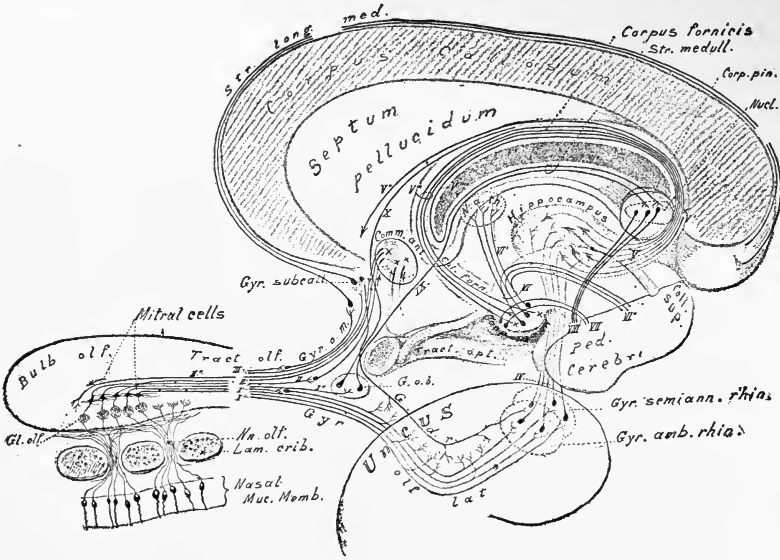
Olfactory cells from the Schneiderian membrane: 1, from that of a dog; 2, from man; *b*, the olfactory cells; *a*, supporting cells. The hair-like filaments, *e*, on the upper ends of the cells extend outward on the moist surface of the mucosa. (Schultze.)

The Olfactory Apparatus is simple so far as mechanism is concerned, for it consists wholly of peculiar cells embedded in mucous membrane, of neurones, and of centers in the brain.

The olfactory cells are the cell-bodies of non-medullated neuraxes whose teleodendrites are in the olfactory bulbs. They are fusiform cells each with a round nucleus and a large nucleolus in the thickest part of the spindle. Toward the free mucous surface the cells terminate in blunt cones upon each of which stand seven or eight bristle-like filaments, the so-called olfactory hairs, extending out into the moisture of the nasal cavities. Sustaining these cells in place are long columnar epithelial cells branched toward the basement-membrane. Among the branches of these are other cells, broad below and with processes above, resting on the membrane, which are of unknown use. Round about in places are the serous glands of Bowman or olfactory glands, whose cells contain the brownish or yellow pigment of the olfactory region.

THE REGIO OLFACTORIA in man on each side of the body consists of an area of ("Schneiderian") mucous membrane, folded in the middle, and about 2 cm. long by 1 cm. wide. One sq. cm. of the area is on the inside surface of the upper part of the middle of the superior turbinated bone and the other sq. cm. is directly opposite on the nasal septum (von Brunn). Sometimes minute islands of the olfactory mucosa are to be found adjacent to this tract. In these areas alone are the olfactory cells to be found. The region is in color a brownish yellow. It is placed high enough on the superior turbinated bone and nasal septum to be out of the direct current of inspired air and especially of expired air, yet it is sufficiently near the incoming air-stream to be continually bathed in a slow current, and this is the condition best adapted to easiest smelling. In sniffing, the in-rush of air is more sudden and probably reaches directly the olfactory mucosa.

FIG. 214



Tentative scheme of the principal neurone-systems of the olfactory conduction-path. (Barker.)

The nerves of smell are the first cranial pair. There are three orders of neurones between the olfactory cells and the centers in the temporal lobes. The *center* appears to be placed mesially in the uncinate convolution in the anterior part of the gyrus fornicatus, and perhaps on the posterior part of the lower surface of the frontal lobe (see page 73). The sniffing-nerves are those of inspiration.

Some Conditions of Smell.—Nothing is known as to the precise relation of the olfactory cells to the odoriferous particles which stimulate them. It is natural to suppose, however, that the reaction of the olfactory protoplasm in these cells is chemical in its nature, the odoriferous particles in some way altering the metabolism.

There is no hint at hand as to the physical nature of these particles themselves. Whatever they are physically, they are well-nigh inexhaustible in certain cases. One thinks inevitably of radio-activity as the type of the process possibly concerned in this sort of stimulation. There has been much discussion also as to the form in which the odor-bringing substance must be in order to stimulate the smell-cells. Zwaardemaker, for example, and Weber suppose that only gases and vapors stimulate, while Aronsohn claims that weak solutions give up their odors to the cells. Perhaps some particular ions convey this impression to the protoplasm, or at least must be present for its conveyance. Haycraft by experiments on himself determined that even odorous air to be smelled must be in motion. 0.00001 gram of mercaptan disseminated in 230 cubic meters of air in a closed space give a weak but distinct odor, or in the proportion of 0.00000000004 gram to the liter of air. This suggests the sensitivity of the olfactory cells to certain substances, for only a small fraction of this last quantity of course would reach the olfactory region at any one time. Passy determined the threshold-values of eight common odorous substances as follows, the numbers being in milligrams per liter of air:

Essence of orange	0.00005	to	0.001
Essence of wintergreen	0.000005	to	0.0004
Rosemary	0.00005	to	0.0008
Ether	0.0003	to	0.004
Peppermint-leaves	0.0000005	to	0.00001
Camphor	0.005		
Natural musk	0.01	to	0.1
Artificial musk (trinitro-isobutyltoluin)	0.001	to	0.0005

Attempts to classify the odorous substances have been made by many observers (E. Erdmann and Linnes, for example), but with almost obvious failure always.

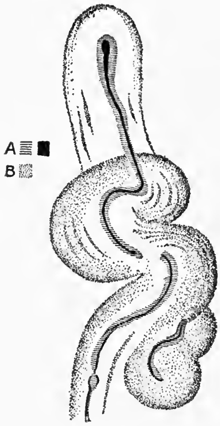
Some odors completely antagonize others, there being here a degree of inhibition found nowhere else among the sensations unless in vision. Thus Zwaardemaker claims that the odor of musk will inhibit the odor of bitter almonds, and iodoform the odor of the volatile oils. Some confusion between smell and taste arises because of the probable presence of taste-buds in the mucous region heretofore supposed to be purely olfactory in function. From this we learn why so many persons confuse, for example, the strong odor and the weak taste of boiled onions.

For both taste and smell individual differences are common and marked. Flavors and savors delightful to one person to the next may be unpleasant. One becomes quickly accustomed to odors at first disagreeable, so that they lose all unpleasantness. Smell-experiences seem to have a sort of arbitrariness about them (somewhat such as one meets with in the study of hysteria) not encountered in the other senses in nearly so marked a degree.

THE TEMPERATURE-SENSES.

The human skin has a sense of warmth and a sense of coldness. Although probably separate more or less in end-organs, nerves, and centers, these may be well discussed together, since in many respects they are similar. At the very outset in trying to give the general usefulness of these senses we are met with the difficulty that although we know what the respective heat and cold end-organs represent, we do not as yet certainly know their general relation to the organism. When we feel cold or too warm it is doubtless by these end-organs that the sensation is started inward from the skin. Their probable relation to thermotaxis has already been discussed under the subject of body-heat (see page 238).

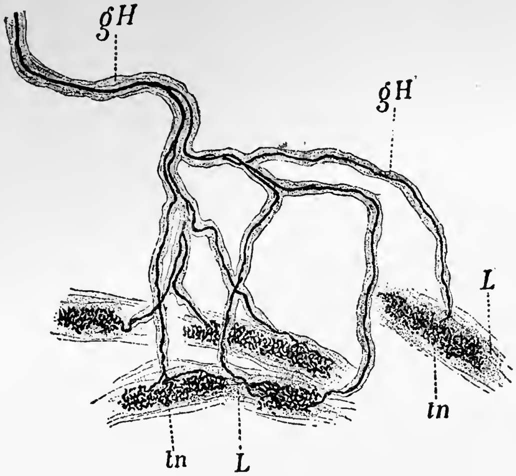
Fig. 215



Krause's end-bulbs: *A*, a twisted form showing the bluntly ending nerve fiber and the lamellated connective-tissue covering; *B*, a corpuscle containing at least six of these end-bulbs. (Szymonowicz.) Perhaps the end-organ of cold.

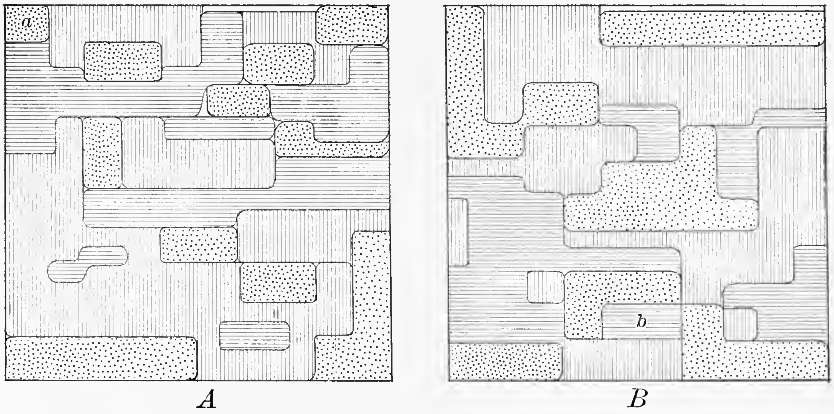
The Apparatus of the Temperature-Senses, including the neural connection, is probably at least not less complex than is that of touch, but we know much less about it. No one so far has published a drawing and labelled it as a representation of the end-organ either of cold or of heat. The nearest to it even is von Frey's suggestion that certain end-organs described by Ruffini (see page 356) and (more likely) the suggestion by Sherrington that the "genital corpuscles" of Krause (see page 368) might be the desired afferent end-organs of the cold-sense. Von Frey thinks it possible, too, that another neural structure found by Ruffini (plume-organ ?), of large size and cylindrical in form, deep in the skin of the eyelid, arm, and hand, may be the end-organ of the heat-nerves. The reason for this long ignorance lies in the impossibility of isolating and stimulating by any known means in man (the only animal who can tell of such sensations) a single isolated afferent end-organ of any sort, because of its smallness and transparency.

Fig. 216



The nerve-endings of Ruffini ("plume-organs") from the subcutaneous tissue of the finger. They have strong connective-tissue sheaths and the varicosities end in knoblets. (Ruffini.) Perhaps the end-organs for heat.

Fig. 217



Two maps showing the topography of the temperature-sensations. Each square represents a square inch of the back of the left hands of two men. Axis of the hand was from left to right. The heat-spots are vertically shaded, the cold-spots horizontally, while the dotted areas represent tactile sensibility. The tactile spot *a* is 0.01 sq. in., the heat-spot *b* is 0.02 sq. in. (Hall.)

The nerves of the thermic organs have not been isolated from the afferent trunks going into the cord by the posterior routes. There is good evidence, however, that each of these senses of heat and cold has nerve-fibers of its own. These impulses probably go upward in the cord either by the numerous short neurones in the posterior part of the gray matter (more or less as pain is supposed to go) or by the posterior median and posterior lateral columns. The cerebral centers connecting with these organs are not definitely known as yet, but the cutaneous sensations in general seem to be represented far back in the Rolandic region. The whole bodily surface is more or less sensitive both to heat and cold, as is to a degree also the beginning of the alimentary and respiratory canals.

Fig. 218

The temperature-spots as Goldscheider found them in the palm of a hand: *A*, heat-spots; *B*, cold-spots.

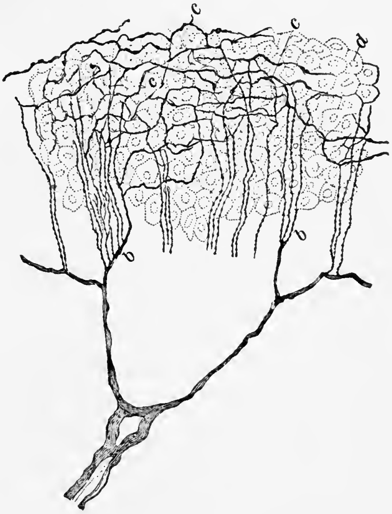
Fig. 217 exhibits two regions, each an inch square, of the same locality of two persons' hands (Hall). It shows very well the mosaic arrangement of the three cutaneous senses so far considered, heat, cold, and touch. Goldscheider suggests that the regions in which none of these sense-spots are to be found corresponds to the blind-spot of the retina—regions over the trunks of small nerves, which are lacking there in branches and end-organs.

PAIN.

In both theory and practice pain is of considerable importance. Several theories, biological and psychological, might be discussed, each involving elements, however, beyond our present range, and each (save that here described) ignoring the physiological evidence of recent years. With one of the theories, that of the evolutionists, *e. g.*, Herbert Spencer, we may say that pain is the mental accompaniment of hindered biological function, just as in the long run pleasure is the accompaniment of furthered biological function. The object of pain, then, is to warn the animal of threatened organic injury or of injury already received. The method by which this is as a sensation is brought about is that of other sensations: end-organs, nerves, and centers. The numerous conflicting theories as to pain rest on, first, the ignoring of the physiological evidence, as too often is the habit of purely book-instructed theorists. Second, they rest on the confusion of the sharp, biting, actual pain with the numberless grades of unpleasantness and the disagreeable. One is an indescribable true sensation, the other a complex feeling allied to the other general "sensations" (see below). The confusion is increased by the fact that oftentimes both the sensation of pain and the unpleasant feelings may be experienced at the same time, somewhat as a man may feel fatigued and suffer from a toothache simultaneously. But if we leave these numerous compound experiences out of our account we find pain as the mental aspect of the functioning of certain sense-organs, while unpleasantness is a psychological subject with which we have just here no concern. Their only apparent common factor is that the animal experiencing them wishes both gone and changed to their opposites, pleasure and pleasantness respectively. We assume, it may be too dogmatically, that a little positive evidence as to pain-apparatus is worth volumes of negative theories in opposition to it. (See also Chapter XII, under Feeling, page 409).

The Sensory Apparatus of Pain was tentatively described about the same time as was that of touch and of the temperature-senses, Goldscheider's name and that of von Frey being especially associated with its discovery. The peripheral nerve-endings or the end-organs, whatever their form, are situated apparently in "spots," as are those of the other senses named. These spots are scattered more evenly than in the other cases over the body's surface, and perhaps to a slight extent within the viscera of the body, especially in the testis, ovary, kidney, and rectum. When stimulated mechanically or electrically by points delicate enough, these spots give rise to a smart, tingling pain whose one only quality is that of pure painfulness, there being nothing connected with it like any other sensation whatever. (On the other hand the touch-spots, heat-spots, and cold-spots lack this pain-character when stimulated.) From the pain-spots pressure-stimuli as small as that of 150 grams per square millimeter elicit this wholly characteristic pain-sensation. Several circumstances besides that of their even distribution serve to distinguish them from the other cutaneous spots. Of these circumstances, their very long latent-period is perhaps the most conclusive, for it is most easily measurable in exact terms. Only less so than this,

Fig. 219

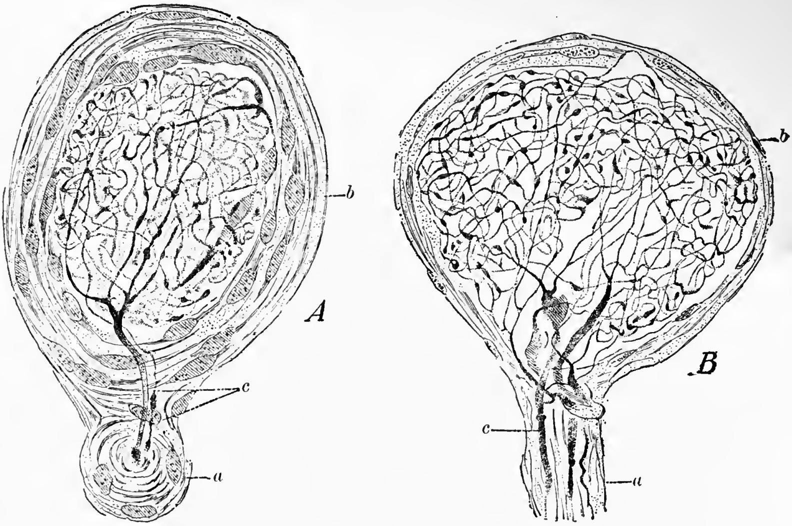


Afferent nerve-endings in the human cornea, according to Klein, oblique section: *a*, nerve-fiber (axis-cylinder); *b*, fibrils; *c*, terminal network among the epithelial cells, *d*. Perhaps these are the endings that represent pain.

however, is their liminal intensity for electrical stimuli, which is lower than that of touch.

The afferent nerves of these spots are unknown. There is much evidence, physiological and pathological, that the impulses pass up the gray matter of the cord for a longer or shorter distance, perhaps only passing obliquely through it or across it. As for the center of pain, Budge found evidence in animals of pain from stimulation of the corpora quadrigemina, but this evidence is inconclusive. Many things go to show that a center is stimulatable with a normal result only by the stimulus coming from its own end-organ, and the pain-stimulus we do not know how to imitate. Cases of analgesia (abolition of the pain-sense) are in themselves alone strong evidence that a neural mechanism of pain is part of the nervous system. It is hard to think how an abnormality could arise which would throw out of action only one set of experiences unless the nerve-arrangements for that set of sense-impressions were distinct in some way. Cases of various sorts and degrees of analgesia are common and similar to the sensory paralysis of other sets of nerves much better known in their courses and endings.

Fig. 220



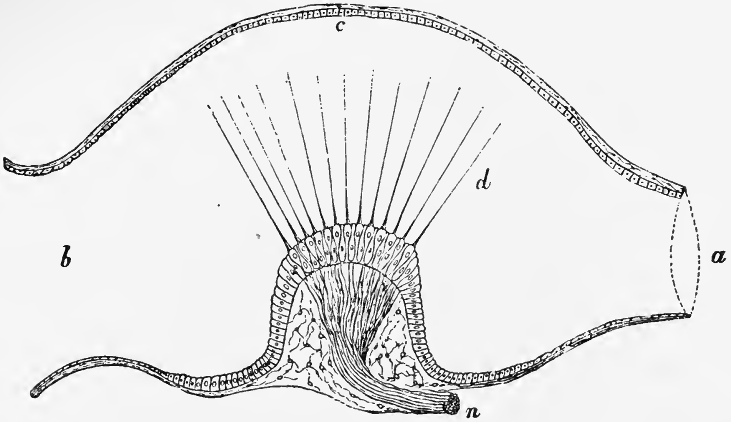
A genital sense-organ from the glans penis of a man: *a*, sheath about the nervelet; *b*, connective-tissue sheath of the corpuscle; *c*, nerve-fibers which ramify inside the end-organ. If the body may be said to have afferent organs of a pleasure-sense, this is probably one of them. (Dogiel.)

Besides the pain-spots of the skin, some of the mucosæ and viscera, notably the heart, the serous coverings, and muscle obviously have pain-organs as a part of their complete mechanism.

Pleasure.—The theoretic status of the sensations of *pleasure* is more vague and doubtful than is that of pain. It seems probable, however, that pleasure end-organs exist (Fig. 221), for example, in certain parts of the sexual organs. It matters not what these be called, whether genital corpuscles or pleasure end-organs, they are certainly destined to incite to the function to which they are attached through the pleasure they or some other sort of end-organs give rise to. If at the same time, as may well be, they reflexly actuate the varied phenomena of coitus and ejaculation it is only in line with the probable action of other various sense-organs throughout the body. They do represent pleasure, and pleasure as a true sensation, distinct from agreeable or pleasant feelings.

There are other conditions which more or less involve various sense-mechanisms. Among these are tickling and vertigo. About the former little worth saying can be given in this place.

Fig. 221

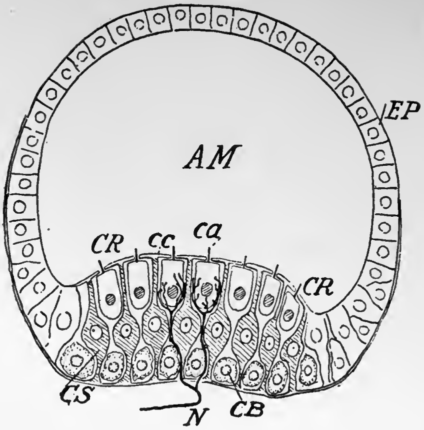


Longitudinal section of an ampulla of the fish Gobius: *n*, nerve; *a*, canal; *b*, entrance into the common chamber; *c*, epithelium; *d*, vibratable "hairs." (Hensen.)

VERTIGO.

This sense is of some practical importance. It arises from the disturbance of the end-organ of the vestibular branch of the eighth cranial ("auditory") nerve. This end-organ consists of the semicircular canals, the ampullæ, and part of the labyrinth connected with the internal ear. This is not properly a sense-organ in the sense that it furnishes sensation, for no consciousness is attached to its action unless its function (mostly that of maintaining reflexly the head's equilibrium) is disturbed. In proper significance, however, that a sense-organ is a peripheral end-organ of an afferent nerve, this organ is a true sense-organ and vertigo a sense. Moreover it may perhaps, or one part of it, have to do with the perception of noise, as we have seen above.

Fig. 222



Diagrammatic cross-section through the ampulla of a semicircular canal: *AM*, ampulla; *CR*, acoustic crest; *CB*, basal cells; *CS*, support-cells; *cc*, cuticle; *ca*, acoustic (noise?) cells and their hair-like projections; *N*, nerve-fiber of the sound-cells. (Duval.)

FATIGUE, THIRST, AND HUNGER.

Fatigue, thirst, and hunger may well be classed together as the most important of the *general sensations*. They each have an unpleasant tone and well illustrate how complex the sensations may be. They arise in the tissues of the body generally, without being sensations in the physiological sense of possessing end-organs, nerves, and cerebral centers. Fatigue, thirst, and hunger, then, are on the border-line between physiological sensations as so defined and the host of psychophysiological feelings.

Fatigue in its origin is chiefly either muscular or neural: our "bodies" may be tired or our "brains," or both. A hard day at trouting in some mountain river of the wilderness is apt to give in its purity the sense-feeling of muscular fatigue; ten hours' work on the books of a bank afford an excellent idea of what is meant by neural fatigue; while a day on foot at a world's fair would combine these two in a particularly tiring way, each sort lending elements of intensity to the other.

In discussing briefly the bodily aspect of the feeling of fatigue, one must discriminate it in the first place sharply from exhaustion. One is physiological, the other pathological. The former may be recovered from within the ordinary periods of rest, but the latter is a matter of incapacity for days in the case of muscles or for many months at times (neurasthenia) when the central nervous system is involved. It is likely too that in muscular fatigue actual tearing of nerve-fibrils has taken place, for it is quite abolished by what we know as training (Hough, Woodworth). By this means the organs of the motor apparatus, muscular, neural, and vascular, have time to develop by growth and repair to their new requirements. In neural fatigue the changes are probably largely metabolic and vascular, while in nerve-exhaustion the shrinking of the nerve-cells (as Hodge has shown) is obvious under the microscope. This is probably of far-reaching import. All degrees of it are perceptible, some arising even from what might be fairly termed normal fatigue (see Fig. 26, page 58).

The general sensations bring out the difference between a massive or voluminous sensation of low intensity and a special sensation which originates in the functioning of a single sort of end-organ. Compare the feelings caused by a day's long climb with those arising in an untrained finger fatigued on one of the ancient Mosso ergographs so common in the laboratories. The latter experience is mostly a localized ache, the former a wide-spread general sensation of low intensity, while neither is like the pain caused by the overstimulation of a few pain-organs by part of the red-hot coal of a parlor-match. Widespread stimulation to their limit of intensity of cutaneous sense-organs is dangerous to life from sheer neural shock. It appears to be the tissue-protoplasm itself which gives the feeling of fatigue. To attempt therefore to trace out nerves or nerve-centers of these sensations is worse than useless, because from one point of view misleading. For fatigue is in the protoplasm of the muscles mostly, although that of the nervous system and doubtless of the glandular tissues have their share. (For the metabolic changes occurring in muscular action, see below, page 382.)

Thirst is also a general sensation (one originating all over the body) dependent on a decrease in the fluidity of the body-protoplasm and of the circulating lymph-plasma. By an arrangement whose nature is not understood, this universal need is referred to one place, the throat and mouth. The principle here as elsewhere is that the protective sensation is felt in the physiologically right place. In this case the sensation requires that the water, needed all over the organism, shall be placed in the entrance to the alimentary canal, for from this organ alone it may be promptly absorbed into the circulation. The condition is general and not local, for it may be promptly relieved by injecting water into the stomach without its touching the mucosa of the tongue and pharynx, as, for example, through a gastric fistula made for feeding the patient in cases of cancer of the esophagus. Again, on taking the required water by the mouth the condition is not relieved as the liquid passes over the tongue, etc., but only after the twenty seconds or so required for absorption from the duodenum into the blood to begin. The sensation may have perhaps a local origin besides the normal one in the general body-protoplasm. Opium, for instance, checks secretion in the alimentary mucosa, as do many other substances, while salt dries the membranes by changing their osmotic relations to the blood and lymph within them. Mild inflammation of the gastric and intestinal membranes reflexly produces sometimes the sensation of thirst, as many persons are apt to know the morning after a too hearty dinner.

The afferent nerves concerned in the sensation of thirst are evidently those of the throat: the ninth cranial (glosso-phargngeal) especially, but also probably branches of the tenth (vagus) and the fifth (trigeminus).

Water is by far the best liquid for relieving thirst, since it is water which forms the 60 or 70 per cent. of protoplasm. Warm water relieves it as quickly as cold, but affects the sensation of thirst less quickly because it lacks the coldness which so promptly relieves the mild inflammation reflexly begun in the throat. An average person will die of thirst in four or five days.

Hunger is a condition similar to thirst save that in this case the body's protoplasm lacks proteids, carbohydrates, fats, and inorganic salts instead of water.

The experience of the general sensation of hunger varies with the habits of the person as regards eating. Many accustomed to omit their meals or food entirely for a day or even two at a time fail to feel the ordinary phenomena of the average man accustomed to go without food for ten hours at the most and that in part while asleep. Normal hunger exhibits a feeling of weakness plus an indescribable sensation in the stomach not unpleasant at first but rapidly increasing to a "gnawing" pain. This is relievable temporarily by taking even quite indigestible matter into the stomach, or by water. After two or three days the feeling in the stomach decreases and disappears and only the ever-increasing feeling of weakness, in addition to the other bodily phenomena of inanition, remains.

What causes these sensations in the stomach we do not know. They are very erratic, sometimes being present when the stomach is full (as in cases of duodenal fistula), and on the other hand entirely absent when no food has been taken for days, as is customary in gastritis, for example. Here, then, as in case of thirst, we have a general sensation normally referred to the organ where the demand is usually supplied. The stomach is really no hungrier than is the kidney, yet the pain is in the stomach, for here the means of relieving it are needed. In this case the impulses go inward along the tenth cranial (vagus) nerve, (the chief sensory nerve of the stomach), and pass to the almost universally connected roots of this nerve in the medulla oblongata. By what peripheral organs the stimuli are started toward the brain we do not know. In most normal cases distention of this hollow viscus seems to provide the opposite sensation, satiety.

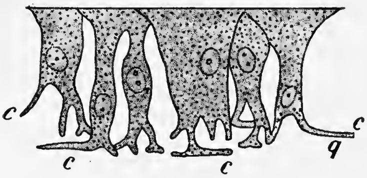
Nausea is another general sensation referred to the stomach, but about it little of a physiological nature is known. It originates from a variety of causes. It comes from local irritation or over-distention of the stomach (especially in children), and from stimulation in the medulla or cerebellum (as for, example, in sea-sickness). It is occasioned by the various central nauseants, *e. g.*, apomorphine, and by many other drugs acting locally on the stomach or centrally on the nerves. (See the description of vomiting, p. 186.)

CHAPTER XI.

MUSCULAR ACTION.

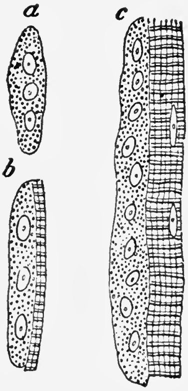
The sense-organs which we have just briefly studied are at the beginning of the typical reflex arc in the nervous system. They originate the impulses which pass into the cord and the brain. The organs which we are now to study for a little are at the other end of the reflex arc and are the chief means by which the individual accomplishes his purposes. These organs are the muscles found in nearly all parts of the body. Homologous to them as active instruments are the glands, and these we have already considered. In general terms the function of the muscles is to cause the approximation of two parts of the body or to constrict a hollow tube or viscus. Biological histology deals with the minute structure of various contractile organs, and to the text-books of this science the reader is referred. In some of the simplest animals, even in the Protozoa (for example, Stentor), one already finds contractile organs. Here they are in the form of very delicate threads technically called myoids, and it is their sole business to cause the animal to quickly shorten. It is likely that something very similar to the myoids of the simplest animals persists in all muscular tissue, in the elaborately evolved cross-striated variety as well as in smooth muscle. The intimate structure of the three sorts of muscle found in man (cross-striated, cardiac, and smooth muscle) must be thoroughly understood in connection with this chapter. Knowledge also of the methods of grouping of the contractile cells into muscle-bundles, of those within the anatomical muscle, and

FIG. 223



Epithelio-muscular cells from a hydra: *q*, muscular prolongations from the cell-body. (Dubois.)

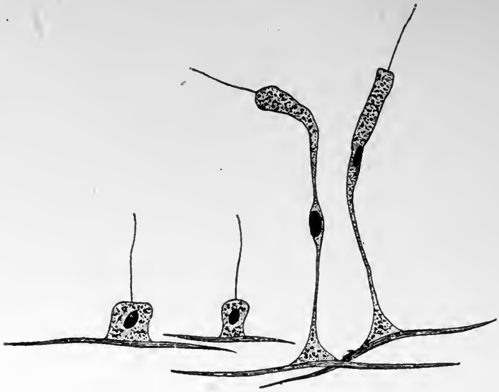
FIG. 224



A diagram suggesting how muscle-fibers originate: *a*, a formative cell or myoblast; *b* and *c*, stages in development of contractile fibers out of the undifferentiated protoplasm in a frog. (R. Hertwig.)

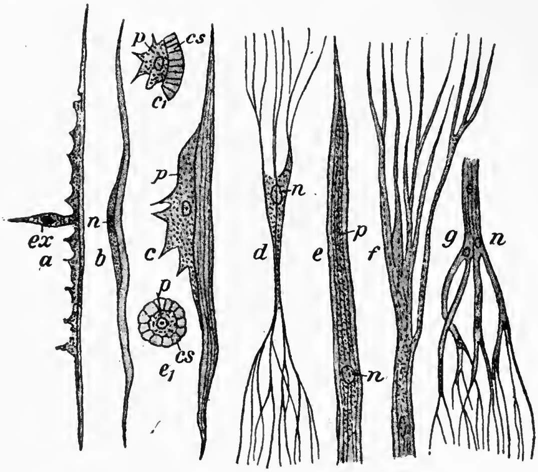
of the relations of the muscles and functional groups to their nerve- and blood-supply should likewise be thoroughly in mind before the study of this chapter is begun.

Fig. 225



Cilio-epithelio-muscular filaments of the parasite Sagastia. At the bottom of each cell one sees the part most like the smooth muscle-fiber of man. (Dubois.)

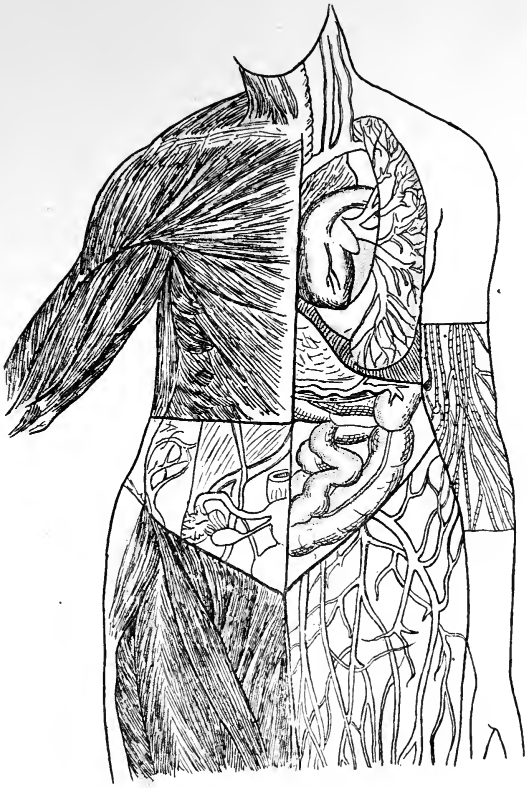
Fig 226



The evolution of muscle: *a*, epithelio-muscular cell; *b*, a subepithelial muscular fiber; *c*, a longitudinal muscular fiber (from a worm); c_1, transverse section of the same; *e*, the same in a bird; *d*, dorso-ventral fiber (from a marine planarian); *f*, the same from a bird; *g*, branched muscular fibers (from the gel of a ctenophore). (Dubois.)

The Contractile System in Man.—It is sometimes ill-appreciated how nearly universal in the organism is some variety or other of contractile tissue—muscle. There are more than four hundred more or less independent muscles classed as cross-striated or "voluntary," ranging in size from the vastus externus to the stapedius and in site from the ends of the toes and fingers to the scalp. Unstriated, smooth, or "involuntary" (reflex or "vegetative") muscle is present throughout the entire vascular system and the lymphatic vessels, placed in almost exery portion of the body; in the wall of the whole alimentary canal from the pharynx to the anus; in the gall-bladder and common bile-duct; in the trachea, bronchi, and bronchioles; in the kidneys, ureters, bladder, and urethra; in the spleen; in the adrenals; in many gland-ducts and mucous membranes; in the skin; in the sweat-glands; in the mamma, mammilla, ovaries, uterus, Fallopian tubes, vagina, epididymis, vas deferens, prostate, tunica dartos, seminal vesicles; in the iris; and probably in still other places. The heart is made largely of a sort of muscle partaking of the nature apparently of both these other sorts of muscle. Van Beneden claims that the rays of the amphiaster-spindle in mitosis are contractile in nature,

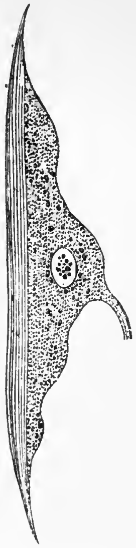
Fig. 227



The universality of muscle-tissue. When one mentally combines the fragmentary views shown here and extends them all over the body it is obvious that muscle is essentially a universal contractile fabric of the organism. Functionally it is not merely a collection of separate organs.

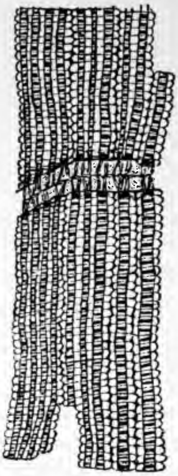
while the cilia and the flagella of spermatozoa are certainly so, although not classed as muscle. Thus, the nervous system, epithelium, the skeleton, certain parts of the sense-organs, the body-liquids, and the epidermal structures are about the only regions (and these of relatively small volume) in which muscle of some sort is not present. Muscle is the organ or tissue of gross (as distinct from molecular) movement, and but few indeed of the active organs of the body do not need its help. Rather more than half the mass of the adult human body is muscle, and this is distributed very widely, as we have seen.

FIG. 228



A muscle-cell from a (nematode) worm, showing an early stage of differentiation. (Claus.)

FIG. 229



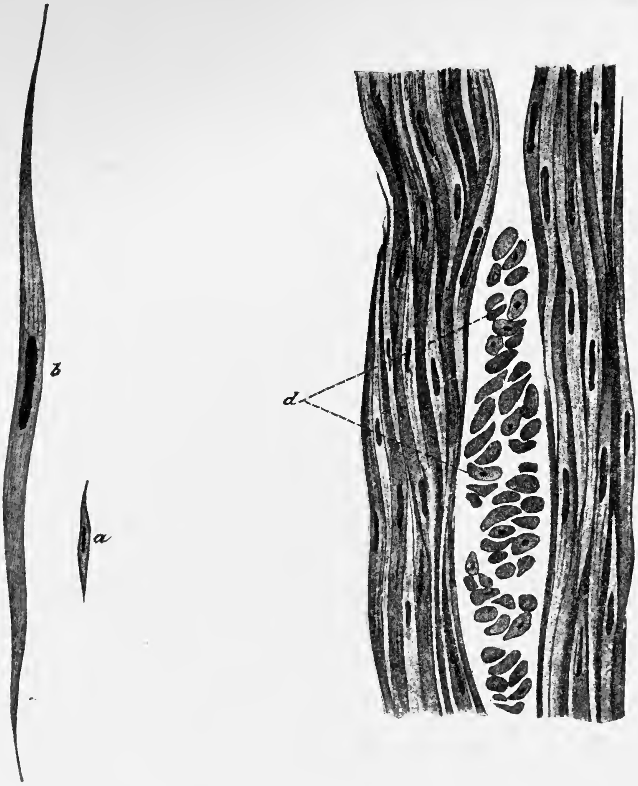
Longitudinal partly diagrammatic section in human heart-muscle to show especially the bridges of contractile tissue extending from one cell to the next. (MacCallum.)

The Structure of Muscle.—Like all the other sorts of tissue in the body, muscle is composed of protoplasm arranged (probably because of the modes of production and reproduction) in cells. In the cross-striated muscle-cells, however, differentiation has gone very far, so that the cellular plan, if we think of an average epithelial cell as the type, as is commonly done cannot very readily be made out. In the smooth variety of muscle and in that of the heart the cellular form is more apparent.

We may divide our brief description of muscle into the three sorts above mentioned: smooth or "unstriated," cross-striated, and cardiac. It seems likely that did we know better the finer structure of muscle these sorts would in part be found to merge histologically as they do physiologically, for the essential fibril is apparently present in all.

Smooth muscle is made up of fusiform anisotropic cells ranging in length from about 0.040 to 0.225 mm., and in width from 0.004 to 0.008 mm. They reach their known maximum size in the uterus in its pregnant state, where they are often more than double the maximum given above. The reticulated nucleus is elliptical and is placed nearly in the middle of the cell. Striations (myoids?) are clearly to be made out running the entire length of the cell. Those about the periphery of the cytoplasm are relatively coarse and straight, while within they are finer and constitute a distinct reticulum. Between the fibrils is the homogeneous and transparent sarcoplasm. The cells are collected together in spindle-shaped bundles, each bundle being enclosed in a delicate fenestrated membrane (as is also each cell) called its sarcolemma. The meaning of the oval openings in this membranous bundle-covering is not yet clear. Several histologists have described fine protoplasmic bridges connecting the sarcoplasm of the cells in the bundle, but these have been declared

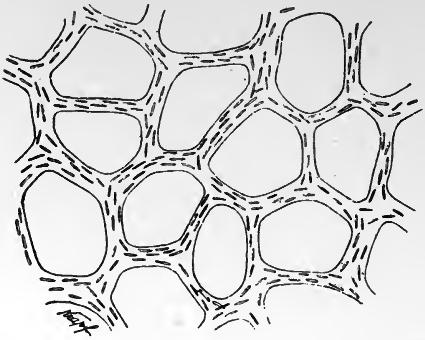
Fig. 230



Smooth muscle-fibers of the uterus: *a*, from a virgin; *b*, from a pregnant woman (Bumm.)

artifacts by others, and hence the matter, so important for the physiology of muscle, must be a little longer considered in doubt. The free transmission of the contraction-wave, for example, in hollow organs like the ureters, makes probable some such mode of connection between the various cells and bundles whether the staining methods at present in use show such connections clearly or not. Each fiber-cell is surrounded by a very delicate transparent sheath which wrinkles more or less when the fiber changes its shape in contracting.

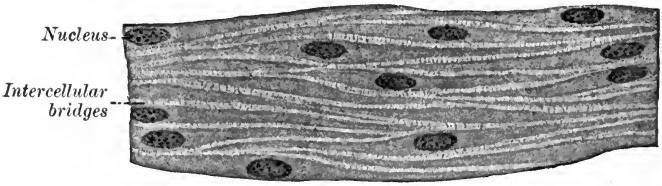
Fig. 231



The smooth muscle in the bronchioles of the dove's lung. (Eberth.)

Cross-striated muscle is the variety most fully under the will's control, and it is therefore often called voluntary muscle; it is frequently attached to the bones and hence is sometimes termed skeletal muscle.

Fig. 232



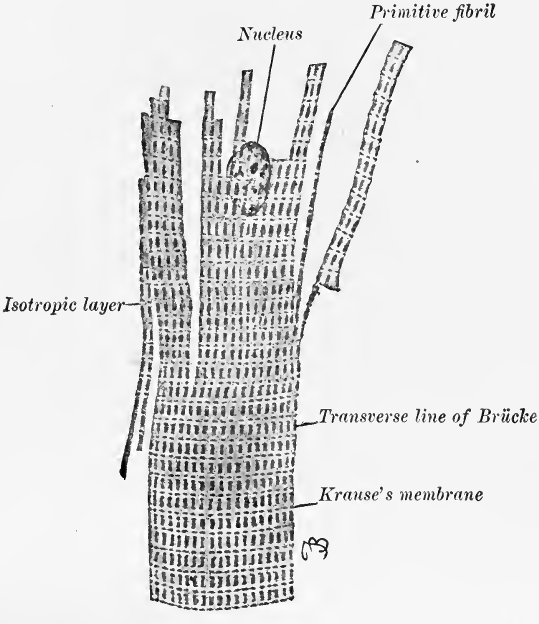
Longitudinal section in the smooth muscle of a dog's large intestine, to show especially the intercellular bridges. $^{530}/_{1}$. (Szymonowicz and MacCallum.)

Cross-striated muscle, like the smooth sort, is made up of fusiform cells. These are, however, apparently of much greater structural complexity and differ much from the others in size and mode of action. The fibers or cells (each fiber being apparently a highly specialized cell), of cross-striated muscle, are more or less cylindrical in shape. In size they may be even as much as 12 c.m. long and 0.1 wide, and they are thicker in the male than in the female. Roughly speaking, the fibers are smaller in the more finely adjustable muscles (such as those of the eye) than in the coarser muscles (like the glutei, for example). Most of the fibers in

FIG. 233

The anastomosis of muscle-bundles as found in the urinary bladder of the cat. Intermuscular nerve-cells and -fibers are to be seen between two of the muscle-bundles. (Metzner.)

FIG. 234

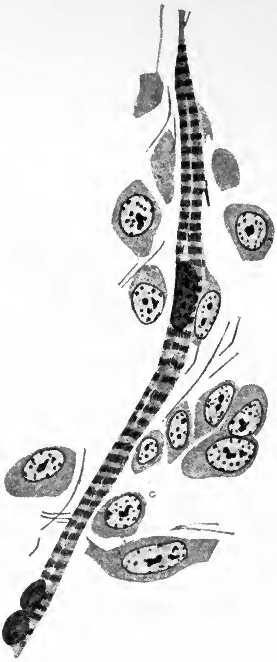


A bit of a cross-striated muscle of a frog, showing the nucleus and the ease of its division both transversely and longitudinally. $^{650}/_{1}$. (Szymonowicz and MacCullum.)

man are not more than 4 c.m. long. The fiber usually ends in its tendon in a quickly tapering single point, but where a layer of tissue such as the skin is to be moved, and in the tongue, the fibers branch repeatedly.

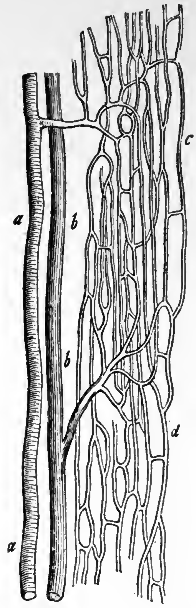
About the fiber is a sarcolemma, a thin, transparent, and tough elastic membrane best seen when the enclosed fiber is torn apart. The muscle-substance itself is elaborately composed of units whose exact status is not yet clear. The regular arrangement of these units (called by Schäfer sarcomeres) is such that under the microscope the fiber seems striated both transversely and longitudinally. A section of units transversely divided constitutes a disk (such as Schäfer shows from a beetle's leg-muscle) but longitudinally considered it is a *fibril* or sarcostyle extending the length of the fiber or cell. Each of these transverse disks is usually about 1.5 microns thick when a muscle is moderately extended, but sometimes not more than half of that. The sarcostyles or fibrils, each consisting of a row of prismatic sarcomeres or sarcous elements, are separated from each other in the fiber by a small amount of transparent substance called sarcoplasm. The fibrils or sarcostyles are in turn made up of fibrils, and by some writers unfortunately it is these which

FIG. 235



A cross-striated muscle-fiber from the epiphysis cerebri (pineal gland) of the ox. (Dimitrova.)

FIG. 236

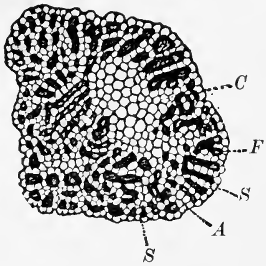


The capillary network of cross-striated muscle: *a*, arteriole; *b*, veinlet; *c* and *d*, the reticulum of capillaries. (v. Frey.)

are termed sarcostyles. Cross-striated muscle is well named, therefore, for numerous striations in both directions divide the protoplasm into many sorts of minute cubical compartments or units whose respective significance is not yet made out either structurally or functionally. The histology of muscle is still further complicated by the complex optical properties of the substance, so that the appearances under one set of conditions are quite unlike those in the same structure under another set, while preserving and staining methods produce very various effects. It is possible, as MacCallum suggests, that the optical appearance of this sort of muscle is partly due to a reticulum with regular meshes extending through the protoplasm, of which, the ultimate fibrils and Krause's membrane, so called, are the chief elements. (See Fig. 278 page 499.)

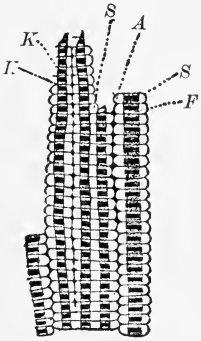
According to a common notion, in the middle of each of these sarcomeric parts, and transversely across it, is Krause's "membrane;" on either side of it an intermediary disk of clear isotropic substance (sarcoplasm or lymph); next a broad dark band which is bisected by Hensen's median (light) disk, and finally this in turn by the median (dark) disk of Heidenhain. Krause's "membrane" appears to extend across the fiber and to be continuous with the sarcolemma. An observation chance made by Kühne seems to place the consistence of the crossing-structures still more in doubt than before. If really membranous, Krause's "membrane" is of only slightly greater consistence than its surroundings.

Fig. 237



Cross-section in human heart-muscle, above or else below the nucleus: *C*, central sarcoplasm-mass; *S*, sarcoplasmic disk; *F*, fibril-bundle. (MacCallum.)

Fig. 238



Longitudinal section in human heart-muscle: *S*, sarcoplasmic disks; *F*, fibril-bundle; *K*, Krause's membrane. (MacCallum.)

It is rather more than possible that the individual fibers are connected by some sort or other of bridges made of muscular tissue.

The nuclei of the cells of striated muscles of man are mostly just within the sarcolemma, but sometimes, as in the red sort of rabbit-muscle, deep within the fiber-cell. About the nuclei is often a more or less granular substance.

The vascular and nervous service of muscle is very abundant, the blood-vessels being large and numerous and intimately distributed, and the nerves of large size and much complexity of course and endings. Lymphatics are abundant in the connective-tissue coverings of the different muscular parts, but do not, any more than do the blood-vessels, extend into the cells, apparently. (For the nerve-endings of muscle, see the preceding chapter, page 329.)

CARDIAC MUSCLE is striated in both directions, but always less distinctly than is cross-striated muscle. Another leading characteristic is the relatively large amount of sarcoplasm, as may be seen in Figs. 237 and 238, by MacCallum. Moreover, the morphological units (cells) are closely connected in such a way as to appear branched, combining in this way to constitute a coarse striated network made up of sarcostyles, which in turn are strings of sarcomeres. No thick sarcolemma, it is said by some observers, appears, but the sarcostyles have sheaths. There may be three or four nuclei in each cell; they are oval in shape with distinct chromatin reticulum and surrounded (as in skeletal muscle) with granular protoplasm whose granules increase with the individual's age. Ultimate fibrils compose the sarcostyles as in other sorts of muscle and pass uninterruptedly from one morphological cell to the next.

The importance of an extension of our knowledge of cardiac muscle for therapeutic reasons cannot easily be over-estimated, the saving of many lives lying in this direction of reasearch.

The Chemistry of Muscle.—This subject is of importance because the muscles, by their metabolism, furnish a large part of the energy and of the heat of the body, and, furthermore, because it underlies the mode of working of the muscle.

In crude and general terms human muscle is: water, 73 per cent.; proteids, 19 per cent., fats, 2 per cent.; "inorganic" salts, 2 per cent.; and chemical sundries, 4 per cent., these latter being mostly carbohydrates, purin bodies, and gelatin. It is not obvious that the water of the muscle is concerned in the actual metabolism of the tissue, but, as we have already pointed out, it is essential to the active movement of these, as of all other organs. The proteids of dead muscle may not be those of living muscle, but of the former we know only a little, and of the latter nothing. There are two proteids probably peculiar to muscle: the globulin, called para-myosinogen (called myosin by Fürth), and myosinogen. These two proteids become myosin under many conditions, this process being probably, for example, at the basis of *rigor mortis*. Dubois suggests an instructive formula by which the katabolism of albumin might conceivably be conducted, and it is reproduced here chiefly as a sort of chemical diagram, infinitely simpler, of course, than the reality, and useful chiefly as a list of the products named.

$$\begin{aligned}
C_{72}H_{112}N_{18}SO_{22},\ \text{albumin} + 20(H_2O),\ \text{water} = {} & \\
& 7(CON_2H_4),\ \text{urea} \\
& + 5(C_6H_{10}O_5),\ \text{glycogen} \\
& + C_{27}H_{46}O,\ \text{cholesterin} \\
& + 3(C_2H_5NO_2),\ \text{glycocoll} \\
& + C_2H_7NSO_3,\ \text{taurin} \\
& + 6H,\ \text{hydrogen}
\end{aligned}$$

It is in part the goal of biochemistry and of chemical physiology to replace this possible outline with the actual formula in all its details.

Carbohydrates are present in muscle only in a small percentage, as we have seen, but their importance in the metabolism of this tissue is apparently great. The two chief carbohydrates present are glycogen and, in much smaller proportion, dextrose. The former, glycogen, present in most animal tissues, if not all, is doubtless the chief source of muscular energy. Manché found that a limb made to contract for about an hour showed about 14 per cent. less glycogen than the corresponding resting limb, and that ligation of the arteries produced a like result. In starvation the glycogen rapidly disappears from the muscle. In muscular paralysis, whatever its cause, glycogen accumulates in this tissue. Most abundant of the elements in the inorganic salts of muscle are potassium (which is preponderant), sodium, calcium, magnesium, chlorine, sulphur, and phosphorus, the three last being represented as the chlorides, sulphates, and phosphates of the others. It is a striking fact that a muscle does not contract spontaneously in aqueous solutions containing no ions, for example, in a distilled-water solution of chemically pure cane-sugar. The large amount of research which has recently been made into the relations of muscular activity and inorganic salts is left to tell us what chemism and electricity have to do with muscular action. Urea, creatin, creatinin, xanthin, hypoxanthin, and carnin are found in muscle, as well as many other nuclein bases. Just how these substances are produced in the katabolism of muscle it is impossible at present to say.

The Modes of Action of Muscle.—It is one thing to understand the structure and composition of a complicated mechanism, but quite another sometimes to know exactly how it works. In the case of muscle this problem is made worse by the minuteness of the structures and by the intricacy of the physics concerned in the action of this highly differentiated kind of protoplasm. As yet we cannot tell how muscle develops its contractile energy, so the best we can do is to describe summarily a few of the various theories as to the matter. Our immediate problem is, then, as to exactly how and why the fibrils of muscle shorten and thicken and then immediately lengthen and attenuate again. Do cross-striated and smooth muscle act in the same way? (See also page 487.)

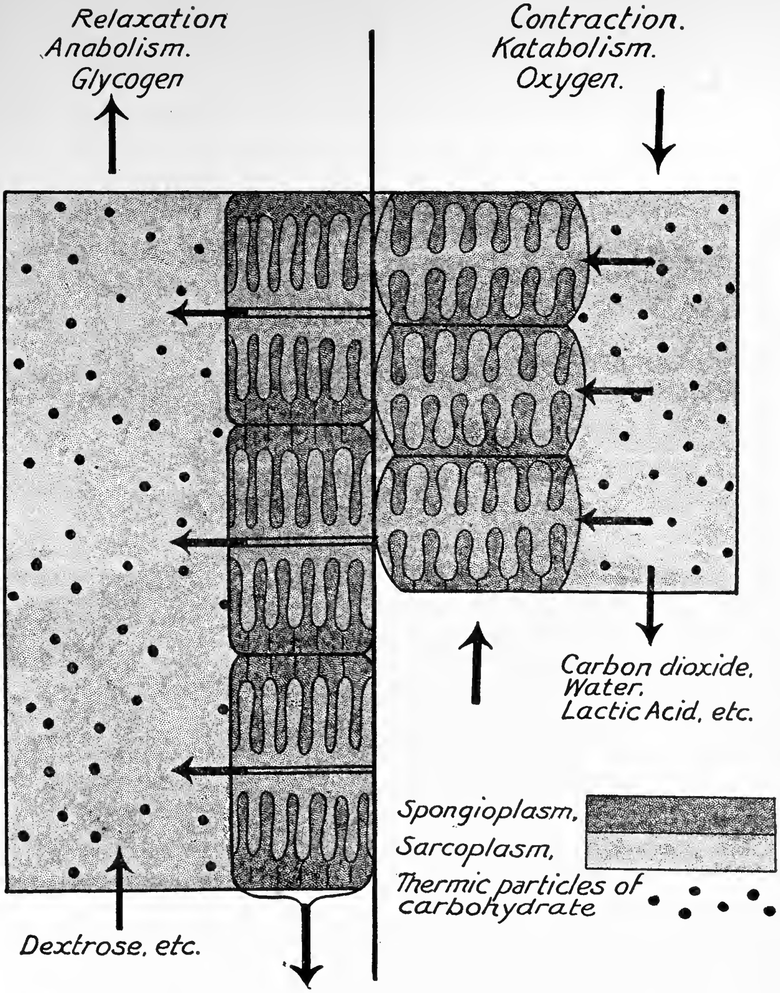
We can go a certain way on relatively solid ground. We know the probable structure of cross-striated muscle, substantially, so far, at least, as appearances go. We know that it consists of two sorts of substances, one (anisotropic) doubly refracting polarized light, the other (isotropic) refracting it singly. We know that when the contraction occurs in cross-striated muscle the latter kind of material changes its place somewhat, while the former kind does not do so. We are sure that the metabolism of all sorts of muscle is, in part, the oxidation of carbohydrates and of protein, sarcolactic acid being a way-product, and carbon dioxide and water among the end-products. The more active the contraction of the muscle the more oxygen it consumes and the more carbon dioxide is liberated from it. We know that, as often happens in protoplasm, the chemism of metabolism gives rise to at least three sorts of kinetic energy: movement, heat, and electricity, for these may be measured and variously studied.

If we start out with the fact that it is chemism undoubtedly which liberates these energies, we have the basis of the chief various theories of muscle-action. To one (Engelmann) it seems clear enough that the chemism gives rise to heat, which, by causing imbibition of sarcoplasm, brings about the contraction. Another "school" (Pflüger, Bernstein, Verworn, Fick) supposes that the chemism directly, *i. e.*, without the intervention of heat, alters the two differing substances in such a way that the isotropic one swells into the anisotropic. A recent group of thinkers (Müller, Loeb) suppose that electricity is involved in causing the contraction. To others (*e. g.*, Weber), the chemism seems to alter the natural elasticity of the myoids or fibrils, making them shorten and then lengthen. Numerous other hypotheses still less probable have been published at various times.

THE THERMO-DYNAMIC THEORY.—The thermo-dynamic theory just now seems perhaps more satisfactory than any other. By means of a coil of platinum wire surrounding a short string of catgut kept warm in a proper solution, Engelmann demonstrated that this form of protoplasm at least shortens when heat is applied to it (the heat was produced by sending an electric current through the platinum wire). Rubber behaves essentially in the same way. The curve made on a rotating smoked drum by both of these substances under these conditions is much like that traced by a contracting gastrocnemius of the frog (see p. 473 of the Appendix). This experiment was at the basis of Engelmann's thermodynamic theory. His supposition, in fine, then, is that metabolism (probably the katabolism) of carbohydrates causes a liberation of heat in or about the myoids of muscle, and so causes them to shorten. The main objections raised to this theory amount to an assertion (as, for example, by Fick) that the heat-increase which actually obtains in a contracting muscle is not sufficient to produce the effects observed. In answering this, Engelmann suggests a rather far-reaching principle, useful, perhaps, in more than this one place: the temperature of some of the chemically acting individual *particles* in a muscle might increase many degrees and yet not raise the temperature of the muscle-mass (two-thirds water) more than a thousandth of a degree. At the same time the heat rapidly produced by means of these relatively few metabolizing particles might very well cause the muscle to contract. In general terms, that which takes place in an ultra-microscopic group of molecules may be very different from what our relatively gross instruments allow us to observe in an organ as a whole.

On the basis of this rapid heating and cooling of minute metabolic parts of a muscle the next supposition of the thermodynamic theory is that this heating of the segments of the myoids or sarcostyles causes the liquid of the isotropic (light-banded) segments of the sarcomere to be absorbed by the dark or anisotropic disks. The lymph or sarcoplasm flows in at Hensen's line and then in the two opposite directions of Krause's "membranes." The work of Schäfer, histological in nature, tends to corroborate the suppositions of Engelmann and to make this

FIG. 239



Muscular action according to the Engelmann-Schäfer theory of plasmic imbibition caused by heat.

theory of sarcomeric imbibition of muscle-plasm more probable than any other. Blindly ending canals seem to Schäfer to constitute the essential part of the minute sarcomeres, these swelling outward laterally and shortening as they fill with the muscle-lymph from the isotropic disks.

If these suppositions are true, there remains to be worked out the thermogenic metabolism and also the spatial relations of the heating particles to the structural elements of the sarcostyles. (See Fig. 239.) On what basis to adapt this working-hypothesis to smooth, "unstriated" muscle is not apparent. Little or nothing is known about the finer structure of the myoids and muscle-fibrils, and this ignorance makes application of so elaborate a theory out of the question at present.

On the whole, then, the thermogenic theory of sarcomeric imbibition cannot be said to be wholly satisfactory; but it is, perhaps, the best so far devised.

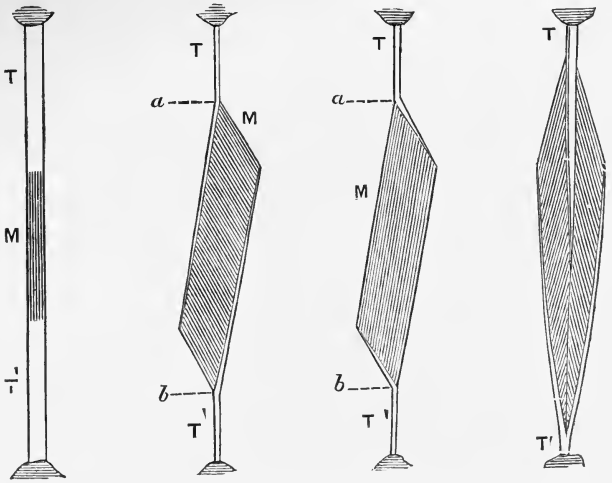
The Chemi-surface-tension Theory.—The chemi-surface-tension theory has been of late perhaps better championed by Verworn than by others. This theory, as set forth especially by him, has already been given briefly in the chapter on protoplasm, but purely from the point of view of undifferentiated protoplasm. Surface-tension is the cause of the tendency to surface-contraction characteristic of liquids. It is this force, for example, which makes a drop of dew on a leaf spherical instead of flat. It is a potential energy of cohesion, apparently, between the adjacent molecules at the bounds of a mass of liquid.

Perhaps we could not do better justice to this theory of muscular contraction than to state it in the terms of Verworn: "During the explosive decomposition of the biogens [protoplasmic units] either in the isotropic or the anisotropic substance (which latter is regarded by Engelmann as the specially contractile element), the chemical constitution of the biogen-molecules is so changed that a molecular attraction arises between them and certain constituents of the other substance. As a result of this, the surface-tension between the two disks (the sarcomeres) must necessarily diminish (or even become zero), *i. e.*, an intermingling, a mutual penetration of the two substances must take place. In this process the isotropic, as the more mobile, substance will necessarily diffuse into the anisotropic, as the more fixed, *i. e.*, the muscle-segment will necessarily decrease in length and increase in breadth. There will thus be in principle the same process as in swelling, except that, as Engelmann assumes, there will be not a simple admission of water, but a chemical swelling, in which along with the water other chemical substances will enter, such as take part in the regeneration of the decomposed biogen-molecules. But in proportion as these molecules are regenerated and by the introduction of oxygen are brought back to the maximum of their labile constitution, a change in the molecular relations occurs, and now, in contrast to what happened previously, a separation of the two substances will take place, which will give to the muscle-segment its original form.

"Although the processes, which for the present are wholly unknown, may in reality take place very differently, at all events the principle of modification of the molecular attraction by changes in the chemical constitution of the molecules, the same principle that explains ameboid movement, appears to be able to elucidate in its essential points the obscure phenomena of muscular movement. Thus, contraction-movements in their most essential points are controlled by the direct interchanges of chemical and mechanical energy without the mediation of another form of energy, such as heat or electricity."

It is to be noted that according to this theory the most essential process preliminary to relaxation is the absorption of oxygen and oxidation. This soon would cause, we might suppose (from analogy with ameboid movement), a loosening of the surface-molecules of the sarcomeres, a lessening of surface tension, and a flowing-backward of the liquid sarcoplasm into the isotropic sarcomeres, lengthening and attenuating the sarcostyles or fibrils to the uncontracted condition. Contraction thus is katabolic, oxygen being absorbed; relaxation is anabolic, oxygen passing out as part of the carbon dioxide excreted from all protoplasm. The two phases are interdependent parts of one rhythmic function.

Fig. 240



Four types of arrangement of the muscle-fibers of skeletal muscles: M, belly of muscle; T, T', tendons of origin and insertion; a, b, length of muscular belly. It is obvious that in a muscle short fibers usually mean small but powerful movement, while long fibers bring about considerable movement of relatively little force. Compare, *e. g.*, the gastrocnemius (type D) with the sartorius (type A). (Beaunis and Bouchard via Gray.)

Other theories of muscular contraction we have here no reason to discuss, for the evidence for them seems at present less than for the two theories already outlined.

When the complexity of the protoplasmic metabolism and the minuteness of the muscular structure is considered, the details of which are as yet largely unknown, it is not strange that the precise method by which muscle works is not yet learned.

The Neuro-muscular Mechanism has been already described in part in this book—the nerve-centers and nerve-paths in the chapter on the Nervous System, and the kinesthetic sense-organs, etc., in the discussion of the senses. It remains here to look at this muscular coördination and control mostly from the side of the muscles. (See Fig. 188, p. 334.)

It has been emphasized that the nerves form with the muscles (and glands and sense-organs) a functional *unity* if not a complete structural continuum of protoplasm, a principle of importance in the theory of muscular control. Philosophically one has to consider the nerve-muscle group of organs as agent of the individual will ready at all times to bring about whatever movement the biological needs of the animal demand. It is only by the intimate union of the nervous system with the muscle system, reaching thereby nearly every body-cell, that the muscles are made almost the universal instrument of every function in one way and degree or another. In other words, the all-pervading "nerve-net" brings, perhaps, into the immediate service of every part of the body practically the whole muscle-mechanism.

The relations of voluntary movement to reflex movement were discussed in the chapter on the Nervous System. It is largely a matter of habit, of repetition until the action is on a mechanical basis almost, that finally turns a laborious new voluntary movement, made only at first by exercise of perhaps strained attention, into a reflex group of movements nearly free of mental effort. The muscles in unity with the nerve-net *learn*, acquire readiness and coördinated accuracy, what, in short, is known as skill or, more broadly looking, cleverness. What is the muscular side of the development of this capacity, one of the most precious of man's powers, one of the largest elements in the evolution of his civilization and culture? While, indeed, "the reign of the brain is plain," it is easy to limit too closely what we mean by "brain" and to forget that the nervous system is above all a system of conducting paths. These are so infinitely devious that in a sense they form a net, and yet they are useless without something to connect, without some way of expressing in the material, practical world that system of adjustments which combined are life. The most immediate agent in this direction is the muscular system. How then does a musculature learn? and in learning, what development does it undergo?

There are two directions in which a muscle may develop: vigor and strength, and skill or delicacy of adjustment. The latter, skill, involves a degree of the former, vigor, but, on the other hand, the vigor may be present with little delicacy of coördination. To some extent, indeed, in their higher degrees these are opposed and in practice rarely present in the same muscle-group. The strong-man in the circus is seldom a graceful dancer, and the expert engraver or musician is only rarely an athlete. The reason for this lies largely in the fact that the time required for one sort of development excludes development of the other kind; but there is a true physiological opposition of a certain degree. In athletic training the endeavor is constantly to overcome this opposition, to acquire skill in playing combined with a large degree of strength. The games in which both mean much, such as tennis, golf, rowing, or base-ball, are then theoretically the best for the general good of the organism.

In developing *strength* the muscles and their nutrition are almost solely concerned, although the exercise involved indirectly tends to develop all parts of the body (see below). It is not easy to find any data of a precise histological nature on the effects of long-continued exercise or work on the muscle-fiber itself, either smooth or cross-striated, but the effects on a muscle in general are fairly well known. In the first place, when a muscle by working becomes stronger, it grows somewhat larger, and this notwithstanding that the thin layers of fat within the muscle are oxidized and disappear. The muscle-fibers probably increase not only in number but in size as well. A second condition obvious in a strong muscle (and a better strength-index than size) is hardness or tone together with an increase of elasticity. The growth of the fiber distends more fully the sarcolemma and that of the fiber-bundles their coverings of fascia. In an abundantly fed muscle the elasticity is greater than in one poorly fed. A fourth change which takes place as a muscle strengthens is a marked increase in the collagen coverings (sarcolemma, fascia, aponeurosis, etc.) of the muscle-bundles. These membranes are very strong and elastic, for their function is to keep in place the muscle-fibers and muscle-bundles which are more than half liquid, allowing them at the same time to glide with little friction over or within each other. In a poorly nourished man, especially if at the same time his muscle be overworked, these coverings are especially prominent, developing out of proportion to the protein muscle-fibers. This consideration has a bearing on the contention of Chittenden that most men eat far too much protein, being against the supposition as applied to those who do much muscular work. A fifth but accessory change in a hard-worked muscle is a development of the blood-vessels to allow of a freer nutritional supply and excretion. There is a corresponding new-growth of nerve-fibrils which more than replaces those lost by metabolic and mechanical wear-and-tear, especially at the beginning of training.

In developing *skill* (delicacy and accuracy of adjustment), a group of muscles develops not only itself and its immediate blood- and nerve-supply, but without a doubt no small part of the nervous system also. A man who is very skilful in one set of muscular movements has acquired much more than adroitness with that one muscular mechanism, for he has learned how to become generally skilled, and his neuro-muscular mechanism has developed to a higher degree of efficiency in every sort of activity.

In just what this sort of development consists so far as the muscle is concerned is not yet known, nor indeed are certain data at hand as to what then happens in the nervous system. Keeping in mind the nature of the nervous system, especially its fibrillar structure, we may suppose that in the muscles there is a proliferation of afferent and efferent end-organs, and that in the cortex cerebri (on both sides of Rolando's fissure or in the cerebellum) a corresponding increased interlacement between neurones develops. This sort of difference between muscles capable of fine adjustment and those incapable of it is apparent in the number of muscle-fibers to one nerve-fiber in the eye-muscles compared with their number in the gluteus maximus or other strong, gross muscle; it is many times greater in the former case. In other words, each muscle-cell is controlled in more detail in a skilled muscle than one which is unskilled. The power of coördination with its neighbors is by this means greatly enhanced, and the resulting bodily movements are within limits of accuracy not before realized.

When this skill in adjusting movements has been acquired by many functional groups of muscles in different parts of the body, the nervous system developing in ever-increasing ratio, we call the individual *clever*, meaning thereby that he can do many things well.

A person becomes clever as an individual, as a "mind," usually only through having done many sorts of things with his neuro-muscular mechanism. This is a firm basis for the philosophy of utilitarianism, and a reason for a large increase in the "manual" training and the "physical" education of men and women. Except to the narrowest individualism, knowing (however clear and deep the insight) without some sort of doing is almost a reproach.

In the actual psychophysical personality, then, we cannot separate that which is the immediate outcome of muscular activity from that known to the older psychology as "mental." These two aspects develop together, stand in the same grade of values, and both take important part in men and women as we would always wish to know them. Perhaps at a later day physiologists will be able to explain this fact, which is more and more obvious to educators, by reference to association-impulses running everywhere in the body, especially in the brain.

Special Muscular Functions.—The means, largely muscular and neural, by which posture, locomotion, speech, and emotional reactions are accomplished seem important enough to receive special description, however brief it must necessarily be in comparison with the complexity of these processes themselves. Speech especially is an intricate subject of importance which can receive here by no means adequate discussion, having to make room for things more immediately practical. These brief descriptions will serve not only to explain these particular neuro-muscular processes, but also as examples of the numberless highly elaborate coördinated movements, etc., which the vegetative and voluntary muscles and the nervous system achieve.

Posture.—We have several times mentioned muscular tone, and it is in discussing posture that we see one of its functions so far as the skeletal muscles are concerned. These latter are not wholly organs for producing active movement, but have another important use in maintaining the body and its parts in the numberless positions into which previously they have placed the body. During life this muscular tonus plays a very important part in our control of our organisms. It is characteristic of life and is maintained even in the deepest sleep. It departs, however, at death unless the conditions are such that it is promptly merged into rigor mortis. If one compare the posture of a sleeping body lying flat on its back with a dead body in the same position, the absence of the tonus in the latter case is obvious enough, and in other bodily positions is still more striking. It is in part then by the tonus of the muscles that posture is maintained.

The central nervous system is probably the organ in which the coordination of muscle-tonus is brought about. How the body's intention to maintain a certain posture is connected with the nerves we have no hint, and here we do not need to inquire. With little doubt the coordinated tonus is maintained in most postures by the streaming of very numerous mild impulses from the muscles' nerve-centers into the muscle-bundles. These do not occasion a full twitch of the muscles, but only just enough contraction to maintain, so to say, the "status quo." These impulses are of somewhat the same nature as those which increase muscular metabolism without causing any contraction, spoken of in our discussion of thermotaxis. They are doubtless, however, of greater intensity than the latter, just as these in turn are of less intensity than the influences which bring about active molar contraction.

It is interesting to observe how widely the intensity of contraction, if not of its stimuli, must vary to maintain a posture under the many varying conditions of resistance and muscular vigor. Either of these mechanical conditions in any case may vary within wide limits, but the nervous system must and normally does see to it that just the right degree of contraction is maintained to preserve the bodily position assumed.

In some cases the maintenance of posture does not rest largely with the muscles, for the bones bear the weight. By this means considerable needless work is taken from the actively metabolic muscles and assumed by the tissues (largely bones, tendons, aponeuroses, cartilages), that serve more or less in a passive way. It is the work of the muscles in these cases to pose the various parts of the body so that they are in equilibrium, and to keep them thus, while the strain comes largely on the bones. In this way only a minimum of exertion is demanded of the muscles. Perhaps the most important illustration of this is in standing.

Standing.—It was formerly thought that the muscles were largely responsible directly for the maintenance of the erect position. The work of Braune and Fischer, v. Meyer, and others shows that the body's equilibrium is almost wholly a passive affair so long as the joint-centers are kept in the "normal position" and the muscle-tonus maintained. In this exact posture the center of gravity of the body and all the joint-centers are in line. The knee-joints, hip-joints, the atlo-axoid, and the ankle-joints lie in the same vertical plane in which are also the centers of gravity of the head, trunk, thighs, legs, upper arms, forearms, and hands. Hence in normal standing each of these parts and joints is in balance and also the whole body together. Braune and Fischer found that the knee-joint's mid-point was 4 cm., the hip-joint's 5 cm., and the atlo-axoid's 3.5 c.m. in front of the vertical plane passing through the ankle-joint's mid-points, while the center of gravity of the head was 4 cm. and of the whole body 4.2 cm. in front of this plane. The center of gravity of the trunk is only 0.6 cm. behind it. Altogether the balance is a very perfect one and is maintained with a very small expenditure of effort in comparison with the considerable weight sustained.

IN SITTING the weight is sustained on the tuberosities of the ischia, and the trunk, leaned either against some surface (as the back of a chair) or else leaned forward, is sustained in balance somewhat as in standing.

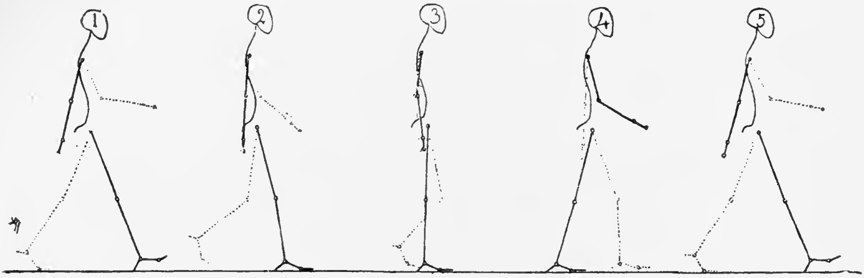
Locomotion consists of some sort of rhythmic alternation of the limbs made in such a way that the body advances as a whole. Aside from jumping and rolling, the chief means of natural human locomotion are walking, running, creeping, and swimming. Of these we need discuss only the first two.

WALKING AND RUNNING.—Braune and Fischer have advanced somewhat upon the classic studies of Weber brothers and of Marey into the phenomena of walking and running. By attaching tiny electric lamps to different parts of the body, accurately photographing in the dark the respective courses of these lights, and afterward working them out with mathematical exactness, these researchers have arrived at many of the actual physical conditions of these important motor functions, and with surprising precision. For a general understanding, however, of these processes the instantaneous photographs of Marey (made in part in daylight from a man running and in part in the dark from illuminated lines and lights attached to the man's costume) furnish us the best material.

The muscles of walking and the process itself are somewhat as follows (Richer): Pushed forward by a muscular action, which will be noted later on, the leg which is swinging falls again by its own weight on the ground. At this instant it is in a condition of almost complete muscular relaxation or rest. As soon as it begins to support the body's weight again, even before the foot is completely on the ground, the muscular contraction begins. The middle gluteus begins to shorten and its energetic contraction lasts during the time of one-sided support to prevent the rotation of the pelvis by the swinging leg attached to it. The middle gluteus and probably also the gluteus minimus directly oppose the lateral fall of the pelvis, and are aided by the upper part of the gluteus maximus and the tensor fasciæ latæ. The gluteus maximus in its entirety, meanwhile, contracts during the entire posterior step and thus prevents the falling of the trunk forward, but its activity stops at the moment of verticality and does not begin again during the anterior step. The quadriceps also is one of the first muscles of the supporting leg to contract, and maintains thus the extension of the weight-bearing leg which else would bend; like the gluteus maximus, it is quite inactive during the anterior step. The muscles of the (lower) leg are all slightly relaxed during the posterior step, but at the time of verticality the posterior and lateral muscles contract vigorously, the contraction increasing to the step's end. The calf-muscles (gastrocnemii and peronei) energetically raise the heel, and the latter, as it leaves the ground, raises and pushes forward the body simultaneously. Hence these muscles are the true agents of propulsion. Flattening of the arch of the foot is prevented only by the powerful action of the lateral peronei. The posterior femoral muscles, flexors of the supporting leg, begin contracting during the anterior step, and the contraction soon becomes marked and flexes the leg off the ground.

The previously supporting leg now becomes the swinging leg. At this moment the gastrocnemii and the peronei relax, and at the same time the extensors of the toes and the tibialis anticus contract, the last serving to raise the toes off the ground to prevent their touching it as the leg swings. The flexors of the leg are contracted, but the flexors of the thigh on the pelvis (sartorius, etc.) contract so as to draw forward the thigh and the rest of the leg. Thus the swinging leg advances, but as it passes the vertical the quadriceps femoris shortens vigorously so as to extend the leg from the thigh; this is a quick movement and is quite finished before the advancing leg has stopped. (The swelling seen in the thigh later than this is due to the relaxation rather than to the contraction of this large mass of muscle)

Fig. 241



The periods of a double-step. The first shows the period of double support, the second the posterior step, the third the moment of verticality, the fourth the anterior step, and the last the period again of double support. (Richer.)

Other accompanying contractions are to be seen: The spinal muscles contract on the side of the oscillating leg, as does also the deltoid, the anterior and posterior fibers of the latter controlling the natural swinging of the arms.

The work of Fischer, then, tends to minimize the old passive pendular movement notion of the Weber brothers and to show that it is largely a muscular propulsion.

In *running* the phenomena are essentially those of walking, the main difference being in the vigor of the supporting leg's action. All the movements are exaggerated and the supporting leg (gastrocnemius) in extending the foot on the ankle raises the body so strongly that the latter entirely clears the ground and falls, a moment later, considerably further forward on the far-extending other leg. Running, like walking, is then a system of fallings first on one leg and then on the other. The energy expended is about double (Marey) that of riding a bicycle, but partly because the number of nervous and muscular movements is much greater, the fatigue is much more than in this ratio. The cerebral center may be the corpus striatum.

Speech.—The neuromuscular mechanism by which we use our voices is one of the most complex in the body. While complicated in the large number of nerves of muscles and muscle-bundles employed, it is doubtless vastly more so as respects its central neural apparatus. This has to put it in intimate relation on the one hand with practically all aspects of our intelligence, and on the other with the centers of many of the motor functions. It is only artificially, then, that we can separate the phenomena of speaking from the more mental principles of language; they are aspects of one and the same broad function, *the expression of intelligence.* Without this we would still be brutes. In writing, the same language-phenomena are employed, but the voice-muscles, etc., partake in it only reflexly and sympathetically. Here we are concerned, then, only with *voice-production* and not at all with language itself or with the other modes of its expression. The physiology of language, merging into the formation of spoken and written words on one side and the abstruse psychology of conception on the other, is outside our present range (see page 417).

The apparatus concerned in vocalization includes the muscles and nerves of most of the external respiratory mechanism; the larynx; the air-chambers connected with the nose; and the mouth-cavity, including the tongue and lips. These all are active instruments of speech. For the detailed anatomy of these parts the reader is earnestly referred to anatomical text-books in order that he may clearly understand the relations of these organs to each other. The most complex part of this mechanism, aside from the nerves connected with it, is the larynx; its parts and their respective functions are even yet, after three centuries of study, only partly determined. The thorax furnishes most of the motive power of vocalization. The larynx contains the vibrating sound-producers proper. The nasal air-chambers are the chief resonators of this sound-producer. The mouth-cavity and the lips, tongue, and teeth within it or part of its walls are largely the means by which the "sound" sent into it from the larynx are differentiated into words and other utterances with a myriad shades of tones and meaning. Controlling all of these and coördinating them into one useful mechanism, the valued servant of the individual, are the nerves and the nerve-centers connected with them.

THE RESPIRATORY BELLOWS is concerned with voice chiefly in the expiratory phase of its movements. In very high-pitched singing or speaking the current sent through the trachea is a powerful one, one estimate making the tracheal air-pressure 70 mm. of mercury or more. In ordinary tones it is probably not over one-sixth of this amount. It is to furnish this draft of the tidal air that the thorax is used in speaking. In this function of the bellows-mechanism of the trunk one sees how perfectly under voluntary guidance the respiratory muscles are. Without this minute and careful control of the air-currents through the larynx the significant functions of cultured and emotional speaking and singing would be quite impossible. When one considers that the abdominal muscles, the diaphragm, and many muscles of the thorax take part in the respiratory movements, the wide-reaching extent in the body of the influence of vocalization is obvious.

THE LARYNX is the automatically adjusting reed-box by which the voice is actually produced except apparently in one sort of whispering. The essential organs of the larynx are the true vocal cords. The tonal conditions of these vibrating reeds are determined and varied by the nine intrinsic muscles of the larynx, not including those attached to the epiglottis. In general terms there are four duties which these muscles perform: to increase and decrease the effective vibratory length of the vocal cords and the space between them. The former pair of functions concern the pitch of the sound, the latter its loudness.

THE AIR-CHAMBERS connected with the throat, nose, and mouth, including the antrum of Highmore, are resonators of the tones started in the larynx. Without these chambers the sounds produced by the vocal cords would have little of that volume and richness in some degree characteristic of all voices. It is largely owing to the uniqueness of the combined shape of these chambers in each individual that each voice is different from every other.

The mouth-cavity, including the tongue and the lips, is, like the other chambers above and in connection with the larynx, when closed a resonance-chamber of the fundamentals and partials of the voice. It is, however, much more than merely this, for only by means of its muscular walls, so cleverly trained in the passing centuries, has spoken language become possible. Speech is primarily a large and elaborate system of vocal symbols, and these are produced almost wholly through the proper adjustment and coördination of the muscles in and about the mouth-cavity. Of these muscles, the tongue is by far the most versatile, although the soft palate and the lips also play important parts in enunciation.

THE NERVOUS CONTROL of the mechanism of voice-production requires little special mention, for the nerves actuating the separate parts of the mechanism have been already discussed, while about the central connections producing the complicated coördinations nothing in detail is known. To the student of mental processes especially this neural apparatus would have great importance could he know it, since it serves better than any other in the body perhaps to link the events of idea-formation with the motor events expressing them—it "connects" more closely than elsewhere, it may be, the body and the intellectual aspects of the mind. We must think that the mental aspect of an idea is somehow intimately associated with its symbols of motor expression to others, but we do not know just where or even in what manner to look to discover its material mechanism. Vocal movements, like other gestures, involve muscles and the nerves which coördinate them, but the relations of the speech-center with other aspects of body and of mind we can as yet but guess about. Here in especial degree hypotheses are vain, so far apart in character are an idea and the moving parts which express it.

The chief nerve-trunks containing fibers concerned in speech and respiration have already been mentioned. The larynx is supplied by the superior laryngeal and by the inferior or recurrent laryngeal branches of the vagus. The other nerves vitally concerned in speech are practically those of deglutition and of mastication.

The *speech-center* in the child, according to Gowers, like most centers, is probably bilateral, but it gradually builds most of its connections into the left hemisphere. Whether or not the common and unfortunate development of one-sided hand-function, "right-handedness," is the cause of this unilateral location of the speech-center is as yet not known. More likely than not, however, this is the reason of it. In left-handed persons the center is in the right hemisphere. There is considerable evidence that in childhood or later if one speech-center area be destroyed the same region of the opposite hemisphere may take up its function of remembering the motor ideas, etc., of speech. We have seen above that the real motor-center of the vocal process is in the ambiguous nucleus of the vagus, the influence coming to it (by way of the spinal accessory?) from some part of the cortex cerebri above by some road as yet not sure. By its association-powers this knot of fibers wherever it be placed in the cortex, over-sees or perhaps controls the more mechanical and truly motor centers in the cerebellum, medulla, or cord, it contains the kinesthetic traces used in articulating words.

The exact location of this supervising associating center in the cortex was determined by Broca following up valuable work by Bouilland, who in turn was inspired (Howell) by the work of the famous pre-scientific phrenologist Goll. It is seated undoubtedly in the third or lower frontal convolution in the region surrounding the short anterior vertical branch of the fissure of Sylvius. In this area of four or five square centimeters of knotted neurones are somehow stored and associated the kinesthetic directions for moving the speech-organs via other centers in the medulla. It is to be noted that this center is part of the so-called "motor area" of the brain, or at least it is close to the region representing all movements of the neck, face, and mouth. Just below this area, on the other side of the Sylvian fissure in the superior gyrus of the temporal lobe are traced the memories of the word-symbols themselves in their relations to the senses and other yet more purely psychical conditions. From this former region the motor fibers extend deeply inward to the posterior part of the lenticular nucleus and then downward to the medulla as above mentioned.

Aphasia.—The various kinds of aphasia are practically important sometimes for locating cerebral disease, and theoretically of great interest because of the light they throw on the psychomotor apparatus of speech and of language. They are varieties of speech-defect corresponding to the different aspects of the total function of these processes. Removal by cyst, tumor, or wound of the motor speech-area noted above causes loss of speaking-power. The memory-directions for working the right muscles in the right order then no longer exist, at least in this cortical region of voluntary use. This defect is motor aphasia, *aphemia*. In case the motor inability is in using the hands for writing instead of the throat, etc., for speaking, it is *agraphia*. When there is not a complete loss of speech, but only a defect (as in paresis, intoxication, etc.), it is called *ataxic* aphasia. Other kinds of speech-derangement, caused by mental rather than by bodily motor disturbance, are rather misleadingly called sensory aphasias. Thus *amnesic* aphasia indicates a loss of memory of either some words or all words. The forgetting of proper names, especially those of persons, is its most common and least abnormal form. There is *word-blindness* and *word-deafness*, wherein the words are read and heard properly but not recognized as symbols of meanings, not "apperceived." In *paraphasia* the word-sounds or word-shapes are recognized but associated with the wrong meanings, wrongly apperceived. The opposite condition is a variety of ataxic aphasia relatively common in which the patient has the meaning in his mind properly but uses the wrong words in trying to express it. There are many combinations of these various conditions found at times, but for description of them works on nervous and mental disease should be consulted. These aphasias are all of much interest physiologically as examples of direct psychophysical relations and of the vast complexity of brain-processes.

Emotional Reactions.—As will be pointed out more explicitly in the next chapter, the bodily aspects of the actual individual, as distinct from his mental aspects, are not all related to his "will" (voluntary), or to carrying on reflexly the vegetative, somatic, and protective functions of the body. Besides these there is a class of movements and tendencies to movement called strains which form part of the emotional feeling-aspects of the individual. These are commonly called emotional reactions or emotional "expressions," but they are also essential parts of feeling-phenomena too simple and feeble to be called true emotions. Thus, when we feel surprised our muscles make at least our faces show it, unless (as is likely) we have trained ourselves to inhibit these muscular movements. If we feel very glad of something and are alone, that is, have no reason for inhibiting the natural movements and "repressing our feelings," we are apt to smile and laugh and perhaps be more lively and expansive than usual. When we are suffering from an acute sorrow the opposite tendencies are obvious in our "manner," that is, in our muscular conduct. In terror our face-muscles move in a certain combination and make us "look frightened," and if we are angered the infant even recognizes it instinctively because of the particular set of muscle-movements characteristic of the emotion of anger. The classic works of Darwin, Piderit, Lavater, Rudolph, etc., describe and finely picture this wealth of emotional reaction in man and other animals. The striking thing about the matter physiologically is that every feeling and emotion has a different set of movements involving, when strong enough, practically the whole body. In these complex sets of movements the muscles of course play the chief part, whether in the wall of an arteriole or of the gut, in the diaphragm, or in the face. Epithelium also takes part. Our present inquiry asks how these motor reactions are coördinated and the principles, if there are any, underlying the different sets of movements. The more psychic aspects of feeling are discussed in the next chapter, so here we briefly glance only at the "reactions" in so far as they are a muscular function.

We have seen that the motor nervous apparatus works probably on the reciprocating plan: when one muscle-group is caused to contract its antagonist is correspondingly inhibited and relaxed. About the hinge-joints are two opposed sets of muscles, the one flexor and the other extensor in function. There are pronators and supinators, elevators and depressors, adductors and abductors, sphincters or constrictors and dilators, the members of each pair being opposed or opposite in action to each other. Again, there is another sort of antagonism of a vascular sort in the vaso-motor mechanism. When vaso-constriction occurs in a more or less well-defined area of the body vaso-dilatation is brought about to compensate in some other area. Finally we find, if we compare various emotions, that there is antagonism in the degree of muscle-activity: in grief, for example, we tend to use our muscles little, in joy and gladness and pleasure much.

These basal antagonisms in the action of the muscles have been studied not a little in relation to emotions which involve them in some characteristic ways. Mixed up with the theories of pleasure and of pain, for example, is the degree of general activity: pain hinders metabolism and activity, and pleasure furthers it. In general, however, the only correspondence which can be made out between aspects of feeling and emotion and these motor oppositions (besides that just mentioned) is a general agreement between pleasant emotions and contraction of extensor muscles and unpleasant emotions and the action of muscles classed as flexors. To this rule even there are many exceptions, just as some beneficial things have a bitter taste and many deadly poisons are sweet. Some emotions lack more or less any tone of the pleasant or unpleasant, yet have well-marked muscular reactions. It is possible that some quality of the mental side of an emotion other than pleasantness or unpleasantness determines the motor combination. It is even possible that we may have finally to look to the intricacies of the nervous "net" and to its connections with the elements of the muscle-fabric in order to account for the motor aspects of emotions. Meanwhile there is always before us for admiration this marvellous structure of muscle and nerve and other tissuess whose parts and action-principles even centuries of self-rewarding but tantalizing research may not exhaust.

CHAPTER XII.

MENTAL FUNCTION.

Another of the various modes of activity which are in one way or another directly connected with the human organism is consciousness, or mind. Reduced to its very simplest biological terms, this is the feeling of being alive. It is necessary to discuss this aspect of the individual for several reasons, the most important of which perhaps is the fact, obvious but often ignored, that every person is not merely a body but also a mind, neither being complete or easily thinkable without the other. It is one of the greatest defects in the practice of the scientific medical art that many far too often disregard the mental aspect of the individual. Indeed, only in very recent years has the medical profession as a whole begun to realize the importance of this mental "half" of his patients. These two aspects practically inter-act in almost every phase, and the mind is scarcely more dependent on the body than is the body on the mind. In no sense, however, is the mental process a function of the body but rather in reality the body is only the material instrument of the mind. We have no intention of entering for a moment upon any metaphysical discussion of the relations of body and mind. It is only necessary here to assume the common theory that these "two" probably are different aspects of one reality. If we take Fechner's famous simile of the arc of a circle, the bodily events are like the outer aspect of this curve and the mental process the same line as seen from the inside. Consciousness, properly speaking, cannot be defined. Its only definition consists in living it, and yet we may say that in a narrow sense the mental process is the experience that an animal has of its external and internal environment.

Consciousness is inherently a process, and psychology no longer pursues its ancient search after a substantial soul. The soul for modern thought is an ethical thing and psychologically that which James has made known the world over as the stream of consciousness. In the following brief description of the mental functions all that we wish to examine is facts, the "what" without the "how" and usually without the "why." We desire only a simple, straight-forward description of the outlines of the human mental process in those aspects most closely connected with the organism. This is properly a part of physiology, not only because from any and every point of view mind is connected undeniably with organic function, but because the physician and the student need to know much better than they often do the other side of man's nature, about his "fire" as well as about the structure of his "clay." The time has nearly come when the scientific physiologist will no longer shy at hearing the word consciousness or even at the sight of the psychologist in his laboratory, for the truth is marching on that the subject-matter and the methods of science do not, after all, conflict with or even necessarily concern the honored interests of philosophy. In merely describing in a simple way the phenomena of mind, we need never go outside of science, nor indeed outside of physiology considered as the general science of vital processes.

There is nothing in consciousness more difficult of understanding than many of the functions and structures already described, of the kidney, the brain, or the lung. The impression to the contrary, so common among medical students, arises partly from the novelty of the mental topics but more from the fact that these psychic objects cannot be literally handled but must be felt otherwise and studied as they stand before the mind in the imagination. Bones may be taken out of the box and their tuberosities compared visually with the pictures in the text-book, and brains and muscles may be handled in the dissecting-room, cut open, and preserved. We are accustomed to this mode of studying material things, and it is easy for us. Here, on the other hand, are only sensations, emotions, percepts, ideas, objects not material but objects none the less, well-defined, separate in a way, with qualities, relations, and real. Indeed the aspects of consciousness are the realest of all real things. Who is there whose life has not been influenced more by some ideas or volitions or feelings than by every sort of material object whatsoever? For every man crushed by a falling rock or an overturning car dozens are crushed by mental objects such as these others. These things, then, are significant and real and can be taken apart somewhat, observed and examined, analyzed, synthesized, classified in many ways —in short, scientifically studied.

Terms different from those of anatomy of course will have to be employed at times and psychological expressions with technical meanings. In no other way can things be scientifically, that is tersely and accurately, denoted or described. The terms, however, are mostly simple compared with many in the text-books of anatomy, histology, and chemistry to which we are accustomed. It is their novelty alone which makes them now and then somewhat forbidding.

The "Functions" of the Mental Process.—In reality the mental process as experienced by individuals has no function; it is the essential part of the personality. Properly speaking, then, it is only the body which has functions: that it may serve as the temporary instrument of the personality. None the less, from a purely biological point of view we may point out one or two uses or functions of this "internal radiance," as Morat rather strikingly calls consciousness. The most conspicuous of these by far are those which inhere in memory and in the synthetic activities of mind. It is easy to think of an unconscious organic machine which would receive and preserve impressions (such as those which produce light and sound) from the environment, but it is perhaps impossible to imagine any means, other than that we call consciousness, by which all these experiences could be summarized, systematized, and recalled at any future time for the benefit of the organism. Minot's formula for this fact is that consciousness dischronates the products of experience. It does more than this, however, for it combines them, allows or causes them to interact and so produce results often entirely new and of the utmost use in the evolution of humanity.

Without consciousness human life were well-nigh inconceivable. It could have no interest either to God or to man, would be nothing more than a self-repairing and self-reproducing material process, part of the inert universe of matter which is dead and meaningless. There would be no persisting unity in this automatic mechanism—without consciousness in its sensory aspects our very feet would be foreign bodies to us. In fact, we could not speak of "our" or "us" at all, for there would be no unity, or if a material unity could be maintained, there would be nothing to lend it value, no self-consciousness, no significant human life. It is only from such points of view as these that we can mention certain "functions" of consciousness.

Certain General Characteristics of the Mental Process.—When we closely observe for a time the stream of consciousness as it passes in our experience we find at least three conspicuous characteristics which are universal (James).

We shall be most strongly impressed perhaps with the continual *changefulness* of the content of this passing "stream." Indeed, if we examine closely or think over the nature of that which "passes through our minds" for say one minute, we are apt to be struck with the fact that although similar experiences may recur meanwhile, the same thought for example, twice, these are never twice exactly alike. There is perpetual change here as elsewhere in Nature and especially in organic life. We never actually experience anything more than this process, this ever-changing yet persistent conscious tide, now narrow and swift, now broader and gentle and slow. This changefulness seems to be dependent all the while on the changing bodily life—although perhaps we never can discover exactly how. If the mental process has one constant characteristic it is this of constant change, and "nought is constant in the world but change."

Because the bodily life is similarly in "perpetual flux," in continual molecular and molar movement, it is natural to say that the former changefulness is in some way related to the latter changefulness just as a sensation involves movements in a sense-organ and in certain nerves and centers. One need only look backward and review the functions of the organism to appreciate that material movement and activity are universal in them. Protoplasm itself is largely water in order that its essential function, adapted and varied activity, may be carried out. Anabolism and katabolism everywhere go hand in hand and both have as their essence none other than molecular change. Into all the sense-organs is continually pouring a stream of stimuli, which are themselves activity and which produce activity in every portion of the nervous system. Every muscle-fiber is continually in a state of at least tonic contraction, and every viscus of the thorax and the abdomen knows only a relative sort of rest. Thus changeful is the "physical basis" of the mental process, but how it is not here our business to inquire.

Another characteristic of the stream of consciousness is that while thus made up of "parts," yet these more or less merge into each other and form a *unity*. In technical terms consciousness is a continuum. In a similar way an hour is a continuous series of minutes and seconds, and a river, although made up of drops or gallons, is yet a continuum of water flowing as a stream. A little later we shall see something of the nature or at least of the origin of these quasi parts which pass into the continuum of consciousness. As long as life endures the mental process stops no more than does the metabolism of the heart or the chemical activities of the brain, although its intensity and its breadth and depth vary greatly from minute to minute, and become much lessened especially during sleep. Heraclitus of old used to say that a man could bathe in a river only once, for the river in which he bathed the second time was no longer the same. Closer analysis of the stream of consciousness suggests that a person cannot bathe in the same river even once, for even while he is bathing the stream is changing around him. It is the chief purpose of descriptive psychology to make plain the numerous shifting but recurring qualities of this conscious river.

The third characteristic of consciousness of which the introspecting individual is always aware is that its states are invariably referred to a unifying *personality*. Continually there is self-reference, a certainty of a personal identity. It is only in abnormal conditions whose physical "basis" is unknown that the mental process related to any organism loses its identity and splits into two or more personalities. Here is one of the paradoxes which continually remind us of the intricacy of things. Notwithstanding this, however, we may be sure that the mental process of the normal man or woman is always unified by an underlying sense of individuality. The feelings we experience and the thoughts we think get their value for us only as they come directly or indirectly into relation with this personal subjectivity which behind, beneath, and all through this tide of changing experience persists unchanged. By this alone consciousness is made real, kept in range of flesh and blood, made something more than the evanescent shadow of a dream.

This individuality not only experiences the stream of consciousness, but directs it to a greater or a less degree. We cannot only control and force our thoughts into any desired direction under normal conditions, but our feelings are more or less subconsciously determined by the nature of our personalities as developed by our experience. What one sees and takes an interest in is determined by no means wholly by the nature of what his eyes actually see. What we perceive is often to a large extent decided by what is already present in our minds. A lumberman, for example, sees in a forest the size and straightness and number and proportions of the trees. An artist sees in the same trees only their beauty. A trapper sees them as the homes of animals and as sources of firewood. The forester and the botanist find in them chiefly a subject for study. Yet the forest of trees has mostly the same physical properties for all. It is the nature of the perceiving self, as determined largely by its habits or its will, that decides the direction of the consciousness of that individual. We should expect, for example, a clergyman who saw a street-fight to try to stop it in some way, but if a passing pugilist did so we might be somewhat surprised. The nature of the selfness then determines not only the trend of the internal consciousness but the external bodily activity as well.

Besides these three general characteristics of the mental process, we find differences in quality, quantity, and intensity. The qualities we shall soon attempt to discriminate and briefly to describe. An example of quality is painfulness. The quantity of the mental process at any time is what is technically known as the extensity of the experience. As an example, the exposed nerves of four teeth give a more extensive pain than that of one would give. The intensity of consciousness at any one time means the degree of interest which it has for the individual. A severe ache in a tooth is more interesting than a milder one would be.

There is one other general attribute of the total stream of consciousness which must be noted: it has at different times every degree of fulness. The range in this respect is from the most conscious experience (the most intense pain, the most exquisite pleasure, or the deepest thought) down to the vanishing-point of sub-consciousness at the "lower" levels. From the physiological point of view these sub-conscious mental processes merge into protoplasmic forces, especially into nervous impulses.

The Descriptive Aspects of Consciousness.—Introspection of our passing mental experience shows us that it has three dominant aspects that we may denote as feeling, willing, and knowing.

The term aspect used in this sense is theoretically important as well as descriptive. The aspects of consciousness are not parts of it, but rather precisely what the term itself with sufficient clearness indicates. If in every period of adult human consciousness we can discover elements of feeling, willing, and knowing, it is not that these are in any sense separate portions of the conscious stream. At one time one of them may be the most conspicuous and the next moment perhaps another. These three are various ways of looking at the mental process, aspects abstracted for the purposes of scientific description from a continuum which is not objectively separable into different processes. Every temporal portion of consciousness (with exceptions which will be noted later) has all of these three aspects of feeling, willing, and knowing. These phases are mentally abstracted for purposes of description as if they were actually separate.

Feeling.—The word feeling is the psychological term for a class of mental events, and it must not be confused in any way with the term used so variously in common speech—feeling a touch, feeling cold, feeling a pin-prick, etc. These, as we saw in studying the senses, are sensations.

The feelings proper are more complex experiences, some of whose characteristics we shall shortly describe; it is necessary first to learn about feeling in general.

Feeling may be considered the primary or primal aspect of mind. By primal here is meant the most basal, possibly the simplest and the most closely related to the matter of the body. Perhaps besides it was the first aspect of consciousness to develop on the evolution of dead matter into protoplasm. In the new-born infant feeling certainly is a very conspicuous part of the consciousness, far more so than are its knowing functions. In the human fetus (as possibly in the simplest animals) feeling more largely still predominates over knowing and willing. In the human adult it touches the personality more closely than do these other aspects of the mental process.

SENSATION.—We can describe feeling in general best by taking up its elements and observing what mental events compose them. At the basis of feeling, indeed of consciousness itself, undoubtedly are sensations. A sensation may be defined as an abstracted aspect of analyzed consciousness representing the activity of a sense-organ. As to how it represents it we know absolutely nothing. Of all the relations and problems in physiology the precise relation between the material, protoplasmic sense-organ and its centers, and the accompanying consciousness seems the most insoluble. The description of the sense-organs and their actions in a previous chapter have shown how various are these end-organs of the afferent nerves and how numerous are the modes of their activity. Attempts to estimate the number of elementary sensations at the basis of consciousness have been various; as accurate as any other doubtless is that of Titchener:

Eye	30,850	Tendon	1
(Brightness, 700; colors, 150.)		Joint	1
Ear	11,550	Alimentary canal	(?) 3
(Tones, 11,000; noises, 550.)		Blood-vessels	?
Nose	(?) 10,000	Lungs	(?) 1
Tongue	(only?) 4	Sexual organs	1
Skin	3	Ear (static sense)	1
Muscle	1	All organs (pain)	1

These fifty thousand are the different qualities of sensation, but they do not for the most part represent the various intensities of the sensations (the quantity, so to say, of each) and of course not the number or the local signs of the sense-organs which produce them. From one point of view a strong sensation (one of great intensity) is a very different sensation and experience from a weak sensation arising in the same end-organ. For example, while the skin may have only four sorts of sensation (touch-pressure, heat, cold, and pain), it has of course many thousands of end-organs serving these four senses, and the experience coming from each end-organ (as we have seen) may be different from that of every other, especially by that space- or locality-element known as its local sign.

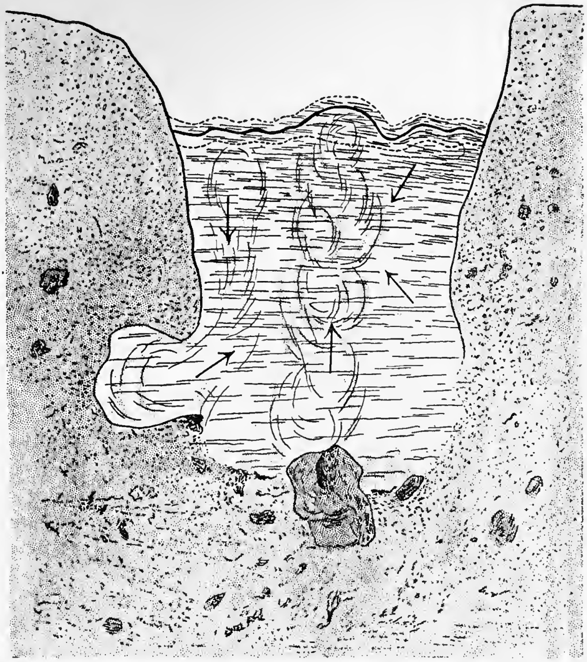
Before we try, however unsuccessfully, to understand how the "product" of the myriad end-organs fuse into the continuum of consciousness, let us look at the nature of a sensation in general from the descriptive standpoint. It is true that a sensation, properly speaking, cannot be described, but it can be marked off from the other aspects of the mental process in a way which amounts more or less to description. Suppose, then, a newly born infant waking from sleep in a room brilliantly lighted by sunlight entering through bright crimson window-shades. For a longer or a shorter period this newborn infant's consciousness we might suppose would be largely a pure sensation of redness. This redness-sensation it is obvious can be described only by reference to similar experience—no mere words could ever make one blind from birth realize what redness is like. To this child whose consciousness as yet had not had time to develop its various latent aspects, the red-sensation would for the time be all-inclusive and it would be essentially a pure unmixed sensation, namely of redness. Now suppose an adult awakening gradually in the same sun-lit room early in the morning after too few hours of sleep. When his eyes opened the sensation of redness would more or less monopolize also his mental process, and his whole consciousness might for a few seconds be only of this one all-pervading redness. Theoretically, then, even an adult may have sensations unmixed with the other aspects of mind, "pure" sensations. In fact, however, pure sensations in the adult are both rare and very brief. Thus, in the example cited, within a few seconds other conscious elements would begin to fuse into the sensation of redness, elements of knowing and of willing. The man would begin almost at once to think and to intend or to wish or to fear or to enjoy or to do something else among the numerous possible processes of his mental action. The flood of crimson sunlight would continue to pervade his experience, but previous experiences with all their multiform traces and activities would have already begun to arise in the man's memory and to take possession of his mind. He would then no longer experience a pure sensation in his mind, but rather the usual complex, variously composed of feeling-elements more or less mixed with elements of cognition and of will. Thus, then, we see what sensation as such is: it is the consciousness corresponding to the activity of one sort of sensory end-organ. Sometimes only one of these end-organs may be concerned in a sensation, but often there are thousands, as in the example given. The number matters not so long as the resulting consciousness is a strictly homogeneous experience of the sort now sufficiently suggested.

Fusion is one of the most basal operations of the mental process. Its simplest form brings about the cohesion of the sensory elements (really represented by sense-organ elements) into actual sensations which, for the naïve multitude, are themselves elementary. The trained musician, the tea-taster, the skilled color-mixer, whether artist or artisan, the introspective psychologist, all and many others, have more or less the means of reducing perhaps even to their lowest, that is organic, terms, the sensory complexes given somehow wholly or in part through the sensory end-organs. One has to think of this process of fusion as almost the chief underlying activity of consciousness. As to its means, nothing is known. We see anatomically discrete sense-organs and other protoplasmic units—we experience in ourselves the products of their fusion. No present facts or theories satisfactorily bridge this gap in our understanding of our consciousness. Unsupported hypothesis is not enough in science, else we might perhaps attempt a solution of the problem by supposing that it is the general body-protoplasm which represents consciousness rather than the nervous system (including its disparate sense-organs) alone.

The various degrees of activity of the sense-organs in the body imply many degrees in the intensity of the sensations they represent. Each sense has a range of intensities from the threshold to that at which no further increase of sensation is possible and the sense-organ is injured. But what of the effects produced by stimuli below the threshold-intensity? In the case of a frog's gastrocnemius muscle, it will be seen, on reference to the laboratory experiments (No. 45) in the Appendix, that there exists a summation in stimuli which singly are inadequate to produce a contraction. In other words, if the threshold-stimulus of a muscle be found and then stimuli of less intensity be repeatedly thrown into the muscle a few seconds apart, contraction finally occurs. The slight stimuli do then influence the muscle and leave traces in it which summate and after a while reach the threshold-value and occasion a contraction. One sees the same thing in the sensory realm. It is, for example, an almost universal human habit to knock repeatedly rather than once on a door when one would attract the attention of those within, in part on this same principle of summation. Stimuli, then, below the threshold do affect the organism's protoplasm, and leave some sort of an impression more or less persistent. This fact, as we have seen, is easily proved by actual experiment, and so proved becomes the basis of an important principle in the relations of the stimulus to the reaction both psychical and somatic. It leads to an understanding, in a way, of the far-reaching phenomena of the "sub-conscious" aspects of the mental process.

In a text-book of physiology we need not be concerned even for a moment with that interesting but futile scholastic doubt whether a sensation, an aspect of consciousness, can be said ever to be unconscious. We cut the doubt promptly here, as in the chapter on the senses, by the fourfold assertion that it is a matter only of terminology; that "sensation" is not in all cases an accurate term, in so far as it usually implies conscious experience; that there are all degrees of consciousness, the lesser degrees merging into (neural?) influences which singly have no consciousness capable of being felt; and finally that these subconscious influences constitute the place, the time, and the means wherein the mental process fuses into the other processes which physiology describes. What these influences or impulses or conditions of activity are and where they originate we do not know completely. We think we know that the neural maze is their pathway through the body. We suppose that some of them, under various conditions of intensity or of other requisites, are always risen into what we call full consciousness, and that the others are meanwhile concerned in carrying on the vastly complex processes of the neuro-myo-glandular mechanism of the body. These former and these latter combine to constitute the "bulk" or "mass" or "substance" of the mental process as physiology understands it, while the sum of the latter influences alone constitute what is known as subconsciousness. In general terms our total consciousness during normal sleep tends to be of the subconscious sort, although apparently nearly always, perhaps always, blended with attentive consciousness also. We have to think subconsciousness as made up, then, of "sensations" (and other mental aspects) which do not at the time occupy the conscious *attention* of the individual, and this might serve as a rude definition of subconsciousness. (For the other subconscious aspects of the mental process see below, under Willing and Knowing.) The description of

Fig. 242



A metaphorical cross-section of the "stream of consciousness." The shifting, free attentive consciousness of the individual may be aware of nearly anything on the earth below or in the heavens above. Beneath it is the mass of varied sensation, and this below merges into subconscious mental processes, and these in turn into the neural and general vital energies of the body-protoplasm. The obstructions and personal peculiarities of the body affect markedly all aspects of consciousness, as these are the structures by which the mental process is supported. The dependence of the conscious stream on the integrity of the protoplasm by which it is guided is peculiarly close.

the subconscious is, however, as difficult as its physiology is important. E. von Hartmann has described it once for all in his weighty but oppressive "Philosophy of the Unconscious," while numerous students of abnormal mind, of the phenomena of hypnosis, of suggestion, and of sleep, of multiple personality, etc., add continually to the knowledge of its influence, and (but much more slowly) to that of its more precise nature in physiological terms.

The relations of the subconscious aspects of mind are perhaps best illustrated by the admirable, if trite, simile of a stream: Let the water of a deep and rapid river, then, represent the sensory mass of consciousness, its rocky bed the basal organism, its surface the thin and changing focus of attentive consciousness, and the manifold and active mass below the subconscious parts of the mental process. These lower portions are not readily appreciated, for they flow deeply and more or less darkly beneath the surface, down near their unexplained channels in the protoplasm. On these lower strata of the stream the upper layers rest. It is only the surface which is fully realized at any moment. Any disturbance below (in the subconscious) produces changes above, while, on the contrary, any commotion of the surface (conscious) portion of the river may influence only to a less degree and less easily the depths beneath—especially little those which are deepest and closest to the bodily functioning. Obstructions in the minor channels in this river-bottom (say an inflamed nerve) produce upheavals not only in the mass (the subconsciousness), but also on the surface (in full consciousness). This stream never stops so long as its banks are present to direct and continue its movements, but its foggy surface may at times be all but invisible (as in coma), although perhaps always in existence. With the ultimate destination of the river physiology is not concerned any more than with its primal origin. It is enough now if we realize that its relations both to the attentive consciousness above and to the bodily substratum below are most intimate—even if still undefined.

THE FEELINGS AND EMOTIONS.—As we have just seen, in the adult mental process pure sensations, untinged and unexpanded by other aspects of mind, scarcely exist as such. What we experience mostly are sensations, feelings, volitions, and cognitions fused together. Feelings in one sense and figuratively speaking are largely made out of sensations. The canvas and the richly varied pigments of a beautiful painting are somewhat like the sensations; the picture itself, significant and valuable, tingling with life, is like the feeling itself. In one sense, then, the feeling is made up out of the sensations, but always it is immensely more, even as the beautiful picture is greatly more than a yard of canvas and an ounce or two of paint. These additional affective elements come from the fusion and the interactions which take place between the parts of the mental function.

Feeling in general has at least three characteristics in addition to its basis found in the muscular, joint, glandular, and visceral sensations underlying and, in a sense, causing it. These three qualities are some degree of excitement; the directing of the conscious attention toward the things causing the feeling (termed the object); and a tone of pleasantness or of unpleasantness. Another element of feeling, a necessary consesequence of the others named, is an increased self-reference. The excitement means in physiological terms that the activity has increased, and the element of attention directed toward the feeling's object implies only that a new relation has been set up between some object or condition and the mental process as a whole. It is the tone of pleasantness or of unpleasantness and the various combinations of bodily sensations which are the distinctive marks of the feelings and emotions (if we leave out of our consideration now the bodily movements which actuate the sensations). These certainly are the two elements of a feeling most conspicuous to the person at the time, although either element may be always inappreciable in certain feelings and when of low intensity in many feelings. The tone of pleasantness or of unpleasantness (as the case may be) of a feeling or emotion, however, may be of almost zero intensity. Who could say whether even a violent emotion of anger or of surprise, for example, were pleasant or unpleasant?

The characteristic sensation-complex (and the affective tone) of the feeling or emotion are usually sufficiently well-marked to be describable. We find developed in man certain fixed sets of bodily "expressive" reactions or movements each of which is more or less characteristic of some emotion. Each expression is accompanied by the particular set of sensations which these movements and strains in the muscles, joints, skin, and glands would inevitably produce in them through the sense-organs (James). On the other hand, most of the feelings and emotions are either distinctly pleasant or unpleasant, and it is by this criterion that they are usually classified. The typical pleasant emotion is joy, while a typical unpleasant one is sorrow or fear. If one observes intelligent dogs, apes, savages, or young children while experiencing such emotions as these it will be obvious what the "expression" of each of these emotions is, and it will be seen that each tends to be physiologically alike in all similar animals. In civilized and cultured men and women, however, these characteristic "expressions" have been hereditarily repressed, and the latter are not to be found under normal conditions in these men therefore in their physiological purity. Even in such constrained animals, however, we can see that joy tends to general expansion and is enacted by the extensor muscles much more than by the flexors. Sorrow, on the contrary, is restricted and condensative, and "expresses" itself more largely by the flexor muscles of the body. The smile and laugh are the characteristic expression of joy, but, on the other hand, tears flow both from sorrow and from an extreme degree of mirth. Technically, this term the "expression" of an emotion is misleading, for the bodily actions are at least as primary as the sensation-feelings accompanying them.

As for the various different feeling-experiences and sets of actions, the feelings and emotions, they are numberless and unclassifiable. To say that they are of four or five general sorts, such as sensuous, intellectual, moral, esthetic, is only to erect wholly artificial barriers between a multitude of feelings many of which have the characteristics of two or even of all of these. The student of ethnology will realize how closely allied at their bases are some of the feelings, for example, of religion and of sex, and the dividing line between the esthetic and the sensuous feelings is likewise quite indefinite. The feelings have not yet been described because so numerous, so complex, and in some cases so indefinite. A few of the stronger and more elaborate of the emotions, such as joy, anger, grief, hate, shame, surprise, contempt, have very well-defined phenomena, and descriptions of some of these are to be found in the technical literature and monographs. The majority of the lesser emotions and the feelings into which they merge have no such marked characters, bodily and mental, and remain for physiology something like a chaos of ill-defined activities. One principle, however, seems common to them all: each tends to involve actions which either by the nerves or the circulation or both often implicates every portion of the body. The bodily aspect of a feeling or an emotion, then, is not a matter of activity in a few muscles or a few nerves. Changes in blood-pressure, diffusion in the central nervous system, local vaso-motions, affections of the alimentary, respiratory, muscular, or glandular systems, involve practically the whole unified body more or less in every feeling or emotion of fair intensity. The recent work with the reflecting galvanometer (Morton Prince) shows how intimately related are the electrical resistance of the organism and affective excitement even of the lowest degrees. Such physical facts open up wide regions for the study of the relations of mind and body. (See also below, p. 418.)

Willing.—The second or willing aspect of the mental function is denoted often by the synonymous terms volition, conation, or action. From the purely biological point of view the will of any animal is basally its vital principle. Its will to live is the sum of its exceedingly complex vital processes, until by evolution this somatic phase of the living animal merges into the psychological aspects of the will. We can no more draw a sharply dividing line between the psychological will and the physiological life-movements than we can between a subconscious sensation and the nervous impulses, etc., related to it. Inasmuch, however, as the will of an animal, man for example, is describable only through some sort of movement, it is customary in modern times to discuss the will, as also the emotions, in terms of the actions of the individual.

From this point of view we speak of four aspects of volition. The first of these is the *reflex movement.* Underlying this kind of activity there is a mass of nervous influences for each one of the countless different reflex actions, while directing this mass of sensori-motor influences is the inevitable motor idea of the movement. This has already been described under the head of kinesthesia in the two preceding chapters, and consists of the traces left in the motor portions of the brain by the numberless active and passive movements already made by the animal. In the case of this reflex kind of willing the motor idea is subconscious: either practically unconscious or of such a nature as to occupy some portion of the attention of the individual. This variety or phase of volition is inherited from our ancestors and constitutes primarily the chief part of the mental (sensori-motor) inheritance of the infant.

The second sort of action thought of as will is the *habitual voluntary movement.* If we take the closure of the eyelid at the sudden approach of an object as a typical reflex volition, a good illustration of an habitual voluntary movement would be the act of walking as it is performed by the adult. This process is a reflex movement with conspicuous conscious voluntary aspects. Underlying it is the same mass of nervous influences present in reflex movement. In this case, however, these nervous influences are in larger part sensory. By this means they keep the conscious individual so fully aware of where he is going and what he is walking on that the process may be accurately directed and controlled. In addition, then, to the mass of nervous influences and sensory impulses (the motor idea) in habitual voluntary movement, there are elements of deliberate attention more or less conscious. Numberless examples of these habitual voluntary movements will readily occur to the reader, for most of the every-day routine actions involving cross-striated muscle are in this class. They are all essentially voluntary movements which have become sufficiently reflex to require less conscious attention than formerly. (See Expt. 88 in the Appendix.)

The third sort of will given us in terms of actions are *new voluntary movements.* Were the student of medicine to undertake to artistically engrave an intricate monogram on a silver vase, he would have in his experience a striking illustration of a new voluntary movement. If we analyze this experience physiologically, we shall find in it the same mass of nervous influences and sensory impulses that were present in the habitual voluntary movement. In the present case, however, the nervous influences are almost all accompanied by clear kinesthetic sensations. Besides this, there is required a large degree of deliberate attention to the movements and strains of the arms and trunk, and in addition to this a continually exerted choice that the movements shall continue in just the right way. In psychological terms we have here the motor idea coming into the brain from these exclusively voluntary muscles plus forced and carefully directed attention plus deliberate choice to continue. All of these, it will be observed, are highly conscious processes. It is only in this third sort of volition that the aspects of will as commonly known to the average man become conspicuous. In such movements as these, made by the motor nerve-centers and the cross-striated muscle often under great stress of effort and continued only by great fatigue and even pain, every man would recognize the exertion of his will. The other two aspects of will which we have just described are volitions from a somewhat more biological point of view.

The fourth and last sort of will which we need to briefly describe is that which may be best perhaps called *choice,* or free-choice decision. It is almost wholly about this aspect of willing that our philosophical ancestors talked and wrote so much in the century before the last. In those days the discussions (mostly with a religious bearing) concerning volition were almost wholly arguments as to the "freedom" of the will, as to whether the individual was free to determine alternatives for himself independently of all else. Into this discussion, still undecided from the biological point of view, we have no idea of going here more than to suggest that every normal personality believes unalterably, whatever he may say and argue, that his will is free. The whole system of human justice rests upon this intuitive certainty. Physiologically, however, it is very difficult to define any basis for this sort of willing. There may be a bodily movement present or apparently there may be none in any particular determination of choice. When a muscular movement is present, there are motor ideas and motor nerve-impulses accompanying it. These perhaps would not actually contract the muscles but only change their tonus. When the choice is wholly a matter of thought, the motor side of the process is probably located chiefly in the mechanism of speech (see pages 394 and 420).

The normal willing-process in general, comprising a stimulus and a motor reaction thereto, requires an appreciable and easily measurable period of time. As any one familiar with the processes of the complicated neuro-muscular system would expect, the time differs for every combination of events. Thus, if electrical apparatus be arranged so that some part of the skin is to be touched and the reactor is to press an electrical key as soon as he can after he feels the touch (the type of all determinations of reaction-time), the time is longer when it is the toe that is touched than when it is the ear. It is shorter to pressure than to light, but longer to sound than to pressure. If the reactor has to decide which of two possible sorts of stimuli it is (as for example red or blue) before reacting, the time is longer yet. It is longer to weak stimuli than to strong; becomes shorter by practice; is longer in dull persons than in bright persons, etc. By this general means many of the relations and processes of mental function have been studied and thousands of exact time-measurements made with the chronoscope, measuring accurately to the thousandth of a second. Some individuals are accurate and quick, some accurate and slow, some inaccurate and quick, and some inaccurate and slow. Some persons recognize the stimuli quickly but react slowly, and others are quick of muscle but slow of sense. In general terms the smaller a muscle the more quickly it reacts. Habit, however, has more to do with the shortness of the reaction-time than anything else: for example, one reacts sooner with the index finger than with the fifth. It is not difficult by practice (habit) to make a voluntary movement practically automatic by continued repetition under constant conditions; the reaction-time then is also much shortened.

On the average a person touched on the hand can move his finger in about 0.110 second; if the stimulus be received through the eyes, in about 0.180 second; and if through the ears, in about 0.120 second. If the reactor be thinking of the stimulus rather than concentrating his attention on the movement to be made, the reaction to light is about 0.270 second (instead of 0.180 second). This indicates the extent to which the inertia of muscle (and nerve?) may be reduced by holding the organ in the utmost tonic readiness. If one has to discriminate between colors in the stimulus, the average reaction-time is over 0.300 second, while recognition of a printed letter or short word requires 0.020 second longer. It is found that in general a quantitative choice or judgment and choice (between two stimuli, that is, of the same sort but different intensities) is about 0.060 second. When it has become automatic the discrimination between two colors may require no more than 0.011 second, quality-difference being more quickly perceived than quantity-difference.

These reactions, it will have been observed, are under conditions which represent the ordinary will-actions of every-day life reduced for exact measurement to their very lowest terms. It has been objected (as by Cattell) that experiments on fragments of actual will-process so small as these have comparatively little practical use, however important they may be theoretically. The movements of every-day life are immensely complicated in every way, and fuse together so as to make a medley of activities in muscle and nerve-center far beyond our present power of comprehension or of measurement. Our consciousness derived from them is at least correspondingly complex.

Habit and Instinct.—An instinct is essentially an hereditary impulsive and unstudied habit concerned in the biological interests of the individual or of the race. It is a complex variety of habit which needs but little separate discussion here especially because the many varied instinctive activities have in them only a minimum of attentive consciousness. The mechanism by which the instincts are so carefully bequeathed from parent to offspring century after century is part of the vital faculty hidden in the body-protoplasm. Our search must be briefly into the nature of habit, in which instinct partakes.

Habit is a motion of very general significance in nearly all aspects of the world. It means in the widest usage the adaptation of a material to the activities of that material, and is therefore by no means confined to organisms. Rain-water running down a hill-side gradually forms grooves in the soil and leads to the formation of habitual water-courses. Wild animals make paths through the forest to the ponds and springs. Complicated machines run much better after a certain amount of use has adapted the adjacent moving parts to each other and into a habit of normal usage. In protoplasm, probably the most complex of substances, this universal adaptation is more complicated and consists not only of action but of reaction not possible in inorganic machines. Owing to the extreme plasticity of the material, organisms can work in a host of different ways, each making an impression on the mechanism in proportion to the number, the frequency, and the vigor of the activities concerned. Thus, right-handedness unfortunately becomes a settled and almost unbreakable habit in most persons' organisms before five years have passed and simply because during the development of voluntary movement the use of the left arm is neglected. What the traces are which determine the habitual usage in the body remains to be discovered. We have to think of them, however, as actual traces in the protoplasm especially of the nervous system, but perhaps in part also of the muscles and other tissues. This is witnessed by the larger size of the whole right side in right-handed persons. The logical limit of this process of habituation is to be seen in the so-called "automatic" organs: glandular epithelium, the heart, the ureters, the musculature of the intestines, etc. The lesser degrees of it are known to all in the thousand physiological minor habits of every-day life.

Of essentially the same nature, doubtless, are the so-called mental habits of feeling, of willing, and of thinking.

The function of habit is almost obvious. By means of this continually greater ease in the performance of an action, "mental" or "bodily," those movements which necessarily frequently recur become more and more reflex or automatic. In this way the voluntary aspects of the brain are relieved of directing a host of mechanical operations that are biologically necessary but which would needlessly consume a large amount of the time and attention "of the cortex." The central nervous system is thus left free to learn new things, to progress in capability, and to assist in the development of civilization and of culture.

Knowing.—The last of the three chief aspects of the mental process is the faculty of knowing objects, qualities, relations, and so on, outside or inside the organism. Synonyms for this process are cognition, ideation, and intellection. In the most general sense this aspect of the stream of consciousness may be called the formation of ideas. An idea may be roughly defined as a mental image of any object whatever outside or inside the mind. In this definition the expression "object" is used in the very general sense which includes not only the so-called material things but the qualities and relations of a purely abstract nature.

The physical correspondents of this cognitive process are narrower in bodily range than are those of feeling and of willing. In general terms we may denote them as chiefly the movements and reactions, nervous and muscular, which are employed in any mode of expressing language. The physical basis of cognition, in other words, is mainly the neuromuscular mechanism of psychical, spoken, written, pictured, and manual speech.

Analysis of the knowing aspect of mind gives us several steps in a process which is continually some sort of fusion. We may distinguish the fundamental process of sensation, and upon that as a basis "the mind" conducts the various operations of perception, conception, understanding, and reason. The means by which this very complicated fusion accomplishes the interaction and development of the original sensation-mass is hidden from us in the largely unknown relations of the nerve-paths especially of the brain. That these fuse in some way so as to elaborate the higher products of the knowing faculty, there is little doubt.

The things which are known in cognition are of two general sorts: things "outside" and those "inside" the mind. A chair, for example, which we look at standing before us and think of, is obviously an object outside the mind, while if we then close our eyes and observe our memory-image of the chair just seen we are evidently cognizing an object "inside" our consciousness. Further consideration of the former of these processes, however, shows us that when we looked at the chair what we really experienced was not a chair but a sensation of seeing, and that what we thought of in both cases was a curious sort of mental representation of a chair. Thus, we see that in both cases in reality what we know is "inside" the mind, although we appear clearly enough to see the chair itself or its mental representative at will. This is the view of the thoughtless, the naïve realism of the mass of mankind, and the view also, we may see, assumed to be the better for physiological purposes though all the while believed in reality to be a false view and one which is philosophically misleading. Thus, we may go on and describe cognition as a process which knows (at different times) objects both outside the mind and inside the mind. It will appear shortly that without the inside-the-mind-object process the outside-the-mind-object process would give us no knowledge worthy of the name. The sensations might enter the mind from objects, but without the internal process they would be of little or no use as knowledge. We might then have knowledge of, but not knowledge about, the objects.

First, then, as to the process of knowing objects outside the passing current of consciousness. To make this clear we shall have to consider sensation, perception, and conception. These are the different aspects and degrees of this fusion-process which is in itself single and devoted to the sole end of making the conscious animal (man in this case) familiar as may be with the parts of his environment. It will be seen that on this process almost the whole fabric of language and so of civilization itself depends.

Sensation has already been discussed sufficiently for our physiological purpose. We have seen how various are the sorts and shades of the sensations; that they are the simplest elements of consciousness, coming closest to the physical forces of the environment and to the physical protoplasmic basis of mind; that they represent the environment to the individual only to a slight extent, being largely subjective in nature; that they fuse together in large numbers for the most part so as to be indistinguishable as units; that they are hardly ever experienced in their pure state, being always mixed with the other mental aspects (feeling and will) in greater or less proportions; and that it is proper to consider that the mass, so to say, of the sensation-stuff constitutes the subconscious part of the mental process, close "down" among the nervous impulses and possibly the other protoplasmic activities. The sensations represent the energy of the environment acting against the energy of the animal, and it is on this account perhaps that they are so little objective, that as sensations merely they tell so little about the qualities of objects.

Perception.—Sensation is essentially subjective in nature, while perception is inherently objective. Let us revert to our former illustration of the crimson light we used in discussing sensations (page 405). This might flood our consciousness as a sensation of redness but technically would be perceived only when we had awakened enough to realize it as an objective quality or thing in the objective world affecting ourselves as subjects. This objectivity of perception is one of the marvels of consciousness. To the thoroughly naïve mind, it is the basal property of the knowing "faculty." Even in thought in which the subject knows objects within the mind the objectivity of consciousness is at least as conspicuous a quality as is its subjectivity. It is one of the powers of the mental process that it can perceive objects outside itself as well as parts of itself.

Besides the objectivity of perception its leading characteristic perhaps is its process of synthesis or fusion. In our study of the sense-organs a conspicuous fact always was the smallness and the multitude of the individual sense-organs (considering the rods, cones, and fibers of the membrana basilaris separate organs). Not only are the sensations from these put together by the mental process in perception, but also the unlike sensations from different classes of sense-organs. When we perceive a flower we may perceive not only color and form but odor and perhaps its softness and coldness and stickiness and taste of sweetness. By all these means and more at once we may obtain a percept, as it is called, of a lily. Various sorts of sensations have been thereby combined into a representation in our minds of a particular lily. To explain this marvellous process is at present quite beyond us, unless indeed we be content to suppose that it is accomplished by the close association or fusion of sensory impulses in the brain.

Conception.—If our knowing "faculties" went no farther and were no more complex than perception, civilization would never have evolved even as far as it has. Speech would have been undreamed of, as it probably is still among the brutes. Perception in some way connects consciousness with particular, individual objects or groups of objects, thus giving us a mental image of them. Conception goes much farther. It picks out the characteristic qualities and relations of objects, combines and fuses them, and leaves us possessed of a general idea of the object or of its qualities and relations by which a similar one can again be known.

The concept is then the product given us by the process conception, the nature of which is best indicated by an example which will bring out how it differs from perception. Perhaps we can do no better than to use our old illustration of a black-painted wooden chair standing before us but never perceived by us before. How do we know this chair? Only through our senses, certainly. Only because the color of the object differs from that of its background more or less, vision shows us its shape and size and (indirectly perhaps) that it occupies space and is not a painted image on a screen. This last is inference merely, for a sufficiently cunning artist might paint it on a screen so as to quite deceive us. If we go up and touch the chair we shall find it hard; if we saw off one of its legs we shall see that it is made of wood, screws, etc., of certain forms and colors; if we examine this wood with a microscope we shall see its structure; if we lift the chair we shall find it of a certain weight, etc. It is only simple facts like these that perception by the senses gives us, although the facts as to an object may be numerous to almost any conceivable extent. We all really know much more about this black wooden object, however, than our perception could ever give us. In the first place we know what a chair is, an object to sit on, and that it is called in English a "chair;" we know perhaps how it was made, about how much it cost, how much it is worth, that it would burn, float if thrown into a pond, hurt us if we ran against it, be too low for a young child at table, etc. Furthermore, more or less unconsciously, perhaps, we compare it with other chairs in some or many of the respects which pertain to chairs. We are perceiving only one chair, this one, but we have in mind all the time more or less unconsciously many of the chairs we have seen, bought, used, broken, heard of, read of, and told about. In short, we all have in our minds a *general idea,* notion, concept, expressed in English print and speech by the symbolic characters chair. The parts of this concept chair in the minds of each are many, and they were derived from very many sources. Each person's concept of chair differs theoretically from that of every other according to the percepts and the concepts which have united and fused together to form each one's concept. If one of us is an artist, he knows chair-concept in one way; if one is a furniture-dealer, in another way; if one be a lover of ease, in another way; if one be cold for want of fuel, possibly in still another way; and so on without end. Each of us, then, has a notion of chair in his mind provided he ever saw one or a picture of one, or heard of one, or read of one before. Yet each of our chair-concepts is different from every other.

This then is the process of conception: the abstraction of the qualities, characteristics, relations, categories, uses, etc., of objects, real or ideal, and the combination of these qualities, relations, etc., into general notions. Only because of "the divine gift of speech" was this abstraction and conceptualization possible—man gives a name to a thing, and a concept of it becomes forthwith attainable for all men's use. In the name of an object is epitomized for us the key by which we can recall the details, qualities, relations, etc., which for each of us make up the concept of that object.

Besides concepts of objects there are concepts of every sort of quality, relation, use, etc. These fused together make up our knowledge of life. Each of us has in his mental process not only concepts of quality, but concepts of relation of innumerable sorts, of shape, weight, hardness, porosity, value, perceptibility, inflammability, salability, usefulness, space, causality, reality, infinity, etc. All these and many other sorts of concept have united to partake in our knowledge of the world and all within and around it and above it. Our knowledge is in terms of concepts and not in terms of percepts. A farm-hand, for example, sees more blades of grass in a day of haying than a city-child might see in its lifetime, yet if the child were to study botany or vegetal physiology a week she might know more about blades of grass than the farmer would learn in fifty years of raising and curing them. The farmer would have acquired an enormous perceptual knowledge of blades of grass, and the student some conceptual knowledge about blades of grass. For almost every purpose the knowledge about is worth more than the knowledge of.

UNDERSTANDING can be described only in the same way as we have suggested the fusion-process in conception. This indescribable multitude of concepts which the human adult of average intelligence has somehow stored in his brain combine and interact and develop what we call the understanding of things. As the material of this marvellous process, every man has concepts of a multitude of different kinds of objects ranging from his collar-button to the sublimest notions of Ultimate Reality. He has stored away in his nerve-paths concepts almost without end. These in some way fuse together in his mind and brain and give him an understanding of the facts and principles on which our human life is conducted. (See also Expt. 88 in the Appendix.)

THE REASON.—A very perfect synonym of the term reason is the expression common sense. It means more than a large store of varied concepts, and much more even than understanding, for it indicates our capability of so uniting the elements of the understanding as to produce new aspects of things and to develop new truths about the relations of objects. In no one of the human mental faculties do the mass of men differ more than in their gifts of reason. Many have good understandings of essential principles who seldom combine their energies in new ways so as to produce new results. This reasoning process is the highest and most advanced of the human mental functions.

The physical basis of the understanding and the reason is to be sought in the same process of neural fusion which we have seen everywhere present in describing the stream of consciousness. The products of the understanding, the multitude of concepts, and the percepts interact to produce mental products which are entirely new, of large value in the conduct of personal and social life and in the advancement of the world.

The Relations of Body and Mind.—We have now suggested in a very brief and inadequate way some of the facts which can be observed on introspection as to the stream of consciousness of any normal human individual. As has been sufficiently emphasized, this stream is a process and in no sense a substance. The other chapters of the book describe in somewhat more detail the bodily processes, the stream of material movements. These last are no more substantial than the others, although they continually have reference to something that we call the body which appears to us to be substantial. The mental process is a series of movements in consciousness. The bodily process is no less a series of movements in "matter." Our next inquiry very briefly refers to the relations between these two series of movements which continue as long as life endures. We shall keep as far as possible from the ultimate metaphysical relation of these two series, for our entire object is to point out some of the almost obvious facts of their relationship.

Before doing that, however, we may merely mention some of the theories of this association. These are of three sorts, two of which are monistic theories and one dualistic at least for scientific purposes. The theory of pure idealism maintains that the conscious series is the real one and that in some incomprehensible way the bodily series is but an aspect of consciousness. The opposed hypothesis, now clearly given up by philosophy as a living belief, is the materialistic point of view, namely, that the conscious process is only an epiphenomenon of the bodily life, the product of the activity of protoplasm. The dualistic theory of the relations of body and mind supposes, at least for scientific purposes, that there are two kinds of series running along always just side by side but of essentially different natures. When these two series are postulated as entirely independent of each other, we have the theory of psychophysical parallelism. When they are assumed to be continually interacting, we have the theory of interaction.

Some biologists have supposed that only man was conscious, others that the mental process has its basis only in the nervous system, and others still that all protoplasm has consciousness as part of its life. If, furthermore, there be a few who suppose that consciousness is attached to the whole creation, it is no affair of ours in this connection, but concerns rather the speculations of philosophy.

We may perhaps best suggest a few of the most obvious relationships of mind and body in addition to those already intimated above, if we take up in turn the three aspects of the mental process, feeling, willing, and knowing. Far from attempting to say how mind and body are related, we only mention some of the instances in which a relation is especially apparent.

In the aspect of feeling, willing, and knowing which we call sensation it is clear in what way the bodily mechanism is concerned. In the chapter before the last we studied the sense-organs. We saw that in every case physical force of some sort impinges on these thousands of sense-organs on the surface and in the interior of the body, and that the nervous impulses actuated by these movements in the afferent end-organs go as influences into the central nervous system. In every case, moreover, whether we can define it accurately or not, such impacts are followed by reactions in the central nervous system and efferent nerve-influences stream outward. There is little doubt at the present time that this complicated and multifarious maze of nerve-impulses going and coming everywhere through the body, forms the "basis" of the mental process. Some of these nervous influences are probably directly and intensely conscious to the individual, but of the others he knows nothing directly. Inasmuch as sensation (based on these influences) is a conspicuous part in almost every mental process, we have here a chief respect in which the body and the mind are related.

In the mental process known as feeling and emotion we have, as it were, summarized for us this conspicuous mass of afferent and efferent nerve-impulses representing much of the stream of consciousness. As we saw in discussing these aspects of mind, every well-defined feeling and every emotion has as an essential part of itself a complex of movements within the range of the efferent nerve-impulses. These are largely muscular contractions and strains and changes of tone, but they are in part also innervations of epithelium. Preceding all these we have to suppose a somewhat corresponding multitude of afferent nerve-impulses coming from sense-organs or perhaps only from portions of the brain or the spinal cord. Altogether these represent every portion of the feeling aspect of consciousness through bodily movements and strains, either molar or molecular. These movements and impulses it is the business of psychology to define and describe much more in detail than has yet been done save in the case of three or four emotions.

In the phase of consciousness which we call volition the bodily accompaniments may be no less universal than in feeling. Here too are concerned the multitude of afferent impulses from the sense-organs which determine especially the reflex aspects of will, while the other side of the nervous arc is concerned with the vegetative musculature, although it may involve any muscle in the body. The actions which are classed physiologically as voluntary or deliberate probably lack these afferent impulses in some degree, and from the fusing process perhaps in the cortex of the brain impulses pass downward which actuate the cross-striated muscles as well as those of the smooth variety. The accompaniments of the willing process are physiologically of two phases, actuating and inhibitory, but these alike doubtless involve nerve-currents passing to or from nerve-centers. In the determination of choice we can point out the least of bodily concomitance. Morat supposes that there is a continual circulation of nerve-currents in the cortex, and that these in some way accumulate force which the individual uses in typically voluntary movements.

In cognition the bodily accompaniments are probably as before the sensation-mass represented by almost universal nerve-impulses. Besides these there may be an ill-understood process of fusion in the intricate maze of the cerebral paths. Besides this general relationship, however, the entire mechanism of speech represents the intellectual functions. When a man thinks clearly, he thinks only in terms of words, usually either spoken or written. When a subject in the laboratory is asked to pick out from one hundred the ten chance ink-blots most like a certain one shown to him, he cannot do so ordinarily without having a clear notion of the similarities in verbal terms in his mind. When one thinks, it is likely that the brain sends out the same impulses that it would send out to the muscles if these words were spoken. The intellect, moreover, does not develop normally if speech of every kind is by any means prevented. In general, then, ideation is impossible without the kinesthetic impulses and motor-innervations which form this physiological basis. Many of these innervations are subconscious, but they may not less effect the mind on that account.

If there is a speech-center, then, in the brain, it is not because the intellectual processes involve only this small area of the brain, but because some directing knot of neurones is necessary here as elsewhere. Apparently all the centers, nerve-paths, and muscles concerned in speaking, writing, drawing, or otherwise representing ideas as concepts constitute the special physical basis of cognition. (See the discussion of speech in the latter part of the chapter on the Muscles, page 394.)

Jennings' work on the mental process of infusoria is of fundamental value in the theory of the relation of body and mind.

MEMORY is the faculty by which organisms retain their experiences. As we have already noted, it is the basis on which habits are formed, and in general terms mental and bodily processes are inconceivable without it. Corresponding with memory must be traces of some sort in the body-protoplasm, but of the nature of these records no one as yet has the slightest notion. We know only certain of the laws which appear to underlie the function in the organism.

Almost more than any other attribute of mind, memory is a natural gift, and it varies greatly in its perfection in different individuals. A good memory is a true gift of fortune for it ordinarily does as much as any other thing to bring success in life, since he who has it possesses a double and quadruple store of percepts and of concepts at his instant command. This is the more important because it appears that the memory is little capable of true development. One may acquire the habit of trying to remember and thus practically enlarge to some extent his memorizing powers, but observation no less than actual experiment in the laboratories shows that the grasp and range of this recording and recalling faculty can be little developed by any known means. We have to look especially in the nervous system for the innate difference in memories, and it may be surmised to have its basis in some unknown plasticity and tenacity of protoplasm especially of the neural variety: "wax to receive and marble to retain."

Sleep is another condition quite as evidently physiological as psychological. From either view-point there are many things about it still unknown and the subject therefore of dispute. Still, much that is definite about its psychophysiology is fairly well settled. In ancient times the mystery of sleep found expression in some of the most striking suppositions and superstitions of all anthropology.

The reason for sleep lies obviously in the fact that all finite, material things wear out, and to continue acting require renewal. Entirely deprived of sleep a person would live only about a week—perhaps not so long. A few organs which work intermittently, for example the heart, rest amply between actions, but the majority work continuously, as it were, for longer periods and demand corresponding periods of rest in order that the wear and tear may be repaired and that anabolism may restock the tissue with efficient energies. For this repair in the muscles or in the glands sleep is not required, for these refit themselves for work by simple cessation of activity. It is the neural tissues apparently that demand the peculiar conditions of sleep for the recovery of their coordinating energies. Meanwhile, however, every portion of the body rests more or less completely, for quiet in the nervous system normally implies repose in the other tissues. Did we know the nature of the nervous impulse and of nerve-katabolism generally, explanation of sleep would probably be forthcoming, or so far at least as its metabolic accompaniments are concerned.

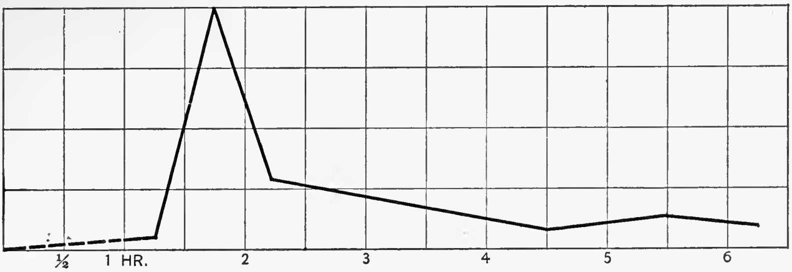
The metabolism of the whole body is doubtless lessened during sleep. All researchers into respiration, for example, find the oxygen-carbon-dioxide exchange decreased (according to Johansson, 31 per cent.), and this is of course the best criterion of energetic expenditure. Most of this loss probably comes from the greatly decreased action of the voluntary muscles, but some is derived from the lessening of activity in the other tissues. We do not know to what extent the accumulation of lactates (from the muscles especially) influences the sleep-conditions in the nervous tissue. Perhaps it has nothing to do with it, for mental fatigue easily produces sleep and the metabolism in nerve is certainly very much less than that in muscle. When nervous fatigue is too great and verges on either acute or chronic exhaustion, sleep sometimes does not come. This too well-known fact would seem to indicate that the occasion of sleep is a chemical katabolic product of nervous action rather than of muscular activity, since muscular exhaustion does not show the same abeyance of sleep—unless it be from muscle-pain. But the truth is that the real immediate occasion ("cause") of sleep is still unknown.

During sleep the heart slows its rate somewhat and the breath-rate is markedly lessened, deepened, and made more regular (because uninterrupted by speech, swallowing, etc.). Howell showed by means of the plethysmograph that the volume of the hand and forearm gradually increases from the beginning of sleep up to the end of an hour or an hour and three-quarters, remains this size until about forty-five minutes before waking, and then returns rather quickly to the normal. The "general" blood-pressure generally sinks because of the lessened heart-activity and the dilatation of the peripheral (and intestinal?) capillaries. It is likely enough that this abdominal and peripheral dilatation is for the purpose of reducing the blood-supply and the consequent metabolism of the brain, for cerebral anemia is regularly observed in sleep. If a man be delicately balanced on a tilt-board and then goes to sleep, his head-end rises while his feet-end descends, and this tilting is due to the descent of blood from the head into the trunk and extremities. For the same reason one feels drowsy after a hearty meal, the blood then going to the alimentary canal.

The pupils of the eyes are contracted during sleep, and their smallness is to some extent an index of the depth of the sleep. This action is apparently due to some central irritation; other sphincters (*e.g.*, of the anus and the bladder) are usefully tightened in a similar way. This tonic contraction is more or less inhibited by afferent sensory impulses. Like the other voluntary muscles, those moving the eyes are relaxed during sleep, with the result that the eyeballs turn somewhat inward and a good deal upward. General complete relaxation of the voluntary muscles on retiring is an important habit to acquire, for only so are they free of tonus, and this, as we have seen, is a condition of partial activity. The unique position taken by the cadaver while lying flat is the type and limit of this sort of muscular relaxation.

Sleep varies not a little in its soundness at different times during the night. It has been found (by comparing the intensities of sounds necessary to awaken the sleeper) that the depth of sleep slowly increases (Mönninghoff and Piesbergen) for 1.25 hours, then deepens very rapidly (see curve, Fig. 243) for half-an-hour, and becomes speedily lighter during the next half-hour. From this time on until the middle of the fifth hour sleep very gradually becomes lighter, deepens slightly for another hour, and then becomes slowly but progressively less deep until awakening occurs. Thus a person retiring at ten o'clock is most profoundly asleep at quarter before twelve, and after the second hour the sleep is comparatively light and easily disturbable. Children sleep the most soundly, but men more soundly than women.

Fig. 243



Graphic representation of the varying depth of a natural sleep lasting about six hours. Light for 1.25 hours, it rapidly deepens during the next 0.5 hour; becomes as rapidly lighter for the next 0.5 hour; then more slowly for 2.25 hours; deepens slightly for 1 hour more; then becomes slowly lighter until some slight stimulus is enough to recall the person to the waking consciousness. (Altered from Piesbergen.)

The mental relations of sleep are difficult to describe with certainty. We think of sleep-consciousness as continuous but as lowered in intensity and, which is more important, as *separated* in some manner from the waking-consciousness. In abnormal cases one waking consciousness is similarly shut off by forgetfulness from another, this amnesia giving us the phenomena we call double or multiple personality. Aside from dreams so vivid probably as to partially awaken us, we do not remember the mental events experienced in sleep. Yet there is excellent and widespread evidence that consciousness persists continually, for the more suddenly a person is awakened the more certain he is to find himself in the midst of conscious experiences of some sort. This is not to be accounted for on any supposition other than that consciousness persists at least until death. On this principle, demanded by the continual advancement of knowledge about the relations of body and mind and the nature of subconsciousness, coma might give a subconsciousness down to its vanishing-point, perhaps, in death. In this state, however, the conditions are different and abnormal, the essence of the state being one of depression quite unlike the partial rest of sleep.

Dreaming and its congeners somnambulism, etc., probably represent the activity of certain more or less localized parts of the nervous system separately. One could almost suppose they might depend on the vagaries of the cerebral vaso-motion. The dream is an unusually vivid experience out of the subdued sleep-consciousness and, however long a time its content may represent, lasts only a very short time. On the vasomotor supposition it would be represented by a temporary dilatation of some little region of the brain-capillaries, this congestion setting up for a moment a more active metabolism and function. Similar in origin may be the delirium so common when the vaso-motor centers are apt to be deranged, as in high degrees of fever. This notion as to the relation of dreaming to local cerebral vaso-dilatation has never been demonstrated and stands as an hypothesis allowable only where facts, except as to the actual existence of cerebral vaso-motion, are lacking.

It is a common experience that dreams are more or less dependent on sensory stimuli. Thus, a child from whom the bed-clothes had fallen dreamed of a frolic in a cold snowstorm, and an over-burdened stomach readily transfers its load to the oppressive weight of a night-mare. Strains or pressure on the nerves of the arm may readily give rise to indescribable impressions of being overwhelmed by boundless waves of indefinite matter. Such an experience forms, moreover, a striking example of the widespread and absorbing mental impression which may come from the stimulation of a single nerve-trunk. A common characteristic of the dream-experience is its freedom from the restraints of common sense and fact, not less than from other sorts of law: "In sleep a king, in waking, no such matter." As men grow old they dream less and less, while women maintain their early frequency in this respect and dream at all life-periods more than do men (Heerwagen). According to Jastrow it is "the vividness of the emotional background elaborated by the imagination that furnishes the predominant characteristic and tendency to dreams." It is between the ages of twenty and twenty-five that dreams are vividest, while in childhood they are by far the most numerous.

Despite the evil dreams that come at times, sleep makes up much of the happiness of life, just as it constitutes about one-third its duration. Very few persons can work or feel well on less sleep than seven hours daily, although six suffice some; rarely, after childhood is passed, does one need over eight hours of rest. Sleep is indeed to the world's multitude

> ". . . the certain knot of peace,
> The baiting-place of wit, the balm of woe,
> The poor man's wealth, the prisoner's release,
> Th' indifferent judge between the high and low."

It is unfortunate that so relatively little yet is known about its psychical status as well as about its physical basis. Especially does science need to know the nature of the break in memory between the sleep-consciousness and that of waking hours.

Hallucinations, Illusions, and Delusions.—These three sorts of mental experiences are, strictly speaking, more or less abnormal, but they are of such fundamental importance in the theory of insanity and so instructive physiologically that we may describe them briefly here. It is, however, only the exceptional "normal" man (and normality is a very indefinite sort of thing) who does not often experience in some degree, usually as a victim, various illusions and delusions. Furthermore, about one-tenth of the public have some time or other, if only for a few seconds, been under the strange spell of a true hallucination. (See the "Census of Hallucinations" made by H. Sidgwick.)

An *hallucination* is a percept without objective occasion or representation, while an illusion is a wrongly interpreted percept. A delusion, on the other hand, is of a conceptual rather than perceptual nature, and is a system of notions and beliefs contrary to the facts.

It is plain from these definitions that hallucinations and illusions are of the same general nature and they probably have the same neural basis. In normal perception the stimulus comes in through a sense-organ and goes on into the perceptual brain-centers, each percept employing doubtless very many neural paths. In normal imagination these same brain-centers are doubtless employed, but whether the sense-organs and the afferent paths also are we do not know. When an hallucination occurs these perceptual centers are stimulated in the same way or to the same degree as when a percept is formed, and not in the manner of the imagination, and no one ever mistakes the product of imagination for that of perception. How it is that these centers are stimulated so as to give the same sort of experience as in perception, no one as yet knows. It is a process of imagination changed to the vividness, objectivity, and reality of actual perception. Sometimes the individual is deceived into supposing the hallucination a true perception, but more often, owing to contradiction between the hallucination and perceptions, the false "object" is realized to be fallacious.

In *illusion* there is some sort of objective occasion or stimulus, and the afferent neural apparatus (end-organ and nerve) employed is the same as in perception. The result given to the brain is wrongly interpreted by that organ, so that the person perceives differently from the objective reality. For example, if in looking at the short curved lines of dried bacilli on a microscope-slide one sees them bend and infers therefore that they are alive, he is the victim of illusion, and illusions are easy and very common in microscopy. A white stump in a swamp at midnight is much more apt to seem a ghost than as a portion of a dead tree. These are illusions and obviously differ from hallucinations in being wrongly interpreted perceptions; in hallucinations the latter are wholly absent. The physical basis of both of these experiences is evidently much like that of dreams. Hallucinations are about half as frequent again in women as in men, and more common in Brazilian women, for example, than in English women.

Delusions exist wherever knowledge about the relations of things is deficient, mistaken, or deranged. Thus, one thinks of Eddyism as a delusion which for obvious reasons has had a certain popularity. The delusions' names, like their natures, in the history of civilization have been legion, but with the advancement of learning they continually become fewer and less dangerous. In the individual delusions are of all sorts, all degrees, and all importances. Some of the dearest beliefs the world knows are delusions: surely Santa Claus is the precious birth-right of every child.

It is with the delusions at the basis of paranoia (monomania), paresis, etc., that mental and legal medicine are most often concerned. Sometimes these are based on hallucinations or on illusions. Whatever their source (and we have no idea of it in pathological terms), the delusions of an alienated mind often make him, long before he is put in a hospital, one of the most dangerous of beings, so cunning and so cruel are the purposes of such unfortunates apt to be under the unnatural stimuli of these delusions. These are unknown derangements in the powers of the reasoning aspects of the mental process.

Anesthesia.—This term commonly means not only the absence of "feeling," as the word itself implies, but also the absence of pain, *analgesia*. In the use of laughing-gas (nitrous oxide), for example, pain may be lost and feeling retained, and this is the case also in the lightest degrees of the effects of ether- and of chloroform-inhalation. Analgesia and anesthesia may be either general or local. In the former case the anesthetic is inhaled and, entering the circulating blood through the alveolar walls, is taken quickly to every part of the body. It is its action on the nervous system especially which causes the disturbance, shutting off, or "loss" of consciousness. Local anesthetics seem to act by cutting off the else painful impressions passing inward on the afferent nerves. We are concerned now only with general anesthesia, and then only so far as consciousness is concerned.

General anesthetics in one way or another (just how is not yet certain) check the conductivity in the neural tissue and thus prevent that unification of numberless impressions which we call the mental process or consciousness. People widely vary in their mode of reaction to anesthetics, but very often (aside from the feelings of suffocation, etc., incident to taking the drug) there is experienced a vast hurrying of some great mass that is very variously described. Most often, perhaps, this mass very early begins to rotate, sometimes around the anesthetized subject, sometimes with the latter on its edge, or within it. Then the speed rapidly increases until the mind is in a vortex of tremendous energy but without any suggestions (usually) of terror or unpleasantness. No limit of time can be set by the subject to these long-remembered impressions, but often they seem to continue throughout the anesthesia.

In reality it is rather the memory of their presence and nature which fades as the effect of the anesthetic deepens into the deep subconsciousness of surgical anesthesia. Doubtless these two ("unconsciousness" and entire loss of memory of consciousness) are the same so far as the future recall of the experience is concerned. The reports of anesthesias strengthen the presumption long ago made that it is the break in memory which is the critical phenomenon of all conditions commonly called unconscious rather than that any condition of real "unconsciousness" can exist during "life."[1]

The physical basis of the action of anesthetics is still obscure. Lately it has been suggested, however, that the general anesthetics are substances which dissolve fats, and the fatty substances cholesterin, lecithin, etc., are probably constituents of every cell-wall. Perhaps the circulating ether or chloroform dissolves some of these complex substances out of the guarding envelope of nerve-cells and nerve-fibers, and thus by disturbing its osmotic interchange alters their metabolism enough to destroy their conductivity and so the fusing unification on which attentive consciousness in some way depends.

For the bodily changes made by general anesthetics the reader is referred to treatises on general and dental surgery.

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[1] Accounts of experiences during general anesthesia are sought by the author, and questionaire-blanks for this purpose will be promptly mailed on application to him.

CHAPTER XIII.

REPRODUCTION AND DEVELOPMENT.

The eternal changefulness of things is impressively typified in the rapid succession of generations consequent on man's inherent mortality. It is this which makes reproduction one of the three or four universally essential functions of all organisms, for individuals die and must be replaced if the races are to persist. The means by which this replacement is brought about constitute one of the most elaborate of all psychophysical mechanisms, while the record of the process of the individual's growth to maturity and his subsequent decadence are the history of life and death, are physiology itself. To these two important subjects, reproduction and development, so interwrought with life's happiness and misery, so vastly complex in all their details, we can here pay but inadequate attention and give but insufficient space. We can discuss briefly the bare outlines of only the somatic process, in part the physiology of the organs concerned, but must leave undescribed entirely all that great mass of psychological, social, anthropological, and criminological facts which from any adequately broad view-point constitute part of the deep problems of sex and of racial progress—basal truths in human physiology considered as the science of man's normal living. Even medical men, the proper teachers of mankind, because of the hereditary prudery of the race still reserve from common knowledge reproductive facts and theory which would be of immense value to mankind, making happy the lives of multitudes of boys and girls which without this needful information will be stained with unnecessary disease and misery.

It is inevitable that with so large a number of dissimilar animal forms as there are (a million or so), there should be many processes of generation. All the forms of reproduction may be classed, however, either as asexual or sexual except in the one-celled animals, the protozoa, in which we find budding, simple division, spore-formation, and one or two other more or less similar processes. The asexual process in multicells is seen chiefly as budding in some form or other. The sexual process proper involves the union of special reproductive cells which have small part in the general functions of the body, and largely serve this function of reproduction. The special germ-cells coming from one (the male) sex are termed spermatozoa, those from the other (female) sex ova, and usually their combination in fertilization is necessary for the origination of a new individual. In a few cases, however, the female cells (ova) develop into infertile animals parthenogenically, that is without being fertilized by male protoplasm. In sexual reproduction the ovum stands for body-material and for relative passivity, while the spermatozoon is the supplier of the activity and the energy by which alone the body-matter becomes spontaneously motile and, in short, *alive*. Both aspects of the actual animal are essential, a material body and the activity whereby that organized material may adjust itself to its environment.

The cellular reproduction of man, as of all other mammals, takes place by mitosis (karyokinesis), as distinguished from the amitosis or direct cell-division of many protozoans and some metazoans. An outline of the mitotic process was given in the chapter on Protoplasm (see page 45).

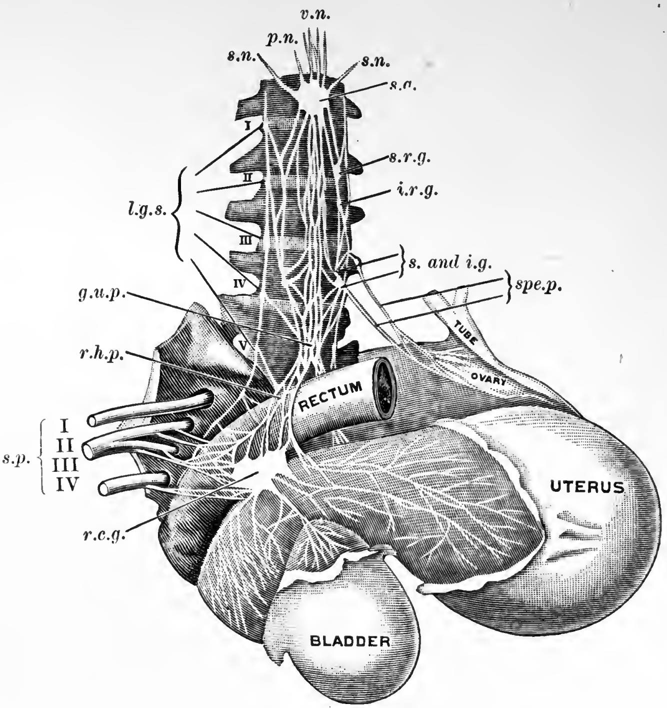
PUBERTY AND MENSTRUATION.

Our first inquiry must be as to how the reproductive apparatus is made ready for use in the developing adolescent, especially in the girl, as a preliminary to a description of that use—the fertilization of the woman by the man. Here, as in the other functions, a detailed knowledge of the genital apparatus of each sex, to be obtained from anatomy, is presupposed.

Puberty in the Male.—From the beginning of voluntary control during the latter part of the first half-year of extra-uterine life the boy-baby shows in some slight respects his functional difference from the girl-baby—he has especially more tendency to the initiative and is on the average bolder in his activities. None the less, up to the age of twelve or fourteen the nature of the boy is like that of the girl in a much greater degree than ever again it can normally be. Many perfectly normal girls up to this age and sometimes beyond it do boyish things, and vice versa. It must be deemed physiologically a distinct advantage to both sexes that the boys and girls should mingle freely and naturally up to the age of twelve and freely also, if not quite naturally, beyond that time. Such association keeps the boy from becoming, sometimes, a "boor," and the girl from becoming a prude.

When about fourteen or sixteen years of age, in temperate climates, the boy's organism begins to change and with it his mental nature more or less, although to a much smaller degree perhaps than in case of the girl. The testicles rapidly increase in size and become more pendulous and the dartos tunic more contractile. The penis grows in length and soon develops in its cavernous bodies an increased power of erecting, while the prepuce becomes more easily removable over the glans. The vocal cords develop and elongate especially, and during these changes are apt to be badly controlled in speaking. The shoulders broaden and hair grows on the lower part of the face, in the axilla, and on the lowest middle part of the abdomen, over and around the penis. The moral sentiments become more conspicuous in the nature of the boy, and beauty especially becomes for the first time a reality to him. Around his whole being floats a consciousness of new powers, new interests, and new life, for this sexual flood-tide pervades without his realizing it perhaps every portion of his two-faced mental and physical nature. In some respects this is the climax of the delight of mortal experience, this opening of the world's real life to the childish mind. By a study of the phenomena of puberty including the far-reaching bodily changes not less than the all-pervading alterations in the mental process, one learns to appreciate how completely intermixed is sexuality in most of the affairs of life. Its instinctive influence surpasses that of all other functions save nutrition, and these two accord in being irrepressible.

Fig. 244

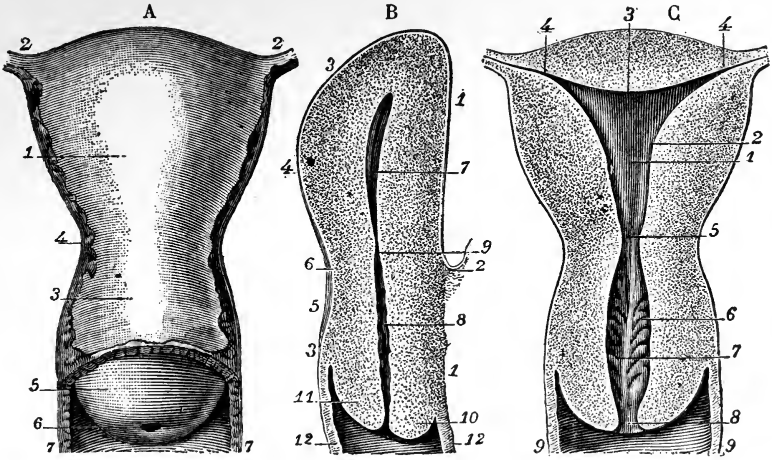


The female reproductive organs, to show their nerve-supply: *p.n.*, phrenic nerve; *s.n.*, splanchnic; *l.g.s.*, lumbar ganglion (sympathetic); *g.u.p.*, great uterine plexus; *r.h.p.*, right hypogastric plexus; *s.p.*, sacral plexus; *r.c.g.*, right cervical ganglion; *v.n.*, vagus; *s.g.*, solar ganglion; *s.r.g.*, suprarenal ganglion; *i.r.g.*, infrarenal ganglion; *s. and i.g.*, superior and inferior genital ganglia; *spe.p.*, spermatic plexus (ovarian nerves). (Frankenhäuser via Edgar.)

Puberty in the Female.—More profound by far than the changes that constitute puberty in the boy are those which make of the maiden child a woman. The average young girl while a child is more like a boy than the average boy is like a girl—that is to say, the pubertal changes of the female are more revolutionary than are those in the male.

They come about somewhat more gradually, and soon after the age of twelve in temperate climates (sometimes as early as nine in the tropics) the proper sexual changes begin. As one may read in Aristotle, menstruation begins when the breasts are two fingers' breadth high. The whole body takes part in this evolution, which fits the individual to bear children. The specific gravity of the blood rises and the pulse-rate accelerates, although somewhat less than in boys. The chest enlarges, but so much does the pelvis grow, especially laterally, that the hips become very much more prominent in comparison with the shoulders. Deposits of fat about the limbs and between the muscles cause all contours to become more rounded. The face changes in a marked degree and in some indescribable manner becomes the face of a woman. The larynx enlarges and the voice nearly doubles its range. The breasts develop their adult rotundity, as does also the abdomen. The sexual organs proper, especially the uterus, develop in size and shape, each of them changing in many particulars into the condition of greatest fitness for its particular part in the momentous process of procreation. All the glands concerned markedly develop and play no small part in the new experiences of the new woman; the vascularity especially of all portions of the genital system increases greatly. Hair grows on the mons veneris, etc., and in the axillæ.

FIG. 245



A virgin uterus (twenty-two years).

A, from in front and below: 1, body; 2, angles; 3, cervix; 4, opposite the os internum; 5, vaginal part of the cervix; 6, os externum; 7, vagina (distended).

B, sagittal section: 1, anterior face; 2, utero-vesical cul-de-sac; 3, posterior face; 4, body; 5, cervix; 6, isthmus; 7, body-cavity; 8, cervix-cavity; 9, os internum; 10, os externum's anterior lip; 11, os externum's posterior lip; 12, vagina.

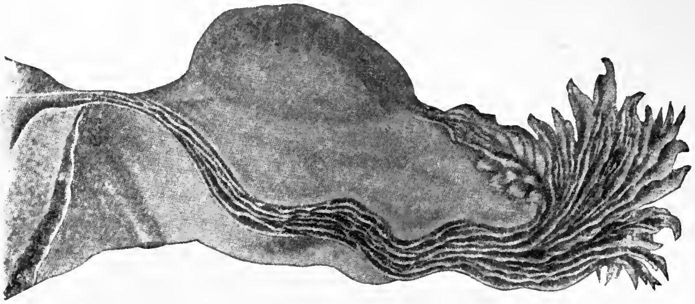
C, transverse longitudinal section: 1, body-cavity; 2, lateral wall; 3, upper wall; 4, horn; 5, os internum; 6, cervix-cavity; 7, arbor vitæ cervicis; 8, os externum; 9, vagina. (Sappey.)

The mental changes of the commencement of womanhood we may not attempt to describe. They are homologous to those occurring in the male, and all have their physiological meaning and explanation in the new tendencies toward and fitness for fertilization and the bearing of children. It is from this, biologically speaking, that these new desires and thoughts and emotions get their sweetness and their worth, as indeed the normal woman finally learns to realize.

Of all the new activity in the female organs the two new functions of ovulation and menstruation are in a way probably the most essential, the former in particular. It is not yet known how these are related biologically, hence we describe them separately as two processes rather than as parts of one.

Ovulation is the process in which a matured ovum breaks out of the ovary and is started down the Fallopian tube toward the uterus. Every lunar month at least one of the Graafian follicles makes its way to the surface of the ovary, but just how this passage through the stroma occurs and is controlled is not understood. When it arrives there and projects beyond the general surface of the ovary, the outer walls of the follicle may degenerate and give way, thus freeing the ovum and the plasma about it in the follicle on the ovarian surface. The follicle's rupture may come from its over-distention with lymph, from excessive congestion of the ovarian stroma, or from the reflex active contraction of the ovarian musculature in the excitement of coitus. The last-mentioned possibility has been usually overlooked. The inner lining of the Fallopian tubes, including the trumpet-shaped fimbriæ, is ciliated, and the cilia all wave so as to cause a slight but continuous stream of lymph down the tubes toward the womb. If the fimbriated end of the tube embraces the side of the ovary during ovulation, it is easy to see that the minute ovum (0.2 mm. in diameter) would very probably be drawn into the wide openings of the tube and, once started, be passed slowly along one of the very narrow channels into the uterus. The rate of this passage averages perhaps 20 mm. per day. In trying to define how this functional connection between ovary and tube can take place so regularly (abdominal pregnancies are relatively uncommon though by no means rare), it must be kept in mind that there are no open spaces in the abdominal cavity,

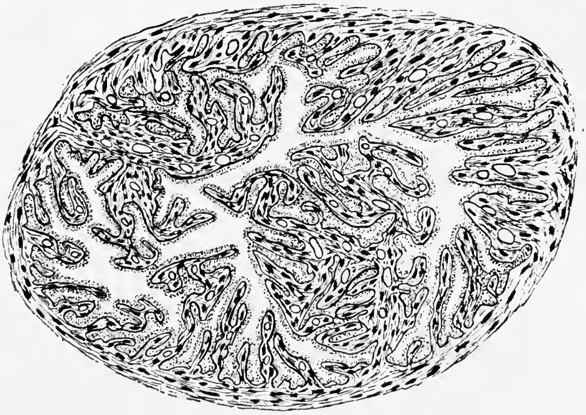
Fig. 246



A sectional view of the left Fallopian tube, showing its numerous channels, its widely spreading openings, and its close connection with the ovary. (Sappey.)

for the viscera fit snugly together, and that the few spaces there are between them are filled with lymph. The plasma poured out with the ovum serves undoubtedly to float the latter into the stream trending into the tube, for else the peculiar nature of the follicle is unintelligible. There is however, also a permanent anatomical connection between the tube and the ovary by means of the ovarian fimbria, and it is likely that it is by this channel that the ova usually pass, the other fimbriæ being present perhaps to pick up the stragglers from this straight and narrow way. Sometimes the ovum becomes fertilized on or near the ovary and fails to reach the safe channel of the tube, the fetus then developing as an abdominal (ectopic) pregnancy. Maturation occurs either just before or just after the follicle's rupture, and fertilization, while occurring usually in the peripheral part of the tube, may take place at any time after the rupture, even in the uterus. The relations of the two ovaries as regards ovulation are unknown, but there is a likelihood that both ovaries ovulate every month.

Fig. 247

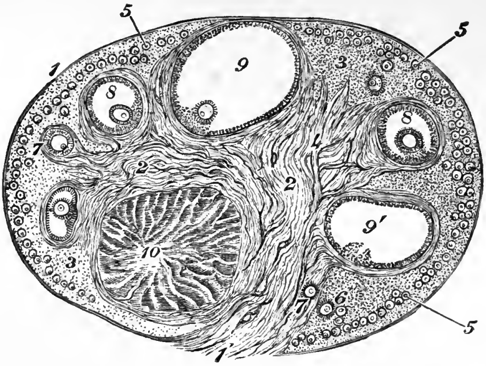


Section through the Fallopian tube. (Bates.)

The Corpus Luteum.—When the follicle has burst and freed its ovum its duties as a follicle are done. If we may trust, however, the recent work of several men, and especially of Fränkel, the follicle forthwith takes on a new function, that of producing an internal secretion, which stimulates the growth of the muscular parts of the sexual organs, and perhaps of others (heart, for example?), to meet the demands of the expected pregnancy. Aside from the experimental evidence for this, the hollowness and the large size of the Graafian follicle in themselves are additional testimony. These conditions apparently are not necessary merely for the development of (and maturation of?) the ovum but rather preparation for the corpus luteum. This glandular (?) organ is formed according to von Baer substantially as follows: When the follicle bursts open in ovulation to allow of the ovum's release, blood escapes into the drained cavity of the follicle, whose walls, especially the stratum granulosum, remain. These latter cells degenerate and the internal layer beneath them by proliferation soon gives rise to a cellular mass sufficient to fill the now restored sphere of the follicle. Trabeculæ of fibrous tissue, containing an abundance of blood-vessels, soon divide the little body into lobules. The cells composing this new mass are colored yellow by lutein, a lipochrome of unknown composition which gives the blood-serum its faint yellowness.

In case the liberated ovum be not fertilized, in about three weeks the yellow cells become more and more white like connective-tissue of a special cicatricial sort, and in course of time, this, now called the corpus albicans, almost disappears. If we suppose, as many at present do, that ovulation takes place normally about a fortnight before menstruation, it is clear that the contents of the corpus luteum might well enough influence the changes, constructive and then destructive, which occur in the uterus previous to the outward flow of uterine debris. The sexual apparatus is constructed and acts, however, on the supposition of continually repeated conception and pregnancy, and yet in the above manner it provides for disappointment.

Fig. 248



Section in the ovary of a cat: 1, free peritoneal border of the ovary; 1′, attached border; 2, central stroma, fibrous and vascular in its structure; 3, peripheral stroma containing unstriated muscle-fibers; 4, blood-vessels; 5, Graafian follicles in the earliest stage (about 36,000 in number altogether); 6, 7, 8, more advanced and larger follicles embedded more deeply; 9, an almost mature follicle containing a conspicuous ovum; 9′, a follicle which has accidentally lost its ovum; 10, a corpus luteum. $^6/_1$. (Schrön.)

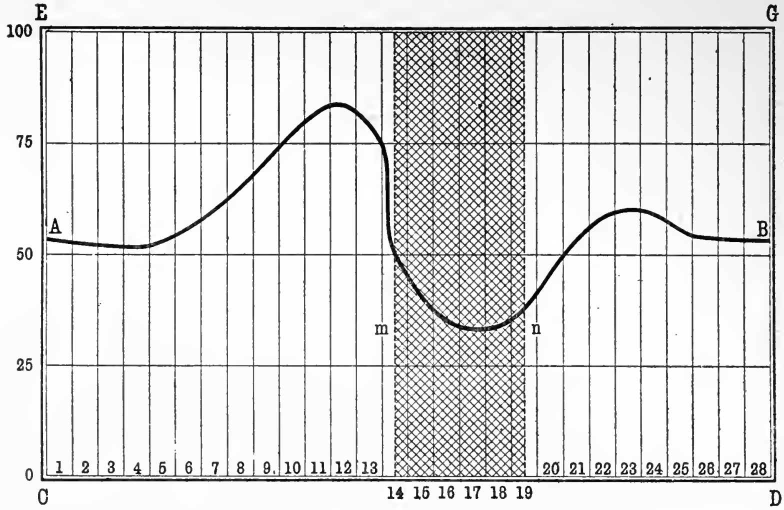
If, however, the ovum be fertilized within a week or so after ovulation (the ovum will persist at least as long as this), the corpus luteum vera, as it is then called, becomes more fully developed and larger. More than this, it persists in its entirety until after parturition, when it degenerates in practically the same way as does the corpus albicans. On this hypothesis, then, the hollow sphere from which an ovum has escaped becomes forthwith filled with epithelium which provides a stimulant for such temporary development of the organism as is required for the growth and birth of the new being. In case fertilization fail, the stimulating material ceases to be produced and the uterus rids itself by menstruation of the now useless growth in its mucosa (see below). Things fit together too well on this hypothesis to warrant its rejection unless disproved. None the less, at present it is a theory only.

While it is true that the ovary probably discharges an ovum each lunar month, the exact time-relation between this event and menstruation is still a matter of research and discussion, a discussion which can be made clearer when the facts and theory of menstruation have been given.

MENSTRUATION is the monthly hemorrhage which occurs from the uterus in women and in some of the higher apes. It occurs (but not monthly) in the females of many other species, such as the equine, bovine, and canine animals. It begins its periodical routine at puberty (as early as the ninth year in Africa and as late as the seventeenth in Lapland), and continues normally, except during the pregnancies and lactations, until the menopause at the forty-fifth or fiftieth year. Some women, but not many, menstruate throughout pregnancy; very rarely even fertile women do not menstruate at all. Individual differences as regards menstruation are great in the frequency, the amount of hemorrhage, the duration, the ages of commencement and cessation, the secondary phenomena, etc. On the average, however, the occurrences are as follows:

At intervals of twenty-eight days a flow of blood comes from the uterus and continues for four or five days. Many women are unwell every three weeks and fewer show an interval of thirty-two or thirty-three days, these being the normal limits. The more civilized and "cultured" the woman the more pronounced is the flow, it being much less in the savage races. Preceding the actual hemorrhage there are apt to be many varied premonitory signs of its approach: indefinite and irregular pains, chilliness, nervous instability and irritability; in many women these signs of a general stimulation of the nervous system are seen especially about a week before the flow begins. The breasts are enlarged by the congestion and made firmer and somewhat tender to the touch. The amount of urea excreted becomes smaller. The bloody discharge begins very gradually and is apt at first to be somewhat watery. In a day or so the flow becomes established often with no little uterine and ovarian pain (dysmenorrhea), continues more or less abundantly for one or two days, and then in one or two days more gradually stops. The quantity of blood ordinarily ranges between 100 and 200 c.c., but is often very scanty, especially in anemic young women who have too little physical exercise. Often, too, it is as much as 400 or 500 c.c. in amount. It is because of this habitual loss of blood that women stand severe accidental hemorrhage better than do men. In a degree the ancient Jewish notion of the catamenia as a means of purification is physiologically justified, for many women are "more normal" in many ways just after menstruation than before. This relief doubtless originates reflexly in the decrease of the congestion in the sexual apparatus and to a lesser extent in that of the whole body. Another possible source of relief lies in the fact that the body temperature is highest a short time before menstruation. Sexual desire is increased over the average just before and also after the menses, the period itself being the time of heat or rut in the brutes. In the human male also there appears to be a somewhat similar periodicity of desire dependent doubtless on the accumulation or else on the liberation from the testicular tubules of spermatozoa. It is not apparent that the moon has anything to do with the periodicity in either sex—the notion is one of the many from the superstitious past. The social, medical, and legal relations of menstruation make it and its accompaniments (such for example as nervous instability), matters of no small practical importance.

FIG. 249



Graphic suggestion of the fluctuations of the vital processes as related to menstruation. The days of the lunar month are indicated on the abscissa-line *C D;* menstruation lasting part of the six shaded days, *m, n.* The percentages of intensity of the life-processes (including pulse-rate, blood-pressure, heat-radiation, muscular strength, lung-capacity, strength of respiration, reaction-time of patella reflex) are indicated numerically along the ordinate-line *C E,* by the varying height of the curve *A B,* in the ordinary way of the graphic method. Thus, just before menstruation vitality is at its height, ready to be reproduced. (Nagel.)

The *uterine phenomena* causing the monthly flow are relatively simple. The columnar ciliated epithelium of the uterine body, together with the outer portions of the mucosa beneath it, degenerate more or less and are washed out of the uterus and vagina by the flow of blood from the capillaries and smallest arterioles lacerated in this process. In some women this epithelial degeneration may be almost or quite lacking. Both the uterine glands and the tissue between them undergo fatty degeneration and are excreted, the layer of tissue given off being from 3 to 6 mm. thick, and appearing sometimes as a complete cast of the uterine interior wall. The blood passed into the vagina because of its large admixture with mucus does not clot. The ammoniacal odor is due largely to needless decomposition in the vagina. The normal biological odor sometimes to be distinguished about menstruating women is a very different odor; it comes from the skin, and is somewhat aromatic and by no means unpleasant (Ellis). The mucosa partly given off during the periods is regenerated in a week or less after the flow ceases.

The relation of ovulation to menstruation is still somewhat uncertain; the most likely theory has already been discussed. That there is a relation and a dependence may not be doubted, as we have seen. Yet girls sometimes conceive and bear children before they have menstruated, and so occasionally do women years after their menses have ceased at the climacteric (menopause). It is certain, then, that menstruation is not essential to normal conception, while ovulation obviously is, for without the freeing of the ovum the sperms could not gain access to the latter. The chief problem then is as to the function of the monthly flow. Another question not less important, practically as well as theoretically, is the time-relation of menstruation to ovulation, since everywhere the menses are used as a sort of almanac for predicting the date of delivery. These problems are made yet more difficult by our ignorance of just what happens in the ovaries during the reflex excitement of coitus. On Fraenkel's hypothesis, ovulation should occur rhythmically once a month two weeks before menstruation, the rhythm depending on entirely unknown conditions perhaps in the ovarian tissues. From this point of view coitus would have little influence in rupturing Graafian follicles, and the musculature of the ovaries fails of a known function. If we suppose, then, that menstruation is occasioned by the degeneration of the uterine mucosa after being disappointed in its expectation of feeding a fertilized ovum, we shall be as near to an explanation of the menses as can be had at present.

The evidence that some internal secretion of some part of the ovary occasions the monthly flow is very conclusive, for removal of all of both ovaries stops menstruation permanently, while if only a small part of one ovary be left the process continues. This is quite in line with the conditions under which enzymes in general work. Moreover, after complete removal, with cessation of the catamenia, the successful transplantation (Glass) into the abdominal cavity of a fragment of ovary again starts the menstrual rhythm. In the over-radical gynecology of a decade ago there were all too many opportunities for testing these now well-known facts. Experiments on the transplantation of corpora lutea only remain to be performed.

IMPREGNATION.

Biologically considered woman is female in order to bear children and to nurture them during their uniquely long childhood. The first step in this long and complex process in which the girl becomes a woman is a willingness at least to be sexually loved, whereby alone, speaking generally fertilization of her ova is possible. This function, coitus, is a very complex series of activities differing somewhat in the two sexes, but in each homologous to that of the other. Strictly speaking, the muscular actions are of the voluntary sort, but they tend under the perfectly normal conditions of sexual vigor to become practically reflex in nature, as are plainly the secretory processes and the emotional accompaniments. For a detailed description of these important events the reader is referred to the various scientific discussions in the more elaborate treatises on physiology, psychology, and obstetrics.

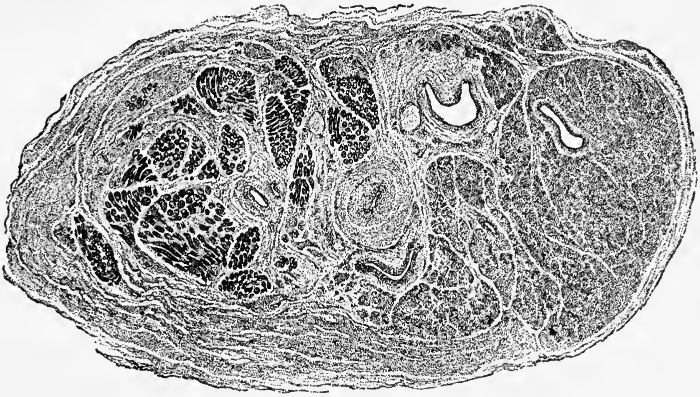
Fig. 250

The erectile bodies of the vulva: 1, symphysis; 2, pubic bone; 3, ischium; 4, ischial tuberosity; 5, vestibule, including the mouth of the urethra and the vaginal entrance; 6, anus; 7, glans of the clitoris; 8, suspensory ligament of the same; 9, dorsal plexus of the same; 10, corpus cavernosum; 11, Bartholin's glands; 12, crus of the clitoris; 13, bulbo-cavernosal muscle. The erectile parts are injected, and the four labia are cut away. (Rauber.)

Semen is the term given to the complex viscous fluid poured out by the male during the orgasm. It has long been known that the spermatozoa are its only essential elements, the other parts being but physical and chemical menstrua for the conveyance and continued vitality of these sperms. Each cubic centimeter of semen contains about fifty millions of these male cells. This substance is an opaque, whitish, streaky fluid with a quite characteristic odor, and wholly insoluble in water. Chemically it contains nuclein, the base protamine, proteids, lecithin, cholesterin, inorganic salts, and fat (Miescher). Crystals found in dried semen are supposed by some to be a phosphate of a base called spermin, and to cause the odor of semen. Camus and Gley found an enzyme in the prostate's contribution to this liquid, the function of which is apparently to partly coagulate the ejaculated semen, a process which occurs also when semen is placed in water. The respective functions of all the various liquid constituents of the semen are as yet, however, by by no means certain. The secretion of the prostate seems to preserve the vitality of the spermatozoa, while that of Cowper's gland is a mucus which prevents their too wide dissipation in the vagina.

The amount of semen deposited in the fornix at each coitus depends on the vigor of the sexuality of the male and on the time since ejaculation previously occurred. In normal cases, that is when coitus does not take place oftener than six or seven times per month, the average amount is 3 or 4 c.c., but it may be much larger at a single emission and much more abundantly produced. In old men semen is produced many years after the power of erection and intromission has gone. The spermatozoa are easily killed by the Röntgen rays, etc., and in some cases spermatogenesis appears to stop, at least for many months. In young men it is apparently the distention of the seminiferous tubules with the constantly secreted sperms, etc., which raises the irritability of the sexual nerve-centers and thus leads to sexual desire; in the woman these conditions are largely lacking, for no such pressure can arise. Under the influence of erotic impressions, nervous or imaginary, the semen is rapidly secreted and this distention may become almost painful. There is some evidence that semen contains some substance (enzyme?) that when absorbed into the circulation stimulates metabolic vigor. This action is apparently often to be seen in the physical improvement of newly married women.

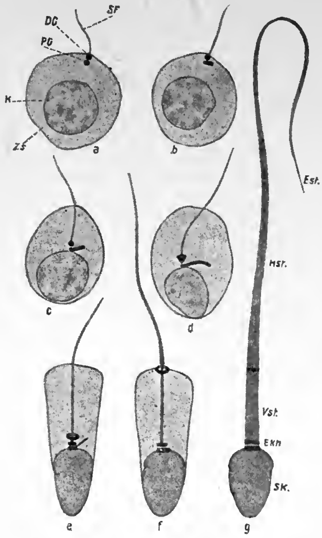
Fig. 251



Section through the round ligament of the human uterus. (Kölliker.) On the left are many bundles of cross-striated muscle-fibers, and on the right is the smooth musculature. In the center are vessels. Thus we see that the movements of the uterus (as in coitus, etc.) may be under many sorts of influence—perhaps voluntary as well as reflex.

Fertilization in the more technical sense is the union of the spermatozoa with the ovum. This leads to the development of the latter into a new individual possessing the characters of both parents. In a broader sense it is the woman that is fertilized not by the union of the sexual elements merely, but by the whole generative process. It is one of the most basal instincts of the adult female to be fertilized, just as it is of the adult male to fertilize. Next to that of self-preservation this is the strongest of all our instincts, the cause of untold happiness and often the occasion of unimagined misery and crime.

FIG. 252



The development of a spermatid into spermatozoön. Figs. *a* to *f*: *Zs*, cytoplasm; *k*, nucleus; *PC*, proximal centrosome; *DC*, distal centrosome; *SF*, tail-thread. Fig. *g*: *Sk*, head; *Ekn*, end-nodule; *Vst*, connecting-part; *Hst*, chief part; and *Est*, end-part of the tail. (Meves.)

FIG. 253

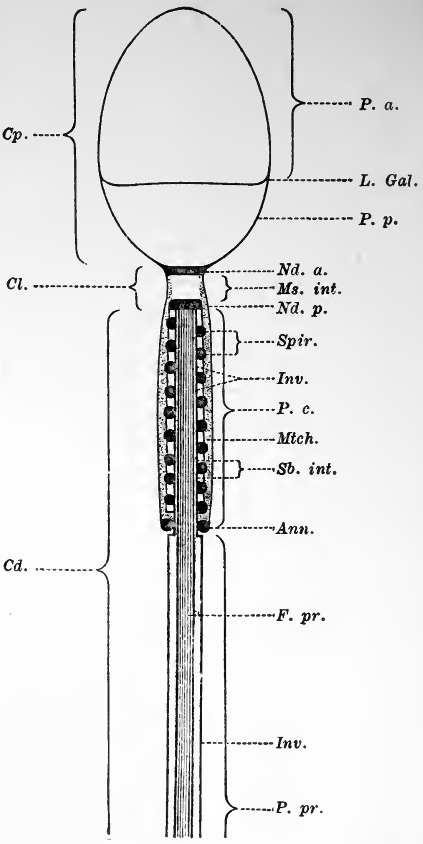


Diagram of the front part of a human spermatoözon: *Cp*, head; *Cl*, neck; *Cd*, tail; *P.a.*, anterior part of the head; *L. Gal.*, edge of the valve; *P. p.*, posterior part of the head; *Nd. a.*, anterior nodule; *Ms. int.*, mid-part of the neck; *Nd. p.*, posterior nodule; *Spir.*, spiral thread; *Inv.*, involucrum of the connecting part, *P. c.*; *Mtch.*, mitochondria; *Sb. int.*, intermediary substance; *Ann.*, annulus; *F. pr.*, chief thread; *Inv.*, involucrum; *P. pr.*, chief part of the tail. (Meves.)

The male elements of the seeds are deposited either at the entrance to the uterus or slightly within its neck. The next inquiry is how these sperms, two hundred millions or so of which are in every normal deposit of semen, reach the distant ovum in the further end of the Fallopian tube or on the surface of the ovary. The alkaline secretions of the mucosa of the uterus and vagina are adapted to preserving the life of the spermatozoa until they reach the tubes. The spermatozoön is an independent motile cell with a very long and active flagellum (tail). By rapid undulations of this flagellum the sperm is forced ahead, the movements being not too unlike those of a frog-tadpole when its tail is at its longest.

In the chapter on Protoplasm (see page 43) we suggested the various forms of barotaxis, or reaction of certain organisms to pressure, and found that rheotaxis, the reaction to a current of fluid, was a common cause of movements in small animals. This rheotaxis apparently helps the spermatozoa to pass up through the Fallopian tubes to the ova or ovum. As has been already said, the current of lymph in the tubes under the influence of the cilia set always from the fimbriæ to the uterus. If, then, the sperms are negatively rheotactic (that is accustomed to oppose a current rather than to go with it), we have a tentative explanation of how they reach their goal many centimeters away from the uterine cervix, where they are mechanically deposited in a preservative and stimulating menstruum (Adolfi). Chemotaxis also may aid in this ascent, for in some plants it is the chief means to fertilization. Hundreds at least of the spermatozoa approach and surround the ovum, and the place of meeting appears at present to be usually the upper part of the tube. The time required for this passage is not known, but it is probably hours at least and it may be a day or more. The sperms appear to travel in their normal liquid about 150 mm. per hour, but we have no evidence that in the actual and devious conditions of the vagina, cervix, uterine body, and tubes they can make anywhere near this speed, especially because of the strong contrary lymph-current in the 120 mm. or so of the tube. As frequent ectopic gestations attest, the place of fertilization may be on the surface of the ovary sometimes and probably in any other part of the ovarian-uterine path. Inasmuch as the location of the ectopic growth is determined by the arrest of the descending fertilized ovum rather than by any condition of fertilization itself, the usual place of the latter is very hard to learn either by this or other means.

Oviposition is the passage of the fertilized ovum down the oviduct (in woman the Fallopian tube) and its implantation in the uterine mucosa ready to develop. In birds reptiles, etc., the egg when laid, compared with the human egg, is independent, requiring only a proper environment. All placental animals, however, lay their eggs into the uterus, a special organ of development and birth.

Fertilization, as has been said, ordinarily occurs in the Fallopian tube from a few hours after a fertile coitus up to perhaps even three and a half weeks (Dührssen). The average period after coitus that an ovum is fertile is estimated by Issmer at sixteen days (McMurrich). It will thus be seen that the time of conception (fertilization) is impossible of exact calculation in the human female because so many of the facts are unknown. One large group of cases indicated that after a single coitus the average length of pregnancy was 275 days, and this implies that in such, usually vigorous, cases fertilization is prompt after copulation. Ordinary cases in which coitus may take place at all times in relation to menstruation are much harder to calculate. The long life of the sperm and ovum after coitus would seem to indicate that were all the concerned organs normal, fertilization would almost invariably follow a normal copulation, as is the case in general with the brutes that are the less artificialized by domestication.

The means by which the fertilized ovum is transported down the tube to the uterine cavity have been already described. The cilia lining the different divisions of the tube bear it along at a slow rate, while development goes on. Several days, probably about six (2 cm. daily), are required for the ovum to reach the uterus, which meanwhile has been making ready for it. The mucosa of the uterine fundus has hypertrophied and become soft and active from increased vascularity, and the blood-vessels extend outward to form long villi. This new-growth is known as the decidua vera, and it forms a soft nest for the segmenting ovum when it arrives from up the tube. Meanwhile the outer covering of the ovum has been changing somewhat similarly, so that when it reaches the uterus its villi soon interlock with those of the uterus. It thus becomes in a short time firmly embedded. Then the decidua vera grows upward about the ovum (forming the decidua reflexa), and shortly encloses it. The growing ovum is embedded firmly in this way in a soft and vascular matrix, with which for nearly ten lunar months it can develop, growing meanwhile after an inherent pattern of its own yet influenced more or less by many conditions in its maternal environment.

PREGNANCY, PARTURITION, AND LACTATION.

Inasmuch as the direct influence of the father ceases with the fertilization of the ovum, we may now turn our attention wholly to the means by which the child is fostered in its mother's womb, born "into the world," and nourished until fitted to eat food other than mother's milk. These three processes are respectively pregnancy, parturition, and lactation, and because the subject-matter of an art and science by itself (obstetrics), they require here but relatively brief discussion.

Pregnancy is that physiological period, in round numbers forty weeks long, which elapses between the fertilization of the ovum and the beginning of the child's expulsion from its mother's belly. Too often, perhaps, it is looked upon as other than a normal functional part of a woman's life, but biologically woman is female only for this purpose.

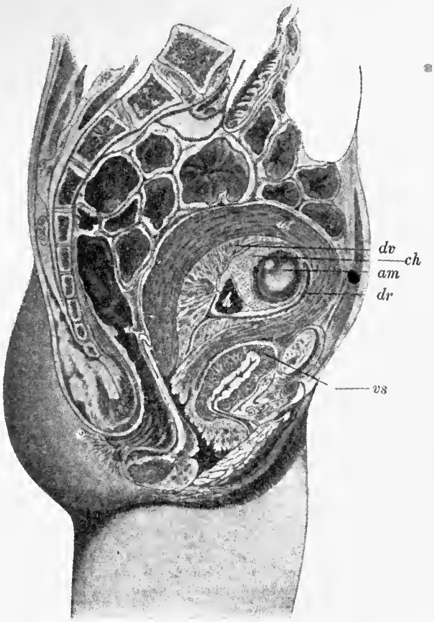
The physiological changes which occur in the maternal psychophysical organism during pregnancy affect in some degree nearly all its aspects. We may divide them into three classes: those which concern respectively the reproductive system proper, the remainder of the body, and the mind (Edgar).

THE CHANGES IN THE REPRODUCTIVE ORGANS in pregnancy are such as one would expect to find in any organic apparatus during a period of functional activity, namely, an all-round development. The body's changes in general are all directed to this end of supporting the additional activity of the sexual system.

Alterations in the Body Generally.—These we may classify under the heads of changes in the digestion, circulation, respiration, nervous system, urine, thyroid, and skin. This is only a classification for convenience of description, for without doubt practically the whole organism develops to meet the demands made on it by its production of a substantial new being more or less a replica of its mother.

The changes which the *digestive function* undergoes are in two directions: one physiological, an increase in activity, the other accidental and scarcely pathological, an increase in the irritability of the stomach with a hindrance of excretion from the colon. The growing fetus and the enlarging tissues of the mother's reproductive apparatus require an increased amount of nourishment, especially in the latter half of pregnancy, and this new demand brings about oftentimes an enlarged appetite for food. This is more noticeable in women who do not usually eat more than the organism requires, although probably these women are to be found only, as a rule, among the poorest classes of Society. The extra food demanded by the pregnant woman is especially proteid in nature.

Fig. 254



Sagittal section of the belly of a woman pregnant two months: *ut*, uterus; *dv*, decidua vera; *ch*, chorion; *am*, amnion; *dr*, decidua reflexa; *h*, hemorrhagic clot between chorion and reflexa (occurring before death?); *vs*, urinary bladder. (Ahlfelds.)

The disturbances of digestion appear to depend on the growing and congested uterus, which irritates the abdominal nerves and impedes intestinal movement. The former cause results in nausea ("morning-sickness") lasting sometimes almost from conception onward even for four months or more. Sometimes it brings about a curious craving for all sorts of unusual articles of diet, as well as for the chalk, earth, lime, etc., often craved by young children.

The *blood and its circulation* undergo changes of much less practical importance. The changes which occur are less than was formerly supposed; for example, Ehrlich denies that the number of the blood-corpuscles is changed in any recognizable degree. Measurements of the erythrocytes of twenty-two pregnant women (Rosthorn) showed no change in their size, although there were many of a diameter greater than normal. No nucleated red corpuscles could be found, yet the indications were that regeneration of the corpuscles was unusually lively. The percentage of hemoglobin increases slightly and considerably (15 per cent.) postpartum. There is a very moderate leukocytosis. The blood's alkalinity is slightly lessened; its specific gravity is unchanged from the usual figure (1055).

It is likely that a certain amount of what one might call functional hypertrophy of the heart at least obtains as in all muscles when used more actively than before, but its degree is slight; no increase in blood-pressure for example, is discoverable. The heart's apex is displaced upward by the abdominal pressure, and it was this which formerly gave the impression of enlargement. The right heart seems to be under more extra strain than does the left heart. It is not at all likely (von Rosthorn) that any pulse exists characteristic of pregnancy.

Respiration is rendered difficult to a degree dependent on the increase in size of the abdomen. Despite the additional demand for more oxidation made by the fetus, the hypertrophied uterus, etc., the inspiratory movements are more or less impeded by the presence of the enlarged uterus in the belly. This gives rise to a degree of dyspnea that is usually however, of small annoyance.

The nervous system during pregnancy becomes both more sensitive and more irritable. The former change shows itself in the additional acuteness which the senses exhibit. The increase in irritability is manifest in numerous ways, especially in "nervous" primiparæ, for conditions which before did not trouble or worry them now become occasions of irritation.

Changes in the *urine* are many, but it is not certain that they may all be said to be normal. In general the amount is increased, with a corresponding decrease in density. In about 5 per cent. of pregnancies (some observers say many more) some degree or other of albuminuria is to be found. Glycosuria too is to be found in a variable percentage of pregnancies. Acetonuria is to be found in all cases of pregnancy, but in only 28 per cent. (Stolz) does its degree overstep the normal figure. The sulphates of the urine and especially its phosphates are lessened in amount, being used perhaps in forming the fetus. The ammonia of the urine increases during pregnancy.

The *skin*, especially in brunettes, has a marked tendency to show an increased deposit of pigment in its lower epidermal layers. The areola of the breasts, the abdomen, and the vulva are the chief areas concerned. About the navel there may be deposited a ring of sigment, and a line of similar nature two or three centimeters wide tends to connect the mons and the sternal cartilages. Truzzis supposes these pigmentations to be the result of trophic changes set going reflexly from the genital apparatus. White lines, more or less circular in form, coming from the mechanical stretching of the skin, tend to appear on the abdomen. As in menstruation, skin-eruptions tend to be more common during pregnancy. The growth of hair is accelerated or stimulated, as is also the production of the dermal secretions (sebum and sweat).

The *thyroid* is well known to swell during pregnancy (as after coitus), resuming its usual size after labor. The exact reason for this hypertrophy has so far not been learned. In some important way the gland is probably closely related to the genital functions generally.

Mental Changes.—During pregnancy a number of psychical alterations occur, and as we do not know fully the physical basis of mind, they must be mentioned in a class by themselves. They are of no little practical importance to the mother, but it is not apparent (despite centuries of superstition to the contrary) that they exert any influence on the offspring within her.

With the increased tendency to insanity during pregnancy we are not concerned. This is the natural result of the additional strain placed by pregnancy on a nervous system already burdened with a more or less neurotic taint. These effects (melancholia or mania for the most part) are more common in unmarried women, the mental stress being then sometimes unduly great.

The psychical changes in normal women while pregnant are to be seen largely in the affective, or emotional, aspect of mind. Sometimes the whole disposition is changed, many a husband finding his wife happier and more ompanionable while pregnant than at any other times. But the opposite change may occur and women usually good-natured become peevish, irritable, and unhappy. To some extent the causes of these changes lie in the woman's mental attitude toward children, toward pain, and perhaps even toward their personal safety. Those who look forward with normal delight to the possession of the promised child will in general be happy while pregnant, the whole organism being dominated by the child-forming process. To many even strongly feminine women, however, the dread of the unknown experience of labor, with its usual pain and usually much exaggerated danger, directs the feelings throughout all of pregnancy, and makes the more or less obvious bodily inconveniences worse to bear. These mental changes are none the less important because not exactly definable, and form no inconsiderable part of the phenomena of pregnancy in the average civilized woman. As regards the declining birth-rate in many regions, these degenerative mental attitudes of women are more important probably than any other circumstance, the rate being lowest in just those localities where these considerations are most apt to be depressive and prohibitive of conception.

Parturition.—This is the complex process by which the now complete fetus and its accessories are forced into the world from its mother's womb. This event, the especial field of obstetrics, we need discuss only in its purely physiological aspects.

Obstetricians divide the process of birth into three stages, partly for convenience of description. The first stage extends from the first effective contraction of the upper half of the uterus to the time when the os uteri is forced open enough for the head of the child to pass through it. The second stage lasts from then until the child is fully born. The third stage comprises the expression of the membranes and placenta. It is obvious that the first two stages are physiologically continuous with each other.

The causes of the beginning of delivery are doubtless several in number, but are all included under the term ripeness; on the other hand the occasion of the commencement of the event may be any one of many. Here as elsewhere the conditions are numerous and complex rather than single and simple. On the average, about 280 days after the beginning of the last menstruation the fetus has reached maturity, and then the metabolic balance between the oxygen and the carbon dioxide in its tissues begins to lean toward asphyxia, and in consequence the placenta begins to degenerate. Thromboses tend to form in the placenta, and soon this organ begins to act like a foreign body and to break away from the uterine wall. Perhaps the excess of carbon dioxide passed into the maternal medulla oblongata actuates the parturition-center as it always does the respiratory center. For several weeks or even months prior to delivery the uterus shows painless rhythmic contractions, these being either inherent in the smooth muscle-protoplasm or directed by resident ganglia. Perhaps the placenta and fetus, beginning now to act like foreign bodies, stimulate the mother's uterine center in the spinal cord so that the rhythmic contractions increase in force up to the effective degree. Such being perhaps the causes of the beginning of labor, the slightest disturbance of the nervous apparatus, of the circulation, or of the muscular (uterine) nutrition would set the reflex neuromuscular mechanism in action. Although the child may furnish some of these exciting conditions, it can supply little or nothing of the motive power for its own extrusion into the world.

The first stage of actual labor begins by uterine contractions of increasing severity. As is probably the case with most smooth-muscle, the uterine walls have both a tonic mode of contraction and a rhythmic mode. The former tends to lessen the diameter of the uterus and to keep it small, while the latter sort of contraction is the slow, progressive peristalsis characteristic of all the tubes and sacs. The peristalsis of the uterus in labor affects only the upper part of the uterus down as far as the "contraction-ring." Each "pain" lasts about a minute, but they recur irregularly rather than in a complete rhythm, and each is harder than the preceding. In consequence every succeeding contraction gives rise to greater pain than the one before it. The first pains of labor are caused by the violent stimulation of the uterine nerves, whose delicate endings are injured by the strong compression of the hardening uterine walls. As the compressions become stronger the pain is radiated over the abdomen generally. Each peristaltic wave leaves the uterus narrower and in consequence longer than before, but the pressure in the sac about the fetus does not reach more than that of 10 cm. of mercury. The liquid forms a sac in front of the now somewhat advancing head, and serves until the sac ruptures as the best of dilators for the external mouth of the womb.

In the second stage of labor the abdominal muscles are put in action to aid the uterine contractions, and rhythmically contract, thus powerfully pushing from above upon the elongated uterus now closely pressing the child on all sides save in front. The vagina is, then, the path of least resistance, and gradually and slowly the advancing head makes its way through it along the curve of the pelvis. At last, after a few minutes of excessive pain (properly always relieved by an anesthetic), caused by the over-stretching of the nerve-filled vulva, the relatively rigid head emerges from the maternal body. The softer shoulders and body so on follow, and the second stage of labor is finished. These two stages differ greatly in length. The first stage averages about thirteen hours in primiparæ and nine hours in multiparæ, while the second stage lasts about one-and-one-half hours in both. Sometimes, however, the first stage lasts two days or more, and seldom less than an hour, depending on the variable relations of the size of the child, of the pelvis, and the muscular powers of the mother.

The third stage is the expulsion of the placenta by the uterine contractions. It is usually complete within ten or twenty minutes after the child is born. The coming-away of the placenta gives rise to more or less hemorrhage, the average amount being about 400 c.c. After the placenta is delivered the uterus normally contracts strongly, thus preventing further and dangerous hemorrhage.

The muscular phenomena of labor may occur by direction of the spinal cord alone, for the whole process from conception to delivery is possible in dogs whose spinal cords have been severed at the first lumbar vertebra (Goltz). As we have said, the movements of the uterus are largely "automatic," but are regulated and adapted by the inherent nerves. They may be initiated by reflex impulses from any part of the reproductive tract (*e. g.*, the nipples) or even from the brain, as when fright causes miscarriage.

Lactation.—After the muscular and mental strain of labor a few hours of sleep are usually necessary and are very beneficial. The child being then put to the breast, the sucking-process reflexly causes the uterus to contract, thus more surely preventing hemorrhage. It also removes the colostrum from the mammary glands and makes them ready to secrete true milk. The latter begins to appear about twenty-four hours post-partum and normally becomes abundant within the next day. Nursing should be allowed only once every two hours between six in the morning and the mother's bedtime at night, and only once in the night. After six or seven weeks the two-hour period should be lengthened by a half-hour, and after four months by an hour. Once in three hours is then the most beneficial arrangement for both mother and child, and night-feeding is usually unnecessary after the first four months. As is the case with other neuro-muscular mechanisms (*e. g.*, defecation), the habit of vigorous promptness is important and hence nursing should be accomplished in fifteen or twenty minutes, and from each breast alternately, one breast at a meal. Regularity in taking food is of very essential importance to the child, the danger of feeding too seldom being much less than that of eating too often.

The mother's best diet for large and adequate milk-production is of the ordinary sort save that it should be generally rather more abundant and richer in proteid (fresh meats) and in liquid. Sufficient muscular exercise out-of-doors is important in maintaining an ample milk-supply. A large proportion of the infants who die in summer from intestinal disease are babies fed on food other than mothers' milk.

DEVELOPMENT.

Our concern thus far in describing how the adult racial individuals are reproduced has been largely with the parental part of the process. We have glanced at the operation of the generative mechanism and have discussed the formation of the egg of the new being and the complicated way in which it is made fruitful. Now our view-point changes somewhat. We shall look at things hereafter from the offspring's stand-point and make it our business to outline, if dimly, some of the tangled processes which culminate normally (but how often not!) in the average adult man or woman. Forty weeks of these forty years the new being passes in its mother's womb, and meanwhile is physiologically, even if not morally and legally, a part of its mother's being. This is the fetal life. From the hour of birth until puberty is another period of development, about fourteen years long, and this we may for convenience term *childhood.* For the next thirty or forty years or less *maturity* keeps up a somewhat variable level of strength. Beyond this, evolution is apt to become involution, and this period of *old age,* commencing almost imperceptibly, ends inevitably in death. Contrasting the human adult with the once-divided ovum, one realizes what "development" means. Only an expert embryologist could tell the human ovum at this stage from that of any of a thousand other species, yet the adult man or woman has a physical and psychical nature which is unique and, taken as a whole, the summit of organic evolution on the Earth. This is so, however, not because the protoplasm on which this nature is somehow based is superior in any way to that of other animals and plants, but because this human nature goes far beyond that of these others and reaches values which are probably both permanent and real. With all these more actual human values biology as such has nothing to do save to recognize their existence and to admit its own inadequacy as a science of human nature.

Fetal Life in a broad sense of the term includes the period of development between the union of the nucleoplasm of the male and female pronuclei and the completed birth of the child. This is the subject-matter of human embryology, and partly because this science is considered a portion of anatomy rather than of physiology, we do not discuss it here.

Childhood.—The fourteen years or so between birth and puberty we may, although not technically, know as childhood. Its beginning is the separation, for the most part, of the new individual from its mother's body. Its other terminus is the commencement of the time when this new being may in turn become mother or father to another generation. In most all respects childhood merges into adulthood gradually. It is only in the reproductive phase of bodily function that entirely new events begin, although these widely pervade in one way or another both the body and the mind.

The commencement of childhood so far as the various bodily functions go is likewise gradual in some respects. Yet the unique act of being born, the beginning of respiration, of digestion, of excretion, the changes in the circulation, and the beginning of action in most of the sense-organs make the extra-uterine life sufficiently different from that within the womb. Formerly the fetus was influenced from without itself almost wholly (aside from mechanical impacts wholly) through the mother's blood. Now, however, it begins a much more varied career and becomes more nearly unified with its environment through many various channels and in a large number of respects. As Fiske long ago pointed out, it is because of man's uniquely long childhood more than anything else that his general predominance in the world is due, for meanwhile he imitates his parents.

The ovum has increased in mass more than nine hundred million times by the time the child is born, and has seen the "division of labor" in case of its original functions go on in hundreds of directions and in thousands of steps. The human animal when born (although made up of cells basally like the ovum) has a cellular tissue-complexity and differentiation beyond all understanding. At the birth of the individual these myriad cells take on a new set of relations to each other. The child begins a new group of developmental changes—his long second step toward maturity. Let us glance at the most important of these sorts of growth.

Weight.—The average weight at birth of the female child of American parents is about 3150 gm., or 7 lbs., and that of the male child is 100 or 200 gm. more. Largely for the reason that the average infant assimilates little nourishing food for the first day or so, its weight falls in two or four days 175 gm. and often more. In babies fed from vigorous breasts however, this loss is often much less or even none. At ten days old the child weighs 100 gm. more than at birth. For the first six months, speaking roundly, the infant gains 25 gm. daily, and for the next six months 15 gm. The birth-weight is about doubled at five months and trebled at fifteen months. When a year old the child weighs 9000 or 9800 gm. (20 to 21 lbs.), and this weight is doubled at seven years and quadrupled at fourteen. Breast-fed babies gain in weight much more regularly and certainly during the first half-year, but later the difference between these and those fed from the bottle with modified cows' milk is not so marked. As before remarked, the liability to death is very much greater in bottle-fed infants, especially if the milk be improperly modified and cared for.

The proportions of the various organs differ not a little in childhood and adulthood, Of these the relative weights of *brain* and *spinal cord* to the body are most conspicuous. According to Bischoff, the brain at birth weighs one-eighth as much as does the whole body, at the end of one year one-sixteenth as much, and at fourteen one-twentieth as much. In the adult the brain is only about one forty-third of the body by weight. Similarly with the spinal cord: at birth it is one five-hundredth as heavy as the body, but in the adult only one fifteen-hundredth as heavy. This relative preponderance of the nervous system is clearly seen in the conduct of the child. The actuating aspects of the nervous system are especially conspicuous, while its inhibitory functions are relatively little developed

The *liver* and *adrenals* are relatively large in childhood, the *spleen* relatively small, while the *heart* bears about the same proportion to the body-weight at all ages.

Height.—The average length of babies when born is 49 or 50 cm. In a year this has increased to about 70 cm., in two years to 79 cm., in three years to 86.5 cm., in four years to 93 cm., and at the end of five years the average height is almost a meter. After this period the child grows not far from 6 cm. yearly, so that when he or she is fifteen the height is just about treble that at birth, or 150 cm., its doubling having occurred at the beginning of the seventh year. Rotch notes that growth in height is fastest in the spring.

Nutrition in children is in general more normal and vigorous in all directions than it is in adults, excepting in the first few months. The full powers of the digestive enzymes do not develop all at once, but more or less gradually in the first third or half of the first year. This is particularly true of the amylolytic juices, and starch is particularly ill-digested in the first months. Normally, that is in woman's milk, the only carbohydrate ingested is lactose or milk-sugar. In general, however, the child from three years onward digests more vigorously than the adult does, for the supply of digestive juices is proportionally greater and the alimentary movements more active. It is by this means that the child's commissary organs are able not only to replace the protoplasm worn out by the intense youthful activities, but to do more—to cause the rapid growth of the body. As we have just seen, this causes a doubling of the body-weight between seven and fourteen years. The child's digestive system, like all his others, is more plastic and more adaptable than the adult's, for it has not as yet become habituated to certain ruts in part of mental origin but always in the nature of defect, such as most grown-up persons fall into.

Muscular action in childhood is more lively but inherently less accurate than that of the adult. The ultimate usefulness of youth lies in its ability to elaborate the neuro-muscular mechanism into the wonderful perfection seen in the capable and clever adult. All know how vastly complex is this machine, and how countless its coördinations and its combinations of movement. In the infant up to four months or so voluntary movements are of no immediate use at all, for they are so much at random and so grossly inexact as to be only general tendencies of action toward some object or end. From this, the merely formative stage of neuronal inter-knitting, up to the expertness of the clever craftsman or performer in a thousand different ways, the development is in the direction of the acquirement of better and ever better and more numerous coördinations and neuromuscular adjustments. For this the new individual was created.

The *circulation* during childhood differs from that in adult life chiefly in its irregularity and variability. Especially is this so in girls and during the first six or eight years. This is due to several causes, among which are the greater elasticity and variability of the tissues, particularly the blood-vessels; the incomplete development of the circulation-regulating nerve-centers; and the greater irritability of the nerves. There is often a better-marked dicrotism in the pulse of a child than can be found in adults, due doubtless to a greater elasticity of the arterioles. The pulse-rate appears to lessen from its beginning early in fetal life (up to about seventy years, when it increases slightly), and to be always faster in females than in males. As was said above, in the fetus it is from 160 down to 110 or so; at one year it is about 110; at four years, 100; at eight years, 85; four years later, 80; and in adult years from 70 to 80. For girls the rates are considerably higher. According to Vierordt the *circulation-time* at birth is twelve seconds, while recent research has shown the time required in the adult to be about forty seconds. There is little satisfaction to be had clinically in the child's pulse, because it is so variable a process even in perfect health, especially up to the ninth or tenth year.

Owing to the more active muscular life and metabolism of the child, his *lymph-flow* is livelier than that of adults, and the vital process is correspondingly strong while the lymph-glands and the lymph-vessels are relatively larger. Digestion, especially of fats, is relatively better in childhood, and the lymph takes an important part in the process and in nutrition in general.

Respiration during childhood differs likewise from the adult process chiefly in its greater activity and in its larger variability under different circumstances. The breath-movements are more diaphragmatic and abdominal than in the adult, the intercostal muscles being relatively weak. The respiratory movements of the chest, according to Uffelmann, are at birth 35 per minute; at one year old, 27; at two years, 25; at six years, 22, and at twelve years, 20. Very often, indeed, however, one sees breath-rates averaging five higher than these figures indicate. The breath-rhythm is very vague during the first years of life, and varies greatly from little causes, such, for example, as emotions, muscular activity, and physiological variations in body-temperature. Periods of apnea of short duration are normal, while the rate on either side of such a period may vary many breaths per minute, being at one time 70 and at another 40. The imperfect connection of the various vital centers in the medulla plus the relative strength of the emotional expressions will in part explain these irregularities.

The bronchi and trachea are proportionally larger than in adulthood, while the alveoli are relatively smaller. Partly because of this we find the common pneumonia of infancy to be of the bronchial type, while that of middle life affects the alveoli more especially: lobar pneumonia.

Body-temperature is another function of the child-organism which is characteristically variable and irregular by the adult standards. For a few days after birth, owing to the lessening in the metabolism from lack of assimilation, the degree of heat may fall a degree or so below the daily average of about 37.2° (99° F). Exposure decreases the temperature readily. Raudnitz found that a cold bath raised the temperature (as indicated in the rectum) in vigorous new-born children, but lowered it in feeble infants. If we take 37.2° (99° F.) as the average temperature of the first ten years, it must be considered the same as all averages—that is, as more or less artificial. The causes of variation in temperature are numerous, and many of these in childhood frequently produce effects much more marked than they would among adults. Thus, excitement, especially mental excitement, and intestinal irritation of a trivial degree, weak toxins, or fatigue may raise the temperature of the child of two or three years in a way not observed in the child of ten nor in later life. This great variability is especially marked in girls, but in both girls and boys it constitutes the chief peculiarity of the temperature during childhood. A temperature of 39° (102.2° F.) in an adult usually means something of consequence, but in a three-year-old it often signifies nothing which a movement of the bowels will not promptly dispel. Here, as elsewhere, we see the signs of neural incompleteness and of nervous instability.

The *senses* of children are in general more acute than are those of adults, save in so far as training is involved in developing the actual sense-organs. Sensations, however, by themselves are of little use comparatively, aside from their meanings to the individual. The child is relatively deficient in his apperceptive power and does not yet know, moreover, how to use his senses to the best advantage. Hence the effective result of sensation in general in childhood is far below that of the adult, although the latter's actual sense-organs may be less perfect as mechanical instruments than are those of the child. (See the preceding chapter.)

More marked, even, than the bodily characters of childhood are those of the *Mental Aspects* of the individual when young. Into these, so amply discussed are they in pedagogical and psychological literature (*e. g.*, by Stanley Hall), we cannot go here. Three principles, however, may be mentioned which are more or less important in medicine. First, the young child lacks mostly whatever degree of voluntary control over the physiological and reparative processes the adult mind exerts. This makes the child a more passive and more plastic patient as well as pupil. Its physiology is perhaps to be found in the incomplete command over the so-called "voluntary" musculature which is so conspicuous an aspect of childhood. How far this control extends over the vegetative functions in the clever and accomplished adult we do not as yet commonly appreciate.

The child is relatively naïve and open to all kinds of influences. Habit in this period of life has not yet laid its all-encircling and resistless fingers on both the body and the mind. Children therefore are more amenable to all sorts of therapeutic and hygienic measures, and especially to those which, like suggestion, do their work through the mental processes.

Worry has not yet fixed its hold on the normally cared-for child. In the adult this is a source of harm whose importance it would be hard indeed to exaggerate. Chronic emotion of fear as worry is, its asthenic effects on bodily processes are certain, and none the less so because the mode of its action is not fully made out. It is hard not to believe, as has been suggested, however, that worry through the trophic nerve-impulses depresses the metabolism and so undermines the resistance of many kinds of tissue. Working in the opposite direction of invigoration and stimulation, joy and happiness exert a wholly beneficial effect on the vital functions. Childhood, normally the joyful age in our perhaps too strenuous civilized life, receives the full benefit of this continual sthenic influence. Not a little of the versatile freshness of the child's bodily metabolism may come from this sort of mental stimulation—as it may come to all humanity centuries hence, when the old-time worries, largely based on the struggle for existence and good health, may be outgrown.

Maturity or adulthood is the general subject-matter of ordinary physiology and needs here no separate discussion. So far as the general activities of life most useful to the world's evolution are concerned, it is preëminently the period of achievement. It is, for example, the period of reproduction, biologically one of basal life-functions. It is the epoch of the bodily strength which in the childhood before it has been developing and which in the senescence after it will gradually lessen again. This gradual accumulation of experience, wisdom, etc., during the period of maturity changes the nature or quality of the individual's capacity, and (as when one wrongly tries to compare the values of men with those of women) one finds comparison therefore between maturity, childhood, and old-age more or less illogical except in terms of bodily strength and the somatic functions. These latter maturity exhibits at their best, but no one should fail to see the more substantial compensations of the life-period which follows it in a portion at least of the individuals who are born.

Old-age is the fourth period of the epochal differences which we need to consider—and the last. How, physiologically, does it differ from the average status of maturity? We may in a word suggest all these differences (save as has just been mentioned) by the term decline, "a bending-downward" toward death, a general weakening of an inherently limited organism. In the preëminent respects above suggested, then, senescence is a superior condition, but in most regards it is the inevitable decay of the "unremaining glory of things that soon are old."

The *weight* and *stature* both are regularly less in old-age than in the epoch of maturity.

The causes of the slowly progressive decrease in *weight* are chiefly the lessening of the water-content of the skeleton; the disappearance of the fat from the body generally, but especially from the muscles; the skrinkage of the muscles (and glands?) from their relative disuse; and the weakness of the nutritive process, making now the growth-balance negative instead of positive, as in childhood, or zero, as in middle-life. Fat represents especially the storage of nutritive tissue, and in old age, unless the digestion be unusually vigorous, this surplus is not produced and stored. The bones become more brittle as age advances: they lose water, collagen, and fat, and become more calcareous.

The reasons why the aged body is less in *size* than that of middle-age are in part those just cited as explaining the loss in weight. The stature is less because of the shrinkage of the interosseous cartilages generally, and especially of those between the vertebræ. These plaques lose collagen and chondrigen and in so doing become both thinned and less elastic. In persons accustomed to much manual labor that requires a stooping posture the spinal column has acquired a dorsal bend which further decreases the stature.

Nutrition in old-age shows the most fundamental differences belonging to this epoch. In no one respect especially, but in all of them, the assimilative process has degenerated. Mastication is imperfect because few or many of the teeth are gone or broken. Digestion is defective partly because the alimentary movements are weakened with the other muscular activities and partly because the digestive liquids have no longer their former abundance or (probably) strength. It seems likely that the failing power of mastication is the more important of these deficiencies, although the muscular atonicity of the gut must be also a weighty factor, for we see much harm coming from constipation.

The chemical defects if any in the digestion, absorption, assimilation, and excretion incident to old-age are not as yet well known. Habit must play an important part, for it extends even to the chemism of the nutritive processes.

Next to nutritional defects those of the *circulation* are undoubtedly most characteristic of old-age, and are perhaps even more frequently the cause of death. The most important perhaps of these changes is the sclerosis or hardening of the arteries. In old age this is physiological rather than pathological, and is always present in some degree after fifty. It consists of an atheromatous condition of the arterial wall, especially in the larger tubes. Sometimes the change is fibrous, but much oftener calcareous, the essential elasticity of the arteries being in either case diminished or almost lost. This makes it necessary that the heart should work harder to keep up the activity of the capillary-circulation, and it therefore becomes enlarged. Often the heart-walls too are affected in like manner. If a large brittle arteriole burst in the brain, there is apoplexy and resulting death sooner or later; if the heart gives way or fails to meet the demands put upon it, there is likewise death, either at once or after weeks of dropsy, dyspnea, etc. Minor degrees of these conditions are essentially normal after old age has begun, but that they would be so common did not people so often over-use alcohol, dissipate, under-exercise, and eat too much, no man at present can be sure. It remains to be learned through statistics whether lactic acid (found in butter-milk) if taken continually would prevent or lessen this arterial sclerosis so frequent among people more than fifty years of age.

The *pulse-rate* is increased in old-age five or ten beats, this increase being necessary, as well as the heart's hypertrophy, to compensate for the inelasticity of the arteries.

Body-temperature.—In old age the temperature is slightly higher on the average than in middle-age, and nearly equals that of infancy. This is brought about, despite the lessened metabolism of advanced age, by the decrease of vaso-motor power. The peripheral vessels are relatively more rigid and smaller than in middle life and so lose less heat from the blood within them by radiation; and less sweat is produced. Despite their rise of temperature, old persons usually feel chilly unless their environment be warm, and frequently when in good health, even in high temperatures.

Respiration declines in old-age largely because of the defects in the circulation, but also because of the hardening which the costal cartilages undergo, and also from the weakening of the intercostal muscles. Expiration especially becomes more difficult because these cartilages are less elastic. This is one reason why broncho-pneumonia is so common and fatal in old persons: the difficulty of coughing and expectoration allow the irritating mucus, bacteria, and other substances to collect in the lungs.

By the lessening of the respiration the great oxidative process of the tissues is decreased. This is one condition of the smaller metabolism so general in old-age: the fuel is lessened and the vital fire burns ever more dimly out.

The *muscular activity* in old-age is greatly diminished. The bones lose their small degree of pliancy, the tendons and cartilages stiffen, the muscles lose part of their strength and their power of endurance because of the lessened circulation and nutrition. The joints move with more or less difficulty. All these conditions combine to decrease to a minimum bodily movements of a voluntary sort and to lessen the activity of the vegetative smooth muscles. In addition the perfection of adjustment and coördination is lost. When the muscular weakness is considerable, the graceful balancing of youth and middle-age at last gives place to a trembling and uncertain mode of movement characteristic of very advanced age and called decrepitude.

The *senses* undergo changes often some time before other alterations are apparent. The accommodation of normal eyes begins to lessen even in infancy, and by fifty years the lens has become so rigid as to necessitate the use of convex lenses in order that near objects may be clearly seen. The general hardening of tendons, etc., has by sixty years often checked the free adjustment-movements of the ossicles of the ears and made slightly less movable the membrana tympani. The sense of touch is regularly blunted and that of pain somewhat so. In general the mental processes are slowed and rest becomes natural in larger proportion than formerly, in a way corresponding to the lessened strength.

Death.—Physiologically, death is not development but the cessation of development and of that "continual adjustment" and ceaseless chemical and physical change in which bodily life essentially consists. Metabolism stops and thereupon the former protoplasm is no longer protoplasm but only animal matter liable at once to that retrograde series of changes which ends in distributing the elements of the former organism into other shapes, whether living or dead.

There are two sorts of death, corresponding to the two orders of units, the cell and the individual animal. Let us look briefly at cellular death first.

The essential thing about the death of a protoplasmic *cell* is the cessation of its metabolism, because it is in that process largely that life inheres. Whether the nucleus or the nucleolus or the centrosome or none of these organs controls the cell's activities we do not as yet know, and hence we can state nothing as to the process of its death. Pathology is that branch of biology which discusses the various steps toward death to which cells are liable, and to the text-books of that science the reader is referred for the facts and theories as to cytological death. The important thing for us here is that cell-death of one sort or another, in one organ or another, is always the cause of the death of the entire individual, the higher unity, just as in turn a race dies only from the death or decay of the individuals composing it. When, as always happens in all animals save unicells, the death of some cells precedes that of others, we have the condition termed by Schultz necrobiosis (death-in-life). Poikilothermous animals show this process best, and it is because of it that frogs and turtles and batrachians generally are so useful to humanity for studying some of the conditions of life. Homotherms die all over much more rapidly. This is apparently due to their more elaborate nervous systems in part, but chiefly to the fact that when the circulation stops, body-temperature rapidly falls, and this disturbs in many ways the osmotic and chemical metabolism. Even in mammals, however, certain sorts of protoplasmic activity continue a considerable time after the animal as an individual is dead. Thus, the cilia keep up their rhythmic swaying three or four days, and the leukocytes, still more independent, continue their ameboid movements for a week or more, these being still surrounded by their usual nutriment, the plasma. Just in proportion, then, as a cell is immediately dependent on its environment for nutriment, heat, and removal of its waste, does its death closely follow the cessation of the circulation and of the respiration. (See Expt. 51 in the Appendix.)

Hibernation has to be thought of as a partial cessation of cell-life, for the circulation and respiration (*i. e.*, nutrition) then continue only in a very restricted manner. As we have seen already, human hibernation is sometimes induced voluntarily, as by the fakirs of India. Even normal sleep perhaps is a low degree of this lessening of the general cellular activity of the organism.

On the other hand, the exact biological status of the dried state in which certain minute animals of our aquaria, notably Tardigrada, can pass, remain months, "or even years," and yet revive readily on being immersed in water, is at present quite unthinkable. It is unlike death as at present defined by biologists, but yet it seems to fail of the death-conditions only in its persistence, the non-decay of its protoplasm, and in its power of recovering the usual activities of life. This state seems to imply that it is only the decomposition of protoplasm, its katabolism unaccompanied by anabolism, that prevents the continuance of life so long as body-decay can be prevented and its protoplasm be still unpoisoned. But so long as we do not know as yet whether what we call life is a uniform thing, essentially alike from Haeckel's "monera" to man, or whether it may not be of many sorts rather, nothing worth the reading need be speculated in this direction. The phenomena of complete drying followed by revival, however, suggest strongly that in the tardigrades, etc., at least, the cessation of cell-metabolism may not mean the death of the individual animal. (See Fig. 129, p. 236.)

The nature of *individual-death* has already been suggested in the foregoing. It is a less scientific term and a more practical and legal expression. Oftentimes a person thought dead is not so, but very seldom is a person who really is dead supposed alive. On this account the danger is considerable and the means of knowing when an individual is really dead, that is unrevivable, are important, and that too aside from the legal relations of the problem.

The common law generally recognizes a person as dead when his heart has ceased to beat. As we have seen recently, the heart is about the first organ to begin to move in the fetus, and in Daphnia, for example, on drying up it is the last to die. This presumption that the cessation of the pulse or of the apex-beat is the forerunner of death is a proper and usually a precise one. Life is mostly dependent on metabolism, and this in turn immediately on a supply of nutriment and of heat, and on a prompt removal of katabolic waste. The instant the circulation all over the body stops metabolism with certain exceptions comes at once to a standstill. The brain is especially dependent from second to second on a rapid stream of normal blood. Suppose a person in the standing position to be shot with a large bullet through the heart, or that the heart of a man with myocarditis bursts or stops short in extreme diastole. In any of these cases the skeletal muscles instantly lose their tone because the vast multitude of impulses which pass continually from the motor centers to these sustaining muscles immediately cease. As a result the man drops almost instantly when the blood-stream has ceased, and that is immediately. In parts of the body other than the nerve-centers the effective metabolism continues somewhat longer, and yet not long enough to sustain the body-heat for any appreciable time, for the body cools much as would one artificially heated when the source of heat is removed. Recent work on the heart has shown that in cases where the organ is not materially injured (as from lightning-stroke or from blows over the solar plexus) it may be often started beating again by cardiac massage either directly or through the pericardium. This indicates that the nervous inhibitory shock has no permanent influence over the heart's rhythmic pulsations. (See Expt. 15 in the Appendix).

Respiration is another function whose cessation promptly kills, but it does not do so as quickly as the stasis of the circulation, for survival sometimes occurs after the intake of air has been stopped for as long as five minutes. The modes of death other than nervous shock, the stopping of the pulse, and the cessation of breathing we need not consider. It is already obvious how individual death differs from cellular death. The former term means the end of the general faculties—movement, sensation, posture, etc.—of the whole organism so far as appears from without. The latter expression means the really essential physiological death. Individual "death" may sometimes be recovered from; cell-death, so far as we know, never.

Physiology has at present no concern with the chief personal problem of the human race—persistence after death. This subject even psychology still almost ignores, and scientific ethics knows next to nothing of it. Death, indeed still "the Arch Fear in a visible form" to many unthinking men, must from considerations other than these receive its quietus in the soul of humanity.

APPENDIX.

Containing directions for performing certain fundamental physiological experiments, with brief theoretical notes on the same; a list of topics suitable for essays and conference-discussion; and conversion-tables of various sorts.

LABORATORY PHYSIOLOGY.

The following pages relating to the work in practical physiology in the laboratory contain some of the theory underlying the experiments, but more must be obtained from the text-books in which adequate discussions of all important matters are set forth. There follow also concise, but indispensable, directions for doing in an orderly and scientific way numerous basal experiments, together with the physiological principle which it is the chief purpose of each experiment to demonstrate. To do the laboratory work without a full understanding of its various theoretical relations would be, of course, only the training of an artisan.

Every experiment is to be performed successfully and well before the next is taken up. To prove that this guiding rule of the laboratory is lived up to, every experiment is to be demonstrated at the time it is being done to the instructors in charge, or when the graphic method is employed, evidence to the same effect in the form of the original curves, properly labelled in all their details, pasted into the note-books. The excellence of these curves recorded in the note-books largely determines the standing of the respective students in the important practical part of the Course, but good notes are next in importance to good curves. These are to be written in the laboratory directly from the experiments. Make *notes*, then, and not pictures merely, which shall record your own observations. *You have to use your common sense all the time!*

I. PROTOPLASM AND SIMPLE ANIMAL FUNCTIONS.

The first work in the laboratory consists of a series of careful observations with the compound microscope of a number of selected animalcules. We do this chiefly for two reasons, the first that you may become familiar with protoplasm in its less differentiated forms (the human body consists of highly differentiated protoplasm). The other reason is that each of these animals, however small, exhibits all the basal functions possessed by any animal, yet in a form so simple as to be much more readily analyzed and appreciated than is possible in the most evolved forms. The life of any order and species of plant or animal is as perfect as that of any other.

There is here immensely much to be seen by him who has brain and eyes to see it, and life is one, apparently, whether in infusorium or in man.

> "Flower in the crannied wall,
> I pluck you out of the crannies;
> Hold you here, root and all, in my hand,
> Little flower—but if I could understand
> What you are, root and all, and all in all,
> I should know what God and man is."

Each student will get out of the laboratory work in physiology, and especially out of this first portion of it, that which he is fitted by his intelligence, training, and industry to acquire.

Experiment 1.—The first slide given out contains some of the simplest forms of living *vegetal* and *animal cells.* The vegetal cells are here growing filaments of a common alga, Spirogyra, or of another still more common, called Edogonium, seen as lines made up of rectangular yellowish cells more or less filled with protoplasm colored green with chlorophyll (plant-green). Use first a No. 3 objective to find a filament made up of cells as large as possible. Note the geometrical, rigid structure of the cellulose cell-walls, and that the cells are lacking in means of locomotion. Now employ a No. 5 objective and draw in the note-book any changes observable in the arrangement of the essential living protoplasm within the cells. Make large drawings of all observed detail.

Compare with these vegetal cells the minute infusoria rapidly swimming about them—animal unicells made up wholly of soft protoplasm not confined in rigid cellulose walls. Note that the animal protoplasm probably is uncolored by the green, hemoglobin-like pigment chlorophyll; a lack which prevents animals from synthesizing starch out of its inorganic elements. Note their rapid movements, in search of food, by means of cilia; and that they seldom or never quite collide with each other. Observe if possible individuals each about to divide into two new animals smaller than their parents but otherwise similar. Make numerous drawings showing all possible details. (See Chapter I.)

In a mixture such as this practically only one thing usually distinguishes plants from animals, and that is the presence of the green pigment chlorophyll. The usual criterion of animality employed for higher forms, the rapid movements, will not answer with these simple forms of life, for some of the green plants have active swimming movements and some of the animals are motionless and green (see Euglena). Still many plants contain no chlorophyll—and there is left no strict standard whatever for discriminating a plant as such from an animal.

Expt. 2.—The second allotment consists largely of a very much mixed mass of common saprophytic *bacteria* and *cocci* which grow on nutritious liquids when exposed to the air and light. Observe the minuteness of these vegetal cells; their vast multitude and their spontaneous movements.

For knowledge of the bacteria see the text-books on bacteriology.

Expt. 3.—The third slide contains the important protozoan rhizopod *Ameba proteus.* (See Chapter I.) Use a low-power (two-inch) objective to find one of these, *the simplest of living animals.* Note its transparency, its extreme simplicity, the nucleus, the metaplasm, and the vacuoles. Watch its slow creeping along the slide and their quite characteristic and unique use of protoplasmic streaming into pseudopodia for locomotion, and for surrounding food-particles. Observe how it tends to contract in area on being stimulated and that it gradually extends numerous pseudopodia again when allowed to rest. No cell-wall can be discovered. Observe food-prehension and vacuole-bursting.

Make drawings of as many shapes of one ameba, in definite successive periods, as possible. If necessary, use the warm-stage.

This observation of Ameba (because the type of relatively independent undifferentiated protoplasm) is one of the most important experiments possible in class-work in physiology. Here is the very essence of spontaneous vital activity. Do not miss obtaining much from it in the hours allotted to it. See text-books of biology for details.

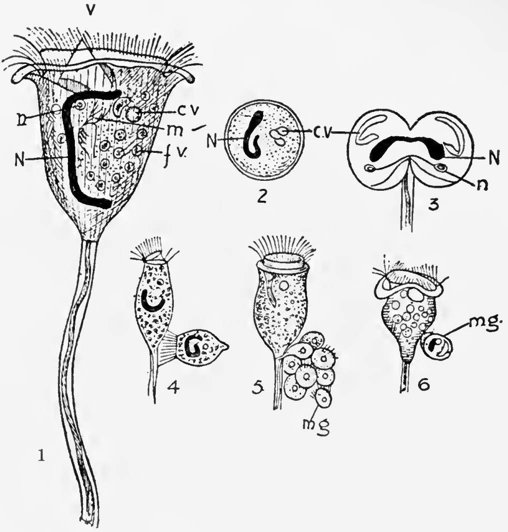
Expt. 4.—The fourth allotment on the slide contains one or more species of the ciliated infusorium *Paramecium.* Use first the No. 3 objective and observe this unicell's mode of poking about among the vegetal and mineral debris in search of food, much as fishes do. Note its various movements, backward and forward with almost equal facility; its mode of turning shows well the fluidity of the protoplasm. A large paramecium is said to weigh about 0.00017 mgr. and to be capable of raising 0.00158 mgr.

Now adjust the No. 5 objective and kill the animals by gentle heat or poison them with a drop of a 1 per cent. chloral hydrate solution, which gradually slows their movements without quickly killing and disintegrating them. Observe among other things their ciliary movements and the various elemental organs within. Make careful drawings of these animals, with all discernible detail, at intervals if necessary to indicate changes. Paramecium merits all the observation and study that may be put upon it. Parker in his *Biology* has an excellent description of this animal as well as of others of like interest. See Jennings for the mental processes of Paramecium, and Conn.

The infusoria are so named because they appear in multitudes in the course of a week or two in infusions of hay, dead leaves, and similar nutritious substances. Ameba is the most difficult to be sure of having at any given time, and Stentor is often scarce; but Vorticella, Tubifex, the Rotifers, Cyclops, and Daphnia (the second a worm and the two last crustaceans) can generally be found in balanced aquaria from which fish and large larvæ are absent. Cyclops and another crustacean, the bivalved Cypris (of little use to us because its shells are opaque), are much easier to keep year after year than is Daphnia; nearly every permanent pool contains these forms in abundance. Ameba readily persists year after year in aquaria where fish are present, although they disappear at times temporarily.

Expt. 5.—The fifth specimen is a remarkable ciliated infusor named *Vorticella.* We have already probably seen early stages in the development of this animal as small spherical transparent masses of protoplasm rolling about through the drops of water on the previous slides. A later stage shows a circular fringe of cilia developed on one side of these spherules and a pointed short projection on the opposite side of the animal. A still later stage shows animals with this process developed into a long contractile filament, the muscle-stem of this unicell, which the vorticella drags behind him as he rapidly sucks his way through the water by means of the cilia at the vortex. Soon a sort of hook develops at the end of this filament and catches upon some mass of vegetal matter and thus anchors the animal for the rest of its life of a few days. Draw all these forms. See also if possible the colony-form, *Zoöthamnium.*

Fig. 255



Vorticella, showing various phases and the modes of reproduction: (1) *N*, macronucleus; *n*, micronucleus; *cv*, contractile vacuole; *fv*, food vacuole; *m*, gullet; *v*, vestibule; (2) an encysted phase, with 3, its mode of division; 4, a free-swimming unit dividing off; 5, formation of several small units (*mg*); 6, conjugation of a small zoöid (*mg*) with one of larger size. (Bütschli.)

Observe in the anchored variety of Vorticella (1) the vortex of water (and contained food) passing into the animal; (2) the internal organs; (3) the very quick spiral contraction of the stem-muscle when the animal is jarred or otherwise stimulated; (4) the gradual probably passive extension of the animal on the end of the uncoiling stem; and (5) that the muscle soon becomes fatigued and fails to respond to stimulation.

Count the number of spontaneous contractions of the more or less rhythmic smooth muscle of the stalk occurring in ten minutes. (See *Comptes Rendus Soc. de Biol.*, 1904, lvi, p. 764.)

The difficulty of defining individuality is finely shown by a comparison of Vorticella and Zoöthamnium.

Expt. 6.—The next specimen (to be studied with objective 3 first and then with 5) is *Stentor.* This infusor is more clumsy and many times larger than Vorticella, but has the same general mode of life. The contractile stem in this case is surrounded with cytoplasm largely lacking in Vorticella. The internal movements of Stentor are produced by the simplest sort of muscular fibrillæ longitudinally arranged about the periphery of the thick body-stalk. The animal sometimes secretes a delicate temporary cup-shaped shell about its foot, into which it quickly withdraws. Some forms, however, are free-swimming only.

Expt. 7.—*Euglena* (viridis).—This is a unicell of the flagellate sort from 0.05 to 0.15 mm. in length. As its name implies, it is brightly green and it is one of the organisms which sometimes color stagnant water. This infusorian has a cell-wall (cuticle)—note how it limits the shapes of the animal as compared with Ameba. Its movements are, however, various and characteristic. Euglena contains granules of some carbohydrate. The chlorophyll is contained in one or more chromatophores at the body-center. The bright red spot near the anterior (flagellated) end is the eye—a mass of pigment which can make the animal aware only of degrees of light and shade. The flagellum arises from the bottom of the mouth and draws food-particles into the gullet by the vortex which it makes, and the same movements draw the animal through the water.

Draw all possible shapes of this minute protozoan and make notes of its peculiar features. It is well illustrative of the unity of Nature that the botanists claim Euglena as a plant-cell.

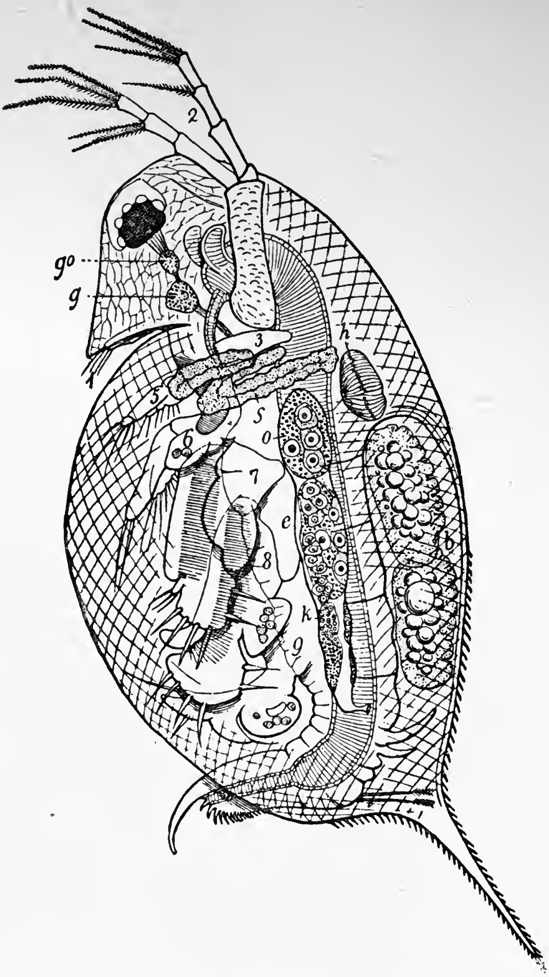
Expt. 8.—*Brachionus.*—This little animal is common in the sand at the bottom of ponds and fish-containing aquaria. It is one of the very curiously shaped class of Rotifers (wheel-bearers). It is a multicell of relatively complex organization, having an alimentary canal, a celomic cavity, excretory organs, reproductive glands, a nervous system including sense-organs, and muscles. It has also an elaborate body-wall.

Make out the trochal disk from which is extended in front the long proboscis-like organ with a prehensile arrangement at its end. See the conspicuous eye of red pigment. Study the telescopic nature of the trunk and especially of the long and slender "tail" with a pair of nippers at its end for holding fast to bits of vegetal debris by a complex muscular arrangement of claws. The tail in this species consists of four or five segments completely telescoping when the animal retracts. Note its inch-worm mode of travelling.

Another rotifer, Philodina, inhabiting our aquaria in large numbers, must not be confused with Brachionus. Its trochal disk is much more conspicuous, and is oftener open.

Expt. 9.—The next specimen is *Tubifex,* a multicellular round-worm living everywhere in the mud at the bottom of ponds, ditches, etc. Easily seen with the naked eyes, use objective No. 3 to study the often transparent protoplasm of this animal. Note especially near the posterior end a large slowly pulsating dorsal artery—about the first observed sign of a heart as one looks "upward" in the animal "series." Make

FIG. 256



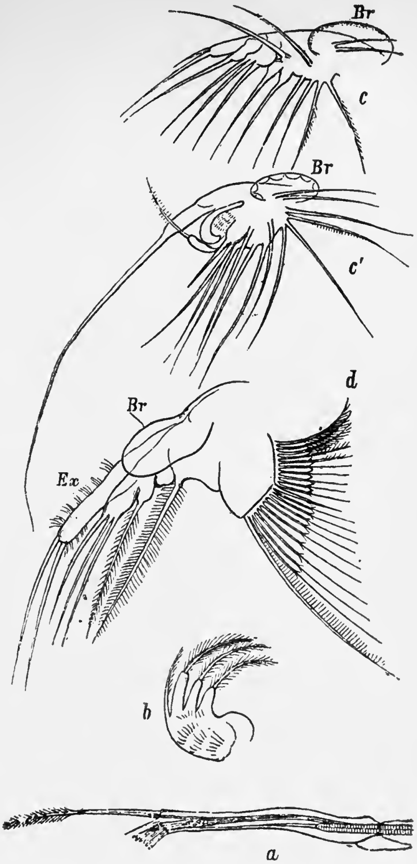
Daphnia pulex, De Geer: 1, antennules; 2, left antenna (the right not being shown); 3, mandible; 5 to 9, gill-feet; *b*, embryos in the brood-sac; *g*, brain; *go*, optic lobe with the eye above it; *h*, heart; *k*, *e*, *o*, various stages in the degeneration of the aborted eggs into food within the intestine. The long spine at the lower dorsal corner is a means of defence after the animal has dived into the silt at the bottom. The curved claw-like projection in front and below is used for removing intruding objects from without. (Hertwig.)

drawings of Tubifex, if possible, showing any interesting structures to be seen in the animal.

Expt. 10.—*Cyclops* is one of many genera of the Crustaceans which inhabit stagnant waters both fresh and salt. Note the general shape of the animal, and his antennæ in front with which he jumpingly swims rapidly through the water. Study the prominent alimentary canal (a yellow mass in the middle line) and its peristaltic surging back and forth. Note the single eye, a spot of pigment, above and in front. Note the symmetrical masses of eggs or of embryos which the females carry about, one mass on either side.

Expt. 11.—*Tardigrade* is used as a type of the animals which survive the dried and hibernating condition. Two-day demonstration of revival after drying. (See Fig. 129 and its legend.)

FIG. 257



Parts of Daphnia pulex, De Geer: *a*, the antennule of the male; *b*, maxilla; *c*, the first "gill-foot" of the female; *c′*, the same of the male; *d*, one of the second pair of gill-feet; *Br*, respiratory sac; *Ex*, exopodite. (Claus.)

Daphnia (*Expts.* 12 to 19).—The last of the microscopic animals we may study at present is *Daphnia*, a fresh-water cladoceran crustacean of great value and interest in physiology because of its extreme transparency combined with a relatively high complexity of development. The animal is to be studied flat on a slide with water too small in amount to allow of its jumping about. Note (1) the general striking effect of movement in every part of the animal at once; (2) the conspicuous heart, and the blood-corpuscles circulating over the body; (3) the single but compound eye, composed of omatidia (single eyes); (4) the eye-muscles in constant action; (5) the brain; (6) the alimentary canal with its surging yellow-green contents and its movements of peristalsis; (7) the gill-feet; (8) the brood-sack and its probable embryos in some stage of development from mere eggs to forms almost like their mother; (9) the antennæ with which it jumps in a characteristic manner through the water, etc. Add a drop of methylene blue in thin mucilage to the water close to the animal.

We study Daphnia as an *advance epitome of animal functions,* and perhaps nowhere else might we find so clearly and easily displayed so much basal physiology for the mere looking, without preparation of any sort. We may readily behold in little Daphnia the fundamental portions of the blood's physical composition and its circulation, respiration, nutrition, the nervous system, muscular action, and reproduction (especially embryology). We will divide our observation of these basal activities orderly as follows:

Expt. 12.—*The Blood and its Circulation.*—Careful watching of the head-region, especially between the eye-muscles, shows clearly even with a one-third objective the many-shaped one sort of blood-corpuscles of this colorless blood. These are the *amebocytes* corresponding to the leukocytes of man, but doubtless with even more functions to perform. As the name implies, these cells have ameboid movements. They are relatively few in number, as may be seen; compare the 10,000 to the cubic millimeter present in man's blood. If any respiratory pigment like hemoglobin exists in Daphnia's blood it is colorless. Its rate of circulation may be clearly seen by means of the corpuscles, as also its general course about the wide membrane-formed sinuses under the shell. The most conspicuous of these channels lies dorsad to the alimentary canal and in it pulsates the heart. Isolate some blood and examine its corpuscles.

Daphnia's heart (see Dearborn, *Med. News,* March 21 and 28, 1903 etc.), is as simple structurally and functionally as a heart well could be. It consists almost wholly of two series of smooth muscle-cells arranged on both sides of the dorso-ventral plane so as to form an ovate saccule open in front and with an ostium (for the blood's entrance) in the middle of each side. By the simultaneous shortening of these blunt fusiform cells the heart is made to pulsate. The rate usually is about 240 per minute, but it varies greatly with the temperature. The embryonic rate (see the brood-sac) is less rather than greater than the adult rate. The pulse-rate persists until the heart entirely stops, and is readily variable by the ordinary physiological salines. Irritation with a fine needle in the abdominal fold stops or inhibits the pulsations instantly. Study the cells of the heart, and its movements.

Nicotine in 2 per cent. aqueous solution gradually slows and stops the heart in diastole after several minutes of great irregularity. Digitalis in 3 per cent. aqueous solution of the tincture slows and invigorates it, but makes it irregular. Curare injected into circulation stops the heart at once. Chloral increases the power and the length of the diastole and slows the pulse-rate. Some of these drugs and many saline influences change the functional size of the heart in a way to strongly suggest the presence of the tonus which is so conspicuous, for example, in the turtle's heart and probably present in all hearts—a slow tonal contraction and relaxation beneath the pulsations. The existence of a two-phased nerve-control over this heart is at least exceedingly probable.

Expt. 13.—*Respiration* is carried on in Daphnia both directly by diffusion through the thin membranous, chitinous shell and by means of feathery gills attached to the four to six pairs of degenerate legs in the ventral middle of the body, when seen on its side. The former means is probably much the more important, the flatness of the animal, its small size, and the broad exposure of blood immediately under the shell making easy the direct exchange between the blood and the surrounding water. The movements of the gill-feet are, however, probably a respiratory reflex for waving the gills rapidly through the water, the shell being open on the ventral side. Occasionally the abdominal end may be seen to vigorously extend for the purpose of removing particles which have entered the shell and are interfering with the feet's free activity. Crush a Daphnia and study the freed gills with a higher-power objective.

Expt. 14.—*Nutrition* (including the preparation of food for the metabolism of the tissues) is mechanically a simple matter in Daphnia. Chemically, however, it may be very complex, for the food digested is largely proteid. The fine hair-like antennule near the end of the beak can be clearly made out, but whether it is an organ of taste, smell, or touch is not known. The mouth-parts are not easily seen. Observe the conspicuous quick peristalsis of the esophagus. Note the digestive gland at the summit of the anterior bend of the greenish-yellow gut close to the brain; this probably secretes the enzymes which dissolve the food. It pulsates as a continuation of the peristaltic waves which pass up the intestine. Sop a speck of cotton bearing croton oil (*poison*) on the animal. This soon causes a marked increase in the intestinal movements. Observe now the pulsations of the digestive gland. The peristalsis of the gut is an antiperistalsis and now, exaggerated by the oil, the waves may be seen to start at or near the anus and to pass in a typical way up the gut as far as the enlargement opposite the heart, but here a less definite surging sort of movement takes the place of the true peristalsis. *Study the peristalsis carefully*, measuring the speed of the waves, their frequency, etc. Within ten or fifteen minutes after administering the croton oil the entire gut is usually free of its former contents. Note the mode of defecation.

Expt. 15.—*Nervous Function and the Senses.*—Note the brain, the optic lobe, the nerve going to the antennules, the trunk extending from the brain. According to Lang, there is a ladder-like ventral cord consisting of seven pairs of ganglia, the foremost of which controls the mandibles and maxillæ, and the remainder the six pairs of legs.

Demonstrate the presence of nerves inhibiting the heart by a light puncture with a very fine bent needle over the caudal bend of the gut. The heart stops instantly. Oftentimes in a few minutes it begins to beat again (as does the mammalian heart after stimulation of the vagus).

The compound *eye* of Daphnia consists of five simple eyes or omatidia. The ocular muscles should be studied carefully and the movements which they give the eye. These movements are in some respects like those of the human eye. Note the nuclei of the muscles, and the thickening of the latter as they contract.

The frontal sense-organs on the antennules are conspicuous but of unknown function. It is possible that the antennæ bear auditory setæ and perhaps touch-hairs.

Expt. 16.—*The muscles* may be studied in both their aspects, reflex and voluntary. The heart, gut, and eye have shown us examples of the former sort. The first joint or two of the antennæ show well the pulley-action of the voluntary muscles in operating the limbs.

Expt. 17.—*Embryology.*—In many specimens may be seen dark-brown cases containing two eggs each, which are intended to persist when all the adults have died either of ice or of drying. These are the "winter eggs." In other females there are from three to eleven embryos crowded in the brood-sac above the alimentary canal. These may be found of every age from the mulberry stage up to the fully formed young daphnias ready to break out of the sac. The brood-sac contains an albuminous fluid which nourishes the young. The eggs begin in groups of four, and part of these break down to nourish the remainder.

The ovaries and testes are simple paired tubes; the sexes are distinct and males are relatively uncommon.

Expt. 18.—*Drug-actions* and similar effects might be studied largely on Daphnia with benefit, for here their action on brain, heart, respiration, and digestion might be actually observed directly in its details.

Expt. 19.—Finally, allow the animal to dry up on the slide. Observe thus the relative persistence of the organs, and also the optical changes which protoplasm undergoes when its water is decreased.

Besides the genera mentioned above, the following should usually be found in abundance in the varied aquaria of the Laboratory: Stylonychia, Hydra, Amphileptus, Philodina, and Chetonotus.

II. CILIARY MOTION.

Expt. 20.—*Direction and Speed of Movement Produced.*—(Apparatus: Frog-board, small cork platform, lead weights (0.5 to 5 gm.), watch, hot normal saline, metric rule.) Pith the frog's brain (see Expt. 35) and fasten the animal well stretched out on its back to the frog-board. Divide the lower jaw longitudinally on the median line and extend the incision through the esophagus. Turn the flaps *widely* back and fasten them with clips. Place the little cork block on the mucous membrane of the roof of the mouth between the eyes. (*A*) Measure with watch and rule the speed at which it is carried downward in millimeters per minute. (*B*) Load the cork with weights and determine the limit of load in grams. (*C*) Warm the membrane with hot (60°) normal saline solution (NaCl) and compare the two speeds. Make ten measurements and average them. Subtract algebraically this average from each measurement. (Place all the arithmetical work in the note-books.) Use the same method in comparing the speed on the warmed mucosa, and state the acceleration in percentage of the cold rate.

Note (1) the direction, (2) the speed, and (3) the great power of the ciliary motion (Bowditch).

Expt. 21.—*Coördination of Cellular Movement.*—(Apparatus: Frog-board, powdered charcoal, hot wire.) With the heated wire superficially cauterize a spot of the ciliated mucous membrane which has been lightly powdered with charcoal. Observe carefully where there is movement still and where it is not. It will be found that the motion is stopped not only on the burned spot, but throughout a small isosceles triangle whose apex is at the spot and whose base is toward the esophagus.

Most of the infusoria we have been studying move by means of cilia; so do spermatozoa. Ciliated epithelium lines the human air-passages, the Fallopian tubes, the cerebral ventricles, the ventricle of the cord, the Eustachian tube, the vasa efferentia, etc. Its general function is to move a liquid or small particles over a surface or through a tube. Nerves are probably nowise concerned.

The cause of the movement of cilia lies in the body of the cell from which they extend, for they have no power of movement when separated from their cells; probably the nucleus exerts the control in some way. Cilia have a rhythm which is broken only by external influences or when the cell is about to rest. Another conspicuous quality of the movement of cilia is the progression of the bending movement from one cilium to the next, each phase being represented by many different cilia at the same time; different rows of cells are coördinated in this rhythm.

The active or contractile movement of the cilia is probably the erecting phase and not the phase in which it bends downward, for this latter corresponds to relaxation. The contractile phase is quicker than the other; contraction of the side of the cilium convex in its resting position pulls the cilium to a vertical position. Reversal of the movement is sometimes observed, but never, so far, in vertebrates. (Consult the literature in the libraries, especially Verworn).

III. NOTES ON SOME OF THE APPARATUS.

Review discussion of electrical physics and *demonstration* of the galvanic cell, the inductorium, the rheocord, the chronograph, Pohl's commutator, the muscle-lever, the electro-magnetic signal, the non-polarizable electrode, the capillary electrometer, the tuning-fork, etc.

However much a student may know about physics (and it is almost always far too little), it is necessary to learn the theory and practice of the simple apparatus used in experimental physiology, else much time and material will be wasted. In this work several matters respecting electrical apparatus are essential which elsewhere often are unimportant—for example, the direction of the current and the relations of the ions bearing it. The more physics the student knows, the better will he grasp physiology, which is largely organic physics and chemistry.

Didactic Rules for Using the Electrical Apparatus, etc.—Dry-cell.—This is a modified Leclanché battery-element, the electricity being generated by the action of salammoniac on the zinc plate and conducted inward to the carbon plate by hydrogen and ammonia anions. Hence the carbon, the negative plate, is the positive pole of the cell, and in a conductor completing the circuit outside the cell the current passes from the carbon (anode) to the zinc (cathode). This is an open-circuit cell and its poles must never for a minute be left connected by a conductor when not in use. Each cell has a pressure of more than one volt. Always remove the wire from one of its poles when its use is finished for the day.

The Inductorium or Induction-coil.—The strength of the momentary currents induced in the secondary coil depend on (*A*) the strength of the battery-make and -break; (*B*) on the closeness of the two coils to each other; and (*C*) on the angle between the rings of wire of the two coils (this angle determining the number of the inducing lines of force). The instrument is used in three sorts of ways: (1) to give single make induction-shocks; (2) to give single break induction-shocks; and (3) to produce a current of alternating induced electricity, each double vibration of the automatic armature producing two alterations of this current. To produce single make or break shocks the left-hand binding-post and the middle binding-post are attached to the battery wires, the short-circuiting key left open, and the battery-current made and broken with the simple key. The break induction-shock is stronger than the make induction-shock (because of the absence of the conflicting extra-currents in the primary coil at the break). To produce (3) the alternating current, the right and left corner binding-posts are employed. Stimulation is applied by opening the previously closed short-circuiting-key on the secondary coil while the simple key in the primary or battery circuit is held closed. The short-circuiting key must be kept closed except while using the alternating current in order to avoid explosive tension at the secondary electrodes. Never bend in any way the vibrating filament of the hammer-armature: ask the instructors to make any adjustments which may occasionally be necessary.

When, as is customary, it is desired to stimulate with a make-shock or with a break-shock only, the other in either case must be carefully kept from stimulating, for else two contractions instead of one would be occasioned. To do this, use the short-circuiting key on the secondary coil in the appropriate way. *To use a make-shock only:* Close the simple key in the circuit (the short-circuiting key being open); this does the stimulating. Hold down the simple key and close meanwhile the short-circuiting key; then release the simple key. *To use a break-shock only:* Close the short-circuiting key; close the simple key in the circuit and hold it down. Open the short-circuiting key; then on releasing the simple key the muscle is stimulated by a break-shock only. This is called "cutting out" the shock not desired.

The common error at first is having pressed down the simple key to at once release it, forgetful that this gives two shocks instead of one. The simple key must always be held down (closed) until the desired reaction has completed itself; then the break-shock will do little harm save toward wearying the muscle or other material.

The rhythmic chronograph consists of a flat steel spring (vibrating at any one of many rates per second and breaking the circuit at each double vibration) actuating the electromagnetic signal. Used in one way it breaks the signal-circuit once a second (caution as to the eyes). Used the other way (horizontally) it actuates the signal either fifty times per second, ten times per second as desired, or at any other rate near these.

The non-polarizable electrodes must be used especially in experiments on nerves whenever delicate quantitative work is undertaken. These prevent disturbance of the ions of the tissues by the chemical action between their salines and the metal of wires, etc. The porcelain boot-electrode is most convenient when the moist-chamber is used, and the camel's-hair brush form at other times. In either form no metal is in contact with the tissue, the electricity being conducted by Ringer's fluid in the boot or the brush.

The capillary electrometer (*A*) measures very delicate electric currents and (*B*) shows their direction. It is in general only in research-work that we care to know the exact values of these electric currents, for they are not known to be physiological; but their direction is of more importance. The movement of the end of the column of mercury in the capillary tube is in the direction of the current, the surface-tension, usually holding it still, being then lessened or else increased as the case may be. If the current be down the tube, the tension is lessened; if up, it is increased. A form with the capillary large enough to be seen readily without a lens is often a convenience and fully precise enough for class-work purposes in schools with the present too-short course of four years.

Pohl's commutator or pole-changer is used in three ways: (*A*) To change the direction of a current. The cross-wires then are in place, the battery-wires (afferent) attached to the posts of the rocker, and the efferent or stimulating wires attached to the pair of posts on one side or other of the rocker. (*B*) To shift a battery-current into either of two efferent currents at will, the cross-wires are removed and the battery-wires fastened in the two pairs of posts ("rocker-posts") remaining. (*C*) As a simple key, the cross-wires are removed and the wires of the circuit concerned are placed one in a rocker-post and the other in a post adjacent to it.

The rheocord is used to subdivide a weak current so that a whole or any fraction of it may be employed; also for gradually increasing or decreasing the strength of a weak current used as a stimulus. In order to reduce the strength of a current, place the two wires carrying the current from the dry-cell in the two corner binding-posts, and attach one of the efferent wires also to one of these posts, and the other in the post to which the movable block is hitched. Then when the block is at the post containing two wires none of the incoming current is taken off to the nerve or muscle; when the block is half-way down the german-silver wire half the current passes out, and when at the opposite corner post all of it. To increase or decrease the current gradually, merely slide the block along the german-silver wire in the direction required. (See Expt. 44.)

The electromagnetic signal is always placed in the primary or battery-circuit and cannot be actuated by the induction-current. It should write immediately beneath the myograph pen.

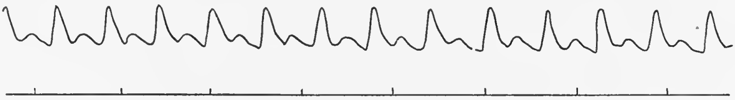
The tuning-fork makes one-hundred double vibrations per second and vibrates fifteen or twenty seconds at a time. It is to be held in the hand and set in action by pinching together the bars and releasing them suddenly. The writing pen is attached to the edge of the end of one bar.

The kymograph or movement-recorder has several speeds. By means of the screw on top of the drum-spindle the drum can be raised off the friction-bearing and may then be spun by hand independently of the clock-work. Keep the kymograph well wound up in order to obtain approximate constancy of speed. The writing-pen should always be at a tangent to the surface of the drum, which must go in the right direction in reference to the tinsel pen and never so as to tend to double it up. In other words, have the kymograph always to the left of the remainder of the apparatus.

IV. THE MECHANICS OF THE CIRCULATION.

Expt. 22 consists of a demonstration of the various parts of the circulation-schema, what they correspond to in the animal, and how to use the apparatus in the laboratory.

FIG. 258

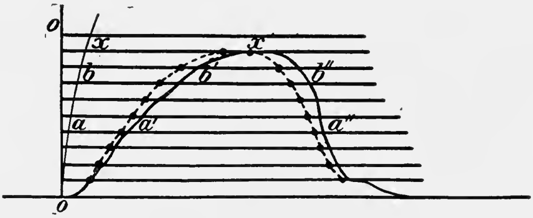


Brachial sphygmograms. Made on the brachial artery with the simple laboratory thistle-tube sphygmograph. To be read from left to right. Time-line is in seconds.

The bulb, representing the ventricles, must always be compressed in the palm of the hand at the rate at which the human heart works, using a watch or the actual pulse as a guide to the correct rate. (A newer form of the circulation schema on the market has no bulb, but an excentric crank-mechanism in its place. The valves furthermore can be more readily changed, making it preferable.) The valve-flaps should be of thin rubber dam. The capillary resistance must be so arranged (by means of the compression-clamp) that the pressure in the arterial manometer is high. Under these conditions observe (1) that the outflow into the bowl is constant. This condition (representing the constancy of the capillary flow) is due to two factors present in the circulation: the great elasticity of the arteries and the high resistance in the capillaries. If either of these be lessened the flow is no longer constant, but intermittent with each beat of the heart. Thus, with extremely relaxed capillaries one sometimes observes a venous pulse. Note (2) the high and relatively constant pressure in the arteries, and (3) the very low pressure in the veins.

Expt. 23.—*The normal sphygmogram* is the pulse-record made with a sphygmograph ("pulse-writer") on the kymograph-drum covered with smoked paper. *Demonstration of the important graphic method,* and of the sphygmograph. Fasten the glazed paper to the drum so that the margins beyond the latter at both ends shall be the same. The layer of soot need not be black, but it should be fairly uniform. Cut off the margins and never re-smoke the paper after this has been done. Keep the kymograph wound up. Use a speed of the drum which will make a sphygmogram one-half as long again as it is high. After applying the receiving tambour to the artificial artery, open the pinchcock to equalize the pressure within the sphygmograph. Insert one or more wooden strips beneath the "artery" if necessary to obtain a good record. The tinsel writing-pen should be at least two centimeters long on the end of a straw lever about 15 centimeters in length. The whole lever should be always held at a *tangent to the cylinder's surface.*

FIG. 259



A simple myogram to show the deformation of the curve by the use of arc-levers and the mode of correcting the error. Each point of the curve save *o* is too far toward the right, but can be put in its proper place by setting it to the left its respective distance as shown in the angle *o, o, a, b, x.* (Weiss.) In practice the error is lessened by having the lever's pivot opposite the middle of the curve instead of opposite its bottom.

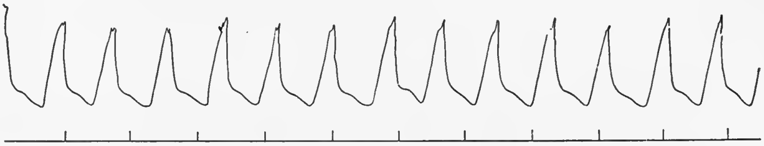
It is fundamentally important that each of the conditions should be normal except the *one* studied in each case. Thus the pulse-rate, the capillary resistance, the leverage, the drum-speed, etc., all must be exactly as in making the norm with which the abnormal sphygmograms are to be compared. A normal curve must, then, accompany each pathological curve. This singleness of variation is of course one of the basal principles governing all biological research, as Francis Bacon and Mill long ago pointed out.

Now, having everything ready, make a series of (1) normal sphygmograms around the drum (pulse-rate of 75, high capillary resistance). Analyze the curve. Observe (*A*) the speed of the uprise of the writing-lever; (*B*) the speed of its downfall; (*C*) the dicrotic notch. (2) Make a series of sphygmograms with a low capillary resistance and compare, in whole and in part, with the normal curve. (3) Make a series with a pulse-rate lower than 75. Make these three sets of sphygmograms directly under each other so that they may be the better compared, the drum-speed being constant. Note the characteristics of each, and study out exactly what each means in the body.

The pathological sphygmogram records abnormalities in the cardiac valves: stenosis and incompetency of both the auriculo-ventricular and the aortic valves. These make up the four common valvular heart-lesions found in man.

Expt. 24.—*Incompetency of the Auriculo-ventricular or Mitral Valve.*—To imitate this condition in the schema, carefully draw out the left-hand valve-tube and turn the thin rubber covering so that it no longer protects the hole in the glass from regurgitation of the "blood." Replace and make a series of sphymograms at the normal rate, and compare with the normal curve. Note that the curve is different from the normal, because much of the "blood" now regurgitates from the ventricle into the auricle at each beat. The shape of the curve may not be much different from the normal, but the tracing is narrower vertically. Replace the rubber on the valve-tube in its normal place (Fig. 261).

FIG. 260



Normal sphygmogram made on the artificial circulation-apparatus. The capillary resistance and the blood-pressure both were high. To be read from left to right. Time-line is in seconds.

Expt. 25.—*Aortic incompetency* is produced similarly on the other valve. Make a series of curves and study their abnormal characteristics. Note the low pressure in the arteries and its great variation; these make a soft and bounding "gaseous" pulse. Replace the valve-dam in normal position.

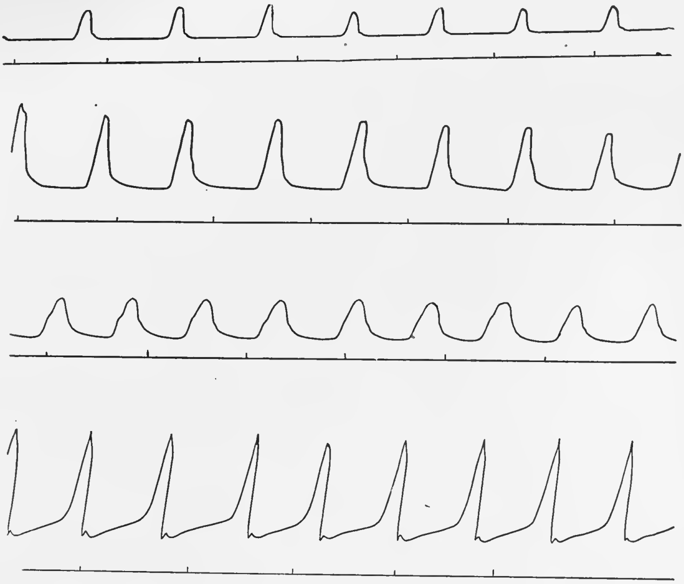
Expt. 26.—*Mitral stenosis* is produced by removing the valve-tube and loosely tying a thread over its orifice so that less "blood" than normally may pass through. Be careful not to tie the thread too tightly. Make a series of sphygmograms and compare them with norm. Observe the shape of the curve. Restore the schema to its normal condition.

Expt. 27.—*Aortic stenosis* is produced similarly on the aortic valve. Make a series of curves and compare them with the normal sphygmogram. Replace the valves in their normal position and wipe the whole instrument dry.

What are the characteristics of each sort of abnormal sphygmogram? Give the hydraulics of each case. Important.

Expt. 28.—*Speed of the Pulse-wave in Man.*—(Apparatus: Two thistle-tube sphygmographs, tubing, kymograph, tuning-fork, adjustable stand-rod, clamps, two chairs, rule, a tall, thin man with strong pulse.) Let the subject sit sidewise in one chair at the table with his bared right foot on its outer side in the other chair in front of him, and his head resting on a folded towel on the table, left ear down. By means of a stand-rod and clamps adjust the sphygmograph with the shorter tube to the subject's right carotid artery. By means of a table-clamp, etc., adjust the transmitting tambour of the long-tubed sphygmograph to the posterior tibial artery of the right foot at a point about half-way between the middle of the inner malleolus and the middle of the bottom of the heel, the foot being naked. Both sphygmographs must be firmly held by clamps and the foot in a firm position.

Fig. 261



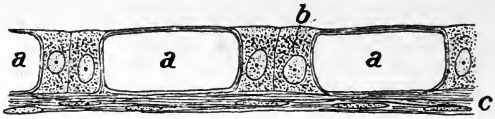
Abnormal sphygmograms made on the artificial circulation-apparatus. The top line represents mitral stenosis; the line next below, mitral regurgitation; the next line, aortic stenosis; and the bottom line, aortic regurgitation. To be read from left to right. The time-line is in seconds.

Adjust the recording tambours one close above the other on the kymograph-drum with their writing-points *exactly* in a vertical line. Spin the drum. Apply the 100 d. v. tuning-fork. Count the hundredths of a second between the uprise of the two levers in several cases. This obviously is the average time required for the pulse-wave to travel from the left ventricle to the foot less the time required for its passage from the ventricle up the carotid. Measure as nearly as possible these two distances. Calculate the pulse-wave speed from these data in meters per second.

Compare this result with the blood's speed.

Expt. 29.—*Demonstration of the Actual Circulation in the Frog's Foot.*—(Apparatus: Compound microscope, stand-rod, clamp, two long, wide slides, wax, small clips, green frog, cloth, tea-lead.) Pith the frog's brain and wrap the animal excepting one foot rather tightly in the cloth and tea-lead previously wet in water. Support the frog and stretch out his exposed foot over the two slides placed one over the other and held in the cork-lined clamp just over the microscope's stage. Secure an outer toe in each of the clips and separate the clamped slides until the web of the foot is stretched over the opening in the stage, catching the clips on the outer edges of the slides. Use a 2-inch objective to find the best spot where the web is flat and level, the circulation lively, and the web free of pigment-cells if possible. Study with the No. 3 objective. (See also page 304.)

Fig. 262



Diagrammatic section of the alveolar wall of a frog's lung: *a*, *a*, capillary spaces; *b*, epithelial cells; *c*, muscle-fibers in the alveolar partitions. (F. E. Schulze.)

Observe how the speed and redness of the blood are proportional to the diameter of the vessel. See the shape and multitude of the erythrocytes and the shape and fewness of the (smaller) leukocytes. (Compare the red corpuscles with those of man.) Note the constancy of the flow, at least after the shock of the pithing has passed off.

Such a preparation is often good for two days.

The phenomena of inflammation may be studied by applying a weak solution of mustard oil or of croton oil to the web. The action of adrenalin also should be observed—a drop of 0.01 per cent. saline solution being applied.

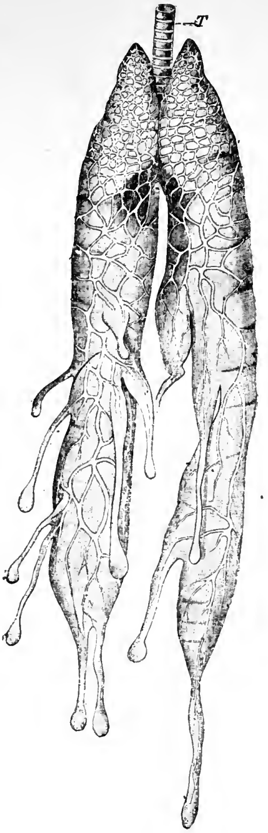
V. RESPIRATION.

Expt. 30.—*The Pneumatics of External Respiration.*—(Apparatus: the schema of the respiration.) *A. Normal Breathing.*—Lower the diaphragm rhythmically and note how the finger-cot lung fills with air falling into it through the open glottis. Observe the slight changes of pressure in the two manometers. What is it that expands the lung?

B. Asphyxia.—Push the glass plug into the glottis, thus closing the respiratory opening to the exterior. Now the lung no longer fills as the diaphragm slightly descends, for the falling-in of air is impossible. Note the great changes of pressure as shown in the manometer in connection with the pleural cavity.

C. Pneumothorax.—Pull out the glass plug which closes the tube connected with the pleural cavity. The diaphragm now descends with great freedom, but no air falls into the lung because no distending suction outward is exerted on the lung-walls. The weight of the atmosphere is equalled by that of the air outside the lung in the pleural cavity.

Fig. 263



Lungs of the chameleon (Chameleo vulgaris). (Wiedersheim.) Observe their relatively great size and their simple sacculation.

Expt. 31.—*Respiration in the Frog.*—(Observation only.) The frog has no diaphragm, but makes the muscles of the floor of his large mouth-cavity serve the same purpose, with the important difference that whereas the descent of the diaphragm in birds and mammals sucks the air into the lungs, here the mouth-floor muscles push it in with a true bellows-like movement.

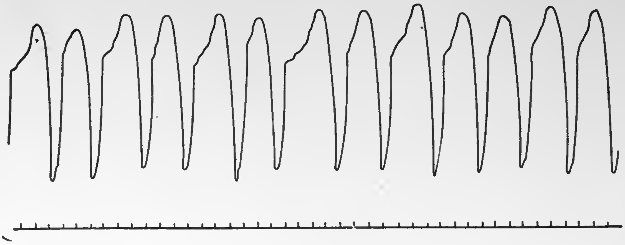
Observe the rhythmic movements of these muscles; the rhythm is easily disturbed by handling, etc., but not stopped long while the animal is in the air. While submerged in the water the frog gets oxygen only through its skin. Note the closure of the nostrils at each inspiration. They are the automatic valves of these inspiratory bellows, opening to admit the air and closing promptly to prevent its return, thus forcing it to enter the lungs, the glottis opening as the nostrils close.

Expiration is here more of an active process than in mammals; the muscles along the sides of the body-cavity compress the viscera and so the lungs, the air passing out in a quick spurt through the opened nares.

Expt. 32.—*The Breath-rate of Anolis. The Normal Stethogram.*—(See Chapter on Respiration.) (Apparatus: Anolis stethograph, and kymograph.) Adjust the stethograph for writing on the smoked drum by means of the aluminum heart-lever. Fasten the lizard (Florida "chameleon") on the board so as to be immovable but uninjured in any way, strapping down firmly the tail and, if necessary, the head. Adjust the animal within the stethograph so that the latter's levers press evenly on either side of the body where the respiratory movement is greatest, close to the forelegs. Warm the animal up somewhat if necessary. With the watch count the number of respirations per minute.

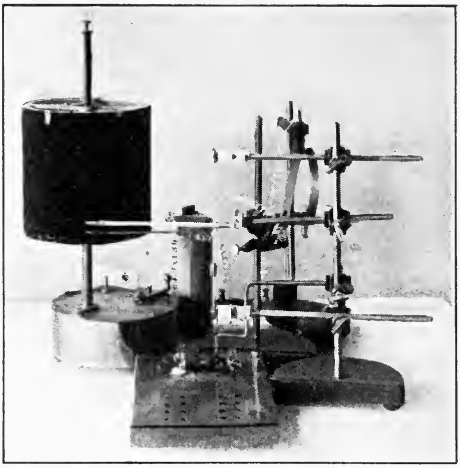
By analysis of the meaning of the different parts of the pneumogram note the characteristics of the respiratory process in this animal. Observe (*A*) that there is no pause between expiration and the succeeding inspiration; (*B*) that there is a slight pause between inspiration and expiration; (*C*) that the inspiratory movement is a strong, quick, active muscular movement; (*D*) that the expiratory curve (the down stroke of the pen) is apt to be broken by a pause at some part of the descent, usually either a slight stay soon after the expiration begins or a much larger one about half-way through it. This expiration is characteristic of a

FIG. 264



The Anolis stethogram. A slightly apneic type of the breath-movements of Anolis. Observe the slight pause after inspiration, but that there is none between expiration and the next inspiration. To be read from right to left. Original size. The time-line is in seconds.

FIG. 265

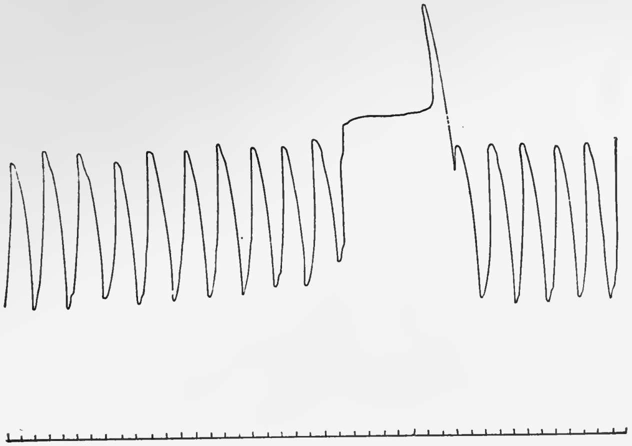


Apparatus (Anolis stethograph, etc.) as set up by students to study the respiration of the southern "chameleon."

passive movement easily obstructed, and of the breathing of lizards generally.

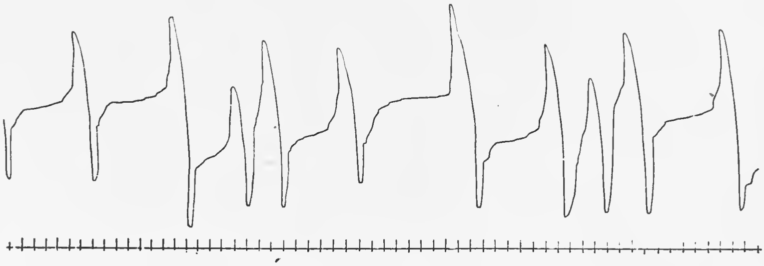
Expt. 33.—*Apnea.*—(Apparatus: Anolis stethograph and kymograph.) Place the animal as in the last experiment and make a normal pneumogram. Stimulate him by tapping his nose very gently with a straw. He will stop breathing for a time and after a full inspiration. Note the number of breaths covered by this pause and the increased depth and frequency of the respirations following it.

Fig. 266



The Anolis stethogram. This shows the inspiratory apnea (so marked a characteristic in the respiration of many lizards) occurring during rapid rhythmic breathing. To be read from right to left. Original size. The time-line is in seconds. (April, 1900.)

Fig. 267



The Anolis stethogram. This shows the strongly apneic type of the breathing of the southern "chameleon." Observe that the inspiratory movements are never interrupted. To be read from right to left. Reduced. The time-line is in seconds.

Expt. 34.—*Anesthesia.*—(Apparatus: Anolis stethograph, kymograph, small wads of filter paper soaked in chloroform.) While the animal is recording a normal pneumogram, place near its nostrils the wad of filter-paper soaked in chloroform. Note the primary stimulating stage (in which the animal struggles), with the acceleration and deepening of the respirations, followed soon by the second stage, in which the respirations become slower and shallower. The anesthetic should be removed at this time lest the animal be killed by cardiac paralysis. Note the gradual return to the normal respiration.

In the remainder of the experiments frog-life may often be economized greatly by arranging the order in which the experiments are performed at each laboratory-period. The order matters little theoretically. Experiments not requiring extensive cutting should be done before those demanding it, therefore, and sometimes observations on the heart may well be made the same day as experiments on the sartorius or gastrocnemius.

VI. THE PHYSIOLOGY OF MUSCLE.

Expt. 35.—*The nerve-muscle preparation* is made out of the bipenniform gastrocnemius muscle, the whole sciatic nerve, and the femur of a large frog. Quick and painless is the killing of the animal by disorganizing its brain and cord with a "seeker," which is thrust into the skull-cavity through the foramen magnum by a *single strong quick movement* at a point to be felt with the thumb-nail as a slight transverse depression in the spinal column. Now with small scissors cut the skin circularly around the lower part of the trunk, and seizing the skin on the back, draw it off the legs with one pull. Cut the frog in two transversely and then separate the legs, etc., by an incision with the scissors exactly in the median line. Now dissect out the conspicuous sciatic nerve from the knee through the thigh to the spinal cord, leaving attached to it a small bit of the latter and the gastrocnemius muscle. Detach the tendo Achillis from the bone and raise the gastrocnemius muscle with the forceps by this tendon. Cut through the middle of the femur (to be used as a handle), leaving it attached to the gastrocnemius. This is the "*nerve-muscle preparation*" so much used in physiology. The removal of both preparations complete from the frog should require not more than five minutes after it has been done two or three times. The preparation that is not to be used at once should be placed on the glass plate and covered with filter-paper wet in modified Ringer's (Locke's) solution, the closest practicable approach to blood-plasma. The nerve should be touched only by the glass rod, and never stretched nor allowed to approach dryness. The muscle, too, should be handled as little as possible (especially with metallic implements) and kept wet. Every stimulation of whatever sort of these now dying tissues shortens materially their life and their experimental usefulness.

The gastrocnemius muscles and the sciatic nerve are the most useful for the purposes of these studies for several reasons. They are easily and quickly dissected; the nerve is the longest and largest in the body; the muscle is distinct; it is of the bipenniform type and thus very powerful;

and it has attached to it a long bone useful as a means of holding it firmly in the apparatus. The advantages of frogs over other animals for this purpose are numerous, but the selection is confined to poikilotherms ("cold-blooded" animals), because in them the muscles when properly cared for will live days in comparison with the hours which the muscles of homotherms can be kept alive with only much greater care.

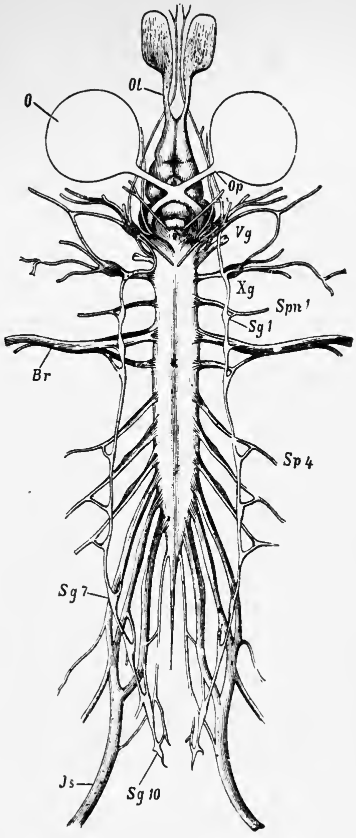
One thing it is pleasant to continually remember: that any considerable injury to the brain or even to the spinal cord produces most certainly, without any doubt whatever, complete abolition of consciousness and the pain-sense, leaving the animal a mechanism only, composed of slowly dying tissues of great scientific usefulness.

Expt. 36.—*Varieties of Energy that will Stimulate Muscle.*—(Apparatus: Gastrocnemius muscle, glass plate, glass rod, key, dry-cell, wires, saturated solution sodium chloride, Bunsen burner, seeker, ice, small beaker.) Muscle can be stimulated by four of the eight known aspects of energy in addition to the normal nervous force of unknown nature. These four are: (*A*) kinetic, (*B*) electric, (*C*) chemic, and (*D*) thermic energy.

A. Kinetic Stimulation.—As the muscle lies on the glass plate prod it with the small sharp end of the glass rod, or pinch it. It will contract.

B. Electric.—Hold the wires on the muscle and close the key (the "make" of the current). The muscle twitches. Open the key ("break") and the muscle contracts again (but not so strongly). Static electricity will stimulate as well as galvanic..

Fig. 268



The frog's nervous system: *Ol*, olfactory nerves; *O*, eye; *Op*, optic nerve; *Vg*, Gasserian ganglion; *Xg*, vagal ganglion; *Spn* 1, first spinal nerve; *Br*, brachial nerve; *Sg* 1 to *Sg* 10, the ten ganglia of the sympathetic; *Js*, ischial nerve. (Ecker.)

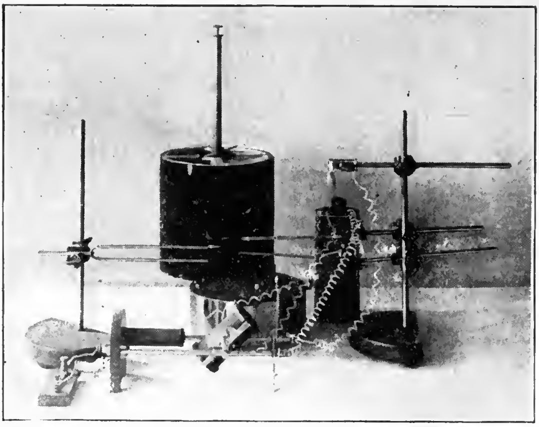
C. Chemic.—Place a small drop of the saturated sodium chloride solution on the muscle. It will soon contract. Wash the muscle. Drying (loss of water from the protoplasm) stimulates the muscle, as may be seen by allowing it to partially dry. Exosmosis of salines is a stimulation: immerse the muscle in a beaker of distilled water. Contractions soon appear

D. Thermic.—Apply gently very close to the muscle a large very hot wire. It will contract. Gently apply the dried wire made very cold by immersion in salted ice. It will perhaps contract again.

E. Normal stimulation of muscle is a universal experience in our bodies.

Expt. 37.—*Analysis of the Contraction of Cross-striated Muscle.*—(Apparatus: Kymograph, etc., for graphic record of gastrocnemius' contraction, altogether called a *myograph*, electro-magnetic signal, tuning-fork.) Raise the drum off its friction-bearing. Place the signal in the primary circuit and arrange it to write as closely as possible under the muscle-lever. Have some one hold tuning-fork so as to write just below or above the signal. Rotate the drum and so draw an abscissa line. Pass maximal make induction-shocks (cutting out breaks) through the muscle while drum is spinning at a rate that makes the contraction-curve (myogram) four or five centimeters long. The height should be about three centimeters. The signal registers the moment of the muscle's stimulation, and the fork measures the elapsed time. Drop perpendiculars (or arcs) from summit of contraction curve, and mark the beginning and the end of the curve. Measure in hundredths of a second (*A*) the combined latent-period; (*B*) the period of contraction; and (*C*) the period of relaxation.

Fig. 269



Apparatus as set up by students to make a simple myogram. The drum, however, should have been at the top of its spindle when the first curve was made.

In analyzing the different parts of the myogram from a cross-striated muscle one has to consider (1) the electrical latent period, (2) the mechanical latent period, (3) the period of contraction, and (4) the period of relaxation. None of these are constant in muscles generally, even in the cross-striated muscles of the same individual animal, for the various elements vary according to many conditions in the muscle itself, with its shape, function, nutrition, irritability, etc. As to the frog's gastrocnemius, *the electrical latent period* (the interval between stimulation and the beginning of negative variation in the electrical state of the muscle) is not over 0.001 second. *The mechanical latent period* is the interval between stimulation at the end of the electrical latent period and the beginning of actual movement by the muscle. This period is about 0.005 second long. Thus the "combined latent period" in the frog's gastrocnemius in summer is not over 0.006 second normally. In addition to this about 0.004 second is taken up by the passage of the nervous impulses, making altogether 0.010 second. This combined quantity is what is measured in the laboratory as the "latent period." In winter it may be somewhat longer, and when the muscle still has blood circulating in it, shorter.

Study of the uprise of the lever (requiring about 0.05 second on the average in the gastrocnemius) indicates that the *contraction* begins slowly and ends slowly, the slow beginning occupying about 0.005 second and the slow ending say 0.015 second. The shape of this part of the myogram depends on many different conditions. The downfall of the lever (*relaxation* of the muscle) occupies about 0.075 second; it begins slowly (0.015 second) and ends slowly (0.01 second).

Expt. 38.—*Galvanic Electricity as a Stimulus.*—(Apparatus: Muscle, myograph or graphic-record apparatus, rheocord, tuning-fork.) Set up the mechanism for making graphic records of the frog's gastrocnemius, connecting the muscle through a key and rheocord with one dry cell. Raise the drum from the friction-bearing and spin it slowly. Apply the tuning-fork and close the key, holding the lever down and using a current only just strong enough to produce contraction. Now open the key and observe that no contraction then occurs: the galvanic make is a stronger stimulus than is the break. Again, with full strength of current, make records of make and of break (here, as always, *separated by holding the key closed while muscle* contracts and relaxes from the make), and observe that the make-contraction is the more vigorous, the lever rising higher than from the break-shock.

Observe also that in case of skeletal muscle no general contraction occurs during the passage of the constant current, but only at its make and break. The muscle, however, is meanwhile in the interesting electrotonic condition.

That the make or application of the constant galvanic current is a stronger and more effective stimulus than is the break or withdrawal of the current needs no special explanation. The addition of energy would naturally result in more activity than the withdrawal of energy already present. It is owing in part to the sudden change in the strength of the stimulus (Du Bois Reymond) that any contraction takes place at the break of the galvanism. (See the next experiment.) There has arisen, however, an elaborate system of explanation based on phenomena whose meaning is obscure: In the case of galvanic stimulation, the excitation on making or *closing* the constant current begins at the *cathode* (C.C.), and on breaking or *opening* the current at the anode (A.O.). Von Bezold first demonstrated this after experiments by Schiff more than fifty years ago. Still no explanation worthy of the name is forthcoming, and the best that can be said, apparently, is that when the current is applied ("make"), the muscles' irritability is increased at the cathode more than at the anode, and so the contraction starts powerfully at the former pole; while when the current is removed ("break"), the irritability is greater at the anode than at the cathode (but less than at the cathode on making). When we have learned the facts about the nervous impulse and muscular contraction these "explanations" may seem less pedantic and more useful than at present.

See also Expts. 59, 60, and 80, the phenomena being essentially the same in nerve as in muscle.

Expt. 39.—*Induced Electricity as a Stimulus.*—Insert the inductorium arranged for single shocks in place of the rheocord of the last experiment. Draw or turn the secondary coil far enough away from the primary so that a make-shock on closing the simple key will just not cause a contraction. Hold the key closed and meanwhile observe that no contraction occurs during the passage of the galvanic current through the primary coil, for induced electric currents are always of only momentary duration.

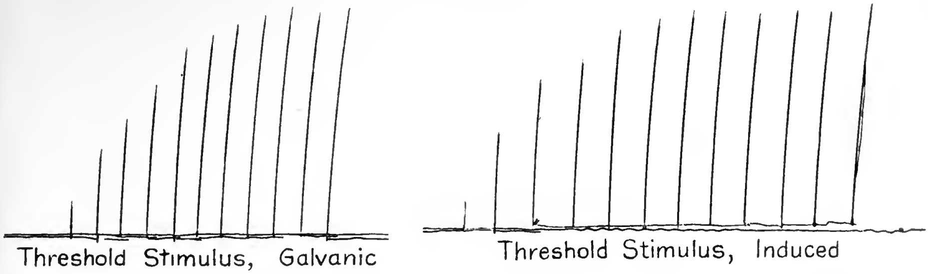
Open the simple key. Contraction then occurs, demonstrating that the induced break-shock is a stronger stimulus than the induced make-shock. This excess is due to the absence from the break of the "extra-currents" which make less sudden the make-shock (as demonstrated previously). Repeat with various strengths of induced electricity, and see, and feel on the tongue, that the break is a much stronger stimulus than is the make; the opposite is true with the simple galvanic current.

The extra-currents referred to as the cause of the lessened stimulating effect of the make-shock are inductively generated in contiguous rounds of the wire of the primary coil of the inductorium, just as induced currents are generated between the rounds of the primary and the secondary coils. These currents are in direction opposite to the regular currents, and it is their opposition that makes the rise to full strength of the regular current gradual instead of sudden. (See Expt. 44.) As regards the break of the regular induced current (a stronger stimulus than the make): when the primary current is shut off both the regular current and the extra current cease at once, and the suddenness of the change of strength of stimulus is maximal, greater than in case of the make, and so stimulates more strongly.

Expt. 40.—*Duration of Stimulus Affects Contraction.*—(Apparatus: Myograph, inductorium, commutator without cross-wires, two cells, sartorius.) Attach one cell to the inductorium for single break-shocks and connect the secondary coil with the two posts of one side of the commutator. Connect the other cell directly with the posts of the opposite side of commutator. Connect the rocker of the commutator with the sartorius myograph in the usual way. Have the drum rotate at its maximum gear-speed. Write an abscissa line. Send a maximal break induction-shock through the muscle. Lower the drum and write another abscissa line 5 cm. below the other. When the drum has rotated at same speed as before to the place of the first curve shift the rocker, thus sending a galvanic make-shock through the muscle. Compare the two curves. The former curve, made with the exceedingly sudden induction break shock will be found to be more acute than that made by the continuous galvanic current.

This briefly sustained contraction of the cross-striated muscle (it is longer in smooth muscle) when stimulated with the galvanic shock is doubtless due to a condition of brief electrotonus, which has no existence when the muscle is stimulated with the almost instantaneous induced shock. The reason that the myogram is broader on top (indicating a sustained contraction) is that the stimulus in case of galvanism lasts longer than it does in case of electricity produced by induction. To stimulate a cross-striated muscle requires a duration of a galvanic current of at least 0.001 second, while to have maximal contraction of a smooth muscle the electricity must be applied from 0.25 to 5 seconds.

FIG. 270



These curves show in general the relations of the degree of contraction of cross-striated (frog's gastrocnemius) muscle to various intensities of stimulus, beginning at the threshold and ending at the maximum. The left-hand set of curves was made with galvanic, the right-hand set with induced, electricity. To be read from left to right. Constant load of 10 gms. Intervals between contractions about thirty seconds. Reduced.

Expt. 41.—*The Threshold and the Maximum Stimulation.*—(Apparatus: Myograph, rheocord, inductorium.)—(*A*) *Galvanism.* Place the block of the rheocord so that the make of the current just does not produce contraction. By gradually moving the slider, increase the current with the key closed until the make of the current just barely causes contraction. Make a record (straight vertical line) of the contraction on the drum while stationary; move the block a few centimeters so as to increase the stimulus, turn drum 0.5 centimeter by hand and make another record—and so on. A series of contractions up to the maximum of the cell is thus produced.

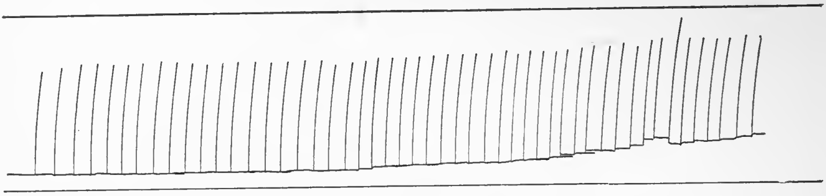
(*B*) *Induction.*—Repeat the experiment, using the induction-coil instead of the rheocord, cutting out (with short-circuiting key on the secondary coil) all the make-shocks. Compare this series with that made with make galvanic shocks. Observe the threshold; the increase in contraction; and that a place is soon reached above which no strength of current would increase the contraction, but rather injure the muscle.

The existence of the threshold is universal wherever protoplasm is concerned. If a sound-stimulus be too faint our ears, as mechanisms, are not set in action owing to their inevitable inertia, and we hear no sound; if a light be too faint, our eyes fail to see it. The threshold is a necessary accompaniment of the inertia of matter, organic and inorganic.

The maximum stimulation of a tissue is of a similar nature logically. A mechanism can work only so hard, a string can vibrate only so far. When a muscle has received a stimulation which corresponds with the maximum of its action, any increase in strength of the stimulus up to a certain degree will produce only the same maximal effect. Beyond that certain degree of strength of stimulus the organism will be injured and its activity impaired in all directions.

Expt. 42.—*Threshold Independent of Load.*—Repeat the latter half of Experiment 41, using no load instead of 10 gm., which is a fair load. Repeat again, using 50 gm.

Fig. 271



The relation of cross-striated muscle's contraction to the increasing strength of its stimulation by induced electricity. The strength of the induced break-shocks increased by degrees, each represented on the inductorium by one notch of the vertical arc-index, then by 3 mm. on the horizontal scale. To be read from left to right. Intervals, ten seconds. (The greater contraction seen near the end is unexplained.) Observe that even ten seconds apart, the electric shocks fatigue the muscle, lessening both its contraction and its relaxation.

It is not obvious why the threshold *should* be in any way dependent on the muscle's load, for, unless the load be so excessive as to tear apart the muscular fibers, it does not affect in any way the action-conditions of the muscle, either in pulling apart the sarcomeres, or in disturbing the relations of the nerves to the muscle. As a matter, however, of precise fact, load does influence in one respect the threshold, for a muscle works more normally in all respects when it has a moderate load than when it has too little or too much. This normal load apparently keeps up the normal tonus of the organ (muscle) and this in all sorts of tissues is a pre-requisite of optimum action. It cannot be doubted, then, that the threshold would be found slightly lower in a muscle with a normal load than in one quite unloaded.

Expt. 43.—*Contraction of Smooth Muscle.*—(Apparatus: Myograph, signal.) Cut four or more rings out of the frog's stomach, tie them together in a line with fine copper wire, and place this long line of rings as the gastrocnemius is usually placed. Use two cells, and put the signal in the circuit. Let the lever write carefully a fine abscissa line. Stimulate this stomach-muscle with one pair of maximal make-and-break galvanic shocks and record on the drum going at the minimal speed of its mechanism. Compare (1) its latent period (several seconds) with that of striated muscle; (2) its period of contraction (thirty seconds or so); (3) its period of relaxation (one minute or so); (4) the general shape of the curve. (All these quantities are very variable with many varying conditions.) These two sorts of muscle are obviously very different in their functional habits, yet they are less different than is sometimes supposed. (The "intermediate" variety, that of the heart, will be studied later on.)

To understand the great differences between the modes of contraction of cross-striated and of smooth muscle, it is necessary to recollect their respective structures. A smooth muscle-fiber is functionally all one piece of protoplasm, massive, and with relatively much inertia. A cross-striated muscular fiber, on the other hand, is made up of very numerous minute portions, each of which, so far as function (contraction), is concerned, is practically a separate muscle-fiber, and one constructed with the greatest readiness for action. Thus, in cross-striated muscle the inertia is divided into many parts, and the muscle therefore contracts very rapidly and very vigorously. The difference between them is not unlike that between a galvanic battery made up of numerous small cells and one composed of only one cell with large elements. The electrical organ of electrical fishes makes this comparison apt, for it is cross-striated muscle modified to produce an electric shock of high intensity, and composed of hundreds of cells like the former of the two batteries above suggested. In a striated muscle the effect is usually sudden and powerful and of relatively short duration, as its structure implies, while in smooth muscle, acting with large and relatively few elements (cells) the contraction is generally the relatively slow, steady, contraction and relaxation we should expect to find in the vegetative, as distinguished from the voluntary organs. In this particular experiment with the frog's stomach the difference between the two sorts of muscle is perhaps unfairly exaggerated because these smooth fibers are circular fibers, and thus give only half as much linear shortening when the rings are thus connected as they would if spread out their full length as are the fibers in the cross-striated muscle compared with them.

The danger in this experiment is that the contraction will not be appreciated because of its small degree and its very long periods. Sometimes an active relaxation apparently complicates matters. Moreover, the stomachs of winter frogs may be very loth to react, either way.

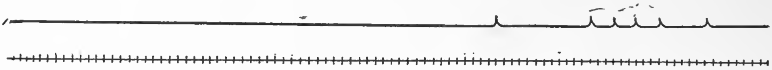
Expt. 44.—*Sudden Change and Gradual Change of the Strength of Stimulus.*—(Apparatus: Myograph, rheocord, two simple keys.) (*A*) *Sudden Change.*—Set up the apparatus carefully as follows: Put two wires into each of the two binding-posts of simple key No. 1, and connect one wire from each post with one dry cell. Of the other two wires, run one to the anode of the other dry-cell and the other to the femur-clamp. From the remaining plate, the cathode of cell No. 2, run a wire to simple key No. 2, and connect the other post of this key with the muscle-lever.

Hold key No. 1 closed. Without making a curve (using the myograph merely to see better the contraction), close key No. 2 and hold it closed, whereupon the make-current from the second cell will stimulate the muscle. Now, with this current still passing through the muscle, open key No. 1, which lets the current from cell No. 1 into the circuit and doubles the intensity of the stimulus. The muscle then contracts again.

(*B*) *Gradual Change.*—Hitch the two dry-cells in series, and interpose between them and the myograph a simple key and the rheocord. Place the block of the rheocord against the anodal binding-post and close the key. Now slide the block along the meter of wire visible on the rheocord to its end and observe that no contraction occurs although the stimulus has risen from below the threshold to far above it. Raise the block off the wire and replace: there is active contraction from this sudden stimulation although no stronger than before.

Expt. 45.—*Summation of Singly Inadequate Stimuli.*—(Apparatus: Inductorium, frog). (*A*) *In Reflexions.*—Tie the wires from the secondary coil about a frog's foot not too close together. Stimulate with make-shocks below the threshold for reflex contraction of the leg. Soon the influences summate and the leg is flexed. (*B*) *In a Single Muscle.*—Place the secondary coil so that the single break-shock is just below the threshold-intensity. After the muscle has fully recovered from the stimulation of this threshold-finding, let a break-shock pass through the muscle (always excluding makes) and repeat at intervals of four or five seconds by the watch. These stimuli after a time will summate to an effective stimulus, and the muscle will contract.

FIG. 272



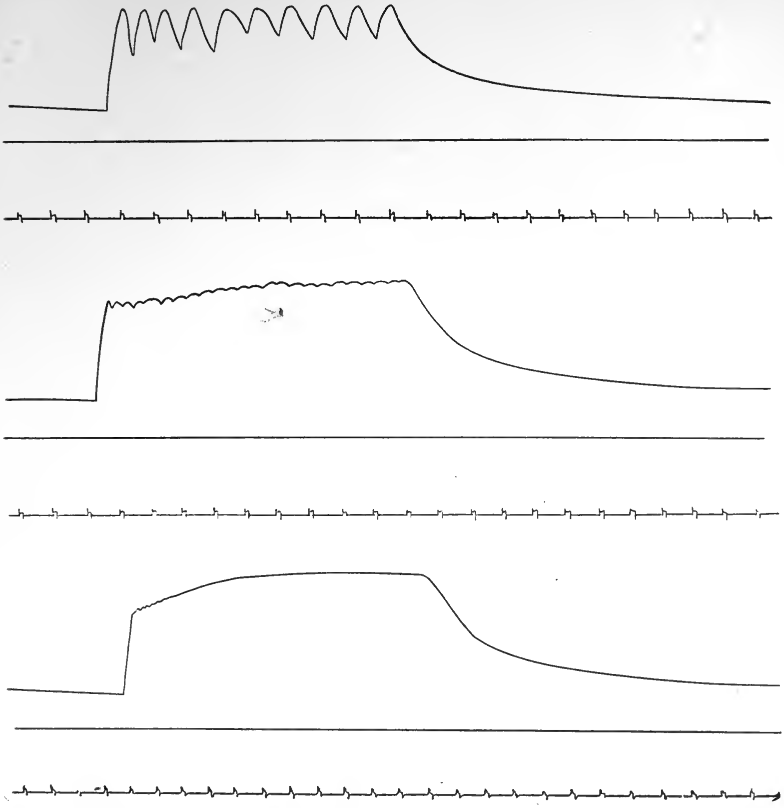
Summation of singly inadequate stimuli, to show a probable katabolic influence on protoplasm. At intervals of three seconds a frog's gastrocnemius was stimulated with break-shocks, each too weak to produce a contraction. After about sixty such stimulations contraction occurred. (To be read from left to right.) The time-line is in three-second intervals. This result, made on a "winter-frog," is not like that seen in the "summer-frog."

This experiment studies the summation of the occasion of contraction just as the next experiment deals with the effect. It demonstrates that even a subliminal stimulus (one below the threshold-strength) has an effect on protoplasm which persists in some form at least five seconds (in fact, twice that time at least). We see this frequently in the sensory realm also. (See Chapter XII.) The precise nature of the impression made on protoplasm by subliminal stimuli cannot be stated, but it lies probably in the direction of increasing slightly each time the tonus or irritability of the tissue.

Expt. 46.—*Superposition of Contractions.*—(Apparatus: Myograph and inductorium.) Arrange apparatus for writing myograms through single maximal shocks, the drum rotating at its maximum gear-speed.

Stimulate by make-and-break shocks separated, as usual, so that the curve from each is complete. Now reduce the interval between the break and the make until relaxation is prevented by a second contraction arising from the break-shock. A compound curve is thus formed, the second part much higher than the first. Compare this height with that from a single break shock.

Fig. 273



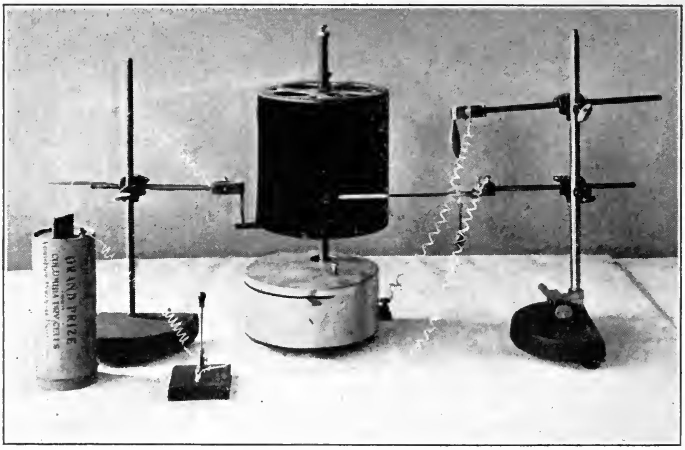
The mechanical nature of muscular tetanus. If electrical stimuli be applied to a frog's gastrocnemius often enough, the muscle does not have time to relax before it is made to contract again. Observe that the more frequent the stimulation the more slowly the muscle relaxes when the stimulation stops. To be read from left to right. The time-line is in seconds.

This superposition of contractions suggests the nature of the contracted condition known as muscular tetanus (not to be confused with the disease tetanus or lockjaw). As has been seen already, relaxation of even a cross-striated muscle requires time (0.075 second), and if another stimulus is imposed upon the muscle before it has fully relaxed, another contraction will at once occur. Because the latent period of contraction is much shorter than the relaxation-period, the two myograms or curves will fuse. This is the mechanical condition of things in this experiment. The shape of the curve, of course, depends chiefly on the time-relations of the two stimulations. (See Expts. 65 and 68.)

Expt. 47.—*Tetanus.*—(Apparatus: Same as in last experiment.) Using the key, stimulate the muscle at first slowly and then more frequently, making a curve for each speed. Determine how many stimulations per second are necessary in order that the muscle may not have time to relax at all, thus writing a curve smooth on top, but up-hill somewhat.

This condition is practically a continuation of the last experiment. Here the stimuli are so frequent that the muscle has no chance to mechanically relax to any degree, and the resulting myogram becomes essentially a smooth line. The number of stimulations per second required to occasion complete tetanus depends largely on the condition of the muscle; fatigue, for example, renders slower the relaxation (as well as the contraction), reducing the number of stimuli per second required to produce this condition. Typical tetanus may be made with induction-shocks coming at the rate of from 30 to 100 per second. Muscular tetanus is of relatively small theoretical importance.

Fig. 274



Apparatus as set up by students to study the superimposed fatigue-curve of muscle.

Expt. 48.—*Fatigue.*—(Apparatus: Myograph with attachment for breaking circuit at each rotation of the drum, signal, inductorium, two stand-rods, two femur-clamps, and strip of spring-brass.) Put signal and femur-clamp holding the brass strip and signal on one stand-rod, and the myograph on the other. Arrange the inductorium for making maximal signal-shocks, placing signals, key and automatic circuit-maker in the primary circuit; the myograph is in the secondary circuit. Keep the kymograph fully wound, or, better, turn the drum with an electrical motor. Load gastrocnemius with 50 gm. Use the maximum speed of the drum. As thus arranged, when the key is closed each rotation of the drum will stimulate the muscle and the myograms will be superimposed, thus allowing of direct comparison of the succeeding curves as the muscle becomes gradually fatigued. Keep up the experiment (with the kymograph always well wound) until the curves are nearly flat. Note in your books the characteristic shape of the myograph at first, midway, and at the last, and also the changes in the different parts of the myogram. If only every tenth contraction is recorded the curves will be more easily discriminated.

The phenomena of fatigue in muscle are of great importance, for it is by muscular contraction that events are accomplished in animal life, whether it be the signing of a name, the starting of a machine, or the composition of a symphony. By thus superimposing the curves fatigue-differences are strongly brought out as follows:

At first the curves (the degree of contraction) increase slightly in height as the muscle gets into its best working order. Then they get gradually flatter, and at length are little more than straight lines. The chief characteristic of the fatigued condition of muscle is a slowing in the processes making up the total complex curve. The latent period increases much, from 0.006 second to 0.3 second or so. The contraction-time increases somewhat, but the most marked change is in the lengthening of the relaxation-time. This is increased many times, and when so increased the condition is sometimes called "contractur." After four or five thousand contractions this slowness of relaxation gradually decreases, but never disappears so that the muscle relaxes as quickly as when unfatigued.

Heat markedly hastens the onset of fatigue, as also does an abnormally large load. White muscle (in the rabbit, etc.) is more easily fatigued than red muscle, and similarly, a supply of blood through the muscle retards fatigue. Recovery takes place rapidly during rest.

Expt. 49.—*Muscular Tone.*—(Apparatus: Stand-rod, femur-clamp, ether, frog.) Lightly etherize the frog and fasten him belly down on the frog-board. Gently open the lower part of the back and divide the roots of the exposed sciatic on one side. Hang up the frog evenly by the lower jaw in the femur-clamp.

On careful observation from directly in front of the frog, the leg whose motor, sensory, and trophic nerve has been cut will be seen to hang lower and to be more limp than the normal leg. The tone of the muscles being lost, gravity draws down the foot farther than the other.

Expt. 50.—*Action-current.*—(Apparatus: Two nerve-muscle preparations with long nerves, frog's heart.) This experiment has long been known as the "rheoscopic (current-showing) frog." (*A*) *On the gastrocnemius.* With the two muscles on the glass plate, lay the nerve of muscle No. 1 longitudinally over muscle No. 2. Stimulate the central end of the nerve of muscle No. 2 with make shocks from one cell, using the platinum electrode for the purpose. If the nerve be properly arranged (use the glass rod), muscle No. 1 will be stimulated to contraction by the action-current passing over muscle No. 2.

B. In the Heart.—Open the thorax of the frog from which the two-nerve-muscle preparations were taken sufficiently to expose the still beating heart. With the glass rod arrange the nerve of a gastrocnemius longitudinally over the heart. The former muscle should contract at each heart-beat. If it does not, snip off the central end of the nerve, place it on the heart's apex and loop the nerve over so that it touches the base of the heart; or even slightly injure the heart-apex mechanically.

It is demonstrated by these experiments merely that when a muscle contracts under experimental conditions an appreciable current passes over it, or at least that a difference of potential is developed in different parts of the muscle. Application of a delicate galvanometer proves this current to be electrical. It may be easily shown that it precedes the contraction of the muscle (see Expt. 69), and that in case of stimulation through a nerve the current starts at its entrance-place and passes over the muscle. (In these respects the contraction-wave is similar.) When one end of a muscle is injured so as to contract less normally, the contracting end is electronegative to the part less active. In an active whole muscle points near its equator are electro-negative to points farther away. The rate of the action-current in frog's muscle (and nerve) is about 3 meters per second, its average duration being about 0.004 second, while its strength in a frog's gastrocnemius is about 0.08 volt. Whether an electrical current accompanies the contraction-wave just as this action-current precedes it is still in dispute. Some find evidence that this electrical condition lasts as long as does the shortening of the muscle.

Expt. 51.—*Electricity Developed in Necrobiosis.*—(Current of injury, demarcation-current.) (Apparatus: Capillary electrometer, normal saline clay, glass rod, nerve-muscle preparations, skin, stomach.)

(*A*) Prepare the gastrocnemius muscle and its nerve with great care, gentleness, and speed. Even with a capillary electrometer no electricity can be found in the muscle when its ends are connected by a conductor (except when the muscle contracts, and that is its action-current). Cut off the lower third of the muscle and bring the end of the sciatic against the cut end. The remainder of the muscle contracts. Apply the electrometer and a vigorous current will be found in the muscle passing from the injured end upward; the injured surface is electronegative to the uninjured lateral surface. (*B*) Try the inside and outside of the frog's skin and the inside and outside of its stomach. The outside is electro-positive to the inside in both cases. (*C*) Roll a small bit of the saline clay into a pencil 3 cm. long and $\frac{1}{4}$ cm. in diameter and bend it in the shape of U on the dried dissecting-plate. Make a gastrocnemius nerve-muscle preparation. Place the nerve near its muscle on one arm of the clay; lift the other part of the nerve with the glass rod and drop the freshly cut end on the other arm of the clay. The muscle will twitch, stimulated by the demarcation-current from the nerve.

These experiments demonstrate the injury-current of the tissues and the great irritability of nerve as well. The term demarcation-current signifies that the injury-current originates at the dividing-line between the normal and the injured tissue. It is also sometimes ill-called the current of rest. The direction of the demarcation-current is always from a normal point round through a connecting conductor to an injured point: the latter is "negative" to the former. Theories as to the cause of the demarcation-, rest-, or injury-current have been various, one sort "molecular" and the other chemical. Du Bois Reymond originated the former, and especially Hermann and Hering have elaborated the latter hypothesis. This chemical theory supposes that the katabolic changes consequent on injury reduce the electromotive force of the part making it less than (negative to) that of the normal region. These theories apply to nerve as well as to muscle.

The strength of this current is much smaller in nerve than in muscle; in the former its strength is from 0.005 to 0.030 volt. In muscle it may reach 0.1 volt. In nerve, owing to the relatively quick death of the tissues, it rapidly disappears. Dead protoplasm gives no current of any sort, nor do normal tissues so far as we know except when functioning. It is then only in necrobiotic protoplasm that this sort of electricity is set free. Its significance is not as yet clear, but its theoretical importance is obvious.

Expt. 52.—*Direction of Current Affects Contraction.*—(Apparatus: Wax, sartorius muscle, rheocord.) Make a wax trough just large enough to contain the sartorious muscle, and place the moistened muscle within it. Place wires from the rheocord (block and anode) on either end of the trough and close the key. The muscle contracts. Place the wires on opposite sides of trough so that current goes exactly across the muscle at right angles. The muscle does not contract. At any other angle than this the current is an effective stimulus. Use various strengths of the electricity.

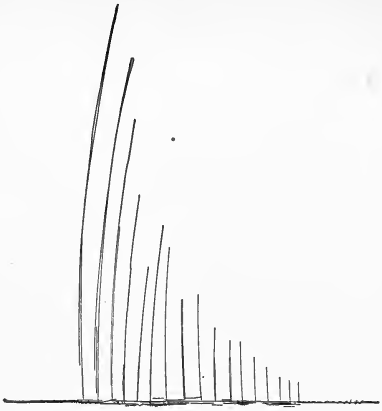
It is not easy to account for this phenomenon definitely, but there are two hypotheses. One is that the lack of response is due to the balancing of the two opposed influences at the cathode and anode, leaving the resultant zero. This could occur only when the current was exactly transverse, hence the difficulty of a good result. At 45° angle the result is less than when the direction of the current is along the fibers. The second "explanation" lies in the much greater resistance shown to electricity's passage across fibers than with them. In nerve, for example, where the same phenomena obtain, the longitudinal resistance is said to be 2,500,000 times the resistance of a like length of mercury, while the transverse resistance of nerve is 12,500,000 times greater. In these cases the electricity might not pass through the excitable tissues at all.

Expt. 53.—*Unipolar Induction.*—(Apparatus: Inductorium, four nerve-muscle preparations.) (*A*) Make four nerve-muscle preparations and place them on a perfectly dry glass plate so that the nerve of each shall be over the muscle of the next except the last. Push the secondary coil completely over the primary, open the short-circuiting key, and set the vibrating armature in motion if not already vibrating.

Connect one binding-post only of the secondary coil with the first of the series of muscles. One after the others will contract stimulated by the induced electricity "piled up" on the pole, for this electricity has many of the characteristics of static electricity.

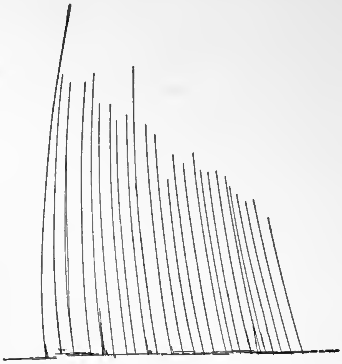
(*B*) Remove three of the four muscles, and while the remaining one is being stimulated as before, hold a moistened finger near the muscle. The latter will contract, the stimulating tension being reduced suddenly by withdrawal into the condensing human body. The practical moral of this experiment is to always keep the short-circuiting key closed save exactly when the induced electricity is being used, thus avoiding explosions of the sort demonstrated.

Fig. 275



Effect on the contraction of much increasing the load. Each curve from left to right represents fifty grams more load beginning with the lever's weight only. Frog's gastrocnemius. Intervals of about forty-five seconds.

Fig. 276



Effect on the contraction of increasing the load. Each curve from left to right represents ten grams more load beginning with the lever's weight only. Frog's gastrocnemius. Intervals of about forty-five seconds.

The theory of unipolar induction is practically given in the directions for the experiment; induced electricity when allowed to accumulate on one secondary-coil pole has a high tension and the consequent ability to jump through considerable spaces of non-conductors. In practical neurology, for example, in testing muscles for reaction in cases of disease, this principle is of great importance, and errors of diagnosis may be easily made by disregarding it.

Expt. 54.—*Influence of Load on Contraction.*—(Apparatus: Myograph, inductorium, sartorius, various weights.) Set up the apparatus for making myograms from the sartorius muscle, used in place of the gastrocnemius. Use maximal break induction-shocks, cutting out all the makes. With the drum stationary, record a contraction when the muscle is loaded with a scale-pan only. Turn the drum (by hand) 1 mm. Add 1 gm. to the scale-pan and stimulate exactly as before. Continue thus, adding a gram each time until the load is 10 gm. Then add 5 gm. before each stimulation and record, and continue until the muscle no longer contracts (1000 grams?). Observe (*a*) the increase in the contraction's height by a moderate load, and (*b*) the decrease as the loads are further increased. (Figure out the power-index of the muscle, keeping its bipenniform shape in mind.)

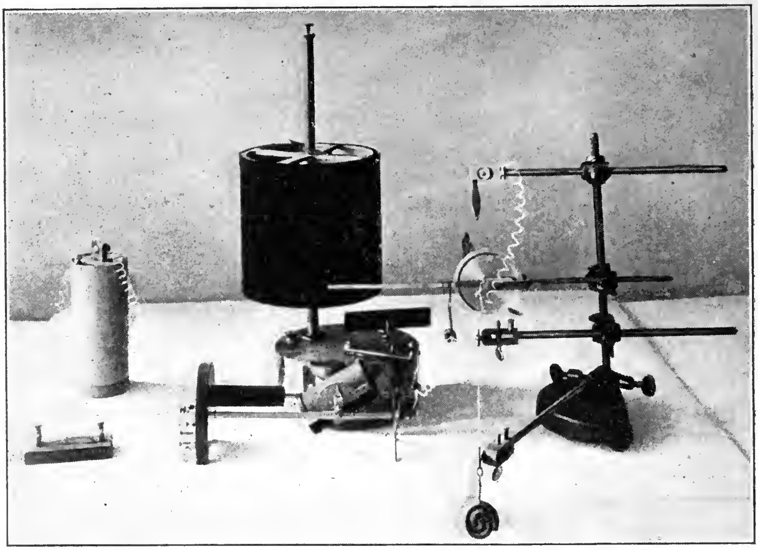
This is further evidence of the important principle that a muscle works best under normal conditions. The average resistance to contraction is one of these conditions, here represented by weights. When a muscle attempts to contract against a weight which it cannot at all lift, it is obvious that the muscle is expending much energy, as, indeed, might be easily demonstrated by calorimetric measurements of the heat, water, carbon dioxide, and nitrogen excreted and of the oxygen and food consumed. Hence in the biological definition of work the space and movements involved are of a minute or even molecular nature.

Expt. 55.—*Volume of Contracting Muscles Does Not Increase.*—(Apparatus: Volume-tube, stand-rod, etc., inductorium, modified Ringer's solution, entire leg of frog.) Place the frog's leg in the tube and hook the lower electrode into one end of it. Fill the tube quite full of the Ringer's fluid, insert the rubber stopper and hook the upper electrode into the upper end of the mass of muscles, being careful that no bubbles of air whatever remain in the tube. Push down the plunger-rod until the solution rises well into the capillary. Now pass a maximal alternating induction-current through the leg, making it contract and continue contracted. The liquid does not rise in the capillary tube, proving that the volume does not increase while the shape changes. Does the volume decrease?

During the contraction of cross-striated muscle (Schäfer) the sarcoplasm of each sarcomere passes into the longitudinal canals of the latter, being stopped by the transverse Krause's membrane in the middle of each sarcomere. Thus the fibril is thickened and shortened, doing its part in this way to shorten the whole muscle and so to approximate its ends.

Expt. 56.—*Effects of Heat and of Cold on Contraction.*—(Apparatus: Muscle-cooler-and-heater, myograph, inductorium, finely cracked ice, salt, Bunsen burner.) Place the cooler-and-heater on a stand-rod high enough so that the lamp or burner will stand far beneath the side tube. Make a gastrocnemius muscle preparation, place the femur in the screw-clamp inside the cover of the cooler, having attached a fine copper wire to the tendo Achillis. Pass the end of this wire through the hole in the bottom of the collar and attach it to the muscle-lever in the usual way, arranged to write on the smoked drum. Fill the space around the muscle-chamber solid full with finely cracked ice and sprinkle on a few grams of salt before covering. When the temperature has reached a degree or two above zero, stimulate the muscle with a single maximal break induction shock and record an accompanying time line. Have the drum rotate at a medium speed and keep this speed throughout the experiment. Make two or three of these curves. Now light the gas-burner (having its smokeless flame not over 3 cm. high) and place it under the outer end of side-tube. When the temperature has risen 5° cause another maximal break shock and record as before. Repeat this for every 5° rise of temperature, having the series of eight or nine curves all on one drum. As the temperature reaches 45° the muscle begins to go into heat-rigor, as is shown by its slight irregular contractions. Now have the drum revolve at a slow speed so as to obtain a graphic record of this, the final dying contraction of the muscle, above the abscissa line.

FIG. 277



Apparatus as set up by students to study the work done by a frog's cross-striated muscle.

Compare the shape of the various curves as regards (*a*) the decreasing lengths of the latent periods; (*b*) the increasing quickness of contraction; (*c*) the increasing quickness or relaxation; and (*d*) the increasing heights of the lever's rise, save at first, until near the end when the extent of the contraction somewhat decreases (as also the relaxation) as the muscle begins to stiffen with the heat.

The degree of heat of a muscle has much to do with the various analyzed parts of the contraction-movements. (1) The latent-period is shortened by increasing the temperature up to about 35°, it being perhaps half as long as at 5°. (2) In general terms, the amount of shortening of the muscle is increased by the upper limit of heat (as shown by height of the myogram), this increase being 40 per cent. or so over that of the muscle at 5°. (3) Generally speaking, the contraction time is lessened, the time of 55° being approximately half that at 5°. (4) Increase of temperature lessens the relaxation-period of the muscle, that at 30° being from 25 to 15 per cent. that at 5°. These estimates are for the gastrocnemius of the frog, and apply in detail to no other muscle, and even here are not at all constant.

Expt. 57.—*Work Done by a Muscle.*—(Apparatus: Work-adder, inductorium, kymograph, centimeter-rule.) Arrange the gastrocnemius muscle above the work-adder so that the lever of the latter will write on the drum, while the thread with 50 gm. on its end hangs over the edge of the table, the weight nearly on the floor. Mark with ink the spot on the thread at the top of the base of the work-adder. Now stimulate the muscle with single maximal break induction-shocks (carefully cutting out makes as usual) every three seconds by the watch. Continue this until the muscle no longer moves the lever or winds up the thread. Have the drum rotate slowly so that the myograms shall be very close together and all on one line around the drum. Mark with ink the thread (at the same level as before) at the end of the muscle's work. Unwind the thread from the wheel and measure the distance in centimeters between the ink-marks. This number multiplied by fifty (grams of weight lifted) gives the gram-centimeters of work the particular muscle did under the conditions of the experiment. Note the changing height of the myograms, and the shape of the curve connecting their summits.

The energy of muscle is derived from the chemical katabolism of carbohydrates (largely glycogen), fats, and proteids. In man about a third may be given out as muscular work. Fick found that of the latent energy in a muscle resisted by a heavy load, one-third may be used to lift this load, while, if the latter be light, not over 5 per cent. is utilized mechanically, the muscle then working at a disadvantage.

A heavily loaded muscle, then, does more work than one lightly loaded. With 70 gm. load the work done may be nearly ten times as great as when the load was 5 gm., while the length of the lift may be much less. The muscles of homotherms are stronger than those of poikilotherms, but the muscles of insects are stronger than others and much more active besides.

Expt. 58.—*The Contraction-wave.*—(Apparatus: Two muscle-levers, two stand-rods, cork clamp, femur-clamp, inductorium, kymograph, tuning-fork, millimeter-rule). Place the cork clamp horizontally in the femur-clamp; arrange the muscle-levers, one on each stand-rod, so that the cork stilts (previously tied on under the levers) may rest on either side of the muscle on the glass plate of the cork clamp, and both write on the drum. It is essential that a line connecting the writing-points of the levers should be exactly vertical, else measurement of the speed of the waves cannot easily be made.

Now prepare a long narrow strip of muscle, including the sartorius, from the thigh of the frog, and place it under the cork clamp (which should be pressed down somewhat lightly) and under the cork stilts of the levers. When the drum is rotating at its maximum speed, stimulate one end of the muscle with one maximal break induction-shock (the tuning-fork also writing its vibrations), using the platinum electrode. The lever nearer the electrode will be pushed upward by the contraction wave first, and the other lever will rise a few hundredths of a second later. Drop from the beginnings of the two myograms perpendicular lines to the tuning-fork's record, and count the number of double fork-vibrations between the two lines. This number will be the time in hundredths of a second required by the contraction-wave to travel between the cork stilts. Measure the length of the muscle between these two points. Reduce these millimeters per hundredths of a second to meters per second and the result is the speed of the contraction-wave in the particular case studied.

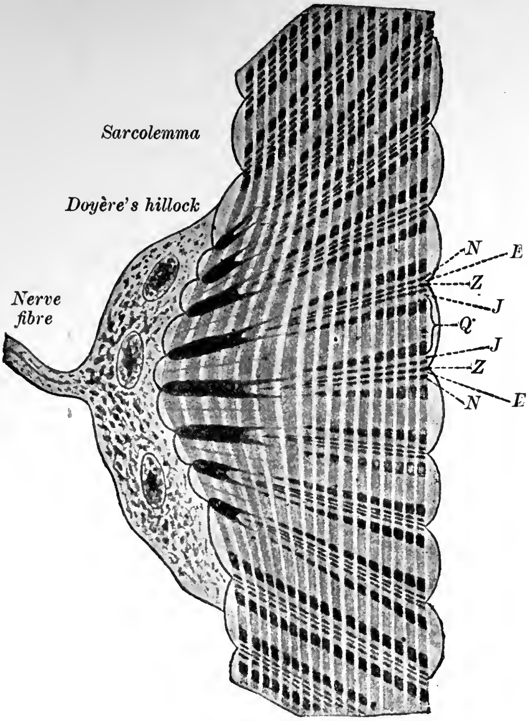
The contraction-wave is to be discriminated from the action-current. The latter is electrical and perhaps an extraneous phenomenon, while the contraction-wave is the actual physical thickening of the muscle which progresses in the likeness of a wave through the muscle at a definite rate. This thickening begins at any point in a muscle where a stimulus is applied to it, and divides and moves in both directions up and down the muscle. It progresses at the rate of about 3 m. per second in the cross-striated muscles of the frog, and faster in those of homotherms. The wave is about 30 cm. long, that is, were a muscle long enough, at intervals of 30 cm. along the muscle the thickening or crest of the wave would be seen simultaneously. In the red cross-striated muscle of the rabbit Rollett found the contraction-wave rate to be about 3.4 m., but in the white fibers it may go as fast as 11 m.; in human muscle the speed is (Hermann) from 10 to 13 m. per second. This progressive wave of thickening of the whole muscle is of course dependent directly on the thickening of the individual striped fibers in the well-known way.

In smooth muscle, according to Engelmann, the rate is only about 0.025 m. per second, while in the frog's heart ventricle (the muscle being, so to say, intermediate in character) the rate is (Waller) about 0.1 m. per second.

Expt. 59.—*Polar Stimulation.*—(Apparatus: Sartorius muscle, rheocord, simple key, and dry-cell.) Slit up the sartorius about one-third its length and lay it on the glass plate. Have the plate and the muscle comparatively dry. Place the anode on the left-hand side of the muscle, the cathode on the right-hand leg. Close the key, hold it three seconds and then open it. On the make, the right side of the muscle (cathode) contracts and on the break the left (anode)—*i. e.*, application of a moderate galvanic current causes stimulation at the cathode, and removal of the current stimulation at the anode.

Expt. 60.—*Physiological Anode and Cathode.*—(Apparatus: Rectus abdominis muscle of frog, rheocord, simple key, and dry-cell.) Connect a dry cell with a rheocord and key in the usual way. Remove the rectus abdominis muscle and lay it well stretched out longitudinally on the glass plate with weights if necessary. Place the anode from the rheocord on one end of the muscle and the cathode on the other. Using a very faint current, send a make-shock of galvanism through the muscle. At the cathodal end of each compartment of the muscle a faint contraction will be seen. Open the key, and a slight contraction will be seen at each anode. The muscle as a whole has no general contraction. This condition suggests the facts as regards the number of physiological anodes and cathodes in any part of the body, *e.g.*, a man's arm when stimulated through the skin. Subsidiary anodes and cathodes then clinically are apt to be numerous and must be allowed for.

Fig. 278



The contraction-wave in cross-striated muscle (Cassida equestris). The beginning of the contraction-wave of shortening and thickening is seen at the left in thick black lines. (Rollet via Szymonowicz and MacCallum.)

VII. HEART-MUSCLE.

Expt. 61.—*The Stannius Ligatures.*—(Apparatus: Kymograph, etc., heart-lever, frog-board, needle and thread, inductorium.) (Cardiograph.) (*A*) *The First Ligature.*—Having pithed a large frog and fastened it to the frog-board, open slightly the thorax and expose the heart by opening the pericardium. Cut the connective tissue from beneath, lift up the heart, pass the moistened thread under the bulbus arteriosus (coming from the ventricle) and around over the two superior venæ cavæ, carefully avoiding the inclusion of the aorta. Tie the thread around the junction of the sinus venosus and the right auricle. Draw the ligature with a surgeon's hitch just tightly enough directly over the whitish "crescent." The auricles and ventricles after a movement or two will stop beating, although the sinus-venosus continues. Touch the apex gently with the needle and observe that the ventricles may be easily artificially stimulated to contract.

(*B*) *The Second Ligature.*—With the first ligature in place, tie a second bit of moist thread around the heart in the auriculo-ventricular groove just above the ventricle. When properly adjusted just over Bidder's ganglion (which must be found by chance more or less in these small hearts), the heart begins again its automatic rhythmic beat, but at a rate slower than normal.

These two experiments, first performed by Stannius in 1851, are more easily carried out successfully than certainly explained. The cause of the phenomena of the *first ligature* is especially obscure, but there are two tentative explanations: The first ligature may stimulate the inhibitory action of Remak's ganglia in connection with the vagus. Another way of accounting for the facts of the first ligature is that, if the beat of the heart originates, as is generally admitted, in the sensitive tissues of the sinus venosus, this ligature may cut off the progress of the impulse, thus making necessary a long pause before the ventricle can gather energy enough to make a beat of its own originating. It is usually considered that the *second ligature* starts up the heart by stimulating Bidder's ganglion in the auriculo-ventricular septum, and that this constant stimulation has the same (trophic?) influence on the ventricle as has the normal influence coming to this ganglion.

Expt. 62.—*Every Contraction Maximal.*—("All or None.")—(Apparatus: Kymograph, inductorium, heart-lever, needle, and thread.) Place about under the bulbus venosus of a frog's heart the first ligature of Stannius, as described in the former part of the previous experiment, bringing thereby the heart to a stand-still. Put the pan of the cardiograph (heart-lever) under the heart without detaching the latter from its anatomical connections, and connect with it wires from the secondary coil of the inductorium arranged for single make and break shocks. Place the secondary coil so far from the primary that neither make nor break causes the apex (ventricle) to contract. Arrange the lever of the cardiograph for writing on the drum while the latter is stationary. Move the secondary coil very slowly and gradually toward the primary until a single break shock causes contraction of the apex. Turn the drum a millimeter by hand and stimulate again with a make-shock. Now gradually increase the strength of the stimulus and make a record each time (allowing at least thirty seconds to elapse between each two) until the shocks are of maximal strength. Comparing the height of the cardiograms, it will be seen that the last is not longer than the first.

In other words, the heart contracts on the principle of "all or none." The aluminum heart-lever may be used instead of the older heart-pan; the platinum electrode is then applied directly to the suspended heart.

As has been learned in the work on cross-striated muscle, the force of its contraction varies somewhat with the stimulus; but the heart, as we see, does not beat on this principle. It is impossible to be sure as yet why this is so. Gaskell, one of the leading authorities on cardiac contraction, thinks this phenomenon (and also that of the refractory period and the fact that the heart cannot easily be tetanized) may be explained by supposing that in case of the heart all the heart-cells are stimulated together by even a weak stimulus; or (on the supposition that the metabolism, both up-and-down, of the heart is slower than that of cross-striated muscle and the energy-material more stable), that they are less easily katabolized in contraction. (See also notes at end of the directions for Expt. 67.)

Expt. 63.—*Muscular "Automaticity."*—("Engelmann's Incisions.") (Apparatus: Fine scissors and a frog.) Expose the heart of the pithed frog; lift it gently by the lower end of the apex, and with a pair of small, sharp-pointed scissors make transverse incisions into the ventricles from both sides, so that those from each side extend beyond the middle line but do not connect. By these means any nerves which might extend from base to apex might be cut. Observe that the contraction-wave passes over the slashed ventricle down the zigzag strip of muscle from base to apex.

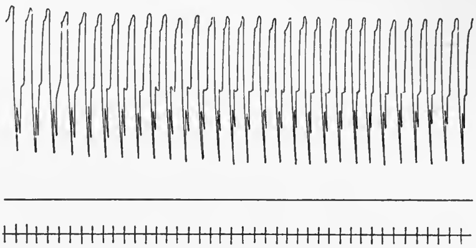
This "automaticity" of certain muscular tissue is a large question, which becomes more complicated rather than simpler. It is essentially the problem whether muscle can act normally without any influence from nerves so long as it is supplied with nutriment and kept in physiological condition. It involves, too, the whole matter of the general function of the nervous system. Lately the ions and the theory of the electrolytic dissociation of inorganic salines have come into the problem. Discussion of the matter is out of the question here, but see the theoretical notes of Expts. 67 and 68, and the discussion in the body of the book, page 293, etc.

Expt. 64.—*The Inherent Beat-rhythm.*—(Apparatus: Dry-cell, rheocord, stand-rod, femur-clamp, key, wires, dissecting-plate.) Connect the rheocord to a cell through a key. From the block and anodal post of the rheocord run wires to the jaws of the clamp so that their ends may be applied to the heart in a fixed position, the hands not being steady enough (do not twist the wires together). Sever the ventricles of a frog's heart carefully at the auriculo-ventricular groove, lay them on the glass plate, and keep them only barely moist with saline. This isolated "apex" does not beat. Now stimulate it (one electrode on each side) with the constant galvanic current, gradually increasing its strength until the make just causes a contraction. At this strength let the current pass continuously through the apex. It will beat rhythmically, such being its life-habit and that of its cardiac ancestors.

From some source (perhaps from a progressive anabolism in the protoplasm, possibly from the nervous system), the normally beating heart receives a constant stimulation. The galvanic current may serve as a substitute for the normal stimulus whatever it is, and occasion similar reaction. Other muscle does the same, for example the ureter, the dartos, and in some cases the intestinal muscle.

Expt. 65.—*No Cardiac Tetanus?*—(Apparatus: Needle, thread, inductorium, key, kymograph, etc., heart-lever.) Apply the first Stannius ligature (around under the sinus venosus) as described in Expt. 61. Place the quiet heart in the heart-lever, connect the latter with the inductorium arranged for tetanizing currents (with the armature vibrating), and arrange the lever to write on a slowly rotating drum. Stimulate the heart with three strengths of this alternating current, weak, medium, and maximal, each for a series of ten or more beats. Nothing like the tetanus-curve of cross-striated or of smooth muscle is produced.

Fig. 279



Normal frog-cardiogram by the suspension-method. The auricular beat occurs first. To be read from left to right. Original size. The time-line is in seconds.

If the frog's heart, however, be warmed to 35° and such a current be sent through the heart, something approaching tetanus is produced in the organ. This is thought to be abnormal; it is perhaps a degree of the torpidity due to heat rigor, or to the coagulative death of the cardiac protoplasm. The matter, however, needs further study.

Expt. 66.—*Temperature Affects Contraction.*—(Apparatus: Heart-lever, kymograph, chronograph, etc., Ringer's fluid at 3° and at about 40°, pipets.)

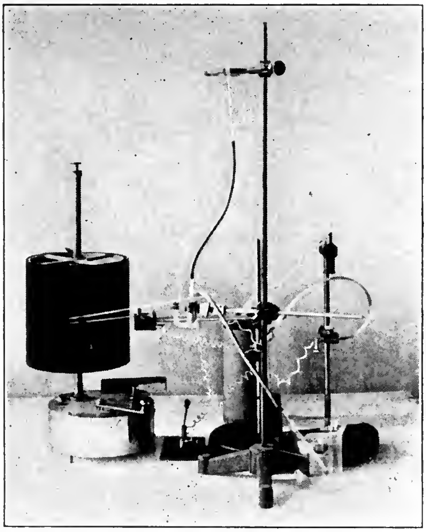
(*A*) Put the normal heart in connection with the heart-lever and make a series of cardiograms on a drum rotating slowly; by a watch make on the curve a short mark exactly every ten seconds, or use the time-marker. This record shows the rate of the heart at a room temperature, about 18°. Determine exactly this rate per minute.

(*B*) Start a cardiogram on a lower drum-level. With a large pipet drop by drop add the modified cold Ringer's solution to the heart. Observe that the heart at once slows. Measure off the cardiogram into ten-second periods as before, and calcutate the cold pulse-rate per minute, and the percentage of retardation.

(*C*) Again push the drum down so that the lever may write in a fresh place just above the normal curve. With the pipet add a few centimeters of the Ringer's solution at 30°. The heart soon beats much more rapdily. Measure off the record and count the beats per minute. (If the degree of heat be as high as 35°, the ventricle ceases while the auricle continues; a few degrees warmer, and the heart muscle dies in heat-rigor.) Calculate the rate and percentage of change as before. (See Fig. 153, page 286.)

There is little that needs general explanation in these results. Almost universally does protoplasm slow its action when cold and hasten it when warmed to a degree somewhat below that of its coagulative death. Poikilothermous animals show this better than homothermous animals could, for their tissues are adapted to these changes. The heart of a frog buried in the mud at the bottom of a cold pool probably does not beat fully all winter, but only hard enough to maintain a very sluggish circulation. The same sort of cardiac acceleration obtains in persons when they have a fever; that is, a relatively slight rise of body-temperature. In Daphnia the changes are much more marked than in the frog. We saw the ameba hasten its streaming movements when it was warmed; when in the water near the freezing-point it is apparently but a tiny drop of almost motionless colloid.

Fig. 280



Apparatus as set up by students to prove the action of electrolytic salines on the frog's heart-muscle.

Expt. 67.—*The Importance of* (*Electrolytic?*) *Salines.—Perfusion with Ringer's Solution.*—(Apparatus: Heart-oncometer, Ringer's solution.)

Tie a piece of the thinnest rubber dam over the top of the arm of the oncometer, and fill it with Ringer's fluid (consisting of a weak solution of sodium and potassium chlorides and of basic calcium phosphate in distilled water). Remove a *large* frog's heart by cutting it transversely with the scissors about midway through the auricles. With a moistened fine silk thread tie the heart over the end of the perfusion cannula so that the latter shall extend just into the ventricle through the auriculo-ventricular opening, and be sure that the openings of the cannula are not obstructed. Press the cork of the cannula into the body of the oncometer and adjust, if necessary, so that the heart shall hang free in the surrounding solution, being sure that the instrument contains no bubble of air. Fill the portion of the inflow-tube above the closed clamp with the solution, and insert the short arm of the siphon in the Ringer's fluid in the beaker above. Adjust to the rubber diaphragm the tiny cork block and above it the light straw lever attached to the cork stopper by a crank-shaped pin. Now loosen the pinch-cock slightly to allow the solution to run slowly down the tube. Gradually raise the upper beaker in the stand-ring. When the pressure has reached that of 10 or 15 cm. of water the ventricle will begin to beat rhythmically. If not, insert fine copper wires in the oncometer and connect them with a dry-cell through a key. It is sometimes impossible to obtain frog-hearts large enough for this experiment; it is difficult to insert the perfusion-cannula into the ventricle of a small frog-heart without obstructing the former.

Only in very recent years has the extreme importance of the salines in the blood become apparent, but calcium, magnesium, sodium, potassium, etc., are now known to be important in the composition of protoplasm. Deprived of their continual supply of these metals by way of the blood, tissues promptly cease to function, while, on the other hand, an isolated heart even of a mammal may be made to beat for hours when perfused with these salines in the proper proportions and kept warm and moist. We are still only at the gate-way of the physiology of the inorganic salts in protoplasm. Perhaps the ions are the real causes of this complex influence of the various saline substances.

Expt. 68.—*The Refractory Period, Extra Contraction, and Compensatory Pause.*—(Apparatus: Kymograph, etc., heart-lever, inductorium, heart.) Place the normal heart in the heart-lever and arrange the latter to write on the drum rotating at a slow speed. Run wires to the heart from the inductorium's secondary coil. Record the normal beat of the heart on the drum. Early in the uprise of the lever at some beat throw into the heart a maximal make induction-shock (cutting out the break). By stimulation within this period no extra contraction is produced. This (the period of systole approximately) is the "*refractory period*" of the heart. Throw in another maximal make-shock just at the height of the lever's rise; the stimulation now causes an extra beat. This is the "*extra contraction.*" Now observe that the next automatic beat does not occur at the time in the regular rhythm when it should, but that there is a pause of the heart until the time of the succeeding regular beat.

This is the "*compensatory pause.*" In other words, the rhythm of the beat is not disturbable during systole, but when disturbed at any other time the inherent rhythm is maintained by a pause of just the right length so that the next beat occurs in the regular rhythm.

All the metabolic processes of cardiac muscle probably take place more slowly than do those in cross-striated muscle. It is on this account perhaps that the heart's refractory period is so long; that the viscus cannot easily be tetanized; and that there is no relation between the power of the beat and the strength of the stimulus (Gaskell). The cause of the refractory period is probably, in fine, then, the absence during that time of energy sufficient to allow of a contraction, the immediate supply of power having been used up by the systole. Indeed, according to Engelmann, the power of responding to very weak stimuli is regained only at the end of the following rest (diastole). Cross-striated muscle, however, has a refractory period, although it is much shorter than the heart's.

The compensatory pause means that when the rhythm is disturbed by an extra beat the heart cannot contract for a long period again because the energy is used up; it takes up, however, the rhythm inherent in the muscle and beats at the time this rhythm requires.

The extra contraction during the systolic period is nowise unlike that occasioned by a stimulus applied to a cross-striated muscle, there being now nothing to prevent this contraction, for the heart has now again an adequate supply of energy.

Expt. 69.—*The Action-current Precedes the Beat.*—(Apparatus: Heart-lever, kymograph, etc., myograph, counterpoise for heart-lever.) Smoke a drum lightly, and weight the short arm of the heart-lever so that it is nearly as heavy as the long arm. Set the cardiograph on the base of the stand-rod and arrange the gastrocnemius muscle in the femur-clamp, etc., above it in the ordinary way save that the lever is above the femur-clamp. (Use the pulley on the muscle-lever so that on contraction the muscle pulls the lever upward as usual, and not downward, although below the lever.) Adjust the femur-clamp to the cardiograph so that the nerve of the nerve-muscle preparation shall rest longitudinally on the heart. Arrange the two levers to write exactly over each other on the slowly rotating drum. At each beat of the heart the sciatic nerve will be stimulated and the gastrocnemius will contract. Note that the cross-striated muscle's record begins at each beat before the heart's record begins. Apply a tuning-fork and try to measure the length of time by which the action-current anticipates the actual action of the heart. (To insure prompt success in this experiment the gastrocnemius and sciatic must be freshly prepared and very sensitive. The result, when obtained, is striking.)

It has been already shown (Expt. 50) that when a skeletal muscle contracts its action-current is an adequate stimulus to muscle like any other electric current of sufficient energy. It is easier to show the precedence of this action current on the heart which beats "automatically."

The impulse occasioning the beat starts at the central end of the large veins and proceeds quickly over the heart, the connection between the auricles and the ventricle being made not by nerves, but by a few slender fibers of muscle extending from the auricles to the ventricle. The speed of this contraction-impulse (mechanical) is great, but very much less than that of the (electrical) action-current. Indeed, the contraction of the heart, including its brief latent-period, requires so relatively long that not only the heart's action-current passes, but it has time to stimulate a nerve and produce contraction in a skeletal muscle before the heart's contraction occurs. The difficulty of the experiment is due to the trouble of placing the nerve so as to receive well the heart's action-current. A lack of sensitivity in the nerve and muscle used prevents a good result.

Expt. 70.—*Polar Inhibition.*—(Apparatus: Flat electrode, cell, rheocord, commutator, key, fine copper wire). With one rheocord-pole connect the flat electrode and with the other the piece of fine wire. Cut off the upper jaw of a frog and expose the heart. Place the flat brass electrode in the mouth of the frog and the end of the fine wire on the beating ventricle. Observe closely the heart-tissue under the end of the fine wire, and with the commutator rocked so that the end of the wire is the anode, close and hold the key. During systole it is clear that contraction does not occur at this point, for the tissue remains red and does not pale like the remainder of the heart. This is the active inhibitory effect. Now shift the rocker of the commutator so that the fine wire-point becomes the cathode, and close the key again. The effect now occurs during diastole: the spot remains pale while the apex relaxes, indicating that the cathodal stimulation inhibits normal relaxation.

The results of this experiment must be taken at present empirically—they cannot be definitely and certainly explained. When a weak current goes through the heart the anodal pole causes inhibition of contraction at that point, while if the cathodal pole be on the heart, concentrated in space, a local inhibition or relaxation occurs. There have been two theories of explanation of inhibition in general—one that it is purely a nervous effect, and the other, more probable, that the influence arises in the muscle or gland directly. On the latter hypothesis the inhibitory influence comes from a cessation of katabolism, activity involving katabolism as surely as rest gives rise to the anabolic process. The former is usually obvious, but the anabolic process, giving little sign, may be hard to appreciate. Gaskell goes so far as to say that the inhibitory influence probably sets up active anabolism, which thereupon checks katabolism. This is called the trophic theory of inhibition. There is at present, however, no surety that these two opposed processes may not go on simultaneously in a tissue. Inhibition is a subject of great promise to researchers into the basal relationship of the tissues and the nervous system.

Expt. 71.—*Tonus.*—(Apparatus: Kymograph, etc., muscle-lever, tortoise.) Chop off a tortoise's head and saw off the lower part of the shell. Pass a fine wire through the auricle of the tortoise's isolated heart and connect it with the muscle-lever, arranged to write on the slowly rotating drum. Note the compound cardiogram, the larger waves representing the tonus of the heart and the smaller vibrations the beats. From ten to forty of the latter occur during one tonus-wave. This phenomenon appears to be widespread if not universal in muscle, but its import is not yet clear. Under certain conditions not yet definable these vasomotor tonal changes occur also in the frog's heart. (See Figs. 157 and 160.)

Expt. 72.—*Muscarine and Atropine* (its antidote).—(Apparatus: Heart-lever, inductorium with platinum electrodes, muscarine-solution, atropine-solution, frog or tortoise.) Set up the inductorium for alternating currents. Expose the heart, and stimulate the pale "crescent" (between the sinus venosus and right auricle) with strong alternating currents. The heart's beat is more or less inhibited. Now, with a pipet add three drops or so of the muscarine-solution to the heart. It gradually comes to a standstill. Stimulate the ventricle with induction-shocks and observe how little irritable the muscle is. Let it alone a few minutes. Now let fall a few drops of the atropine-solution on the heart. It gradually beats again, perhaps more powerfully than is normal. Stimulate the crescent as before. No inhibition now takes place, for the atropine has paralyzed the neural mechanism of the heart.

Muscarine is the alkaloid which sometimes kills people who eat poisonous fungi. As in this experiment, its action is directly on the heart-muscle and not on the cardiac nerve-mechanism. Atropine, then, is the physiological and therapeutic antidote of muscarine, but it acts powerfully on the nerve-cells in the heart. As these are of inhibitory function (see Expts. 61 and 87), no harm follows. It acts also on the muscular tissue and it is here that it exerts its direct antagonism to the muscarine.

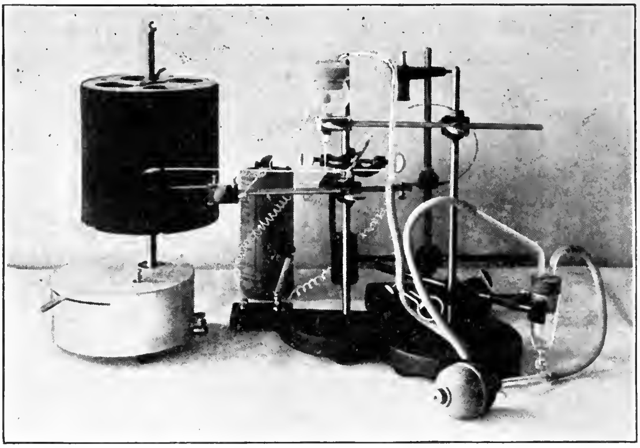
Expt. 73.—*Nicotine.*—(Apparatus: Kymograph, etc., heart-lever, pipet, 0.1 per cent. nicotine-solution, frog, and Daphnia). Expose the heart and make record of its beat on the rotating drum. Now add a few drops of the weak nicotine-solution. The heart slows for a short time and then beats more strongly than before. The slowing is due to a stimulation of the intracardiac inhibitory mechanism, while the augmentation of the beat comes from a partial paralysis of the same nerve-cells. Nicotine in small quantity stimulates and then paralyzes the neurones, especially the cell-bodies.

Nicotine for some, probably chemical, reason has a predilection for the cell-bodies of the neurones, exerting no effect on the neuraxones. Excessive smoking has on the human heart some of this demonstrated effect, making it irregular and rapid. The stimulating result of the four tobacco alkaloids is seen in their action on the cerebral cortex: they incite to mental work and abolish to a marked degree the feeling of fatigue. Their action, however, on the nerve-cells of the walls of the stomach is often disastrous to perfect digestion. (See page 169.) Demonstration of nicotine's action on the heart of Daphnia (see Expt. 12).

Expt. 74.—*Adrenalin.*—(Apparatus: Cardiograph, 0.01 per cent. solution of adrenalin chloride in Ringer's solution, frog's heart.) Make a normal cardiogram as before. Bathe the heart with the solution drop by drop and record the beats just above the normal curve, all conditions else remaining constant. Note the actions of the adrenalin on the pulse-rate and on the power of contraction, and how systole and diastole are each affected.

Expt. 75.—*Carbon Dioxide, Oxygen, Ether, Chloroform, Nitrous Oxide, Carbon Monoxide, Ammonia.*—(Apparatus: Thistle-tube gas-chamber, femur-clamp, heart-lever, kymograph, extra stand-rod, wire, thread, frog's heart, vapors, and bulb for infusing the same.) Arrange the thistle-tube in the femur-clamp directly over the long arm of the heart-lever. Excise the frog's heart, leaving the great vessels long. Pass the wire hook of the gas-chamber stopper through the little mass of the vessels. Pass a thread with a small wire hook on its upper end down through the glass tube and fasten to the long arm of heart-lever near the fulcrum. Insert the wire hook through the ventricle not too near the apex. Place the stopper in position and adjust the fine wire through it so that the beating heart at each shortening will lift the lever.

Fig. 281



Apparatus as set up by students to show the action of various vapors on the frog's heart-muscle.

By means of the bulb-infuser blow a small amount of a vapor into the gas-chamber and close the openings of the latter.

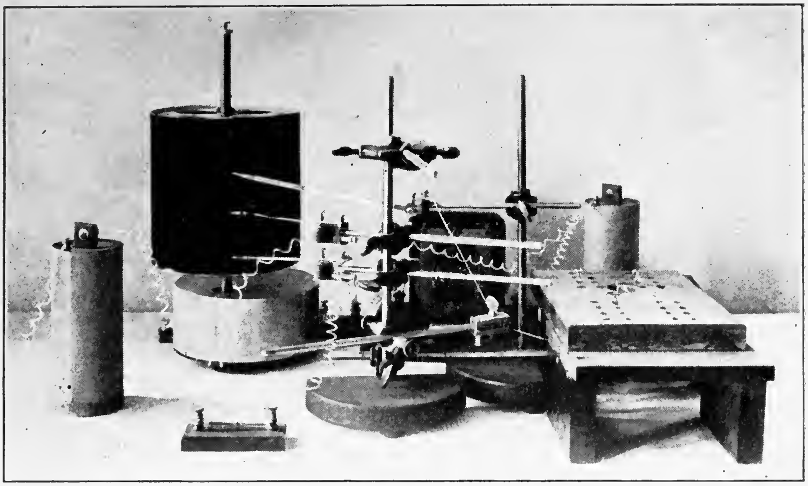
Record these drug-cardiograms and compare them with the normal curve. After each experiment thoroughly wash the heart with Ringer's fluid and allow it to rest a short time.

Expt. 76.—*Lymph-hearts.*—(Apparatus: Frog (or tortoise or snake), frog-boards, seeker, watch). Pith the frog's brain and fasten the animal belly-down on the frog-board, the hind legs abducted. By *short* transverse gentle incisions just above the pyramidalis muscle near the end of the urostyle open into the small triangular spaces on either side of the latter. A small transparent lymph-heart will be seen in each space.

(*A*) Count the number of their pulsations per minute, and compare their rhythm with that of the blood-heart. Do they correspond?

(*B*) Pith the caudal part of the spinal cord and observe that the beatings of these lymph-hearts stops, while the blood-heart is undisturbed.

FIG. 282



Apparatus as set up by students to compare the beat-rhythms of the blood-heart and of the lymph-hearts in the frog.

By boring a hole through the frog-board the beat of the blood-heart may be recorded on the drum, the connecting thread passing over the requisite pulleys. With a Morse key arranged to actuate a signal writing just under the pen of the heart-lever, the time of the pulsations of the lymph-hearts may also be recorded. By this simple means the comparison may be made directly in a graphic way and many altering conditions of the lymph-heart rate may be studied.

VIII. NERVE.

Very great care must be observed in experiments on nerves that they be uninjured by mechanical or chemical influences. Drying (chemical injury) is especially to be guarded against, and to prevent it a nerve should never be allowed to hang free in the open air. In all experiments requiring more than a few minutes the moist-chamber, lined more or less with salined filter-paper, should be used. However inconvenient, these protectors from evaporation are essential in experimental work on isolated nerves.

Expt. 77.—*Neuraxones Conduct in Both Directions.*—(Apparatus: Cell, inductorium, key, sartorius.) Isolate the sartorius muscle carefully and place it on the *dried* dissecting-plate. The motor neuraxones in this muscle divide, one part going to each side of the lower end. Slit up the middle line one-third of the broad end of the muscle, and stimulate with the smallest strength of break induction-shock that will cause a contraction on one "leg" of the divided muscle, both electrodes being at the *end* of the other leg. Observe that with this stimulus, or one slightly stronger, contraction takes place in the other leg of the muscle also. The efferent neuraxones have conducted impulses afferently as well as efferently.

Another place besides the sartorius muscle that this principle may be demonstrated is on the nerves supplying the electrical organ of the electric catfish (Malapterurus), where a single neuraxone supplies a large organ that may be detached from the fish completely, and its nerve studied.

Expt. 78.—*Effect Depends on Connections.*—(Apparatus: Inductorium, key, frog-board.) Pith the brain only of a frog and place the animal belly down on the frog-board. Cut out and away the *upper third* of the spinal column (which extends from the head only *to* the urostyle). With *fine and small* scissors cut away the bone at either side of the remainder of the spinal *cord* (being very careful not to injure in any way the latter), thus having the cord free of its vertebral bony covering. Observe the posterior (afferent) roots and the large anterior (efferent or motor) roots lying beneath them.

(*A*) *Afferent Fibers not Motor.*—Tie a ligature about the largest posterior root close to the cord and cut the root between these. Stimulate with *very weak* single induction-shocks the peripheral portion of the divided root. Practically no leg movements occur. The posterior roots are afferent.

(*B*) *Afferent Fibers Connect with Motor Neurones.*—Tie a ligature about another of the large posterior roots as far as possible from the cord, cutting the root peripherally to the ligature. Gently stimulate the central portion. Muscular contractions occur.

(*C*) *Anterior Roots not Afferent.*—Cut through all the posterior roots of the side on which Expt. B was performed. Stimulate mechanically and chemically the skin of the leg on the same side. No movements occur. Stimulate similarly the other leg. Movements occur in both legs.

(*D*) *Efferent Fibers Motor.*—Ligate a large anterior root close to the cord and sever, as before, between the ligature and cord. Stimulate the peripheral cut end. Contractions occur in the muscles attached. The stimuli must be very weak.

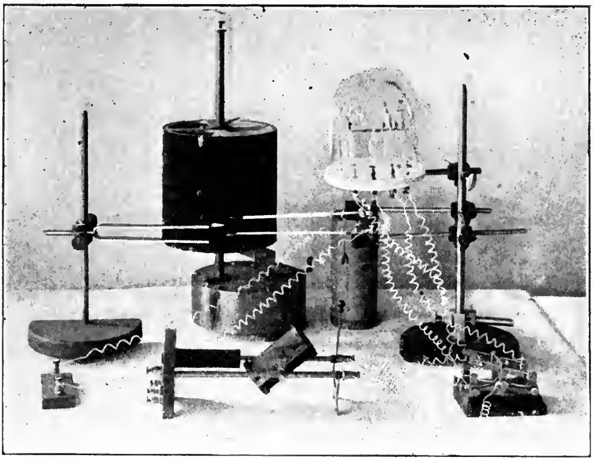
(*E*) *Efferent Fibers do not Conduct Centrally to Motor Neurones.*—Tie another anterior root far from cord, and cut peripherally to the ligature. Stimulate as before near the central cut end. No movements follow.

(*F*) Cut all the remaining anterior roots, and stimulate mechanically and chemically the skin of the legs. Now no contractions whatever occur, all the central connections being cut.

No spinal root, however, is purely either afferent or efferent.

Expt. 79.—*Speed of the Nervous Impulse.*—(Apparatus: Kymograph, etc. (myograph), glass nerve-plate, tuning-fork, electro-magnetic signal, commutator, millimeter-rule.) Twist around each end of the dry glass nerve-plate two fine wires 3 mm. apart, and connect their ends with the four binding-posts of the commutator without its cross-wires. Connect the rocker-posts with the secondary coil of the inductorium. Arrange the myograph to write on the drum, the nerve-plate close to the top of the gastrocnemius, the signal (and the key) in the primary circuit of the inductorium writing directly and exactly under the pen of the myograph's lever. Hold the tuning-fork so that it will write under the signal. Make a gastrocnemius preparation, having the nerve as long and normal as possible. Lay the nerve on the glass nerve-holder over the two pairs of electrodes, one pair near the muscle, the other at the nerve's end. Rock the commutator so that the shock will enter the nerve by the pair of electrodes nearer the muscle. When the drum is spinning (raised by the top screw from its friction-bearing) set the tuning-fork vibrating and stimulate the nerves with a moderate break-shock (cutting out the make). Now lower the drum to a fresh place. Shift the rocker so the current may go in by the further pair of electrodes and make a similar curve with a break-shock, making the time-record also. The time-interval between stimulation and the beginning of the myogram (as shown by the tuning-fork) will be less in the former curve than in the latter. Count the difference in hundredths of a second. This is the time required for the nervous impulse to pass between the two pairs of electrodes. Measure this distance in millimeters and calculate the speed in meters per second.

FIG. 283



Apparatus as arranged by students to show the speed of the nervous impulse in the frog's sciatic.

It was the great Helmholtz who first noticed that nervous impulses require time for their transmission, and he demonstrated it on the sciatic of the frog and on man. Time is required because the setting-up of chemical (or electrical or molecular) change in the millions of complex molecules along the progress of the impulse takes time. The actual rate varies widely in the different nerves of different animals, but along the frog's sciatic (poikilothermous mixed nerve) the rate in the winter-season is usually 20 meters per second. It is often much less. In sensory nerves it is apparently about the same. In man the average rate is not far from 40 meters per second.

Some of the conditions which decrease the speed are the dying degeneration of the nerve, cold, pressure, stretching, fatigue, alcohol, ether, and strong electricity. Heat increases the rate.

Expt. 80.—*Electrotonus.*—(Apparatus: Dry-cell, key, commutator with cross-wires, myograph, glass nerve-plate, 15 per cent. sodium-chloride solution, fine copper wires.) Twist two copper wires 4 cm. apart about the glass nerve-plate and connect their ends with two adjacent posts of the commutator with cross-wires. Connect the rocker-posts with a dry-cell through the key. Adjust the nerve-plate close to top of gastrocnemius in the myograph so that its long and normal nerve will lie over the electrodes.

(*A*) *Anelectrotonus.*—Between the electrodes and 1 cm. from that nearer the muscle, place on the nerve a single drop of the sodium-chloride solution. Rock the commutator so that the nearer electrode shall be the anode. Observe the irregular contractions due to the chemical stimulation by the chlorine. Now close the key. The contractions lessen or cease. Anelectrotonus is in this case a condition of lessened irritability. Sometimes it is not so.

(*B*) *Catelectrotonus.*—Now shift the rocker so that it is the cathode that is nearer the strong salt solution, and close the key. The irregular contractions of the muscle occasioned by the salt are much increased. Catelectrotonus is a condition of increased irritability.

Expts. 59, 60, and 70 suggest the same fact that this experiment demonstrates.

Gotch thus summarizes Pflüger's general conclusions as to electrotonus, which, as its name implies, is only a condition of irritability or tone caused in a nerve by a stimulus: "Under the influence of a constant current flowing through a nerve there is an increase in the nerve-excitability, at or near the negative pole (cathode), a decrease at or near the positive pole (anode). On the cessation of the current these changes are reversed, the cathode being the seat of the fall, and the anode that of a rise in excitability. The alterations in excitability are most intense at the poles, but spread, diminishing with the distance, into the intrapolar and extrapolar regions. At some point in the intrapolar region the boundary between the two polar extensions is reached; this point is therefore unaffected, and is termed the indifference-point. The excitability changes are true for all forms of stimulation, electrical, mechanical, or chemical, and for both efferent and afferent nerves." The condition is explainable at present only tentatively; the most likely theory, perhaps, is that of electrolytic changes by the ions of the nerve-protoplasm, about which little is as yet definitely known.

Expt. 81.—*Afferent Impulses may Inhibit Reflexions.*—(Apparatus: Stand-rod with femur-clamp, inductorium, key, 0.5 per cent. sulphuric acid, acetic acid, beakers, small rubber rings.) (A and B of Expt. 78, as well as many other experiments, indirectly indicate the nature and neural mechanism of reflexions.)

(*A*) Observe that a normal frog placed on its back immediately returns, thus restoring its normal equilibrium. Now put a rubber ring about the proximal part of one fore-leg. The animal no longer rights its position, nor does the unconstricted leg show any tendency toward moving for that purpose. This shows that the effect is in the nervous system and not in the muscles. This inhibitory influence lasts only about fifteen minutes, the reflex mechanism for maintaining equilibrium then becoming tolerant of the unusual stimulus. In a decerebrated frog the returning-reflex is too much deranged to be effective.

(*B*) Pith the brain of the frog and hang up the animal by the lower jaw in the clamp. Lower one foot into the beaker containing a little sulphuric acid and with a watch carefully measure the time (reflex reaction-time) until the leg is withdrawn. Wash off the acid carefully with water and repeat the experiment. Wash off the acid again, and so on ten times. Average the reaction-times. Again immerse a foot and stimulate the other with a strong alternating induction-current, holding the foot down for the purpose. The reflex reaction-time of the leg irritated by the acid will be greatly lengthened or perhaps so strongly influenced that the leg is not withdrawn at all, inhibition being complete.

Expt. 82.—*Vaso-motor Function of Cord.*—(Apparatus: Stand-rod, femur-clamp, and seeker.) Pith the brain only of a frog. Make a small incision in the abdomen and draw out a loop of intestine; expose the heart. Observe these two organs with respect to the amount of blood in each, noting especially the hardness of the heart during systole and the size of the blood-vessels of the gut and omentum. Now carefully with a blunt wire seeker pith the cord of the frog. Note that the blood now collects in the easily distensible omentum.

The cord's vaso-motor centers are normally subordinate to centers in the medulla oblongata, for when the local centers of the cord and sympathetic ganglia are cut off from the bulb (medulla) many days are necessary before the local centers in the cord by themselves take up complete control. The neuraxones of probably all the spinal vaso-motor cells end in sympathetic ganglia (Langley). Sometimes these cells give out rhythmic impulses to the arterioles under their control. The vaso-motor centers can be stimulated reflexly from the blood-vessels, from the afferent nerves generally, or from the emotional centers probably in the optic thalamus. There is an inverse relation between the surface vaso-motor nerves and those of the viscera, as is seen clinically oftentimes in congestions from exposure to external cold.

In this experiment as carried out here all vaso-motor control of the viscera is destroyed and the main bulk of the blood collects where the force of gravitation draws it.

Expt. 83.—*Neuraxones Practically Unfatiguable.*—(Apparatus: Moist-chamber, inductorium, two dry-cells, platinum electrodes, myograph, keys.) Arrange the gastrocnemius nerve-muscle preparation in the moist-chamber in connection with the muscle-lever below and place the end of the long nerve on the platinum electrode connected with the secondary coil of the inductorium arranged through a key for tetanizing currents. On the nerve between this stimulating electrode and the muscle place two fine wire non-polarizable electrodes so that there will be a descending current connected with the other dry-cell through a key. Observe that the muscle contracts when stimulated with the induction-shocks. Throw through the nerve the galvanic constant current, and while it is passing stimulate again. No contraction now occurs, for the constant current acts as a "block" to the transmission of the stimulus by lowering the irritability of the neuraxones. Now leaving the galvanic current running, stimulate the nerve continuously for a long time with the rapidly tiring tetanizing current. Such stimulation would fatigue the "muscle" quickly, but the galvanic block prevents this, although not preventing active stimulation of the nerve between the platinum electrodes and the "block." After long stimulation shut off the galvanic current, thus removing the block, and short-circuit the induction current. Now open the short-circuiting key, thus again stimulating the muscle through the nerve. The muscle contracts quite as well as if the nerve had been unstimulated.

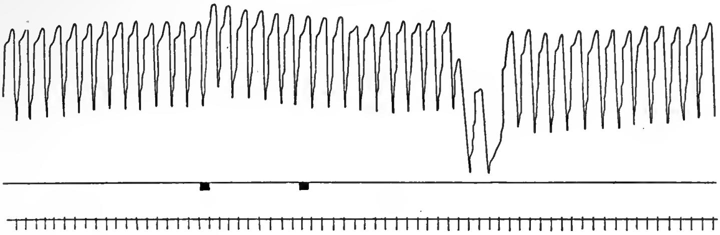
It cannot be surely said that neuraxones are theoretically, that is absolutely, unfatiguable, for it is inconceivable that a form of protoplasm so delicate and elaborate chemically as is nerve should not suffer from exhaustion of its stored energy, whatever it is, when continuously drawn upon for very long periods. There is a normal balance between anabolism and katabolism which must be disturbable after a time. The functioning of nerve may be, however, sufficiently intermittent to allow of apparently continuous performance, just as the heart seemingly works continuously. In reality, as we know, it rests three-quarters of the time, and only for this reason needs no long periods of rest.

Nerve-cells are fatigued with comparative ease, as was shown by Hodge. He kept sparrows flying continuously for many hours, and then compared their cortical motor cells with those of sparrows which had been at rest. The changes both in the cytoplasm and the nuclei were very striking, both being much shrunken. (See Fig. 27.)

Expt. 84.—*The Influence of Strychnine.*—(Apparatus: Pipet, 0.5 per cent. solution of strychnine, seeker.) Pith the brain only of a frog. Into one of the lymph-sinuses lying on either side of the spinal column inject a single drop of the strychnine-solution with the pipet. In a few minutes spasms of the leg-muscles, etc., will be seen, increasing in force. Soon the extensor muscles begin to overcome the flexors, and shortly the legs are rigidly straight. Note the extreme irritability of the whole animal (due to abnormal stimulation of the cord by the alkaloid): a slight pinch of the skin causes universal convulsions. Now destroy carefully with the seeker the spinal cord, and note that the previously noted phenomena cease at once. Strychnine acts on the spinal cord alone.

The precise mode of action chemically of strychnine on the nerve-cells is unknown, but whatever it may be, the drug collects especially in the spinal cord, and violently stimulates the reflex motor nerve cells. Any influence which can disturb the equilibrium of these centers, then, causes strong tonic spasm (contraction) of the muscles. It is apparently wholly owing to the fact that the extensor muscles are more powerful than the flexors that the resulting position of the animal is one of extreme extension. The practical importance of acquaintance with the phenomena of strychnine-poisoning should not be lost sight of.

Fig. 284



Stimulation of the uncut vago-sympathetic in the frog. The weak stimulation lasted between the little squares on the stimulation-line, and the effect took place only about twelve seconds later. To be read from left to right. The time-line is in seconds.

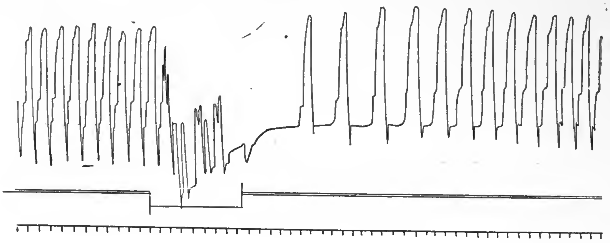
Expt. 85.—*Augmentation of Function.*—(Apparatus: Frog-board, inductorium, shielded stimulating electrode, heart-lever, kymograph, chronograph, etc., signal.) One of the best examples of neural augmentation is the effect of the *sympathetic on the heart.* To expose the sympathetic nerves which influence the frog's heart, pith a frog's or toad's brain, fasten the animal on the frog-board, cut away the lower jaw completely, and excise it below the angles. Very carefully remove tissue until the upper part of the spinal column is completely bared. Now very carefully raise and cut through the flat strip of muscle (the levator anguli scapulæ) extending obliquely outward from the occipital bone. This exposes the vago-sympathetic, the vagal ganglion, and the sympathetic line extending upward from the second, third, fourth, and fifth vertebræ. (This ascending trunk is usually pigmented and accompanied by an artery.) Ligate the nerve as low as possible and cut it below the ligature. Keep the nerves moist with modified Ringer's fluid. Expose the heart and place it in the heart-lever arranged to write on the very slowly rotating drum. (The writing end of the lever should ordinarily move at least

2 cm.) If the heart beats rapidly, slow it with cold solution. Record the normal beat, and mark off exact ten-second periods, or use a time-marker. After twenty contractions or so, stimulate the sympathetic (already ligated and cut) above the ligature with a weak tetanizing current of induced electricity. Count again the number of beats in ten-second intervals and compute the percentage of the acceleration over the normal rate.

In the frog the augmentor impulses leave the cord by the third spinal nerves, go by the communicating branch into the third sympathetic ganglion, up the sympathetic chain to the vagal ganglion, and down the trunk of the vagus.

The ordinary acceleration from stimulation of these nerves is very variable (10 per cent. or several times that), the acceleration being greater when the heart is already beating slowly; it is also influenced by the length of time the stimulation is continued. Excitation of the nerves in both sides at once accelerates no more than stimulation of only one nerve. The speed of the stimulation-wave passing over the heart muscle is increased. (See also Chapter VIII.)

Fig. 285



Stimulation of the peripheral stump of the vago-sympathetic in the frog. The stimulus was an alternating induced current fairly strong, and its time-relations are shown by the middle line. Note the gradual acceleration of the rhythm as the inhibitory influence passed away from the heart-muscle. To be read from left to right. The time-line is in seconds.

Expt. 86.—*Inhibition of Function.*—(Apparatus: Frog-board, small test-tube, heart lever, inductorium, chronograph, signal, kymograph.) Pith the brain only of a frog and fasten the body, back down, on the frog-board. Expose the heart by the removal of the sternum and draw the forelegs far apart. Push the test-tube down the esophagus to distend the tissues of the region. Carefully remove the muscles lying between the angle of the jaw and the hyoid bone in the median line. Observe the three fine nerves which pass upward from the angle of the jaw between the flat muscles; the lowest of these is the hypoglossal, next is the vagus accompanied by a blood-vessel, and still farther forward is the glosso-pharyngeal. This "vagus" trunk is, of course, really the vago-sympathetic.

Divide the glosso-pharyngeal branch of the vagus trunk to prevent disturbing contraction of the muscles. Place the heart in the heart-lever and arrange to write on a slowly rotating drum. Place protected electrodes from the secondary coil of the inductorium under the vagal trunk and remove the coil from the primary. Have the signal in the primary circuit. Record a normal cardiogram, marking off exact ten-second intervals. Now throw a weak alternating induction-current through the electrodes, the signal marking the instant of stimulation. The heart, after a latent period, stops in diastole. Note the length of the latent period, and of the straight inhibition-line made by the heart-lever. The viscus soon begins to slowly beat again and increases its rate even though the alternating current be continued. The inhibitory influence then is not complete, but only of a directing nature. Measure the period of inhibition.

Repeat this procedure with an induction-current stronger than the one already used, then with a weaker one. The mode of inhibition will vary according to the conditions. Observe that on resuming the beat, the sinus venosus always begins first and the ventricle last.

The six sorts of effect due to stimulation of the frog's cardiac inhibitory nerves have been already given in Chapter VIII (see page 295).

Expt. 87.—*The Intracardiac Inhibitory Mechanism.*—(Apparatus: Frog-board, inductorium, platinum electrode.) Pith a frog's brain. Expose the heart and lift it up over with a glass rod. Find the whitish crescent-shaped spot between the sinus venosus and the right auricle. Here are situated the nerve-cells connected with the vagus. Stimulate this "crescent" with the platinum electrode from the secondary coil of an inductorium arranged for alternating currents. After a beat or two the heart stops, but soon begins again despite continued stimulation.

These nerve-cells (Remak's ganglion) situated in the crescent are the inhibitory efferent nerve-cells; the corresponding efferent augmentor cells are in the ganglia on the spinal roots—part of the "sympathetic system." They are probably the trophic centers of the heart in so far as they determine the well-being of the fibers passing from them to the cardiac muscle-tissue, for in a sense the well-being of any part depends on the efferent fibers coming to its tissue. The nerve-cells in this ganglion have one, two, or many poles; some of the unipolar cells in the frog's septum have peculiarities, namely, "a spherical form, a pericellular network, and two processes"—the axis-cylinder and the spiral process wound about the former. It is probable that this spiral process and the pericellular net but not the axis-cylinder are in connection with the vagus. (Retzius and Nikolajew).

Expt. 64 demonstrated that the frog's heart apex containing no obvious ganglion-cells could beat rhythmically. Perhaps then the inhibition by these nerve-cells of Remak's ganglia is due to their quasi-trophic influence over the heart's protoplasm. The matter is not certain.

Expt. 88.—*Functions of the Hemispheres.*—(Apparatus: Decapitated frog, sink full of cool water.) The frog, as given out, has had only the cerebral hemispheres and the olfactory lobes anterior to them removed, the optic thalami, cerebellum, medulla oblongata, and cord being structurally normal. In an hour or less the nervous shock of the operation passes off and the functions of the hemispheres may be demonstrated by noting what the hemisphereless frog does not and cannot do that the normal animal does

(*A*) *Shock.—Note the characteristics of the nervous shock* of the operation: the entire lack of muscular tone, etc. (*B*) *Muscular Action and Posture not Disturbed.* Wait until the shock has passed off (doing some other experiment meanwhile). The heart-beat, respiratory movements, intestinal peristalsis, etc., continue and the eyes are open (and probably seeing, although the frog does not recognize objects). The skeletal muscles have recovered their tone and the posture of the animal is nearly or quite normal (the cerebellum and cord remain). (*C*) *Spontaneity Lost.* Note that, unstimulated, the frog does not move. Were it quite unstimulated, the animal would die of thirst, hunger, or drying without changing its position; intelligence as conceptualization is entirely lacking. (See Chapter XII., page 416.) (*D*) *Equilibrium Maintained.* The frog will not remain in a supine position. If placed on the back of a hand that is then slowly turned over, the animal keeps its equilibrium by the appropriate complex movements, and does not fall off. The optic thalami remain, but spontaneous movement is never made: there is no deliberate will. (*E*) *Vision Unimpaired.* Place some small opaque object (such as a dissecting-case on end) in front of the frog on the table, and pinch a hind foot. The animal jumps, but the object is avoided. (*F*) *Biological Reflexes Persist.* In water deep enough, swimming is perfectly carried out, and the frog may even climb on the rim of the tank and sit there. The sexual embrace is unimpaired. Food put in the mouth is swallowed. (*G*) *Intelligence Gone.* However much irritated, the frog does not hide as a normal frog would do, but jumps only once or twice and then sits quietly again. Every sort of recognition is gone with the fusion-processes of the cortex cerebri. The animal sees the danger, food, water, etc., but not recognizing what they are, cannot make the appropriate actions.

IX. GALVANOTAXIS AND CHEMOTAXIS.

Expt. 89.—*Galvanotaxis.*—(Apparatus: Frog-tadpoles, wax, glass dissecting-plate, two dry-cells, key, commutator with cross-wires, stand-rod, femur-clamp, 0.1 per cent. sodium-chloride solution.) Make a wax trough about 6 cm. long, 2 cm. wide, and 1 cm. deep on the glass dissecting-plate and have it carefully water-tight. Fill with the solution of sodium chloride. Place within it seven or more frog-tadpoles not over 2 cm. long. Clamp the wires from the commutator (with cross-wires) in the femur clamp in such a way that an end of one may be in the saline at each end of the trough. Determine which pole is now the anode and close the key so that three volts may pass through the liquid. A majority of the tadpoles, after being shaken up, collect about the cathode. Reverse the current by shifting the rocker; the animals again turn into line with the stream and generally collect about the cathode. This may be repeated a few times, but after a time a toleration of the stimulus sets up in the tadpole and the reaction is less certain. A young crayfish works more regularly than does a frog-tadpole in the reaction to galvanism.

The various tropisms or taxes (of which galvano-tropism or galvanotaxis is only an example) are the reactions which plant-protoplasm and little-differentiated animal protoplasm exhibit when subjected unilaterally to various external natural influences. Besides reacting to galvanism, such protoplasm reacts among other things to light (phototaxis), to heat (thermotaxis), to chemicals (chemotaxis), to pressure (barotaxis, of which the reaction to contract with solid bodies, thigmotaxis, is a subdivision). One sees phototaxis in many infusoria, as also in plants when the leaves twist around to face the light. It is supposed that it is by the force of chemotaxis that the spermatozoa are attracted to the ova. Thigmotaxis is well seen in the twining of the tendrils of many vines about a small support. (See Verworn.)

Explanation of these reactions as a whole is difficult and at present doubtful in most cases. One has to say that they depend on inherent properties of protoplasm acquired for their usefulness. Some of the reactions can be explained on purely physical and chemical principles.

Jennings has studied these interesting phenomena in Paramecium with great industry and some explanatory success. The simpler the organism the more constant the reaction, for the individual will is least powerful in the lowest forms of life. On this principle even young frog-tadpoles show a less uniform reaction than would, *e. g.*, paramecia or amebæ; dogs or men might exhibit none.

Expt. 90.—*Chemotaxis.*—(Apparatus: Pure culture of Paramecia, wide slide, large cover-glass, wires, fine pipet, carbon dioxide.) Place a large drop of the water containing the paramecia in the middle of the slide, and put wires about 3 cm. apart across the slide on either side of the drop. Place a cover-glass on the water and see that the latter fills as much of the space as possible. Observe with the naked eye or with the biconvex lens that the infusoria are evenly distributed through the water. Now with the pipet force a single small bubble of air under the cover-glass, and then, at least a centimeter away, a tiny bubble of carbon dioxide. The paramecia soon congregate in a ring about the carbon dioxide. This genus of animal, then, is positively chemotactic to weak carbonic acid, as it is to most other acids (Jennings). As the gas more and more dissolves in the water, its solution becomes stronger and the animals soon move away from it—*i. e.*, they are negatively chemotactic to strong carbonic acid.

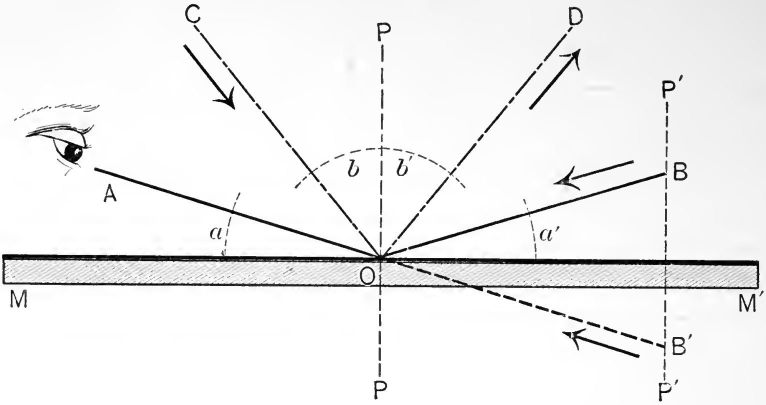
It is this sort of attraction perhaps which causes the spermatozoa to enter the ovum, being aided in their ascent of the tubes possibly by another sort of taxis, rheotaxis, or reaction against the current of lymph setting toward the uterus.

X. OPTICS.

Demonstration of the artificial eye and the electric lantern, including its lenses, used to illustrate it. Complete diagrams of all the optical conditions here illustrated are to be drawn in the note-books (out of the Laboratory if necessary) for inspection.

Expt. 91.—*Reflection by Plane Mirrors.*—(Apparatus: Round diaphragm in lamp, plane mirror.) Let a pencil of parallel rays enter the "eye" and fall upon the plane mirror. Rotate the mirror on its vertical and horizontal axes so that its surface may be at various angles to the rays of light. Observe (*A*) that the angle of reflection is always equal to the angle of incidence, and (*B*) that the incident ray, the perpendicular at the point of incidence and the reflected ray are always in the same plane.

FIG. 286



Reflection by plane mirrors. Angle a' always equals angle a, and always lies in the same plane. So far as mere optics are concerned, an eye at A sees B at B', but there are subjective differences which complicate the experience beyond optical explanation.

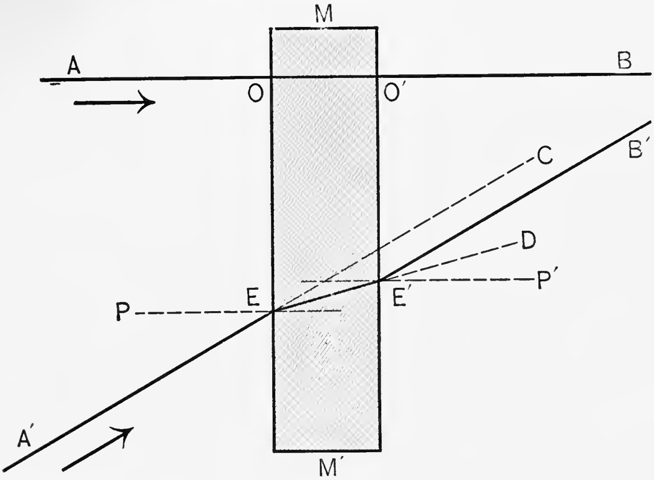
Expt. 92.—*Reflection by Spherical Mirrors.*—(Apparatus: Concave mirror.) Have no diaphragm in the lantern, but adjust the draw-tube so that the rays entering the eye are parallel.

(*A*) *Concave Mirrors.*—Place the concave mirror in the rays and observe the principal focus of the mirror. This is a bright spot 2.5 cm. from the mirror, the latter being a portion of the periphery of a sphere of 5 cm. radius. Turn the mirror at various angles and observe illustrations of principle *A* of the preceding experiment. Place the round diaphragm in the lamp and note the same facts under somewhat different conditions.

(*B*) *Convex Mirrors.*—Remove the diaphragm, and turn the mirror about so that the convex side is toward the light. Note the dispersion of the rays. Draw the diagrams.

Expt. 93.—*Refraction.*—(Apparatus: Square bottle of eosin glycerin, round diaphragm.) Pass a pencil of parallel rays into and through the square bottle of liquid (a denser medium than air) lying on its side on a block. Place the bottle so that its side shall be (*A*) at right angles to the rays. Note that the rays pass into the denser medium and come out again into the air unchanged in direction. Now (*B*) turn the bottle so that the rays shall enter the bottle at the top of the side, the surface being very oblique to the rays. The latter are now deflected, broken (refracted), on entering the denser medium toward the perpendicular erected at the point of incidence and on leaving the denser medium away from the perpendicular. The two bounding surfaces of the denser medium being parallel, the latter deflection is equal to the former and the rays leaving the bottle are parallel to their course on entering it. Observe the reflection also, and the color of the efferent ray.

Fig. 287



Refraction by media with parallel sides. When a ray (*e. g.*, *A*) passes into such a medium at right angles to a side, it continues straight. When a ray (*e. g.*, *A*′) strikes at an angle, it is bent ("broken") toward the perpendicular in the denser medium and away from it again on emergence at *E*′. Thus, the emergent ray *E*′ *B*′ is parallel to *A E C*.

Expt. 94.—*Prisms.*—Let parallel rays in a narrow pencil pass through the prism and note their course. Work out the refraction-angles in passing through the prism and in passing out of it.

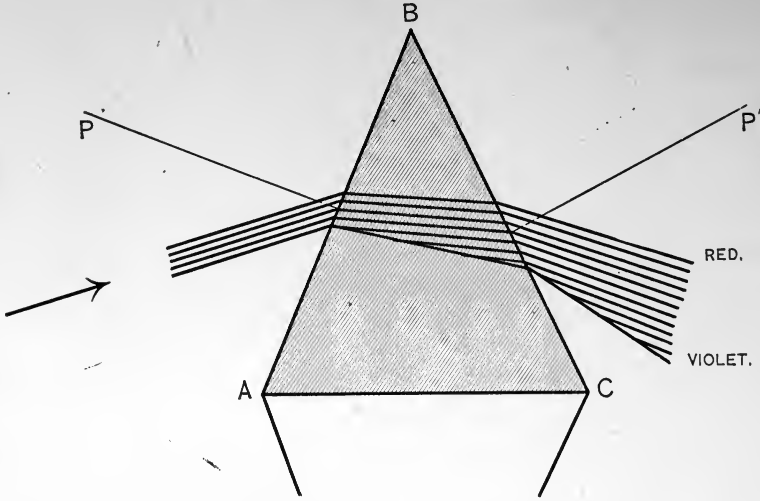
Place the prism in the direct sunlight and observe the *solar spectrum* the rays having the highest vibration-number being refracted most.

Demonstration of the *Spectroscope.*

Expt. 95.—*Aberration and the Use of Diaphragms* (Iris).—(Apparatus: The three diaphragms, ground-glass, and a white card for a screen.) Study the differences of the conditions with convex lenses with and without a diaphragm to cut off the outermost rays.

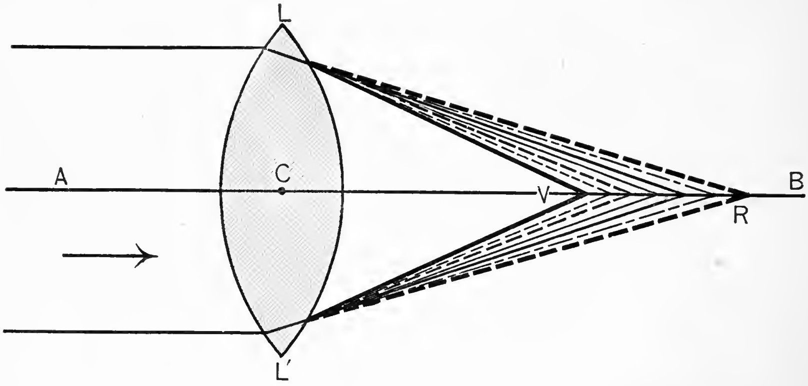
(*A*) *Chromatic Aberration.*—Put the ground-glass plate and the round diaphragm in the slide-way of the lanterns. Make a pencil of parallel rays and have them pass through the +10 D. lens placed 15 cm. away from the ground-glass and just inside the eye (this distance is half-again as long as the lens' focal distance). Place the card (white screen) 15 cm. farther beyond the lens.

FIG. 288



Refraction by media with oblique sides. A ray of white sunlight entering the prism *A B C* obliquely is broken toward the perpendicular and away from it on leaving the denser medium. The violet rays are refracted more than are the red rays of the spectrum.

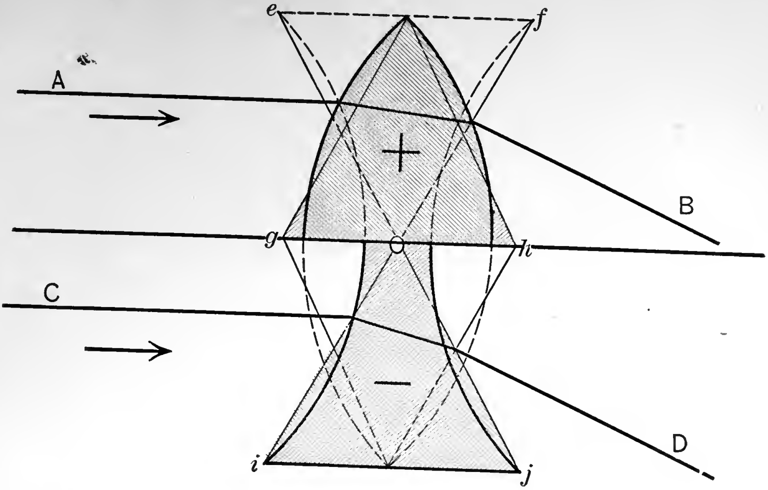
FIG. 289



Chromatic aberration comes from lenses of certain materials because of the unequal refraction of white light into its component rays. The violet end of the spectrum is bent more than the red end, and the focus is indefinite, as in *V R*. This is corrected by using materials for lenses which compensate this unequal refraction.

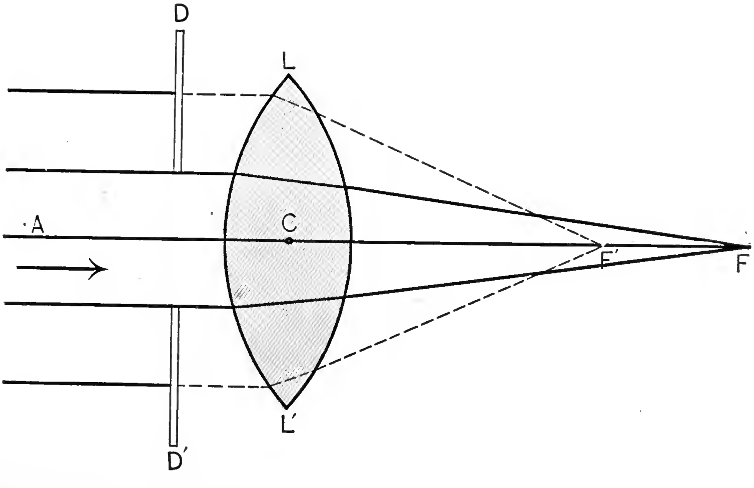
The image of the round illuminated spot on the ground glass seen on the card has a violet center and a red margin. Double the distance of the card-screen from the lens, and the colors change places. The reason

Fig. 290



Refraction. This diagram shows that a double convex lens is optically two prisms base to base and that a double concave lens is two prisms apex to apex. The + lens refracts toward the central ray ($g\ h$), the — lens away from it.

Fig. 291



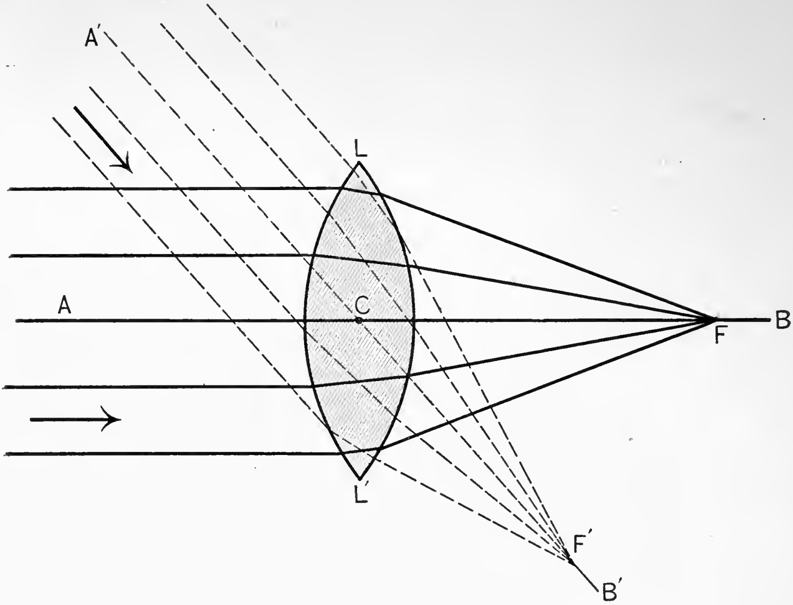
☞ Spherical aberration arises in the natural fact that the rays nearer the lens' center are refracted less than those passing through its peripheral parts. The result is an indeterminate image or focus, $F'\ F$. Diaphragms (as at $D\ D'$) are therefore employed (*e. g.*, the iris in the eye) to cut off the peripheral rays, leaving a relatively clear focus, as at F.

for this lies in the fact that a double convex lens is essentially two prisms placed base to base.

(*B*) *Spherical Aberration.*—Place in the clamp at the "cornea" a diaphragm with an aperture of 1 mm. This cuts off the spherical aberration by stopping the rays which cross within the pencil of rays.

Expt. 96.—*Refraction by Convex Lenses.*—(Apparatus: 10-diopter double convex lens in frame, round diaphragm, L-diaphragm, black screen). (*A*) Let parallel rays enter the eye. Place the lens about 5 cm. from the cornea. Place the screen 10 cm. from the lens and note the focus, and that on either side of that one position the image is indistinct.

Fig. 292



Convergence of the rays in a beam of light is brought about by a convex lens, their point of meeting being the focus F, and in case the pencil be oblique to the lens F'.

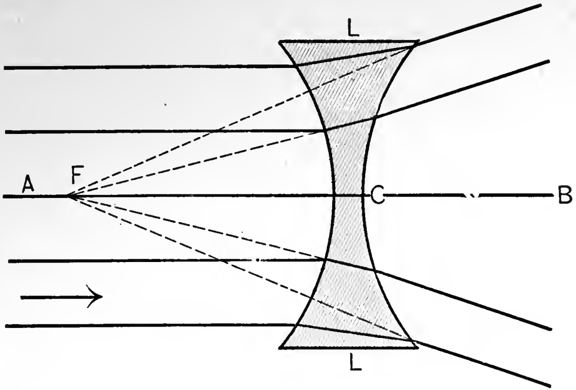
Now replace the round diaphragm by the L-diaphragm and put the screen in the focus. Note that the image of the L is inverted. A convex lens converges parallel rays. (A lens of 10 diopters is one which is a portion of a sphere whose radius is one-tenth of a meter; a + lens is convex and a — lens concave).

(*B*) Adjust the draw-tube of the lamp so that the rays diverge into the "eye" (have the tube close to the cornea). Place the round diaphragm in the clamp outside the cornea; 10 cm. from this diaphragm place the convex lens, the openings in the diaphragm being at the lens' focus. The rays extending beyond the lens are rendered parallel by the lens—the same process as in *A*.

Expt. 97.—*Refraction by Concave Lenses.*—(Apparatus: 10-diopter concave lens, round diaphragm, screen.) Let parallel rays pass into the eye, and through the —10 D. lens. The rays will be diverged.

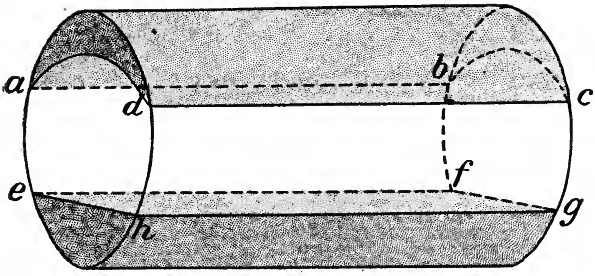
Expt. 98.—*Refraction by Cylindrical Lenses.*—(Apparatus: Cylindrical lens (the thicker one, plane on one side and convex on the other), round diaphragm, L-diaphragm, screen.) Make a pencil of parallel rays pass into the eye and through the convex cylinder placed so that the curvature is from *side to side.* Place the screen at the focus. Observe that the cylindrical pencil of rays is no longer round, but that it forms a vertical line on the screen. Rotate the lens 90°. The line is now horizontal. Move the screen back and forth on either side of the place of clear focus and observe the evident shape of the mass of rays coming from the lens.

Fig. 293



Divergence of the rays in a beam of light is brought about by a concave lens. There is no focus save the mathematical one at *F*.

Fig. 294



A cylinder in diagram to show the principle on which cylindrical spectacle-lenses are made: *a*, *b*, *c*, *d* is a concavo-convex "cylinder;" *e*, *f*, *g*, *h*, a plano-concave "cylinder."

Repeat these procedures with the L-diaphragm in place of the round diaphragm in the lantern.

In the three following experiments the 10 D. lens is to be left inside the eye close to the cornea, representing the lens of the eye.

Expt 99.—*Myopia and its Correction.*—(Apparatus: +10 D.lens, —2 D. lens, round diaphragm, L-diaphragm, black screen. (*A*) *Myopia.*—Let a pencil of parallel rays enter the eye. Place the black screen at the focus of the eye-lens—representing normal vision. Move the screen back from the focus-place 2.5 cm. This is now the usual condition of a low degree of myopia or short-sight, a too great depth of the eye-ball.

FIG. 295

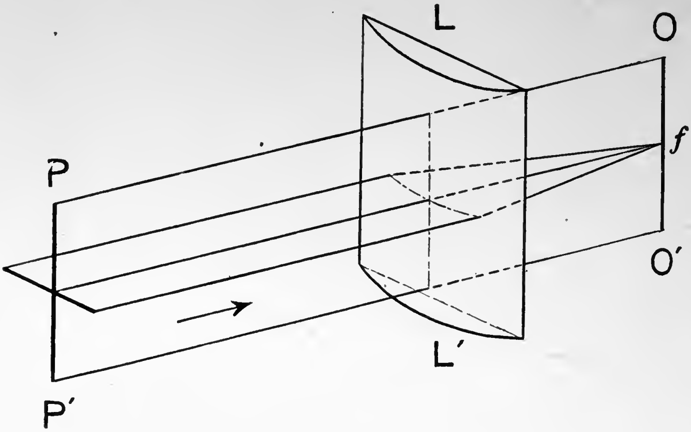
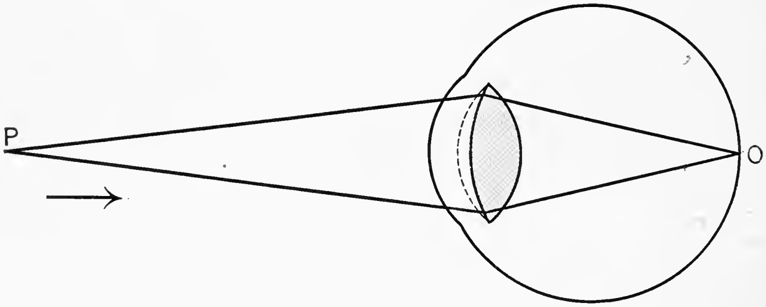


Diagram of refraction by cylindrical lenses. The rays in the vertical plane are not refracted, because the sides of the lens in that plane are parallel. In the horizontal plane the rays are converged by the cylindrical surface of the denser medium. The cross P P' would therefore be falsely focussed as merely a vertical line O O'. (F. R. Ireson.)

FIG. 296

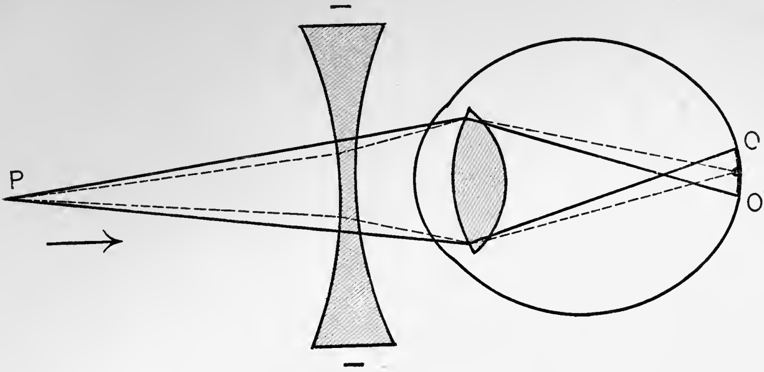


Normal vision, or emmetropia, shows rays from a point (*e. g.*, *P*), focussing exactly on the retina in a point (*O*). The dotted line in front of the lens shows the latter's bulging anteriorly in accommodation.

(*B*) *Correction of Myopia.*—Place the —2 D. lens outside the eye but close to the cornea. The focus is now carried backward to the abnormally situated screen (retina). For short-sightedness oculists prescribe concave lenses.

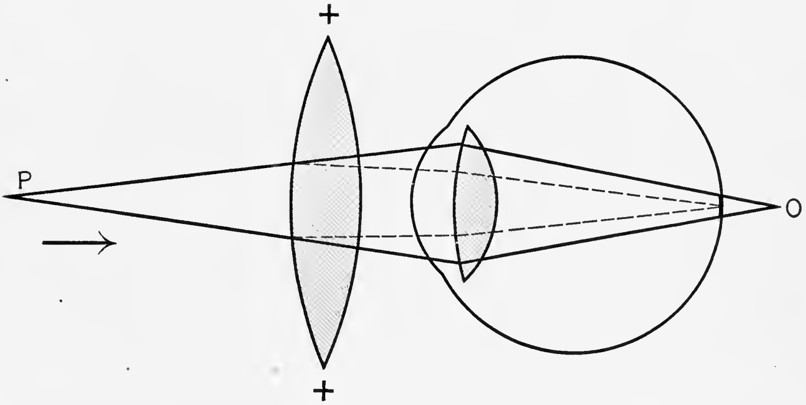
Expt. 100.—*Hyperopia and its Correction.*—(Apparatus: + 10 D. lens, +2 D. lens, round and L-diaphragms, screen.) (*A*) *Hyperopia and Presbyopia.*—Let a pencil of parallel rays enter the eye. Place the screen at the focus of the eye-lens as before, then move the screen forward toward the lens 2.5 cm. This represents the abnormal hyperopic

FIG. 297



Myopia and its relief. In myopia, owing usually in large part to a too great antero-posterior depth of the eye, the rays focus before they reach the retina and an indefinite image results (*O O′*). This common defect is corrected by concave, minus spectacle-lenses, these diverging the rays before reaching the eye so that the rays focus farther back on the retina.

FIG. 298

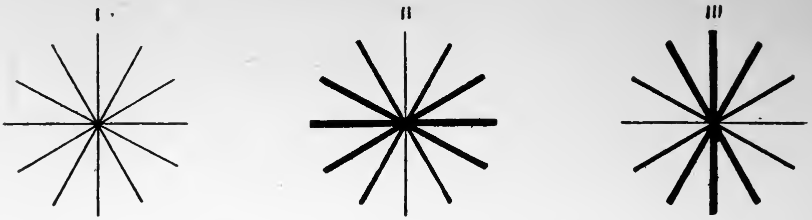


Hyperopia and its relief. In hyperopia, owing usually to a too great flatness of the lens and cornea, the rays coming from a point (*P*) are not converged sufficiently to meet a focus on the retina, but would do so behind it were the latter transparent. This defect ("normal" about fifty years of age) is corrected by convex spectacle lenses, these converging the rays so that they focus on the retina.

eye, except that more often the lens is too convex rather than the eye-ball too shallow.

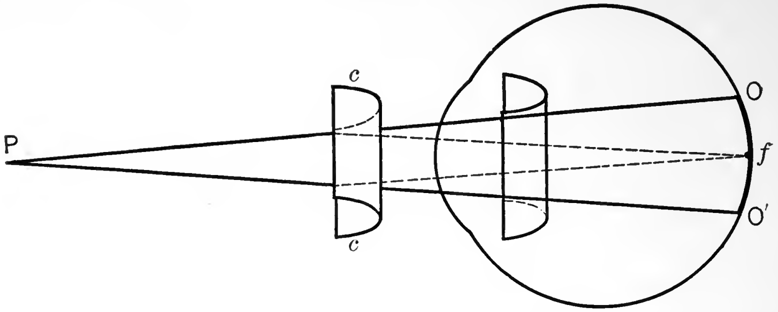
(*B*) *Correction of Hyperopia.*—Place the +2 D. (thin double convex lens) outside the cornea but close to it. The focus is now brought forward to the abnormally situated screen (retina), the rays being more converged.

FIG. 299



The visual defects coming from astigmatism. A figure like *I* tends to appear either like *II*, or like *III*, because of the unequal refraction in the respective axes of the eyes. (Imbert.)

FIG. 300



Astigmatism and its relief. In (regular) astigmatism the refractive media of the eye (especially the cornea) are more convex in one axis than in another. Thus, in the diagram the rays in the vertical plane are not converged at all and the image (*O O′*) is very indistinct in that axis, being a line instead of a point. This defect is corrected by cylindrical spectacle-lenses with the greater refraction in the axis in which it is lacking in the eye-lens, and equal to that defect in degree. In the diagram the spectacle-lens *c c* refracts only in the axis in which the eye-lens refracts none.

Expt. 101.—*Astigmatism.*—(Apparatus: 10 + D. lens, two + 10 D. cylindrical lenses, the three diaphragms, screen.) (*A*) *Astigmatism.*—Place the cylindrical lens (curvature *lateral*) in the other side of the frame in which the + 10 D. (or eye) lens is. Let parallel rays pass into the eye through this "astigmatic lens." Place the screen exactly in the focus of the lens. The image of the circular aperture in the diaphragm is elongated vertically.

(*B*) *Correction of Astigmatism.*—Now place before the cornea of the eye the other cylindrical lens with its curvature *vertical.* The image becomes round. Turn the correcting lens 90 degrees, and the elongation of the image is increased. (See the diagram.)

Repeat these procedures with the other diaphragms until the conditions and principles are fully understood.

It is the cornea which causes usually the cylindricality of the refracting media, and most often the defect is congenital although acquired, and even changing, astigmatism is by no means rare, especially in children. Oftentimes the curvature is irregular and beyond the correction of ground lenses.

All sorts of combinations of astigmatism with myopia or with hyperopia are very common.

XI. OSMOSIS.

Expt. 102.—(Apparatus: Dialyzer and the various solutions). (*A*) *Sodium Chloride.*—Half fill the inner tube of the dialyzer with the solution. Push the capillary tube downward until the solution rises halfway up in it. Put the dialyzer in place. Note the direction of the movement in the capillary indicator. Test with argentic nitrate for sodium chloride.

(*B*) *Dextrose.*—Having carefully washed out at the sink the apparatus, repeat the experiment with the dextrose-solution. Test the liquid in the beaker for dextrose with Fehling's solution.

(*C*) *Glycogen.*—Repeat the experiment with the opalescent solution of glycogen. Test the contents of the inner tube.

(*D*) *Potato-starch Solution.*—Repeat the experiment with the starch-solution. Test the liquid in the beaker with iodine for starch.

(*E*) *Proteid.*—Repeat the experiment with egg-white solution. Test the outer liquid for protein with Millon's reagent.

LIST OF TOPICS FOR DISSERTATIONS AND CLASS DISCUSSION.

Abiogenesis.
Accommodation.
Action-currents.
Adaptation.
Adaptation of diet.
Adipocere.
Adrenals.
After-images.
Air-supply.
Alcohol.
Ameba.
Amitosis.
Anemia.
Anesthesia.
Animal experimentation.
Anthropometry.
Antiferments.
Aphasia.
Apnea.
Aristotle.
Arsenic in protoplasm.
Arterial circulation.
Asphyxia.
Association.
Astigmatism.
Ataxia.
"Athletic heart."
Atmospheric pressure.
Auscultation and percussion.
Bacteria in health.
Bathing.
Bernard, Claude.
Bile.
Blood-composition.
Blood-pressure.
Bodily beauty.
Bodily growth.
Brunner's glands.
Calcium and magnesium.
Calorimetry.
Capillary circulation.
Cardiac massage.
Cardiac tonus.
Cell-division.
Cellular differentiation.
Cerebellum.
Cerebral localization.
Cerebral ventricles.
Cerebrospinal fluid, etc.
Chemotaxis.
Cholesterin.
Classification of proteids.
Clothing.
Coagulation.
College athletics.
Color-vision.
Composition of the blood.
Composition of the feces.
Composition of the sweat.
Composition of the urine.
Consciousness.
Conservation of energy.
Constipation and diarrhea.
Cooking.
Coördination of the heart's movements.
Cortex cerebri.
Cross-suturing of nerves.
Cyclic vomiting.
Ciliated epithelium.
Daphnia.
Death.
Definition of health.
Definition of life.
Deglutition.
Dental hygiene in the schools.
Depressor nerve.
Development of vital capacity.
Development of voluntary action.
Diaphoresis.
Diets.
Dignity of medicine and dentistry.
Diuresis.
Dyspepsia.
Eddyism.
Edema.
Electrotonus.
Elimination of poisons.
Embryology of the circulatory organs.
Embryology of the digestive organs.
Embryology of the nervous system.
Embryology of the respiratory organs.
Embryology of the urogenital organs.
Emotional expression.
Endurance.
Epiglottis.
Erythrocytes.
Estimation of nitrogen.
Eustachian tubes.
Evolution.
Eye-movements.
Eye-strain.
Fasting.

Fatigue and exhaustion.
Fertilization.
Fetal circulation.
Fever.
First heart-sound.
Food-adulteration.
Galen.
Galvanism.
Gelatin as a food.
Geotaxis.
Giantism and dwarfism.
Glycogen.
"Going stale."
Graphic method.
Habit.
Hair.
Hallucinations and illusions.
Happiness and bodily function.
Harvey, William.
Health-value of good teeth.
Helen Kellar.
Helmholtz, Herman L. F.
Hematology.
Hemoglobin.
Hemoglobin and chlorophyll.
Hemophilia.
Heredity.
Hibernation.
Holmes, Oliver Wendell.
Homeopathy.
Human embryos.
Hunger.
Hunger and thirst.
Hunter, John.
Hypnosis and suggestion.
Icterus.
Ileocecal valve.
Immunity.
Individuality.
Inductorium.
Infantile digestion.
Inflammation.
Ingenuity and originality.
Inhibition.
Inhibition of reflexes.
Inspired and expired airs.
Instinct.
Internal capsule.
Internal nutrition.
Internal respiration.
Invigoration.
Invironment.
Ions.
Iron.
Irritability.
Kinesthesia.
Kreatinin.
Lactic acid.
Lecithin.
Legerdemain.
Leukocytes.
Life-periods.
Light.
Liver.
Local signs.
Lymph.
Lymph and bodily exercise.
Lymph-glands.
Manometers.
Massage.
Mastication.
"Maternal impressions."
Mechanics of the joints.
Medical school-supervision.
Medulla oblongata.
Meissner's and Auerbach's plexuses.
Metabolism.
Metric measures.
Micturition.
Milk.
Mitosis.
Movements of the alimentary canal.
Mucus.
Müller, Johannes.
Muscle-fabric.
Muscle-fatigue.
Muscular "automaticity."
Muscular contraction.
Muscular coördination.
Muscular metabolism.
Muscular tonicity.
Myograms.
Myoids.
Movements of the alimentary canal.
Nasal respiratory tract.
Natural organic defences.
Necrobiosis.
Negative variation.
Nervous impulse.
Neurofibril theory.
Neuromuscular mechanism.
Neurone theory.
Nissl's bodies.
Nucleic acid.
Nutrition of heart.
Obesity.
Old-age.
Optic thalami.
Ordeals.
Organic electricity.
Organic heat.
Organic light.
Organic production of water.
Organic soaps.
Organ of Corti.
Origin of blood-corpuscles.
Origin of life on earth.
Origin of lymph.
Osmosis.
Osteopathy.
Overeating.
Ovulation and menstruation
Oxidases.
Oxidation.
Pain.
Parturition.
Pelvic congestion.
Perception of causality.
Perception of space.
Perception of time.

Peritoneum.
Pflüger's contraction-law.
Phagocytosis.
Phosphorus and sulphur.
Physical exercise.
Physicians as teachers of right-living.
Physics in physiology.
Physiological fistulæ.
Physiological superstitions.
Physiology in physical education.
Pigment.
Poisoning from coal-gas.
Pons varolii.
Pregnancy.
Production of urea.
Proteids of the blood.
Protoplasm.
Protoplasm and proteid.
Protoplasmic unit.
Psychology in the medical schools.
Pyloric valve.
Pituitary body.
Psychophysical capability.
Pyrexia.
Quantity of blood.
Rapidity of nerve-force.
Reaction-time.
Reflex action.
Regeneration.
Regeneration of nerve.
Relations of physiology.
Relative heat-values of foods.
Relative values of tissues' metabolism.
Removal of cortex cerebri.
Renal hydraulics.
Rennin.
Respiration of the fetus.
Respiratory quotient.
Rest.
Retina.
Reverse ciliary movement.
Rheumatism.
Rods and cones.
Rumination.
Running as an exercise.
Relations of mind to body.
Renal, hepatic, and intestinal colic.
Röntgen-ray aspermia.
Saliva.
School-room ventilation by opened windows.
Sea-sickness.
Secondary sexual characteristics.
Secretion.
Secretion of foreign substances in milk.
Secretion of milk.
Self-digestion of stomach.
Semen.
Semicircular canals.
Sensation and afferent impulses.
Sensitivity of the viscera.
Sensory cerebral tracts.
Serum-therapy.
Sexual education.
Shock, (surgical).
Shoes.
Similarity of animals and plants.
Simple sense-organs.
Skill and cleverness.
Skin-absorption.
Skin-varnishing.
Sleep.
Sodium and potassium.
Source of muscular energy.
Sources of animal heat.
Specific energy of the nerves.
Spectra of the hemoglobins.
Speech and language.
Spinal paths.
Spinal reflexes.
Splanchnic nerves.
Spleen.
Starvation.
Statistical method.
Stereognosis.
Stimulants versus depressants.
Stuttering, etc.
Subconsciousness and nervous impulses.
Succus entericus.
Sugar as a food.
Superficial burns.
Sweat-secretion.
"Systems" of physical education.
"Taking cold."
Taste and smell.
Tea and coffee.
Teeth.
Tetanus.
Theory of enzymes.
Thermotaxis.
Thirst.
Thrombocytes.
Thymus.
Thyroid.
Tobacco.
Tongue.
Transfusion, etc.
Trophism.
Ultra-microscopy.
Vagus in respiration.
Vagus nerve.
Variation by mutation.
Variation by natural selection.
Vasomotion.
Vasomotion in the brain.
Vasomotor centers.
Vegetarianism.
Velocity of blood-stream.
Velocity of pulse-wave.
Venous circulation.
Ventilation.
Ventriloquism.
Vermiform appendix.
Vesalius.
Vicarious function.
Vocal cords.
Voluntary action.
Voluntary control of the heart.
Voluntary muscular contraction.
Vomiting.
Walking.
What a "nerve-center" is.

CONVERSION TABLES.

Corresponding Degrees in the Fahrenheit and Centigrade Scales.

Cent.	*Fahr.*	*Cent.*	*Fahr.*	*Fahr.*	*Cent.*	*Fahr.*	*Cent.*
100°	212.0°	38°	100.4°	500°	286.0°	90°	32.2°
98°	208.4°	36°	96.8°	450°	232.2°	85°	29.4°
96°	204.8°	34°	93.2°	400°	204.4°	80°	26.7°
94°	201.2°	32°	89.6°	350°	176.7°	75°	23.9°
92°	197.6°	30°	86.0°	300°	148.9°	70°	21.1°
90°	194.0°	28°	82.4°	212°	100.0°	65°	18.3°
88°	190.4°	26°	78.8°	210°	98.9°	60°	15.5°
86°	186.8°	24°	75.2°	205°	96.1°	55°	12.8°
84°	183.2°	22°	71.6°	200°	93.3°	50°	10.0°
82°	179.6°	20°	68.0°	195°	90.5°	45°	7.2°
80°	176.0°	18°	64.4°	190°	87.8°	40°	4.4°
78°	172.4°	16°	60.8°	185°	85.0°	35°	1.7°
76°	168.8°	14°	57.2°	180°	82.2°	32°	0.0°
74°	165.2°	12°	53.6°	175°	79.4°	30°	— 1.1°
72°	161.6°	10°	50.0°	170°	76.7°	25°	— 3.9°
70°	158.0°	8°	46.4°	165°	73.9°	20°	— 6.7°
68°	154.4°	6°	42.8°	160°	71.1°	15°	— 9.4°
66°	150.8°	4°	39.2°	155°	68.3°	10°	—12.2°
64°	147.2°	2°	35.6°	150°	65.5°	5°	—15.0°
62°	143.6°	0°	32.0°	145°	62.8°	0°	—17.8°
60°	140.0°	— 2°	28.4°	140°	60.0°	— 5°	—20.5°
58°	136.4°	— 4°	24.8°	135°	57.2°	—10°	—23.3°
56°	132.8°	— 6°	21.2°	130°	54.4°	—15°	—21.6°
54°	129.2°	— 8°	17.6°	125°	51.7°	—20°	—28.9°
52°	125.6°	—10°	14.0°	120°	48.9°	—25°	—31.7°
50°	122.0°	—12°	10.4°	115°	46.1°	—30°	—34.4°
48°	118.4°	—14°	6.8°	110°	43.3°	—35°	—37.2°
46°	114.8°	—16°	3.2°	105°	40.5°	—40°	—40.0°
44°	111.2°	—18°	—0.4°	100°	37.8°	—45°	—42.8°
42°	107.6°	—20°	—4.0°	95°	35.0°	—50°	—45.6°
40°	104.0°						

To turn C.° into F.°, multiply by 9, divide by 5, and add 32.
To turn F.° into C.°, deduct 32, multiply by 5, and divide by 9.

Measures of Length.

1 Myriameter,	Mm.	=	10000.0	M.	=	6.2137	+	miles.
1 Kilometer,	Km.	=	1000.0	"	=	4.9710	+	furlongs.
1 Hectometer,	Hm.	=	100.0	"	=	19.8840	+	rods.
1 Decameter,	Dm.	=	10.0	"	=	32.8086		feet.
1 Meter,	M.	=	1.0	"	=	39.3704		inches.
1 Decimeter,	dm.	=	.1	"	=	3.93704		"
1 Centimeter,	cm.	=	.01	"	=	0.393704		"
1 Millimeter,	mm.	=	.001	"	=	0.0393704		"

Measures of Capacity.

1 Myrialiter,	Ml.	=	10000.0	L.	=	2641.7890	+	gallons.
1 Kiloliter,	Kl.	=	1000.0	"	=	264.1789	+	"
1 Hectoliter,	Hl.	=	100.0	"	=	26.4178	+	"
1 Dekaliter,	Dl.	=	10.0	"	=	2.6417	+	"
1 Liter,	L.	=	1.0	"	=	33.8149	+	fluidounces
1 Deciliter,	dl.	=	.1	"	=	3.38149	+	"
1 Centiliter,	cl.	=	.01	"	=	.338149	+	fluidounce.
1 Milliliter,	ml.	=	.001	"	=	.0338149	+	"
1 Cubic centimeter,	c.cm.	=	.001	"	=	.0338149	+	"

MEASURES OF WEIGHT.

1 Myriagram,	Mg.	=	10000.0	Gm.	=	22.0461	+	pounds.
1 Kilogram,	Kg.	=	1000.0	"	=	2.2046	+	"
1 Hectogram,	Hg.	=	100.0	"	=	3.5273	+	av. oz.
1 Dekagram,	Dg.	=	10.0	"	=	154.3235639		grains.
1 Gram,	Gm.	=	1.0	"	=	15.43235639		"
1 Decigram,	dg.	=	.1	"	=	1.543235639		"
1 Centigram,	cg.	=	.01	"	=	.1543235639		"
1 Milligram,	mg.	=	.001	"	=	.01543235639		"

COMPARATIVE TABLE OF METRIC WITH AVOIRDUPOIS AND APOTHECARIES' WEIGHTS.

Names.	Numerical expressions.	Equivalents in grains.	Equivalents in avoirdupois weight.			Equivalents in apothecaries' weight.		
	Grams.	Grains.	lb.	oz.	gr.	℥	ʒ	gr.
Milligram	0.001	.01543	....	...	$\frac{1}{64}$	....	...	$\frac{1}{64}$
Centigram	0.01	.15432	....	...	$\frac{1}{6}$	....	...	$\frac{1}{6}$
Decigram	0.1	1.54323	....	...	1.5	....	...	1.5
Gram	1.0	15.43235	....	...	15.4	....	...	15.4
Dekagram	10.0	154.32356	....	$\frac{1}{4}$	45.00	....	2	34.0
Hectogram	100.0	1543.23563	....	$3\frac{1}{2}$	12.00	3	1	43.0
Kilogram	1000.0	15432.35639	2	$3\frac{1}{4}$	10.47	32	1	12.4
Myriagram	10000.0	154323.56390	22	$\frac{1}{2}$	14.8	321	4	3.5

COMPARATIVE TABLE OF METRIC AND APOTHECARIES' FLUID MEASURE.

Cubic centimeter.	Minims.	f℥	fʒ	♏
0.06161	1.0	....	....	....
0.30805	5.0	....	....	....
0.61610	10.0	....	....	....
1.0	16.23	....	....	....
5.0	81.15	....	1	21.15
10.0	162.30	....	2	42.3
20.0	324.60	....	5	24.6
30.0	486.90	1	0	6.9
40.0	649.20	1	2	49.2
50.0	811.50	1	5	31.5
60.0	973.80	2	0	13.8
70.0	1136.10	2	2	56.1
80.0	1298.40	2	5	38.4
90.0	1460.70	3	0	20.7
100.0	1623.00	3	3	3.0
250.0	4057.50	8	3	37.5
500.0	8115.00	16	7	15.0
1000.0	16230.00	33	6	30.0

1 Gram = 15.432 grains. 1 Grain = 0.065 gram.
1 Drachm (troy) = 3.888 grams (approximated 4).
1 Troy ounce = 31.103 grams (approximated 30 or 32) or 480 grains.
1 Avoirdupois ounce = 28.35 grams (approximated 28.5) or 437.5 grains.
1 Kilogram = 1000 grams = 2.2 avoirdupois pounds.
1 Minim = 0.062 c.c.
1 Fluidrachm = 3.7 c.c. (approximated 4).

1 Wine fluidounce = 29.57 c.c. (approximated 30) or the volume of 455.6 grains of water at 62° F.

1 Imperial fluidounce = 28.39 c.c. (approximated 28.5) or the volume of 437.5 grains of water at 62° F.

1 Liter = 1000 c.c. = 2.11 wine pints or 1.76 Imperial pints. or 33.815 fluidounces.

3 Gallons of water = 25 avoirdupois pounds at 60° F. (1 Gallon = 8.331 lbs.)

1 Mm. (millimeter) = $\frac{1}{25}$ of an inch.

1 Cm. (centimeter) = $\frac{2}{5}$ of an inch.

1 Inch = 25 millimeters or 2½ centimeters.

1 C.c. (cubic centimeter) = 16.23 minims or 0.27 fluidrachm or 0.0338 fluidounce.

1 Fluidounce = 29.57 cubic centimeters at 4° C.

1 Grain = 0.06479 gram or 64.79 milligrams.

1 Mg. (milligram) = 0.01543 grain (practically $\frac{1}{64}$ grain).

1 Pound avoirdupois = 453.6 grams.

Rule.—To convert troy ounces to avoirdupois add 10 per cent.

(The difference between a troy ounce, 480 grains, and an avoirdupois ounce, 437.5 grains, is 42.5 grains, or about 10 per cent. of the latter. To be exact, substract 1.5 grains for each troy ounce.)

Rule.—To convert avoirdupois ounces to troy, subtract one-eleventh.

One cubic foot of water weighs	62.425 pounds at 4° C. (39.1° F.)—maximum density.
	62.418 pounds at 0° C. (32° F.)—freezing point.
	62.355 pounds at 16° C. (62° F.)—standard temperature.
	59.640 pounds at 100° C. (212° F.)—boiling point.
	57.5 pounds in form of ice.

1 Cubic foot water = 7.485 wine gallons.

1 Avoirdupois pound water = 27.7 cubic inches.

1 Cubic inch water = 0.03612 avoirdupois pounds.

A pressure of 1 pound per square inch requires a depth of 2.31 feet of water.

The latent heat of water = 79 thermal units Centigrade (or 142.2 units Fahrenheit).

The latent heat of steam = 536 thermal units Centigrade (or 964.8 units Fahrenheit).

Surface-measurement.

1 Square meter = about 1550 square inches (or 10,000 square centimeters or 10.75 square feet.

1 Square inch = about 6.4 square centimeters.

1 Square foot = about 930 square centimeters.

Energy-measure.

1 Kilogrammeter = about 7.24 foot pounds.

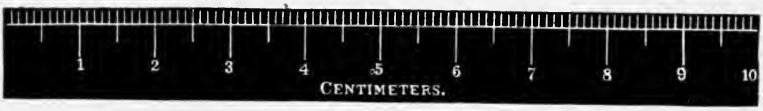
1 Foot pound = about 0.1381 kilogrammeters.

1 Foot ton = about 310.0 kilogrammeters.

Heat-equivalent.

1 Kilocalorie = 424 kilogrammeters.

One Decimeter.



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