THE SIGNS OF LIFE

FROM THEIR ELECTRICAL ASPECT

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VOL. I.—EIGHT LECTURES

ON

THE SIGNS OF LIFE

FROM THEIR ELECTRICAL ASPECT

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PREFACE

THE following monograph embodies the first of a series of lectures on Physiology, delivered by the Physiologists of London in the Laboratory of their University.

The general object of the scheme of which these particular lectures form part, is to present the results of recent investigation by the investigators themselves—orally and with experimental demonstration in the lecture-room—outside the lecture-room by monographs approved by the University.

With the modification considered suitable for the case of University publications, the procedure of the Royal Society as regards the printing of papers in the Philosophical Transactions has been adopted by the Senate of the University of London, the regulations in connection with the official publication of lectures being as follows:—

> "Manuscripts of Lectures delivered, or of the results of investiga-"tions made in the Physiological Laboratory of the University, shall, "in first instance, be submitted for consideration to the Physiology "Committee, to be referred, if considered suitable, to two referees, who "shall be requested to report to the Physiology Committee as to their "fitness for publication.
>
> "Manuscripts shall be accepted only if reported suitable for publi-"cation—
>
> "*A.* By reason of additions to knowledge in Physiology and "Experimental Psychology.
>
> "*B.* By reason of excellence of exposition of recent additions to "knowledge and doctrine in Physiology and Experimental "Psychology."

The present eight lectures embody in large measure the recently published (and unpublished) results of my own current work during the last five years. They are in continuation of a First Series of Lectures on "Animal Electricity," published in 1897. They will no doubt be found to suffer from many of the disadvantages inherent to the nascent state, I hope that they may prove to possess also some of its advantages.

A. D. W.

October 1903.

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THE SIGNS OF LIFE

> "The greatest thing a human soul does in this world is to *see* something, and *tell* what it saw."—RUSKIN.

LECTURE I

Aim and Purpose of the Lectures—The Subject-matter of Physiology—The Signs of Life; The Sign of a Sign is a Sign of the Thing itself—Two Familiar Instances; on Muscle and on Nerve—A Proof of Chemical Change in Seeds—An Experiment on Muscle—Retinal Currents—Vegetable Currents—Terminology—Solution-pressure—Summary.

§ 1. *Aim.*—The aim and purpose of these lectures is extremely simple. By the liberality of the Senate of the University, seconded by the liberality of one of its distinguished graduates, the teachers and students of physiology separately working in the many scattered Colleges of the Metropolis, are enabled to bring to its University, as to a focus, the best they have to bring.

I shall not take upon myself to utter any forecast of the fate of this effort towards concentration, nor attempt to justify our undertaking by any high-flown anticipations. All that I venture to say—on behalf of my colleagues as well as on my own behalf—is that we believe that in Physiology as in other subjects, there exist in this great metropolis, scattered—I had almost said lost—in the several colleges that now form part of the University, the elements which collectively constitute a university school of learning.

And if I might venture to characterize by one word what to my mind is the most essential mark of a teacher of university rank, I should say that it is that such teacher should be an active student—not merely a learn*ed* man, but a learn*ing* man.

And that leads me to what we hope is to be the keynote and dominant tone of these lectures — namely, that they are especially to belong to what may be termed the growing surface of our knowledge. Each one of us is to bring here the knowledge that he has himself gathered at first hand in the particular garden that he has chosen to work in, and of such knowledge it is an infallible characteristic that it is unsatisfied, incomplete—an ever green surface, a surface of encroachment.

And so this, our talking-room, rests upon a foundation of working-rooms, and these in turn ultimately rest upon our working-rooms scattered throughout the colleges of the University of London, at University College, at King's College, at the London medical colleges, and at the colleges for women.

Another point: A critic, a friendly critic, in the days when these lectures were first talked of, wanted to know to whom they were to be given, urged indeed that in this great scattered University of London there are not a dozen students requiring or caring for advanced lectures in physiology; he said that we should have to lecture to each other. I hope we shall lecture to each other and be each other's pupils. Looking to this list, I think I may say that during the last twenty years I have been the pupil of every one of my present colleagues, and I hope I have not finished learning from them; and I am very sure that if this laboratory fulfils its true function, we, the professed teachers, will receive as well as give instruction from and to the students and frequenters of the laboratory.

§ 2. *Subject.*—The subject-matter of physiology is Life—or more properly speaking—living things, vegetable as well as animal. And although physiologists, in common with all mankind, must at times indulge themselves in speculations concerning the origin of life, the existence of vital force, the immortality of protoplasm and other insoluble philosophical problems, their real daily work is the hardly less extensive task of learning how plants and animals live, in what particulars their living organs and tissues differ from the same organs and tissues when they have ceased to live, how quickly they live, how much they live, upon what they live, and how while they live, they absorb, transform, distribute, and dispense the energy stored in food and manifested in each act of life. In one word our task as physiologists is to study the signs of life. To say that these are lectures on the signs of Life is to say that they are lectures on Physiology.

The Signs of Life.

The signs by which we can always recognise that living matter is living are:—

1. Its reducing or deoxygenating power;
2. Its exhalation of carbon dioxide;
3. Its excitability; *and*
4. The electrical signs of its chemical activity.

The present series of lectures will be in chief measure drawn from the fourth head—and I should have taken for their title the *electrical* signs of life, were it not that the electrical signs by themselves should not in my opinion be divorced from other signs; and are indeed, when so divorced, of comparatively small general importance—matter of special and technical interest rather than a chapter in General Physiology.

The point of view to be taken can be formally presented in terms of the classical axiom of the logicians—*nota notæ est nota rei ipsius*—inasmuch as chemical change being a sign of life, and electrical change a sign of chemical change, it follows that electrical change is a sign of life—meaning by "sign" an universal attribute of our subject rather than an occasional or exceptional incident—a "*proprium*" rather than an "*accidens*."

From which formal position we may proceed a step further, and recognise that in the study of electrical change we have the most delicate and one of the most convenient means of approach towards an answer to these two questions addressed to matter that may be living or not-living:—

1. Are you alive?

And when this first qualitative question has been answered:—

2. How much are you alive?

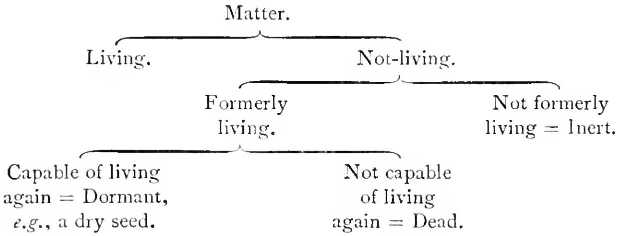
§ 3. *Instances.*—The two instances of electrical effects with which you are no doubt familiar already, are:—

1. The negative variation of muscle; 2. The negative variation of nerve: and I shall presently use the first of these phenomena to illustrate the parallelism between the mechanical sign of life (contraction) and the electrical sign of life (negative variation).

Turning now to the syllabus of this first lecture, you find there several headings that are more or less familiar to you, that I shall nevertheless recall to your attention, for the sake of the point of view I ask you to take.

Omitting any attempt to define "Life and the Living State," we shall in first resort seek to recognise what are the principal differences between matter that is alive and matter that is not-alive. And take note in passing that by this division into alive and not-alive, or living and not-living, we include dead matter as a sub-division of not-living matter, which we consider as falling into the complementary sub-classes of matter that has previously lived (but is now "dead") and matter that has not previously lived (and is called "inert").

And although our physiological problems are in most cases concerned with the comparisons and distinctions that we are able to institute between living and dead matter, we shall find—for the sake of logical discourse in dealing with matter in a state of what has been called latent life or suspended animation—that it is convenient to make a first division into living and not-living, and a sub-division into dead and inert in accordance with this dichotomous scheme:—



This scheme has been drawn up with the particular purpose of showing how, in my opinion, we should logically deal with, *e.g.*, the vexed question whether a seed (or a dry rotifer, or a hen's egg, or a tissue completely "anæsthetised") is alive or dead.

We shall have to recognise that the one general and all-embracing sign of life, whether we consider a complete organism, or a single organ, or an isolated part of an organ, is Movement—movement of the whole mass, or that movement of its molecules which we characterise as physical and chemical and physico-chemical. All living matter is the seat of chemical change, or if you prefer it, physical or physico-chemical change.

Now dry seeds, kept for long periods in hermetically closed vessels, have not been found to manifest any evidence of the most fundamental and general chemical change occurring in living matter, viz., a production of CO_2. Their chemical reply to the question, "Are you alive?" has been "No."

But does this negative answer "not-alive" imply that such seeds are dead? Evidently not, as may be seen if under suitable conditions of temperature, moisture, and so forth, they are found to germinate and grow into plants. So that a seed, in so far as it does not manifest chemical change, is not proved to be living; and, inasmuch as it germinates, is proved not to be dead. Evidently, here is a dilemma; in the absence of an objective chemical sign of life, we have no right to say that a seed is alive; it is, as far as we can tell, not-alive; in the presence of its subsequent germination we are assured that it is living, and that therefore it was not dead. And the usual manner of escape from this dilemma of the seed which is neither living nor dead, is to say that it is in a state of *latent life*, during which there is a complete suspension of chemical changes characteristic of the living state.

I will not, at this early stage, stop to comment upon the contradiction involved in this form of words, nor upon the fact that it involves contradiction of the fundamental axiom that the essential attribute and objective sign of the living state is chemical movement. But I will offer for your consideration a different mode of escape from the dilemma.

It is possible—or rather certain—firstly, that our means of chemical investigation are not refined enough to reveal to us the smallest and most infinitesimal changes that may be going on in an apparently dry and perfectly dormant seed; and secondly, it is possible that chemical change may be completely and absolutely arrested (*e.g.*, by low temperature) without that arrest being of necessity final and definitive.

I will place evidence before you of this first point, which I have investigated at some length. As to the second, which I have not myself investigated, I will only mention that it appears to be established by the observations of Horace Brown,* who found that dry seeds kept for 110 hours in closed vessels at a temperature of – 183° to – 192°, *i.e.*, seeds in which the arrest of chemical change must be considered to have been absolutely complete, germinated quite normally when they were placed under suitable conditions of temperature and moisture.

The inadequacy of our chemical methods to reveal small or infinitesimal chemical changes taking place in seeds is, I think, proved in two ways. We know, in the first place, that kept seeds wear out, that the percentage of seeds that germinate and grow is smaller and smaller with the number of years they have been kept. The deterioration is more or less rapid according to the nature of the seed and the character of its protective coats, but in every known instance there is deterioration sooner or later, and I think you must admit such deterioration to be sign and proof that chemical change has taken place.†

§ 4. *Seeds.*—A still closer and more manageable proof that seeds may be the seat of chemical changes which chemical methods are inadequate to reveal, is, as I shall develop in a future lecture, afforded by an electrical method. As formally laid down above, electrical changes are the token of chemical changes, which are the token of the living state. And these electrical changes are manifested by seeds long before the

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* *Proc. Roy. Soc.*, vol. lxii., p. 160, 1897.—Thiselton-Dyer has gone further, viz., to – 250° to – 252°, *Proc. Roy. Soc.*, vol. lxv., p. 361.

† The continued formation of aleurone granules in very old seeds is in certain instances an objective sign of the occurrence of slow chemical change. The germination of "mummy wheat" must be set down as apocryphal, in spite of the wheat sheaf shown in a Paris museum grown from Mariotte's mummy wheat. The wheat was given to Mariotte by Arabs.

manifestation of any microscopical or chemical signs that they are the seat of a physiological activity. And yet we have not reached a limit; although our electrical test is more delicate and closer-searching than either a morphological or a chemical test, we may not flatter ourselves that it makes sensible to us the real ultimate (or initial) chemical movements of infinitesimal magnitude that herald (or attend upon) the awakening of the dormant embryo—the birth of a renewed life.

And so, if driven to the foot of the wall by the question, "Is this good seed living or dead?" I should answer, "I can't tell by looking at it, nor by chemically testing it, but come back in an hour, and I will show you that this seed, since you say it is a good seed, is an actually living seed; and then, if you like, I will kill it and show you how differently it behaves. At this moment I do not know whether or no infinitesimal chemical change is going on in the seed, but I believe that such infinitesimal change (if it exists) may be suppressed (by low temperature) without thereby making the seed *dead*."

Hence, in verbal physiological specification of a good seed, I should say, in order of logical subordination: Matter—Not-living—Formerly living—Capable of living again.

This has been a dialectical parenthesis. Before leaving the topic let me, however, utilise it in illustration of the answers desired (and in some cases obtained) to these two chief questions:—Are you alive? How much are you alive?

To the qualitative question, "Are you alive?" the seed response is "Yes," "No," or "Doubtful"—"Yes" being an electrical response of considerable magnitude, "Doubtful" or "No" being little or no response.

To the quantitative question, "How much are you alive?" the affirmative response comes in the forms of units, which are fractions of a volt, as in this instance, where seeds (Phaseolus) of different years are submitted to the quantitative question.

It is of course impossible for me to carry out a long series of trials like this on the lecture table; it will be sufficient for the purpose of illustration if I show you three trials—one on an assuredly *living* seed, one on an assuredly *dead* seed (that has been killed by heat), and a third on a very old seed of which I do not know beforehand whether it is alive or dead (but which I believe to be dead as it dates from the year 1860). And at the end of this lecture, if you care to see the trial, I will test some very old seeds indeed, that were given to me by Mr Percy Newberry, who combines the qualifications of botanist with those of Egyptologist. They are seeds collected by himself, and placed by him as dating from the twelfth dynasty, *i.e.*, as being something like 4400 years old. I need hardly say that no such undoubtedly old seeds will give any electrical response, nor will they germinate. I have previously made both tests.

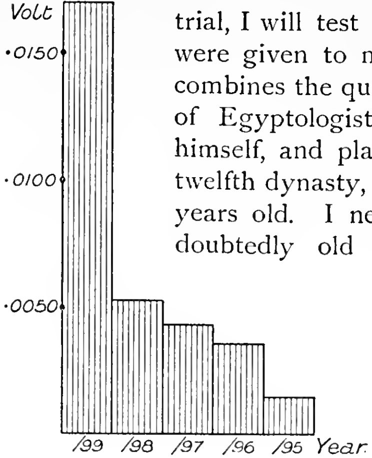

FIG. 1.—Average electrical response of seeds of five successive years. The ordinates represent the average voltage of response, which, as stated in the text, is taken as the index of vitality.*

[*Experiment.*]

The first seed gives, as you see, a large electromotive response. The other seeds give no response at all. The first seed is alive, the others are dead. We shall return to these matters in a future lecture; I wish in this first lecture to exhibit to you two other experimental illustrations as typical of the kind of problem and argument with which we have to deal.

§ 5. *Muscle.*—Muscle is a favourite object of physiological experiment; it gives sign of life by contracting when it is stimulated—either directly, by stimulation of the muscle itself, or indirectly, by stimulation of the nerve that is its motor nerve. And, roughly considered, its mechanical response or contraction is measure of the degree of vitality that it possesses. No one doubts that the contraction of a muscle is sign and proof of its state of life, and that the degree of contraction and the work of which that contraction is capable, are *cæteris paribus* measure

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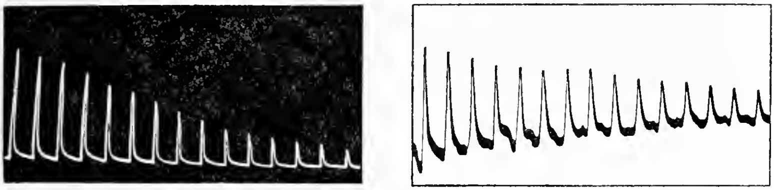
* *Proc. Roy. Soc.*, vol. lxviii., p. 87.

of the amount of vitality possessed by muscle. A weak muscle can do less work than a strong muscle, and a given muscle in the course of fatigue, or of that last act of life that we call death, can give less and less extensive contraction, and effect a smaller and smaller amount of work. *Pari passu* with declining contraction we witness declining electromotive response, and we admit or assume that the common substratum of the decline, whether mechanical or electrical, is decline of chemical activity.

An excised muscle has been set up to show this parallelism between mechanical and electrical response. A lever attached to the tendon indicates to you, by its excursion on a smoked glass plate, the extent or height of the mechanical movements (contraction). A galvanometer connected to the muscle by wires and unpolarisable electrodes, indicates to you, by the excursion of the reflected spot of light, the extent or voltage of the accompanying electrical movements. The muscle is excited indirectly, by excitation of its nerve, and, as you see, the two sets of movements, mechanical and electrical, run an approximately parallel course—both are large together or small together, and if one is absent, so is the other. You would notice, however, on closer comparison, that the parallelism is not perfect, the mechanical and electrical responses are not an exact replica of each other, and the defect of correspondence is particularly apparent in simultaneous records of the two sets of responses.



Mechanical Response. *Electrical Response.*

FIG. 2.—Simultaneous records of a series of muscular contractions, and of the corresponding series of negative variations. The method and apparatus for obtaining such records is described in the Appendix, p. 160, Fig. 63.

I cannot at present enter further upon this difference, I think it requires further study; if you ask which of the two records is the more faithful indicator of the chemical changes of which they are both the tokens, I shall answer that in my opinion the electrical indications are the more faithful; they are without doubt the more sensitive since they are still of quite considerable magnitude when a muscle is so weak as to scarcely contract at all, nor be competent to raise a lever to any measurable height. In the pair of records you have just seen, the electrical indications are reduced to manageable size by shunting the galvanometer.

§ 6. *Retinal currents.*—The third object of experiment is a frog's eyeball set up in a dark chamber between unpolarisable electrodes which are connected with a galvanometer. By opening a shutter the eyeball is illuminated at any desired time for any desired period. When I do this, there is no mechanical movement of the eyeball, at least no coarse mechanical movement,* but you witness a large and obvious electrical change. Holmgren, who first discovered this effect, found by a series of experiments in which he made separate trial of the several parts of the eyeball, that the electrical effect was of retinal origin. Light acting upon the retina excites it; in ourselves the subjective token of that excitation is a sensation; in the isolated eyeball the objective token of excitation is an electrical change. The detailed description of these changes will form the subject of my next lecture, but I should be glad if you would take note of what you have actually witnessed in the present case. The eyeball has been set up on electrodes, so that its fundus rests upon one electrode, while its cornea is touched by the other electrode, the spot of light was deflected to the left during the illumination, and returned to its original position after illumination. I touch one terminal of the galvanometer with a bit of zinc, and the other terminal with a finger of the other hand; the spot moves to the left, the terminal I touched with the bit of zinc is that to which the corneal electrode is connected: from which I conclude that the current during illumination was from cornea to fundus. I choose to call this direction "negative," and shall denote as

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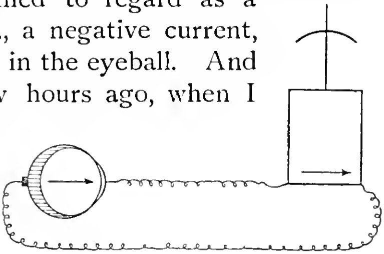
* On closer examination, there may be detected—(1) contraction of the pupil, (2) protrusion of pigment, (3) retraction of cones.

"positive" the opposite direction from fundus to cornea. And I recognise in the deflection to the left that we have just witnessed what I am accustomed to regard as a reaction of the third stage, viz., a negative current, directed from before backwards in the eyeball. And I may just mention that a few hours ago, when I put up this eyeball for experiment (under difficulties inseparable from the presence of belated workmen in a new laboratory), it gave a positive deflection, such as I have learned to be typical of a fresh and normal eyeball, and have chosen to characterise as a reaction of the first stage.



Normal response.

FIG. 3.

These have been details of the laboratory, details that you have hardly followed as I had to do, to make plain to myself (and state to you) what was the direction of current in the eyeball indicated by the direction of movement of the spot of light. Those of you who are actual workers will appreciate the importance of attention to such details, and the hopeless confusion arising from doubtful determinations of direction of observed currents. Those of you who content themselves with the literature of the subject, will find it almost impossible to realise what writers mean by "positive" and "negative" effects.

But the response we have just seen is not of the type that I wish to show in a first lecture; it is of what will be described later as a response of the third type, negative instead of positive; the eyeball may have been kept waiting too long, or have been accidentally compressed in the course of preparation. So I shall repeat the experiment on another eyeball that has just been carefully prepared and set up for me by the assistant.

[*Experiment.*]

And now, as you see, the response to light is a normal response of the first type, viz., positive, for the spot has moved to your right during the illumination, indicating current through the eyeball from fundus to cornea—and I make sure of this direction once more by touching the fundus electrode with a bit of zinc, and seeing that the spot moves to your right.

Let me make one more pair of trials to assure you that it has been luminous radiation in particular, and not thermal radiation, that has excited the retina of this eyeball. I repeat the exposure just as before, with the standard candle at unaltered distance (5 feet), but with an alum cell interposed to filter off most of the heat, and, as you see, the response is no smaller than before. Finally, I take away the alum cell, and expose the retina to the very sensible heat of a black hot surface of metal, and, as you see, there is no response at all to heat without light.

§ 7. *The mechanical excitability of vegetable protoplasm.*—The fourth and last experiment that I wish to show is a very simple one, but in my judgment a fundamental experiment in general physiology. It relates to the mechanical excitability of vegetable protoplasm, and is calculated to convince you of the essential identity between the excitatory responses of vegetable and of animal protoplasm. Those of you who are students of physiology or of physiological botany, are no doubt acquainted with various instances of movements in plants consequent upon mechanical excitation; and you probably know from the observation by Burdon-Sanderson on Dionæa, that these movements are accompanied by electrical effects. You may take it that the excited plant-stuff is the seat of chemical change, that this change is of the nature of a disintegration from large complex molecules to smaller, simpler molecules, that this disintegration has involved an increased osmotic pressure, whence turgor of certain cells, whence movement of petioles and leaves. And with these chemical changes there are of course associated electrical changes.

But these notions are to be extended, and we are to recognise further that any and every living vegetable protoplasm, when excited, undergoes chemical, and therefore electrical, change, whether it actually moves or not.

I have used all kinds of vegetable protoplasm, usually during the months of March and May, and for the experiment now on the table my favourite object has been the vigorously growing shoots of a vine. But in this bleak month of May (1902) the vine shoots have not yet appeared, and I have therefore taken a less favourable object, viz., the petioles of ivy-leaves, which, in comparison with young vine shoots, must be looked upon as rather a sluggish variety of vegetable tissue. So I shall take a stronger mechanical stimulus than usual.

The petiole of an ivy-leaf is fastened by modelling wax to a glass plate; to two points, 5 cm. distant from each other, unpolarisable electrodes are connected, and attached, of course, by wires to the galvanometer. Two slips of wood (weighing 5 grams each) running in vertical grooves, are suspended by catches 1 cm. above the petiole close to the electrodes, which we will call A and B. I let go the slip B, which strikes the petiole near the B end with an energy of 5 c.g.m.m., the spot flies off scale to your right. (I readjust the spot, and when it is steady, let go the slip A, and now the spot flies off to your left.) I test for direction as described above, by touching the galvanometer terminals with a bit of zinc wire, and seeing that by touching B the spot goes to right (and by touching A it goes to left). I know that when the petiole was excited at B there was current

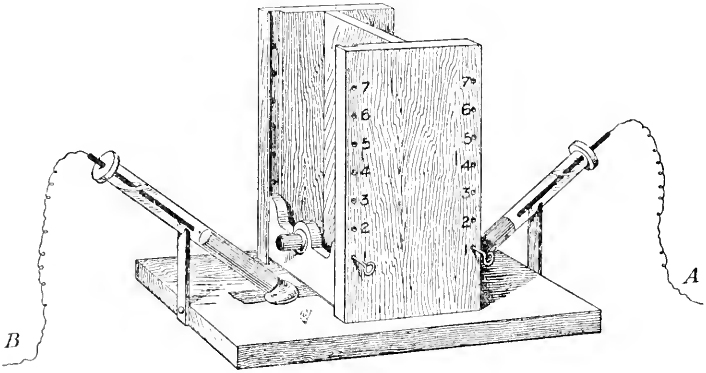


FIG. 4.—"Plant-guillotine" for the demonstration of the mechanical excitability of vegetable protoplasm. The shutter, visible only on one side B, by which the twig or shoot is excited, is represented as having dropped.

through it from B to A (while when it was excited near A there was current in it from A to B).

Is there any doubt in your mind whether these have been *physiological* responses, for which the essential condition is that the ivy petiole should be *alive?* There should be such a doubt in your mind, and you should set the doubt at rest by repeating, or making me repeat, the experiment on a petiole of which the molecular mobility has been abolished, *i.e.*, on a petiole that has been killed or otherwise immobilised. I might kill it at once by plunging it into hot water, but to do this I should have to remove it from the electrodes and replace it, which takes time; and even at best, when the petiole has been replaced as carefully as possible as it was, you cannot be quite sure that I have exactly replaced the petiole. So I shall otherwise immobilise it, in a way that will allow me to leave petiole and electrodes in *statu quo*, viz., by sending through it currents of such strength that the living stuff will be completely stunned: which I now do, and then repeat both trials as before, exciting at A and then at B, without, as you see, any response in either case. The previous effects you witnessed were therefore physiological.

§ 8. "*Zincative.*"—So far so good, there is no doubt whatever about the facts, the excitatory currents are precisely such as are aroused by excitation of animal protoplasm. But how are we to label them?

Following the best authorities—Faraday, Maxwell, du Bois-Reymond—we should say, referring to the pole under our observation, that B, the excited spot, is *negative* to A, the non-excited spot (or A, the excited spot, negative to B, the non-excited spot; but since this confirmatory experiment is confusing we will henceforth omit it, and consider only B excited, and A non-excited).

And as a matter of fact, this has been the terminology followed by physiological writers.

But in course of time, and especially in consequence of the polemic that took place between du Bois-Reymond and Hermann, the meaning of the term "negative" underwent a curious twist. Du Bois-Reymond found that the "resting

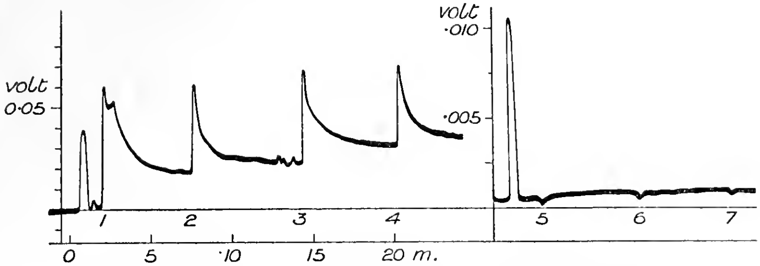


FIG. 5.—Vine-shoot. Electrical Effects of Mechanical Excitation (10 centigrammetres) before and after boiling.

The first four excitations (before boiling) give responses of 0.060, 0.045, 0.045, and 0.040 volt. The 5th, 6th, and 7th excitations (after boiling) give no response.

The deflection preceding the 1st excitation is by 0.04 volt, and the resistance of the stem between leading-off electrodes was 500,000 ohms. The deflection preceding the 5th excitation is by 0.01 volt, and the resistance of the boiled stem was 60,000 ohms.

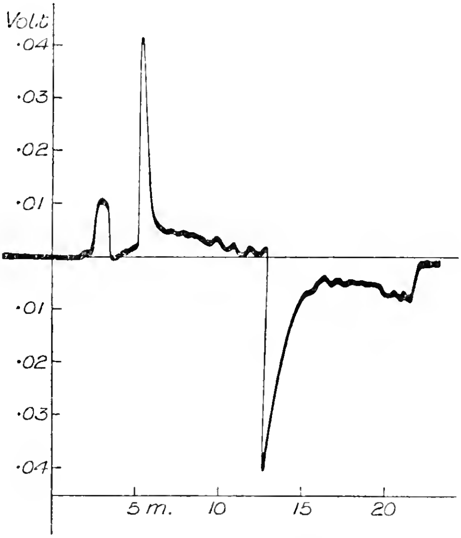


FIG. 6.—*Experiment* (3023).—Bean-Radicle (Phaseolus) 3 inches long and quite etiolated, incubated in the dark at 25° for five days. Led off to recording galvanometer by two unpolarisable electrodes, *A* and *B*. The radicle is struck transversely near *A*, then near *B*, by a bristle fixed to the end of a revolving rod. In each case the deflection is such as to indicate that the struck spot is rendered electropositive (galvanometrically negative) to the unstruck spot. The effects are completely abolished by strong tetanisation.

current" of quiescent muscle and of nerve is diminished when the muscle contracts or when the nerve is excited; he called this diminution "a negative variation of the previous current of rest." Hermann then showed that this negative variation of a current of rest (or current of injury) is only a special case of a more general phenomenon, and that active tissue is, properly speaking, negative to resting tissue, quite irrespective of any previous "pre-existing" current. And from the fact that active tissue is negative, and that the action is propagated in muscle and in nerve, physiologists adopted the expression "negativity of action," and spoke of propagation of a wave of negativity in the excitable tissue. And little by little a confusion of thought established itself; the origin of the expression "negativity" was lost sight of, active tissue was spoken of as being "electrically negative" and then "electro-negative"—which is clearly wrong in the accepted physical sense of this term. In physical language the *negative pole* of a voltaic couple is connected with the *electro-positive element*, the *positive pole* with the *electro-negative element*. And when a writer had escaped an actual misnomer, an ambiguity that was even more mischievous to clear thinking became effective; a state of negativity of action, propagated from active to non-active parts, arouses in the reader's mind the picture of a current directed in the tissue when connected by two points, active and non-active, from former to latter, *i.e.*, from "negative" to "positive." Now this direction is correct, but it is disturbing to one's thought to regard current as directed from negative to positive. And, in point of fact, the language is actually wrong; the adjectives "positive" and "negative" as used by Faraday refer to the poles, current is of course from positive to negative in an external circuit, positive and negative refer to an *external* circuit, and should not be used with reference to the *internal* circuit. It is a misuse of terms to say that current in the tissue is directed from negative to positive pole. The proper thing to say is that direction in the tissue is from electro-positive to electro-negative, that active tissue is electro-positive to resting tissue, that a wave of electro-positivity travels in muscle (or in nerve) from an excited spot.

But, in the present state of our physiological literature, is it wise to attempt to use the proper expressions? No doubt the confusion is very great, no doubt the main bulk of our electro-physiological literature is totally unintelligible to physicists and to most physiologists. Shall we not, however, lay the foundation of a further mass of worse-confounded confusion by any sudden and unauthorised endeavour to call white white and black black, when for the last twenty or thirty years our leaders have been content to call white black and black white?

I hardly like to hazard an opinion, but in presence, on the one hand, of the impossibility of clear thought and speech, with external adjectives for internal relations, and, on the other hand, the mental impossibility of obtaining a sudden reversal of language which is endeared to physiologists by its familiarity and its obscurity, I have adopted a new and barbarous word that avoids the pole name “negative” and the element name “electro-positive,” yet implies both names. And for the present, at any rate, awaiting a better word, or a clearer understanding, I shall, whenever occasion seems to demand the word to make a meaning clear, use the expression *zincative*, to imply “electro-motive like the zinc of a voltaic couple”; zinc is, as we all know, negative as to its external relation by its pole, and electro-positive as to its internal relation in the cell. Current in the cell is from zinc to copper, in the tissue from more active to less active; an active tissue-element is electro-positive to a resting tissue element, or (under protest) an active tissue element is

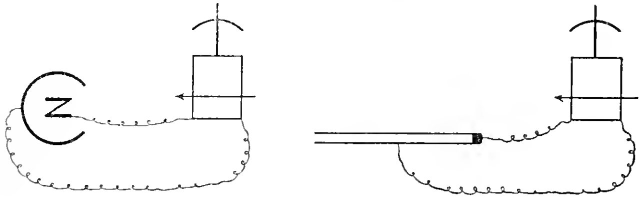


FIG. 7.

The current of a Daniel cell is from copper to zinc through the galvanometer, and from zinc to copper in the cell itself.

A nerve current is from uninjured to injured spot through the galvanometer, and from injured to uninjured spot in the nerve itself. The injured spot is “zincative.”

negative to a resting tissue element; but whether we call it electro-positive or negative, the active element is "zincative."

§ 9. "*Solution-pressure.*"—To those of you who are accustomed to think about currents through electrolytes, in terms of ions creeping through a solvent, this matter should present itself in a very simple light. Active protoplasm takes on a higher "solution-pressure" (in the sense with which Nernst has made us familiar), and electro-positive ions migrate in greater abundance from protoplasm to lymph. There is then "current of action," and I do not think that we need at this stage pause to object whether this increased pressure may be—not of the protoplasm itself—but of paraplasm (? fat, ? carbohydrate) set in motion by protoplasm. Whatever the nature of the ions may be, we must picture them as laden with positive charges, and pressing into the lymph-bath from spots where they have become congregated and accumulated, *i.e.*, in and around the meshwork of living matter. Imagine simple hydrogen kations, or if you like, more complex hydrogen and carbon kations, as issuing forth from a solid coast to a fluid atmosphere, where their oxidation is consummated—forming water, lactic acid, and carbon dioxide as their typical end-products. These notions, in my way of thinking, are the physiological connotations involved in the brief statement that "*active tissue is zincative.*" And if you have gone so far, you will almost certainly go one step further, and imagine that just as a zinc rod that has given off zinc ions to its surrounding medium, is for the moment, negatively charged, so a core or stem of living stuff, immediately after a discharge of positively charged ions is relatively negative. Current of action is thus followed by an opposite after-current; du Bois' "negative variation" is followed by Hering's "positive after-variation." But I do not wish to pursue this point in detail now, for there are no experiments in evidence before you. An opportunity of demonstration may perhaps arise at a future lecture.

§ 10. *Summary.*—Will you think of these things? I will try to place myself in the position of a listener, and offer some criticism of what you have just listened to.

You would find, if you critically compared the lecture with its syllabus, that many points mentioned in the syllabus have not been fairly met by the lecture, that the order of the spoken (and written) description differs from the order of items promised by the syllabus, that points have been talked about of which there is no mention in the syllabus. To which my defence is, that memoranda of a printed paper cannot be placed in the same logical order as the thoughts and comments that arise from experiments in the act of demonstration. And so I have left untouched (for the present) the headings "an excised nerve," "a piece of skin," "a green leaf," "a cut flower," "a stem," in the hope that you may for yourselves realise how these things associate themselves in the mind of any one planning a group of considerations. The reason of such association may perhaps be made plain in the course of these lectures.

You may have found it rather perplexing to be told at some length that positive means negative, and that negative means positive. Some of you have hitherto been quite satisfied to talk about the negative variation of contracting muscle or of excited nerve. I believe that these expressions are nearly always empty to utterers and hearers alike, and I have deliberately tried to disturb your easy acceptance and use of paper language, and put you to the trouble of mentally imaging the facts denoted by the words. The points to be definitely registered from what you have witnessed, are:—

(1) From the muscle experiment: that *pari passu* with its *contraction*, its ordinary and indubitable sign of life, an electrical change is proof and measure of its state of life.

(2) From the eyeball experiment: that we have witnessed an electrical response to luminous stimulation.

(3) From the ivy leaf: that vegetable as well as animal protoplasm, while alive, gives an electrical response to mechanical excitation.

(4) From the seed experiments: that the electrical response to electrical excitation can be utilised as a measure of "vitality."

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Note.—The misuse of the terms " ELECTRO-POSITIVE " and " ELECTRO-NEGATIVE," to which I called attention six years ago in the first paragraph of Lectures on Animal Electricity, is now very generally recognised. In the Oxford Laboratory the remedy proposed is to simply transpose the words ; but until a general agreement is arrived at that " POSITIVE " (*new style*) is to be the equivalent of " NEGATIVE " (*old style*), and *vice versa*, I think the remedy will be even more prejudicial to clear thinking than the disease. I do not think the word " zincative " has yet fully served its purpose, and shall therefore continue to use it when it appears to me to be required.

LECTURE II

The Prospect—Demonstration of Retinal Currents—The Initial Current—The Principal Fact; Subordinate Features—Three Types of Response—Two Opposed Processes—Effects of Complementary Colours—Cause: Effect—Anæsthetics—Retino-motor Effects.

§ 11. *Prospective.*—It is my intention—in the eight days' laboratory excursion which I hope some at least of my present hearers will complete—to visit several apparently disconnected points of physiology. And while I shall not attempt to show you at once that these points are in fact intimately connected, I will name them to you now, and promise that their uniting bonds shall become evident to you in due season—by your own thinking, rather than by my talking. "The Excitability of the Retina"—"The Excitability of Vegetable Protoplasm"—"Skin Currents"—"The Development of a Hen's Egg"—"Secreto-motor Action"—"The Action of Anæsthetics." These are some of the topics that are at present linked together in my mind, as on a thread of intention, towards the next few lectures.

And before I commence to tell the first bead of my chaplet, let me make further confession of faith, and outline to you the sort of purpose and intention by which scientific research may be animated. There are two chief moments in the life of every explorer—the moment of discovery, and the moment of disclosure, when the first pleasure is shared with others. But before this second moment may be enjoyed, a language—not necessarily of words alone—must be common to talker and to hearer. The talker must in a measure generalise his language, the hearer must in a measure specialise his understanding, and learn the meaning of terms and formulæ and labour-saving symbols that are current coin in the daily dealings of every specialist.

I shall do my best to talk in simple language, but I know that we shall often be forced to fall back upon technical terms. The ideal way would be, in first place, to have written a monograph in the dry and freely technical language of a *Philosophical Transactions* paper; in second place, to retell the same story here in the simple words and homely metaphors by which we ordinarily attempt to tell each other what we are thinking about. It will not be possible to me to strictly follow this ideal way, but I shall do my best to justify narrative by reference to duly accredited publications; and as to technicalities, well, perhaps some degree of physiological technicality may be excused in the Physiological Laboratory of the University of London.

Every one here is no doubt acquainted with the physiology of vision, in so far as it is given in the text-books. You have studied the eyeball as an optical instrument, containing a living sensitive surface that receives the focussed (or unfocussed) radiations of light. You have studied the course and the central cortical terminus of the nerve fibres leading from retina to brain. You know that the thing as seen by you is your subjective picture, aroused by the objective retinal pattern of the objective field of vision. You have proceeded to the closer study of the objective retinal change from which the subjective visual sensation takes origin, and have learned that the objective effects of light acting upon the retina of an excised but surviving eyeball are :—a bleaching of its visual purple, a movement of expansion of its pigment cells, a movement of contraction of its cones, and, as in every case of physico-chemical change, an accompanying electrical change.

One more preliminary consideration. Our own retina, that arouses in our own brain the detailed images of complicated objects when detailed images are focussed upon it, gives rise to diffuse sensations of light and to the fantastic appearances called phosphenes when it is stirred into action by direct mechanical or electrical stimuli. Mechanical pressure of the eyeball, or an accidental blow upon it, or an electrical current traversing it, anything, in short, that suddenly disturbs the retina, elicits in consciousness the specific subjective symptoms of a suddenly disturbed retina, formless or fantastic, a blaze of flashing lights, or a succession of colours, in accordance with the accidents and irregularities of such coarse artificial disturbance. And no doubt—could we only detect it—the physico-chemical disturbance is attended by an electrical disturbance The latter will, however, be most easily demonstrated to you with an excised eyeball.

§ 12. *Demonstration.*—Such an eyeball has been removed as carefully as possible a few moments ago from a pithed frog. "Carefully" in this connection means with as little compression of the eyeball as possible, and in point of fact such compression

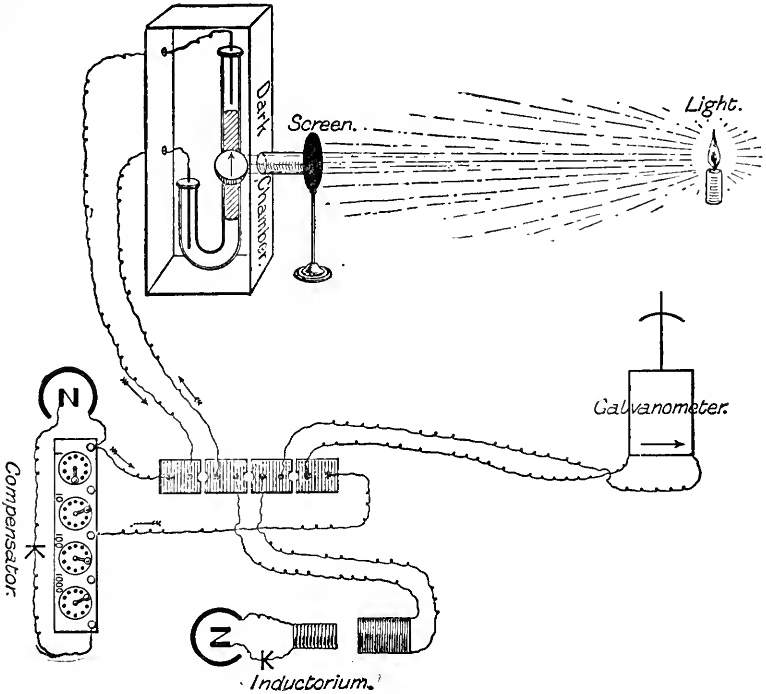

FIG. 8.—Frog's eyeball between unpolarisable electrodes for demonstration of the electrical effects of light and of electrical excitation. The circuit from the eye is completed through a compensator, secondary coil, and a galvanometer. The arrows through the eyeball and the galvanometer indicate the direction of the initial current and of the normal response. Arrows near the compensator wires indicate the direction of a compensating counter-current.

has been nearly quite avoided by cutting the frog's head in half, taking up the fragment with forceps, and trimming away the orbit from the eyeball with scissors. The eyeball is now resting upon the clay pad of an unpolarisable electrode, the pointed pad of the second electrode touches the cornea, the actual contact being by a droplet of salt solution. The electrodes are connected to a galvanometer. The eyeball and electrodes are enclosed in a black box with a hole, tube, and shutter opposite the eye, so that when desired the latter can be exposed for any required time to light of any required strength.

The connections are such that the fundus of the eyeball is attached to the south terminal, and the cornea to the north terminal, of the galvanometer as in Fig. 3 or in Fig. 8, with the keyboard unplugged. (The circuit includes a compensator and a secondary coil, to be used in our next Lecture.)

§ 13. *The initial current.*—Notice as a first point that the natural current of the eyeball has given current through the galvanometer from N to S terminal, *i.e.*, that within the eyeball it has been from fundus to cornea. Notice further the fact that this current is rapidly declining. The spot deflected to your right is sinking to your left towards its zero point.* If we could afford to wait, we should see the spot reach the zero and continue its journey to the opposite end of the scale, indicating to us that the eyeball current, at first directed from fundus to

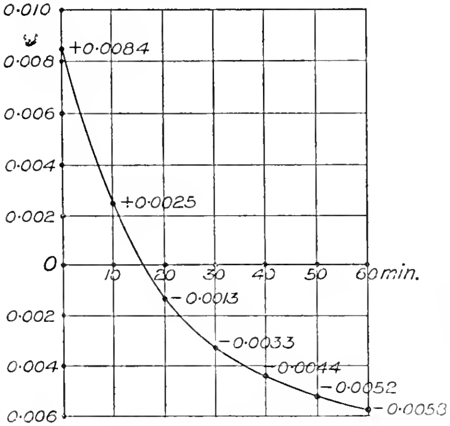

FIG. 9.—Normal declining current of a frog's eyeball. The rate and shape of decline resemble those of a blaze current.

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* The lecture-room is east and west, the former being the lecturer's end. The galvanometer is on a bracket fixed to the east wall of the room, and the movements of its suspended magnet are shown by a vertical spot of light reflected to a transparent scale placed on the lecture-table. The audience

cornea (positive), is ultimately directed from cornea to fundus (negative). We shall get a better general view of this gradual change by plotting a curve of readings taken at regular intervals (Fig. 9). I think you will agree with me that the entire curve, falling with diminishing rapidity towards and beyond the zero value, is badly named when it is called a current of rest, and that it cannot possibly be only a subsiding current of injury at the transverse section of the optic nerve. I think and speak of it as a declining *manipulation blaze* caused by the unavoidable mechanical disturbance that occurs in the most careful possible preparation of the eyeball, for the effect can be at once reproduced by slightly compressing the eyeball, and the current aroused by such intentional manipulation declines just like the current unavoidably aroused in the preparation of the eyeball. So much for the normal or accidental current, which is decreasingly positive and increasingly negative, at least during the first hour or two of observation.

§ 14. *The principal fact.*—We may now proceed to the principal part of the experiment as first made by Holmgren, and subsequently repeated by Dewar and MacKendrick, Kühne and Steiner, Fuchs, and many others.

The eyeball current is steady, the galvanometer spot is sinking with imperceptible slowness to your left, and I expose the eyeball to a brief flash of light by means of an ordinary photographic shutter timed at about $\frac{1}{100}$ second. The galvanometric spot makes a small excursion to your right (positive), indicative of a current through the eyeball from fundus to cornea in response to the flash of light. The direction and character of this response, which are perfectly normal, are nearly sufficient to assure me that we have under our observation a normal and well-prepared eyeball, but I shall not be quite sure of this until I have seen how the galvanometer spot

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faces east, so that the N terminal of the galvanometer is to the left and the S terminal to the right. As far as possible the connections are arranged so that currents in a "positive" or "outgoing" or "ascending" direction shall give deflections to the right, "negative" or "ingoing" or "descending" currents deflections to the left.

behaves itself with a more prolonged exposure of the eye. So I adjust the shutter for such prolonged exposure to light —a minute will be a convenient time—expecting to obtain, if the eyeball is quite normal, a larger and increasing positive deflection during exposure. And now watch the spot rather closely for what will happen when I cut off the light by closing the shutter; as you hear the click of closure, you see that the spot makes a short positive excursion to your right before falling back to its original starting position. All these features will be best realised from a photographic record of the travelling spot; here is such a record, on which you readily distinguish the large positive and increasing response to a prolonged exposure, ending by the small positive response or— as we familiarly call it in the laboratory—the "parting bow"— at the cessation of illumination, after which the current gradually falls to its original level. This has been no exceptional result, but the typical and regular mode of response of a normal carefully prepared eyeball; the photographic record of five such responses taken on a more slowly travelling plate will be sufficient evidence of this. In each case there is deflection in the positive direction at "make" of light, during light, and at "break" of light.

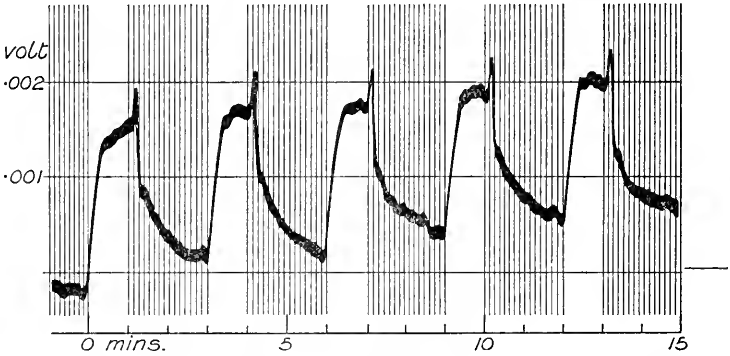

FIG. 10.—Frog's eyeball. Galvanometric record of five successive normal responses to light; each illumination lasts for one minute.

§ 15. *Further points.*—There are several subordinate points relating to the above described typical positive response to light that demand consideration. I will deal with them as briefly as possible. In the first place, it is of no moment as regards the response, whether the accidental current described in paragraph 13 happens to be positive or negative. Kühne and Steiner, who paid particular attention to the point, refer to the fact under the heading, Law of Constant Alteration of Tension, and describe it thus:—

"Reversed direction of the current of darkness (our accidental current) is without influence upon the magnitude and character of the photo-electrical variations, which reverse their signs." That is to say, according to the German designation, that the response of a positive current of darkness is in the same direction as that current, or "positive," while the response of a negative current of darkness is in the opposite direction to that current, or "negative." I have preferred to this correct, but rather confusing mode of description, to say that the response is normally from fundus to cornea or *positive*, whether it starts above or below the line of

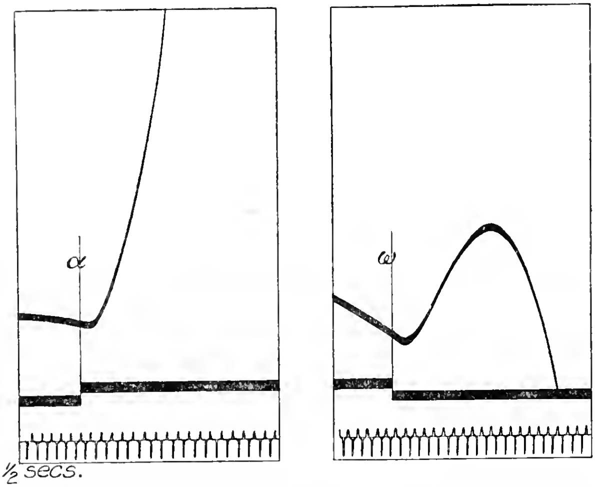

FIG. 11.—Frog's eyeball. Galvanometric record of the normal response at beginning (α) and end (ω) of illumination. The delay in each case is about ½ sec.; that of the galvanometer is ⅓ sec.; the net retinal delay is therefore about ⅙ sec.

zero current, *i.e.*, whether the accidental current upon which it is superposed be positive or negative. Or to use a familiar laboratory mnemonic—the normal excited eyeball always "looks through its own galvanometer." (See Fig. 3).

There is always a considerable interval of time between the incidence of light and the electrical response; sometimes the delay at "make" of light may be so great as to be measurable by a stop-watch, but in such cases the delay at "break" is much less considerable, and I have considered the interval at make as a period of hesitation (*vide infra*) rather than as a true physiological lost-time. But even under the most favourable conditions, with fresh and typically reacting eyeballs, I have never seen the latency as short as given by Dewar and MacKendrick, and more recently by Fuchs—viz., "less than $\frac{1}{100}$th of a second." The shortest intervals I have measured have been of about $\frac{1}{2}$ second, no difference being detectable between the make and the break deflections in this respect. These values have been obtained from galvanometer records, of which Fig. 11 is an example, and are subject to a correction, by

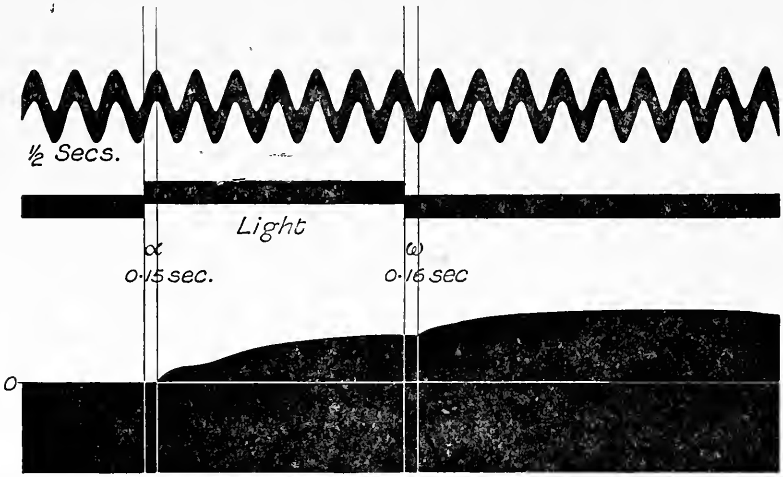

FIG. 12.—Frog's eyeball. Electrometric record of the normal response at beginning (α) and end (ω) of illumination. The retinal delay is in each case about $\frac{1}{6}$ sec., *i.e.*, approximately the same as that of cortical grey matter.

reason of the physical lost-time of the suspended magnets and mirror. With the capillary electrometer, which has no appreciable lost-time, the latency comes out at about 0.15 second—still a very considerable delay, and indicative of a rather surprising physiological inertia of the retinal organ.* (See Fig. 12.)

I had the curiosity to repeat the experiment under precisely similar conditions on an oxidised copper plate, which, as is well known, is acted upon by light, and gives, therefore, electrical currents in response to illumination (Fig. 61, p. 159). There was no detectable lost-time, either by galvanometer or by electrometer—a fact which is of interest in the present connection merely in that it bears witness to the correctness of the retinal data taken by the same apparatus.

When it has been clearly recognised that the regular and typical response of the fresh uninjured eyeball is of positive direction, *i.e.*, directed from fundus to cornea, we may proceed to consider, without losing our way amid a tangle of abnormalities, the varieties of character that present themselves, not merely in the response to light, but in the response to mechanical and to electrical stimulation. And when we have considered such varieties, we shall return to the consideration of the above described typical positive response, and recognise that this positive response is in all probability the algebraic sum of two opposite and not perfectly congruent electrical changes. The terminal positive effect at the closure of illumination, which must have been to us at first sight a somewhat puzzling feature, will then become intelligible to us.

§ 16. *Three types.*—For the sake of distinct description, I have classified the response to light as falling into one or other of three types:—

I. Positive response of the first type, characteristic of the normal fresh uninjured eyeball.

II. Mixed responses, characteristic of transitional states between types I. and III.

III. Negative response of the third type, characteristic of the compressed or partially injured eyeball.

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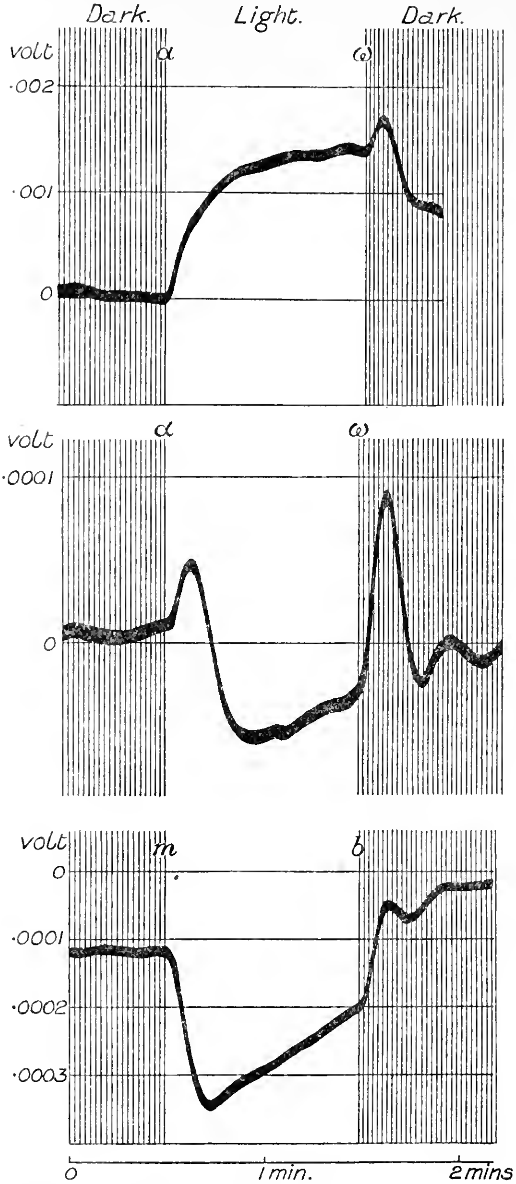
* Gotch has recently and independently made similar observations (see References).



First or normal type.

Second or transitional type.

Third or reversed type.

FIG. 13.—Frog's eyeball. The three types of its response to light, as described in the text.

I have formed the opinion, from a large number of observations and trials, that the principal factor in bringing about that

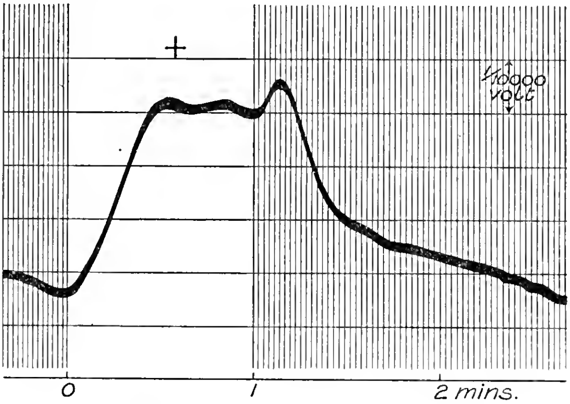


FIG. 14.—Positive—before massage.

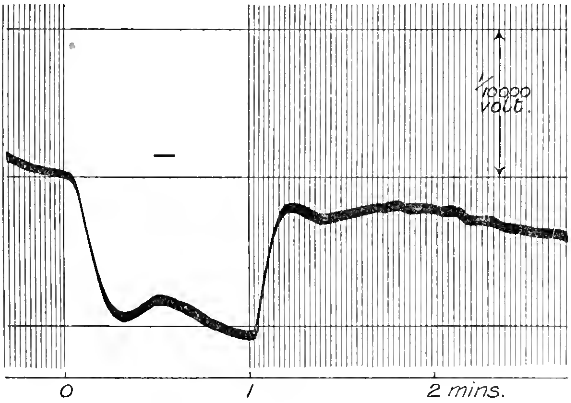


FIG. 14.—Negative—after massage.

Response to light (25 units). The horizontal lines in both these records denote a scale in $\frac{1}{10000}$ths of a volt; the resistance of the eyeball has been much diminished by massage.

state of eyeball in which the response to light is purely negative, is a moderate compression, or shrinking by drying of its retinal coats. A fresh eyeball prepared with such care as to give the typical positive response of the first type can at once be made

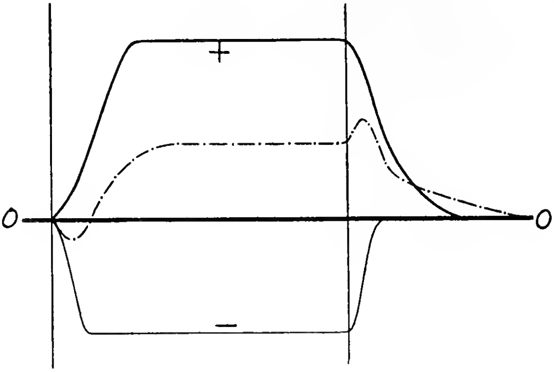


Fig. 15.—Diagram to illustrate the effect upon a galvanometer (broken line) of a simultaneous larger positive current and smaller negative current, the latter commencing and ending more rapidly.

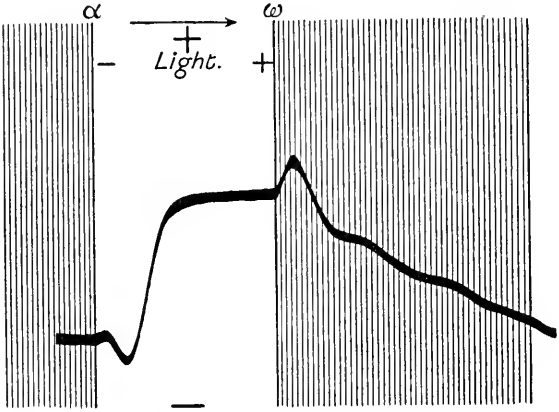


Fig. 15.—Retinal response of the second stage, illustrating the double effect.

to give the negative response of the third type by gentle massage or by steady moderate compression, and in the latter case it is possible with very gradual compression to obtain response of the transitional type.

The conversion of type I. into type III. by means of gentle massage forms a simple and almost an unfailing lecture demonstration. Fig. 14 is the record of a case in point.

§ 17. *A double process.*—I think that any one who has witnessed a great number of experiments of this character, and who has carefully inspected a large number of records such as those figured above, will be forced to the conclusion that the normal positive response is the algebraic sum of two opposite and almost synchronous electromotive phenomena, one giving a positive current that over-compensates the other giving negative current; the first more labile than the second, so that by gentle compression it may, so to say, be wiped out, and the second be thus unmasked.

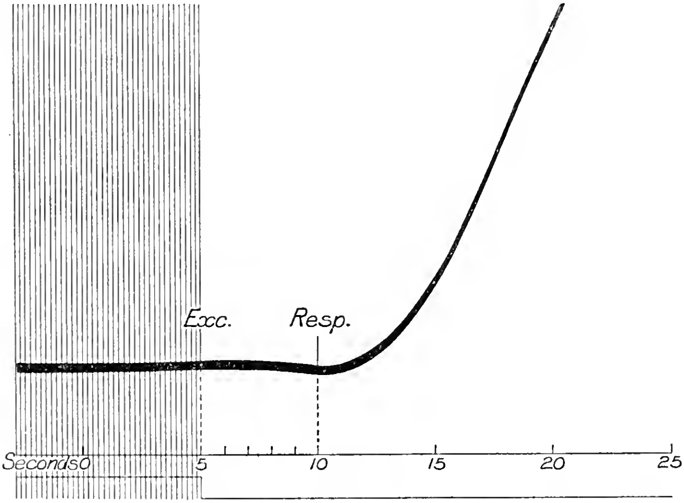


FIG. 16.—Frog's eyeball. False latent period or period of hesitation in this instance = 5 secs.

A careful scrutiny of the manner in which the normal positive response begins and ends confirms this view, and at the same time offers to us a plausible explanation of what has been referred to above as the "parting bow." If during the exposure to light there is a tug-of-war between positive and negative current, with predominance of the former, and if at the end of exposure both currents should cease, but the negative cease more rapidly than the positive, then we should witness what actually does happen, viz., a short movement in the positive direction preceding the return to a state of rest. And finally, on turning back to the nicer examination of the rising effect at the outset of exposure, we find another sign of an opposition between two contrary and all but synchronously developing currents. There is often at this point a false latent period, or *period of hesitation*, perceptible on simple observation, or, better still, by means of records where the beginning of an exposure has been mechanically signalled, amounting to several seconds, and intelligible only on the supposition that our galvanometric magnet is, so to say, trembling in the balance between two opposite and almost perfectly congruent forces. And generally, indeed, on the record of such a false latent period, we may detect signs of such a preliminary struggle, as if an initial positive movement had been forthwith interfered with for a brief period by a contrary negative movement. On some records the magnet remains almost perfectly at rest during several seconds of hesitation; on others it is caught back by a sharp negative jerk; on others still the curve of positive movement is only slightly hitched or notched in its progressive development. All these facts—viz., the transitional responses from positive to negative, the immediate conversion from positive to negative by compression, the initial period of hesitation, the terminal "parting bow"—point to one and the same conclusion, viz., that the retina, when exposed to light, is the seat of two contrary electro-motive changes. And it matters little whether you imagine two single processes or one double process behind the movements of the machinery.

Thus, following a path step by step as it happens to lead us, we find ourselves quite unexpectedly at a place where theory and doctrine seem to be quite familiar to us. We are all of us more or less intimately acquainted with Hering's theory of colour-vision setting forth that contrary processes of dissimilation and assimilation are aroused by complementary colours, white and black, red and green, yellow and blue. And whether or no we happen to believe that, *e.g.*, a red light is katabolic and a green light anabolic, we assuredly do believe in what has been termed by Bernard the axiom of general physiology—that katabolic analysis and anabolic synthesis are inconceivable apart from each other. I think that we should not hastily admit that our double electrical change is presenting us to another aspect of a familiar if somewhat nebulous colour theory; I think we have no ground for assuming that our conclusion means anything more than the old axiom behind a new face. A process necessitates the anti-process, and if the process is attended by an electrical change of given sign, we may expect that the anti-process will entail an electrical change of opposite sign. The chemical changes taking place in living matter are in general *reversible* changes.

§ 18. *Complementary colours.*—One question we may indeed put to the test before passing on. We may see whether or no complementary colours have opposite electrical effects, and whether the excessive action of a given colour favours or disfavours the action of its complementary. I have tried both these points; I had no real expectation that red and green light, *e.g.*, should have electrical effects of opposite signs, nor that the excessive action of a given monochromatic light would promote the subsequent action of its complementary. And in point of fact, neither of these things happened. The effects of all sorts of colours were of the same sign. The joint effect of two complementary colours was practically the sum of their separate effects. And the prolonged excessive action of a given colour fatigued the retina to that colour just as much or as little as to the complementary colour. All colours, in fact, as regards the electrical response they elicit from the retina, give that response of the same sign, and seem to act in the same direction, more or less powerfully according as they are more or less luminous. Thus, *e.g.*, in a given series of trials, the responses came out of the following relative magnitudes:—

Red	+4	Green	+12
Yellow	+16	Blue	+9
(White)	+33		

In other trials the responses were :—

To Red alone .	+5	To Red and Green conjoined	+14
To Green alone .	+10	(To White) . . .	+40

§ 19. *Cause : effect.*—I have upon more than one occasion taken records of the series of electrical effects elicited by a series of illuminations of arithmetically increasing and decreasing strengths. The general question to which this special question belongs is in my opinion one of fundamental elementary importance, coming under our notice in almost every province of study, sometimes in simple and accessible shape, sometimes disguised or hidden by the manifold circumstances and accessories of organic life.

The question is: What quantities of physiological effect, Y, are elicited by given quantities of physical cause, X? And the answers to that question in its various forms will be most conveniently and symmetrically expressed by a curve to the co-ordinates OX, OY, with the physical cause or stimulus or excitation plotted along OX, and the physiological effect along OY.

Generally speaking, we cannot hope to reach in physiological matters an accuracy such as is possible in physical matters. Our data are too rough, perturbed by too many uncontrollable variables, and may not as a rule be formulated in mathematically correct curves characterised by simple equations. The well-known logarithmic law of sensation is at best of very limited application, and a sensation curve actually plotted from experimental data exhibits great divergences from any logarithmic curve that can be fitted to it. Without, however, making any attempt to trim or strain experimental results and fit them with orthodox mathematical curves, we may with advantage plot them out to scale on a simple system of co-ordinates OX, OY, and thus recognise at a glance whether, within the range of the observations made, a given physiological effect has varied (1) as its cause, or (2) more rapidly than its cause, or (3) less rapidly than its cause. I mean of course exciting or proximal efficient cause or stimulus, and not the whole previous chain of principiants resulting in the particular event.

Let us consider the three cases :—

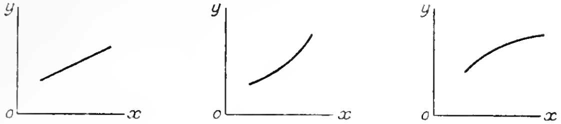


FIG. 17.—Straight. Concave. Convex.

The effect Y varies as its cause X.

Equal increments of cause produce equal increments of effect. The cause / effect curve is a straight line.

The effect Y varies more rapidly than its cause X.

Equal increments of cause produce increasing increment of effect. The cause / effect curve is convex to its abscissa OX.

The effect Y varies less rapidly than its cause X.

Equal increments of cause produce diminishing increments of effect. The cause / effect curve is concave to its abscissa OX.

And now turn to the case in point, where the cause X is the intensity of a light, and the effect Y the magnitude of a galvanometric deflection (which we shall assume to measure magnitude of electrical change, and therefore magnitude of retinal change).

With a light of suitable strength, varied on an arithmetic scale constructed in conformity with the law that luminosity varies inversely as the distance squared, we find the following series of results from the given series of stimuli :—

Stimulation by light .	2	4	6	8	10 X
Retinal change . .	208	248	274	296	326 Y

which, plotted as described above, gives the curve figured below as that of the retinal effects of medium illumination.

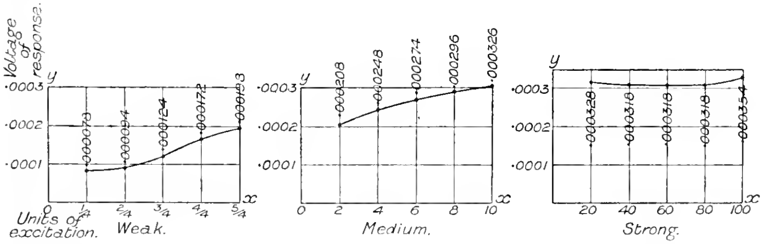


FIG. 18.—Frog. Retinal response to illumination of constant duration and of varying strength. The unit of light is a standard candle at a distance of 10 feet from the eyeball.

Now this curve, concave to its abscissa OX, with the effect Y increasing less rapidly than its excitant cause X, is in conformity with almost every series of observations we are able to carry out on living matter. The familiar logarithmic curve of sensation is concave to its abscissa, sensation Y increases by diminishing increments for equal increments of stimulation X. Muscular contraction, the negative variation of a nerve-current (as I have shown previously), give the same type of curve within at least a certain range of observation. And other cases might be quoted illustrating the general law, that the response of living matter to the excitation of its environment increases by dimishing increments, giving a cause/effect curve that is concave towards its abscissa. And we need not attempt to see whether or no this curve can be neatly fitted with a logarithmic formula, for the fit or the misfit of a curve, constructed from such a formula, would not afford much information beyond what is to be learned from inspection of the empirical curve, and comparison with other curves.

Moreover, one may convince himself at once by somewhat closer observation, that the entire range of any given cause/effect curve cannot be fitted by a logarithmic formula. Above the range of moderate stimulation, we have no further increment of effect, but, on the contrary, a decrement, attributable to fatigue or to shock, or to actual injury by excessive stimulation. And below the range of moderate stimulation, the curve does not spring suddenly from its abscissa and rise by increments diminishing from the very outset, but it rises gradually from zero by increments smallest at first then increasing, so that a first part of the curve instead of concave is convex to the abscissa, and the whole curve S-shaped, convex at first, concave at a higher range. I have urged elsewhere that this S-shaped character of the cause/effect curve is general, and that any well-studied case, where we can plot physical cause along an abscissa and physiological effect along ordinates, will probably be found to yield such an S-shaped curve.*

§ 20. *Anæsthetics.*—In conclusion of this chapter I will briefly remark on the two last headings of the syllabus in

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* Waller.—"On the Excitability of Nervous Matter." Presidential Address to the Neurological Society, 1900. *Brain*, 1900.

your hands; one of these—the action of anæsthetics—I took the opportunity of examining with some care a few years ago in connection with a methodical study of the action of anæsthetics on isolated nerve;* the other—retino-motor effects—I have not worked at myself; it rests upon the authority of Engelmann, who discovered and worked the point with his pupil Grijns.

The ordinary anæsthetics—carbon dioxide, ether, and chloroform—influence the electrical response of the retina to light as might be expected from a consideration of the physiological character and conditions of the response and the relative power of the anæsthetics used. With an enucleated eyeball as the object of experiment, the layer to be anæsthetised is comparatively well protected by the sclerotic coat, and the effects of an anæsthetic vapour are obstructed if only because its access to the retina is obstructed. Still the characteristic effects of the three anæsthetics are produced, although more slowly and imperfectly than in the case of an isolated nerve. Carbon dioxide gives diminution followed by augmentation of the response. Ether gives temporary diminution or abolition of the response, followed (usually) by perfect recovery. Chloroform gives abolition of the response, and the abolition, once it is produced, is apt to be final.

§ 21. *Retino-motor effects.*—The effects studied by Engelmann and Grijns are interesting in two chief particulars: they indicate the possible existence of efferent fibres in that most typical afferent nerve, the optic nerve (retino-motor); and they afford some answer to a question that has no doubt occurred to you, whether, namely, the electrical change occurring in an illuminated retina, belongs to altered pigment or to retracted cones or to both phenomena. The chief points in Engelmann's observations are, that retraction of the cones and an electrical effect can be produced in one eye by electrical excitation of the peripheral end of its optic nerve, or of the central end of

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* WALLER.—"The Action of Anæsthetics on Nerve." Presidential Address to the Section of Anatomy and Physiology of the British Medical Association. Montreal, 1897. *British Medical Journal*, 1897.

the other optic nerve, or by luminous stimulation of any part of the skin. I think we are bound to accept as correct the results vouched for by an observer of Engelmann's experience, yet, I must confess, that I cannot defend myself from a lingering doubt when I remember how sensitive the retina may be to the weakest trace of light (I have seen distinct reaction to a flash of moonlight lasting $\frac{1}{100}$th second, and quite recently, by courtesy of Sir W. Crookes, to the luminosity of radium), and when I consider how difficult it must be to absolutely protect an eye from all trace of direct illumination, while sunlight is reflected on to the other eye or on to the skin.

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LECTURE III

Plan of this Lecture—Electrical Excitation of a Frog's Eyeball—Modification of the Response to Light subsequent to Tetanisation, and during Tetanisation—Effects and After-effects of Single Shocks—"Blaze-currents"—Polarisation Currents—Electrocution—Three Types of Blaze-currents—The Effect is greater than its Cause—Influence of a Galvanic Current—Some Questions—The Crystalline Lens.

§ 22. I propose to consider to-day, and as much as possible demonstrate:—

1. The effects and after-effects of tetanisation upon the eyeball.

2. The influence of tetanisation upon its electrical response to light.

3. The influence of light upon the electrical effects of electrical shocks.

4. The effects and after-effects of single induction shocks (and of condenser discharges) upon the eyeball; and

5. The influence of galvanic currents on the effects of induction shocks.

No small undertaking indeed for a single day's work, nevertheless one that we shall hope to meet by aid of a series of simple experiments. Of course I well know that a string of experiments, perfectly successful it may be, but imperfectly explained and understood, has equal value with a string of conjuring tricks, but I take it that by this time you see your way through the apparatus set out on the lecture table and the diagrams hung at your elbow. Moreover, I can refer you to a paper published last year, on the Blaze-currents of the Frog's Eyeball, that contains at greater length than would be suitable for a lecture the results and considerations that we are about to review. I venture to think that the reading of the paper would help you to understand the lecture, and that the hearing of the lecture may help you to understand the paper.

§ 23. *The effects of tetanisation. Experiment I.*—When one has seen that the stimulation of an eyeball by light arouses

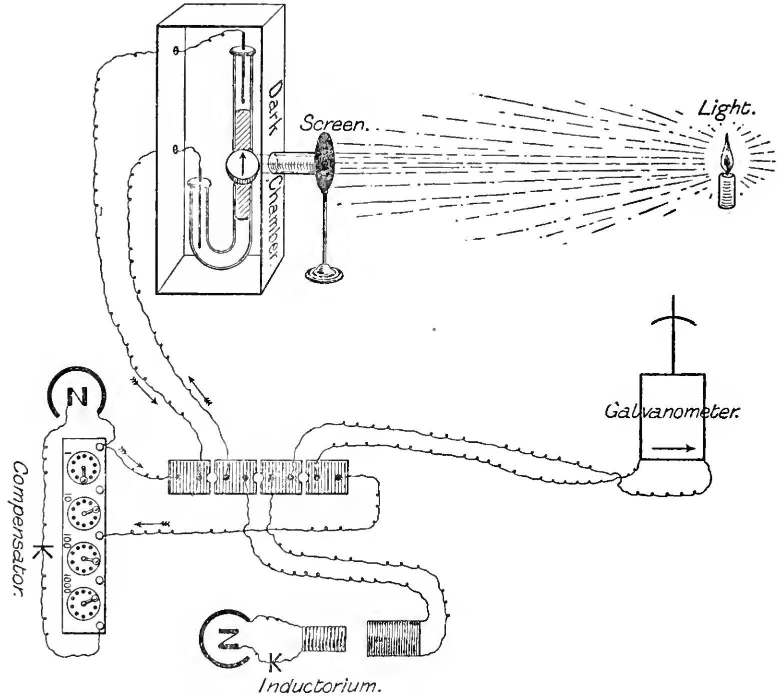

FIG. 19.—Frog's eyeball between unpolarisable electrodes for demonstration of the electrical effects of light and of electrical excitation. The circuit from the eye is completed through a compensator, secondary coil, and galvanometer. The arrows through the eyeball and the galvanometer indicate the direction of the initial current and of the normal response. Arrows near the compensator wires indicate the direction of compensating counter-current.

a positive electrical response (and that any mechanical disturbance arouses current in the same direction), he naturally thinks of electrical excitation, and expects to find that if the retina is stirred up to activity by such means, it will manifest current in that same positive direction. The expectation is realised by the following experiment, in which, as you will readily see from the diagram, a weak tetanising current is to be passed through a secondary coil, an eyeball, and a galvanometer, all the plugs being removed. The tetanising current is so weak that its constituent single shocks, alternating in direction, do not of themselves affect the galvanometer, but do stimulate the eyeball, which gives current in the circuit, current which, as you see from the deflection of the spot to your right, is in the expected (positive) direction.

I repeat the experiment, having turned over a reverser in the secondary (or it might have been in the primary) circuit, in order to reverse the directions of the constituent shocks, and the spot is again deflected to your right. I take it that this experiment needs no comment; it says that induction currents of both pairs of directions arouse a positive electrical response of the eyeball.

In ordinary language, the "effect" of a modifying cause is subsequent to that cause, and is therefore, properly speaking, an "after-effect." But it is in some instances necessary to distinguish between the effect during its cause, and the after-effect subsequent to that cause. You have just witnessed the effect during tetanisation—necessarily during weak tetanisation. I cannot show you an effect during strong tetanisation, since strong induction currents traversing the galvanometer would mask the physiological current of the eyeball. If you should wish to observe the effects of strong tetanisation, you must be content with what are properly speaking after-effects, since I must put the galvanometer out of circuit during tetanisation, and unplug it to receive the eyeball current that may be present as the effect or after-effect of strong tetanisation. And I will do this now, to show that the effect (or after-effect) of tetanisation may be very great indeed. The eye current is exactly compensated so that I can plug and unplug the galvanometer without disturbing the spot. I plug the galvanometer and tetanise the eyeball. Then I unplug and the spot flies off scale to your right, indicating positive current in the eyeball as an effect (or after-effect) of the tetanisation.

§ 24. *The effects of tetanisation upon the effects of light. Experiment II.*—Our next experiment is to show that the electrical response to light is modified by tetanising currents. I had to use very weak currents for the first experiment, I shall use much stronger currents for this one, because I want to show an unmistakable modification of the electrical response to light, and I may use strong currents if while they are passing they are short-circuited from the galvanometer. First notice the response to light, it is about +14 degrees of scale. Now, I plug out the galvanometer and tetanise the eyeball for half a minute. I then unplug, and the spot has flown off scale to your right. That has been what on first witnessing it I called a blaze-current; it has been provoked by the tetanisation to which the eyeball has just been subjected. But for the present it is not our principal concern. I bring the spot back on to scale by means of a compensating current, and as soon as the spot has come to comparative rest—it has been gradually falling off to the left by reason of the gradual subsidence of the blaze-current—we again take a reading of the electrical response to light; it is now 30 as compared with 14, its value before tetanisation, *i.e.*, the normal response to light has been more than doubled in consequence of tetanisation.

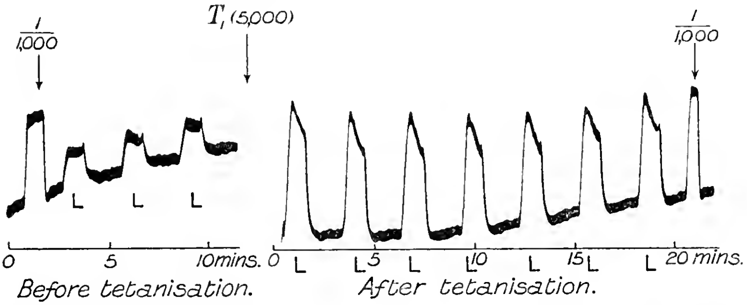

FIG. 20.—Frog's eyeball. Influence of tetanisation upon the normal retinal response to light. Ordinary arrangement of induction coil, fed by two Leclanché cells. Secondary coil at 9 centims. (5000 units on Berne scale). After tetanisation the positive response is considerably augmented, and falls during illumination. The terminal positive deflection at break of light is almost completely abolished.

This marked augmentation of response as to *current* may be due to augmentation of *voltage* or of *conductivity*, or to both factors;

as a matter of fact it is due to both factors, the electro-motive force of the response is increased, and the resistance of the eyeball is diminished. You will recognise both these points on the accompanying record, where the tetanisation has raised the voltage of the response from about $\frac{1}{2000}$ to nearly $\frac{1}{1000}$; you notice also that the standard deflection by $\frac{1}{1000}$ volt has been evidently increased — indicating increased conductivity, *i.e.*, diminished resistance.

§ 25. In the experiment just made you have witnessed a marked effect *subsequent* to tetanisation; a similar effect is witnessed during tetanisation, but it is rather more troublesome to demonstrate properly, and I have not therefore included it in to-day's list. I will content myself with quoting the results of a former experiment in which the deflections in response to light were:—

Before tetanisation 12 degrees of scale.
During tetanisation 36 degrees of scale.
After tetanisation 27 degrees of scale.

§ 26. *The effects of single shocks. Experiment III.*—The very strong currents that you have just witnessed as after-effects of strong tetanisation are—as I hope to prove to you in a future lecture—in chief part of physiological origin, but in minor degree merely the physical effects of ordinary polarisation. Their experimental analysis is a complicated matter that cannot profitably be dealt with before we have become familiar with the less complicated results of excitation by single induction shocks and by condenser discharges. And since for the purpose of our third experiment it is indifferent which of these two forms of electrical excitation we may choose to take, I will use the more familiar apparatus, to show the effects and after-effects of a single break induction shock, first in one and then in the other direction. You understand, of course, that the expressions "effect" and "after-effect" are simply used to distinguish between the two experimental cases, where (1) the induction shock and the response are allowed to pass through the galvanometer; and (2) only the response is allowed to pass, the induction shock (and first part of the response) occurring while the galvanometer is plugged.

It will be most convenient if we make a first pair of trials to witness the after-effects of two single break induction shocks in + and − directions.

It is necessary, in first place, to get rid of the make induction shock. You will readily see by reference to the diagram how this is done. The primary circuit of the inductorium is closed by a spring key, and while this is done, the secondary coil is short-circuited at the keyboard (see Fig. 19, p. 42). Then this plug is removed and the spring-key released so that a break induction shock is passed through the eyeball. And finally the galvanometer plug is removed, so that the current (if any) aroused in the eyeball, traverses the galvanometer and deflects its spot. These steps are quite automatically made after a little practise, and at a quite sufficiently uniform rate; the electromotive response of the eyeball is so prolonged that it is not necessary to hurry; although obviously for comparative trial it is preferable, as well as more convenient, to use a special key that breaks short-circuit of the galvanometer at a regular interval (*e.g.*, $\frac{1}{10}$th sec.) after breaking the primary circuit.* It is evident that in order to plug and unplug the galvanometer without disturbing its spot, all current in circuit must be compensated. This compensation has been adjusted at the outset, and must be exactly re-adjusted before each trial. Then we shall be assured that a given deflection is in reality due to current aroused by excitation, and not to any accidental current in circuit.

I may now proceed with the experiment. I begin by testing the compensation, and, if necessary, adjusting it. I then send a break induction shock through the eyeball in the negative direction, and afterwards unplug the galvanometer. The spot flies off scale to your right. That has been a blaze-current, of positive direction in response to an induction shock of negative direction; it is not a polarisation current; although at first sight by reason of its direction it might have been set down as

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* See Appendix, Fig. 68, p. 166.

such; I characterise it, in distinction from the next variety of current that you will witness, as *equivocal* or *antidrome*. The current is subsiding, rapidly at first, now more gradually, and more and more so as the spot approaches its zero position, sometimes, indeed, we may witness a permanent positive deflection, a current-remainder reminding one of the contraction-remainder of muscle.

I will now test the eyeball by an induction current in the positive direction; so I adjust the compensation and turn a reverser in the induction circuit, send a break induction shock through the eyeball in the positive direction, and unplug the galvanometer. The spot flies off to your right as before. That also has been a blaze-current, of positive direction in response to an induction shock of positive direction; it is evidently not a polarisation current; I characterise it in distinction from the first variety as *unequivocal* or *homodrome*.

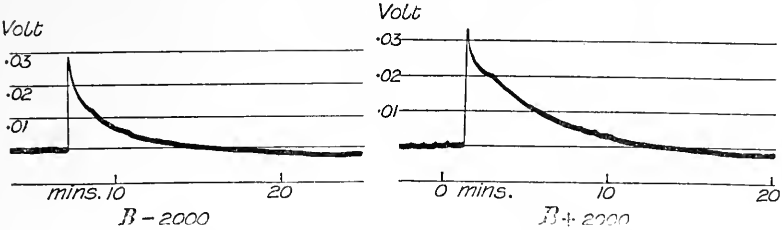

FIG. 21.—Normal blaze-currents of a frog's eyeball in response to excitation by a single break induction current in the negative or antidrome direction (B − 2000), and in the positive or homodrome direction (B + 2000).

This, in my opinion, is a cardinal experiment, and when it was deciphered, became sign-post as well as hinge of further and more general investigation.

But let us complete the experiment. The eyeball—upon which you saw a moment ago that two very large responses in one and the same direction followed excitation by single break shocks first in one and then in the opposite direction—has been plunged into hot water, *i.e.*, killed and replaced between the electrodes. I repeat the test of a right and left induction shock and no movement whatever of the galvanometer spot is to be detected. The dead eyeball gives no blaze-current.

§ 27. *Polarisation.*—But I have been using the galvanometer "at low power," much shunted, in the knowledge that the blaze-currents in the main experiment would be very strong. And to see whether or not there is any trace of response, a "high power" of the galvanometer must be taken by unshunting it. Which has now been done (and you notice by the way that an exact compensation is a little more troublesome to effect), and I repeat the test, right and left. There is just a trace of after-effect—to your left (−) after excitation to your right (+), to your right (+) after excitation to your left (−)—and this is not a physiological response, it is only the ordinary polarisation counter-current exhibited by any electrolyte. I will show it you in more pronounced form with a couple of wires dipping in salt solution, but not now—after lecture, when I shall also test these unpolarisable electrodes.

§ 28. *Experiment IV.*—You have just witnessed the third experiment in one form, demonstrating to you physiological after-effects, and you will have no difficulty now in following the steps by which I am about to make it in another form, to demonstrate to you these same after-effects inclusive of their earliest visible manifestations, which I have referred to as the effects. I do not think that the distinctive words are justified by any distinction of phenomena; their use has, however, been pressed upon me by the necessity of distinguishing between the results of two methods.

A fresh eyeball (that has just been tested by the assistant and found to respond normally to light) is set up between electrodes, and I intend to send through it and through the galvanometer a break induction shock of suitable strength, first in one, then in the other direction. The strength taken as suitable is one that gives through a circuit of resistance equal to that formed by eyeball electrodes and galvanometer, a distinct and equal swing of the spot to the right and to the left, and that if sent through the eyeball is fully adequate to arouse a normal (positive) blaze.

I now send a break shock through the eyeball (and galvanometer) in the positive direction, and you see the galvanometer spot sharply deflected to your right. "Naturally," you say, "since it has been traversed by an induction shock in a positive direction, and 'positive' is to our right." But notice the magnitude of the deflection, notice also, how slowly it is subsiding; that has not been any short kick by an induction shock, but something more, it has been a positive kick heralding our now familiar friend, the positive blaze. And you will be quite sure that this has been so, when you see the effect of sending a break shock through the eyeball (and galvanometer) in the negative direction. Now, you have a short, sharp kick of the spot to the left by the induction shock, and a prolonged large deflection to the right, slowly subsiding, evidently the electrical expression of what by this time we are tempted to call the retinal blaze (but *vide infra* as regards the justification of "retinal").

§ 29. *Electrocution.*—The proof has to be completed by showing that these blaze effects do not occur on a dead eyeball. I killed the last eyeball by putting it into hot water. I will kill * this one by electrocution, a method that has the advantage of leaving the eyeball undisturbed between the electrodes, and then apply the test of an induction shock right and left through eyeball and galvanometer. I strengthen the current, sliding the secondary quite home over the primary, and tetanise for half a minute or so with these strong currents (taking care, of course, to plug out the galvanometer to preserve it from such currents). Finally, I unplug the galvanometer and apply the double test. The positive break shock gives a sharp deflection to the right, the negative break shock gives a sharp

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* It has been objected to me that I cannot tell whether the eyeball has really been killed, may not be merely shocked, would not in time recover. In point of fact I do not think it has been finally killed, but the discussion need not be entered upon further, our sufficient point is, that blaze-currents are not manifested by an electrocuted eyeball, and it does not matter to us whether this inert state is that of death or of shock. A similar objection has been made with reference to capital punishment by electrocution, and in this case accidental recovery is guarded against by a prompt "post-mortem" examination. For the conditions of recovery or non-recovery of electrocuted animals, *cf.* Prévost and Batelli, *Journal de Physiologie et de Pathologie Générale*, 1899, pp. 399, 427, 1085, 1128; 1900, pp. 40, 422, 443, 755.

and equal deflection to the left. There is no blaze. The eyeball is dead, or in that state of latent life, or temporary non-living state to which we give the name of "shock." Evidently,

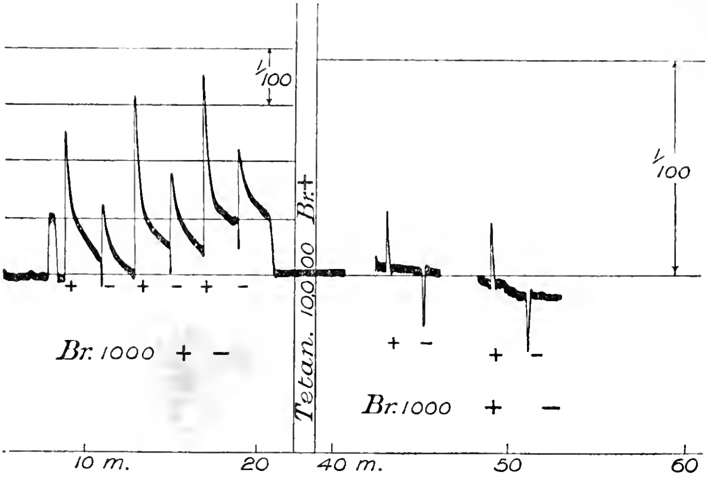

FIG. 22.—Frog's eyeball, induction coil and galvanometer in series. Effects of single break induction shocks in positive and negative directions before and after "electrocution" by strong tetanisation.

as regards the retina, or the eyeball, the blaze reaction is a very nice and convenient "*sign of life.*"

§ 30. *The three types.*—So far, the several experiments that have been grouped together under the head of the third experiment (§ 26), have come off perfectly well, and, in accordance, with expectation and prediction.

It might have been otherwise. I took care to be provided with fresh, normal, uncompressed eyeballs, because I did not wish, in introducing the subject, to have to confuse your first impression of it by interpolated explanation of unexpected results of experiment. And I was careful to be provided with the lively *Rana Temporaria*, as the sluggish *R. esculenta* would probably not have answered as well. Nevertheless, I felt it necessary to have at my elbow a diagram, in which are schematically summarised the various cases that I have met with in various states of the eyeball. I have divided them into three types:—

(1) Both reactions positive; (2) Both reactions homodrome; and (3) Both reactions negative; and although I do not find any

Direction of exciting current . . . .

TYPE I.

The response to excitation in both directions is positive. This is the normal response.

TYPE II.

The response to excitation in the negative direction is negative, and in the positive direction positive.

TYPE III.

The response to excitation in both directions is negative.

DEAD EYEBALL.

The response to negative excitation is positive and to positive excitation negative.

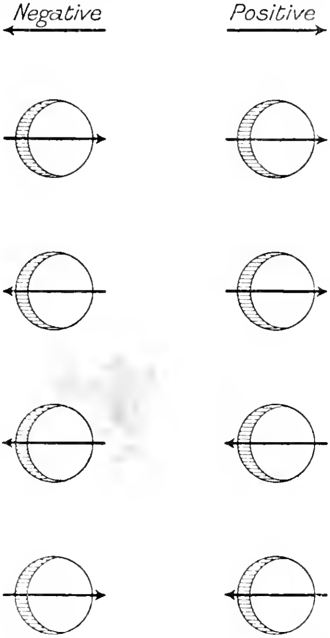

FIG. 23.—Frog's eyeball. The three types of response to excitation by single induction shocks in positive and negative directions.

strict parallelism between these three types of electrical response to electrical stimuli, and the three types described above of electrical response to luminous stimuli, I do find correspondence to this extent that a perfectly normal eye gives positive response of the first type in both series, while a considerably compressed or massaged eye gives negative response of the third type in both series. The extremes in the two series correspond, but I fail to trace correspondence in the intermediate and transitional forms of the two series. It is hardly necessary to point out that the very existence of such a series of responses graded from positive to negative, is confirmatory evidence of the coexistence of *two* contrary electro-motive changes, a conclusion which we saw reason to infer from the effects of light already described.

§ 31. *Cause < Effect.*—I have thought it hardly necessary to repeat to you a series of experiments similar to the preceding, but with condenser discharges in place of break induction shocks. Moreover, time forbids that I should do so, with the explanation necessary to bring out the particular advantages of this method. We may find time for this at a future lecture, meanwhile I will again refer you to the paper already quoted,* where you will find experimental justification for the statement that the electrical energy of excitation is greatly exceeded by the electrical energy of the blaze-current that it arouses.

§ 32. *Galvanisation. Experiment V.*—The fifth and last experiment on our list is to show how the direction of a blaze-current aroused by an induction shock, can be modified by the passage of a galvanic current through the eyeball.

An eyeball is put up as before, the compensator is arranged to give a current of comparatively high E.M.F. (0.1 volt) through the eyeball and galvanometer. I first take this galvanic current in the positive direction, when, of course, the galvanometer spot is driven off scale to your right. I bring the spot back in scale by means of a controlling magnet, and as soon as it is steady, send a break induction shock through the circuit (comprising the eyeball, compensator, and galvanometer in series) first in the positive, then in the negative direction. In both cases the positive deflections are greatly augmented.

Then I reverse the galvanic current to the negative direction, readjust the spot on scale by means of the controlling magnet, and repeat the test. Both the induction shocks, positive and negative alike, now give negative deflections, *i.e.*, blaze-currents in the same direction as the galvanic current. Nothing of the sort happens, I should add, in the case of a dead or "electrocuted" eyeball. If I had made the experiments upon an eyeball giving negative blaze-currents of the third type described above, you would have witnessed an augmentation of these currents during

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* *Phil. Trans. Roy. Soc.*, vol. 194 B., p. 183. 1901.

negative galvanisation, and their reversal to positive currents during positive galvanisation.

I think these points will be best illustrated by the values obtained in some previous experiments of the kind. The values are approximate only, as I did not correct for kick due to the induction shock itself.

Direction of Excitation by Break Shock of Berne Coil at 1000 units, with two Leclanchés in primary circuit.	Voltage of Response.		
	During Galvanisation by −1/10th volt.	Without Galvanisation.	During Galvanisation by +1/10th volt.
+	−0.060	+0.010	+0.050
−	−0.040	+0.010	+0.030
+	−0.024	−0.019	+0.024
−	−0.033	−0.029	+0.019

§ 33. *Some questions.*—Our experiments are at an end, and so is the lecturer's hour. But I will tax your patience for five minutes longer and attempt to answer two questions that must have occurred to you as they have to me. How much of this blaze-reaction is due to the retina, and how much to other tissues of the eyeball? Is the retinal stuff that reacts to light the same as, or different from, the stuff that reacts to an induction shock?

I cannot fully or confidently answer either of these questions. I can only give partial and tentative answers, and I do so far less on account of any value that I place on the answers in themselves, than because I believe you will see how the chief value of a question—somewhere, somehow—we cannot at the outset foresee either where or how—may be wrapped up in our very failure to obtain a neat answer.

At first I thought that the blaze-current was retinal, like the current excited by light. The expression "retinal blaze" obtained currency in the laboratory, and the title of my first paper runs, "On retinal currents excited by light and excited electrically," and the title of my second paper was intended to be "On the 'blaze-currents' of the Retina," but it soon became

"On the blaze-currents of the Eyeball." That the electrical response of the eyeball to light has its exclusive seat in the retina, is proved by the fact that of the two halves of an eyeball bisected into an anterior and a posterior half, only the latter responds to light, and if further—as recommended by Kühne, the retina itself be separated from the remaining coats, electrical response to light persists of the isolated retina, but is absent from the remaining tissues. But a similar procedure in the case of electrical response to electrical excitation taught me that the reaction is not confined to the retina, that it is manifested by the anterior as well as by the posterior half of the eyeball, that the isolated cornea and the isolated lens give blaze-currents. I therefore concluded that tissues other than retinal are coeffective in the electrical response to electrical stimulation of the entire eyeball, and accepted the fact as a hint to examine other living tissues for this presumably common sign of life. Meanwhile, from the retinal sheet in animals excitable by light, my attention naturally turned to the chlorophyl sheet in vegetables presumably excitable by light, and a demonstration of the electrical response to light in green leaves was the immediate result.* I tried petals of flowers in the same way, as one among other control tests of the reality of the leaf response. Petals proved to be absolutely inert in this respect. Yet petals are obviously "alive," so I tested petals by the blaze-test, and found that to this test petals are at once found to be alive. The idea by this time had fully generalised itself in my mind, and I placed all sorts of living things, animal and vegetable, on the unpolarisable electrodes, leaves, stems, seeds, fruits, etc., muscle, nerve, lung, liver, pancreas, skin, hen's eggs, etc., and found that some things reacted well, and others not at all, or irregularly. But these were digressions—digressions, however, that have in my opinion become far more interesting than the original questions.

§ 34. To return to the second of these. To get an indication whether the same or two different substances react to light and to induction shocks, I looked for modifications of the

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* WALLER.—"The Electrical Effect of Light upon Green Leaves," *Proc. Roy. Soc.*, vol. 67, p. 129, 1900.

response to light by strong tetanisation, and *vice versa* for modifications of the response to induction shocks by strong illumination, I also took series of positive responses to light and to weak tetanisation alternated, to see whether or no they would decline *pari passu*. An example of such a series has been

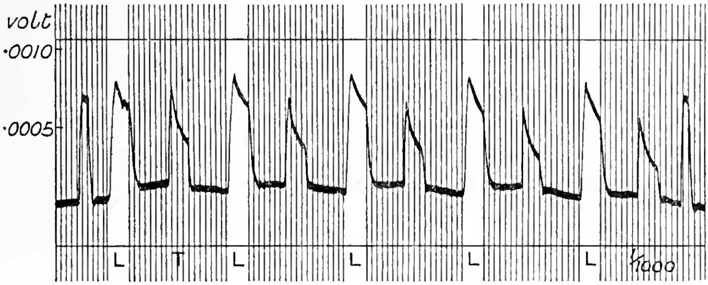

FIG. 24.—Frog's eyeball. Series of normal responses to light and to tetanisation alternated; each excitation lasts for one minute. The response to tetanisation falls more rapidly than that to light.

figured above. The series of responses to tetanisation appears to decline more obviously than does the series of responses to light. But the difference is not very striking, and in other records it is even less so. In fact, when I took the records, I thought they justified me in saying that the two kinds of response wear out in a parallel manner. Clearly, however, the parallelism has not always if ever been absolute; the instance figured above exhibits more rapid decline of the tetanisation responses than of the light responses. The point clearly needs to be tested again. As regards modification of the response to induction shocks by strong illumination, we have seen that no appreciable effect occurs. As regards modification of the response to light by strong tetanisation, we have seen that the regular effect has been an increased response during and after tetanisation. Indeed, the resistance of the retina as regards its excitability by light has been a constant yet surprising feature. The strongest tetanisation at my disposal (Berne coil, 2 Leclanchés, secondary over primary coil, current unbearable by wetted fingers) has failed to abolish its response to light. And strong tetanisation (10,000 units) that has completely abolished all blaze-reaction (as *e.g.*, in the experiment of Fig. 22) has left the response to light unaltered.

On review of all these facts, I am inclined to think that, as regards their action upon the retina, the two forms of excitation act upon two distinct but closely related substances holding to each other the relation of pro-substance and substance, the former acted upon by electrical currents and not by light, the latter acted upon by light and not by electrical currents.

Among the tissues that give most dubious results in a first rapid survey of blaze-currents, the skin was one of the most notable. I therefore studied it the more closely. The next two lectures will be given to the consideration of "Skin-currents."

§ 35. *The crystalline lens.*—Further investigation of the blaze-currents manifested by the anterior parts of the eyeball led to very definite, constant, and, I may add, quite unexpected, results. The observations relating to this matter were made at the sea coast during the months of August and September of last year—principally on the crystalline lens of freshly caught fish—and may be most briefly described by the following quotation:—*

"In the course of investigation of the effects of light and of electrical excitation on the frog's eyeball, I came to the conclusion that tissues other than retinal are coeffective in the response to strong induction shocks, and proceeded therefore to look for blaze-currents in other living tissues.

"The particular point that aroused my attention in the case of the eyeball was the fact that the anterior half of the eyeball was sometimes found to give a larger response than the posterior half, and the present observations proceed from an attempt to determine the principally effective part in such reaction. And I may state at once, as my chief conclusion, that it is the crystalline lens.

"The eyes upon which the determination was made, in the first instance, were those of fish—whiting and mackerel—by reason of the fact that these were for a season at my disposal

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* "On the Blaze-currents of the Crystalline Lens," *Proc. Roy. Soc.*, 4th December 1902.

quite fresh from the sea. I subsequently made similar observations on the eyes of octopus, on sheep's eyes fresh from the slaughter-house, and on the eyes of recently killed cats and rabbits.

"The point that was most striking in these first observations was the great endurance of the reaction in the crystalline lens as compared with its rapid disappearance from the remaining tissues of the eyeball and from the skin, and with the rapid disappearance of the direct electrical excitability of muscle. I should, as an outcome of these observations, look for the last sign of life of a fish by testing the crystalline lens, whereas in the case of man I should test a piece of skin. The reaction—as far as I have yet seen—has been completely absent from frozen fish (salmon) as received from London fishmongers. Its normal direction in the lens is 'negative,' *i.e.*, from external to internal pole. It is abolished by heat (70°) and by pressure. A typical pair of responses is illustrated by the following record:—

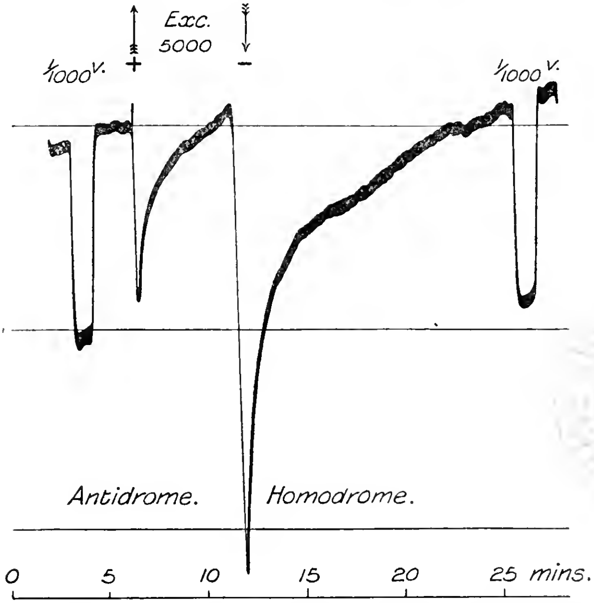

FIG. 25.—Codfish. Antidrome and homodrome responses of the isolated lens, from anterior to posterior pole, of −0.0009 and −0.0022 volt respectively.

"I conclude from this and similar experiments—

"1. That a crystalline lens of suitable size is a good object upon which to study the nature of blaze-currents.

"2. That a 'blaze-current' is a physical sign of the 'living' state.

"3. That a blaze-current may be post-kathodic as well as post-anodic, antidrome as well as homodrome.

"4. That the normal direction of blaze-currents in the crystalline lens is negative or ingoing, *i.e.*, from the external or anterior to the internal or posterior pole."

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LECTURE IV

Skin-currents (of the Frog)—The Normal Current is "Ingoing"—The Response to Indirect Excitation is Outgoing, Mixed, or Ingoing—The Latent Period is Two Seconds—Fatigue—Atropine—Mercuric Chloride—The Response to Direct Excitation is Outgoing—Summation—Effects of Tetanisation—Localisation of the Response by the A B C Method—Terminology.

§ 36. From the preliminary observations alluded to in my last lecture (§ 33), I formulated the following working rule for the experimental distinction between the living and the dead states of matter :—

"If the object of examination exhibits blaze in one or in both directions, it is living."*

One of the earliest objects of examination upon which I tested this rule was the human body, living and dead. I thought that it might be possible to place, *e.g.*, a finger between a pair of electrodes, and to learn from the presence or absence of blaze reaction whether the finger was living or dead. But by reason of the fact that a finger is covered by skin, and that it is impossible to send current by unpolarisable electrodes into the intact human body otherwise than through skin (or mucous membrane), the question has proved to be much less simple than it appeared. It has involved me in an investigation of skin-currents that has taken the best part of two years, and the results, instructive though they are as regards the original question, are, I think, of still greater interest from another point of view. It will be well, therefore, to consider ourselves as entering upon a fresh field, albeit an already much trodden field, in undertaking an exploration of "Skin-Currents."

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* I do not commit myself to the obverse, that if an object exhibits no blaze it is not alive. *Vide infra*, § 82.

We shall study the skin-currents of the frog, of the cat, and of man, also the currents of mucous membranes and the currents of vegetable "skins." To-day we shall confine ourselves to the case of the frog, examining: (*a*) the normal current, (*b*) the effects of indirect excitation, (*c*) the effects of direct excitation.

§ 37. *The normal current.*—A piece of skin of the back, or indeed of any part of the body, carefully excised and placed between unpolarisable electrodes, gives current, directed from outer to inner surface (through the skin). This "ingoing" "negative" or centripetal current increases during observation. A piece of skin spread upon a glass plate with a central hole, and placed between the electrodes as figured, gives current that reflects the galvanometer spot to your left. And, as you notice, the spot is creeping further to the left. Two reflections arise from this observation: clearly the current cannot be due to injury of the internal surface, since in that case it would be outgoing; probably the increasing negative current is due to the subsidence of what in the case of the eyeball we referred to as the manipulation blaze. It looks as if resting skin were the seat of an ingoing current of rest, and as if the increasing negative deflection occurring on the galvanometer scale were in reality a decreasing positive effect caused by the previous disturbance by manipulation. We shall find confirmation of this view later on, when we have learned that direct mechanical and electrical excitation of the skin gives almost invariably a positive or outgoing electrical effect.

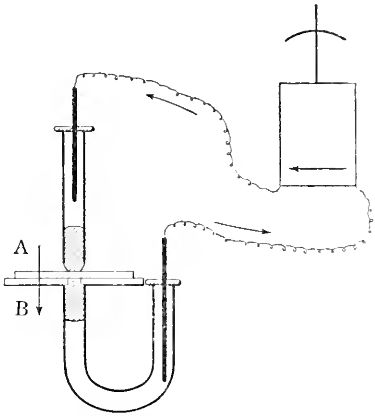

FIG. 26.—Frog's skin on a perforated glass or ebonite plate, between unpolarisable electrodes. The external surface of the skin is uppermost. The arrows signify the direction of "normal current"—"ingoing," from external to internal surface.

§ 38. *Indirect excitation.*—The effects on the skin of excitation of its nerves are particularly interesting; it is easy to demonstrate them, but by no means easy to interpret them in detail. I do not think that any interpretation yet offered has properly embraced all the facts, and I shall not pretend to mend matters much in this respect. But I will lay the facts before you, more completely and more briefly than you will find them hitherto described, by means of graphic records that exhibit better than any narrative the character and dimensions of the phenomena.

The experiment I am about to show you is one that was first made by Roeber (on the suggestion of Rosenthal) more than thirty years ago, and that has since been repeated with variations by Engelmann and by Hermann. The preparation is as follows:—A frog's sciatic nerve is dissected out in the usual way, the foot is cut off, the skin of the leg is longitudinally divided on the anterior aspect and peeled off the leg up to the knee-joint, the leg is cut off just below the knee-joint, the femur and thigh muscles are divided just above the joint. We now have a sciatic nerve in connection with the skin of the leg, and the ends of the femur and tibia serving as a handle. The skin is now laid over one leading-off electrode, and the other electrode is brought into contact with the other surface of the skin, the sciatic nerve is laid across a pair of exciting electrodes that are connected to a coil. We now have a nerve-skin preparation, the analogue of a nerve-muscle preparation, quite as easy to make, and affording, when made, an unfailing demonstration of a current of animal electricity and of the action of nerve on skin. It ought long ago to have become a regular lecture experiment and student's exercise, yet somehow or other it has almost dropped out of notice. Every student of physiology makes nerve-muscle preparations by the score. I wonder how many students or teachers have ever made a nerve-skin preparation, and what would be said if, as a change from the regular round of about six practical experiments (that cannot be properly done in the time allowed) an examiner were to ask an honours candidate to show something by means of a nerve-skin preparation.

Well, our experiment is waiting, and the spot has come to rest. The normal skin current is ingoing and increasing, the spot has crept to the left of the scale, therefore to the left signifies ingoing, to the right outgoing; but we shall verify this presently with a bit of zinc.

I tetanise the nerve for a second or two, and after a distinct interval, long enough to allow the thought that there is no effect, the spot sweeps across the scale to the right, signifying that the skin, aroused by excitation of the sciatic nerve, has given an outgoing current. And knowing what to expect, I took care to shunt the galvanometer, for the resistance of the skin is so low, and the voltage of response so great, that the spot would assuredly have flown off scale if the galvanometer had not been shunted. I wanted, however, to have a measurable effect, such as should allow us to make further trials. Five minutes have elapsed, and I repeat the excitation; deflection to the right occurs again, but is much smaller. It looks as if the nerve-skin preparation were becoming fatigued. And while we wait for a second five minutes to elapse, let us consider matters. How has the nerve acted upon the skin? What is the meaning of the declining effect we are looking for? Is the response always in this positive or outgoing direction?

All authorities who have worked at the subject are agreed that it is upon the skin-glands that the nerve acts, and that the skin effect is the sign of a glandulo-motor or secreto-motor phenomenon. I share this view, and do not think it probable that nerve has any connection with the general epithelial investment of the skin; but, in remembrance of the fact that cutaneous pigment cells are demonstrably influenced through nerves, I make some mental reservation to the assumption that the effect is exclusively glandular. The wearing-out of the response in repetition is not due to wearing-out of the nerve, nor even wholly, I think, to wearing-out of the discharging gland, but more probably to a wearing-out of the junction between nerve-fibre and gland-cell.

The second five minutes is at an end, and now you see that excitation gives a negative instead of a positive response, and thus answers the last of the three questions we put a few minutes ago. Clearly, the response is not always positive or outgoing; you have just seen that it may be negative or ingoing, and I may add, to complete the account, that it may also be "mixed"—negative then positive, or positive then negative, or positive negative positive.*

And now that you have witnessed a representative experiment, I will project on the screen the records of some previous experiments.

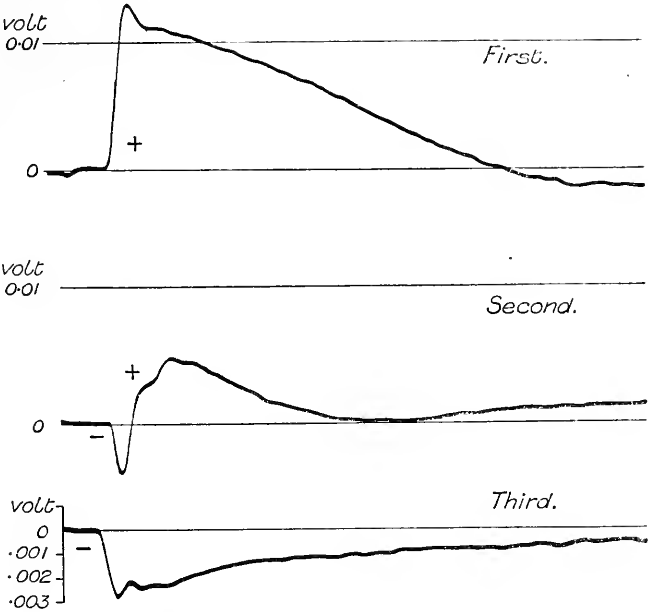

FIG. 27.—Frog. Nerve-skin response.
(1) Positive or outgoing. (2) Mixed. (3) Negative or ingoing.

§ 39. *Latent period.*—Here are a couple of photographic records, taken on a more rapidly travelling plate, in order to bring out more distinctly what was already obvious to simple

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* The accounts given by previous observers—by Engelmann and by Hermann in particular—are not quite easy to reconcile with each other, and with the description given in the text of these lectures. Thus Engelmann, in 1872, concluded that the usual effect of indirect excitation is a "negative variation" of the normal (ingoing) current. Hermann, in 1878, gives the usual and principal effect as being a "positive variation" of the normal current.

The two accounts are summarised in the following diagram, and their inspection—viz., the great delay between excitation and response —about two seconds with a fresh preparation, about three

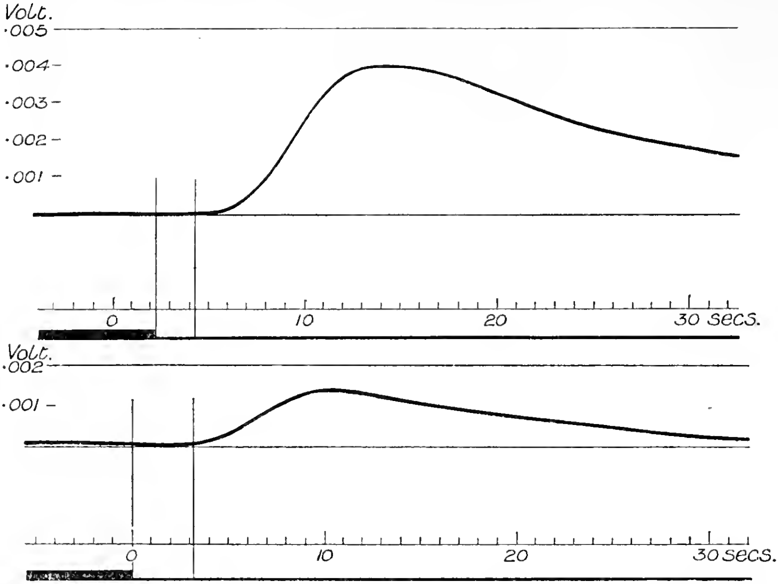

FIG. 28.—Frog. Nerve-skin preparation. Galvanometric records of the lost time of the response to indirect excitation by tetanisation of the sciatic nerve. Lost time = 2 to 3 secs. Lost time of the galvanometer itself = $\frac{1}{3}$ sec.

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relation to that given in the text will be easily traced if it be remembered that there all outgoing effects read upwards and all ingoing effects downwards.

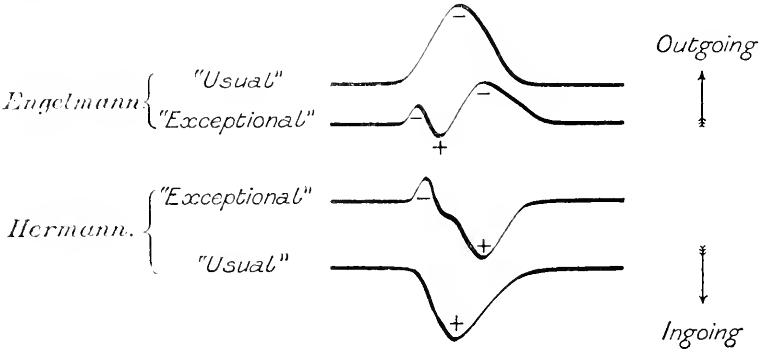

FIG. 29.

seconds as the response becomes more sluggish. And this has been a true physiological latency; it is of the same order as the similar effect that will be demonstrated to you on a mammal, which *a priori* you might have expected to react more quickly (*infra*, p. 105). With the capillary electrometer, and excitation by a single strong induction shock, the latency came out at 0.9 sec.

§ 40. In connection with the action of nerve upon skin, one naturally thinks of atropin—the drug which so promptly abolishes the action of secreto-motor nerve—and remembering how small a dose of atropin dries the mouth and dries the skin in the case of man, you have reason to anticipate that atropin, if it produces an effect at all, will do so when it has been administered to the animal by subcutaneous injection. I have not found this to be the case in two experiments; the nerves of atropinised frogs acted perfectly well upon the skin, but after the drug had been applied to the skin itself, the nerves ceased to be effective. So, in order to demonstrate that atropin acts, it will be preferable to test it by local application; and to show this quickly, it will be best to apply the drug to the external surface of the skin.

A second nerve-skin preparation is set up, for an experiment to consist of three steps. These will be: firstly, to see that indirect excitation (from the nerve) is effective; secondly, to apply atropin to the skin, and see that the indirect effect is abolished, but that an effect can still be produced by direct excitation; finally, to show that this direct effect is abolished by mercuric chloride.

With indirect excitation you see that the large deflection before application of atropin has been completely abolished by atropin. The nerve no longer acts upon the skin. But the response to direct excitation is quite well marked; (and note in passing that it is to your right—in the positive or outgoing direction). I now apply some mercuric chloride solution to the external surface, and you see that direct excitation gives no response. The skin is dead.

§ 41. The effects of *direct excitation* deserve and will repay closer study. The first and only allusion to these effects that I am acquainted with, occurs in Engelmann's paper of 1872, subsequent observers having principally studied the effects of direct excitation on the mucous membranes (Biedermann), and on the skin of the eel (Reid). Engelmann seems to have obtained a negative variation of the current of rest—*i.e.*, presumably an outgoing effect—but he took no account of direction of excitation. Biedermann, in the mucous membranes of the tongue and of the stomach, observed positive and negative variations of the current of rest; but in the case of the tongue two layers of mucosa are under experiment, and in any case a mucosa is not the same thing as the skin.

Reid found that direct excitation of the eel's skin by induction shocks of either direction caused ingoing effects, sometimes preceded by outgoing effects. I have made a large number of experiments on this point with the same disposition of apparatus as that described in a previous lecture in the case of the eyeball, with results that have practically been invariable, *i.e.*, with only one or two exceptions in several hundred experiments. So that I am practically certain that in the experiment you are about to witness, direct excitation of the frog's skin by an outgoing or by an ingoing induction shock will cause an outgoing skin response.

[*Experiment.*]

A piece of skin is set up between unpolarisable electrodes, as in Fig. 26, and connected with a keyboard, galvanometer, coil, and compensator, as in Fig. 19. We are, in fact, about to test the skin for blaze-currents, just as we previously tested an eyeball or a seed. Compensation is established (the galvanometer is shunted because a large effect is expected). With the galvanometer plugged out of circuit, a break induction shock is sent through the skin in the positive (outgoing) direction (spot to your right), and immediately afterwards the galvanometer plug is removed. A large deflection to your right occurs; and to show you what this large deflection with the shunted galvanometer means as regards electro-motive force of the excited skin, I will send current through the circuit from $\frac{1}{100}$ of a volt; the skin response has been two or three times as great, *i.e.*, its voltage has been 0.02 to 0.03; and this is by no means a maximum value, I have seen it as much as

0.10 volt. The positive response is declining, rapidly at first, then more slowly, and as soon as the spot is fairly steady, I compensate and repeat the excitation in the reverse (ingoing) direction, and, as before, you witness a large positive (outgoing) deflection, which, although in the direction of a polarisation counter-current, is a blaze-current, like the antidrome blaze-current of the eyeball (p. 47). Indeed, these skin effects are precisely similar to the effects you have already seen in the case of the eyeball. The positive response to positive excitation is the unequivocal blaze, the positive response to negative excitation is the equivocal blaze.

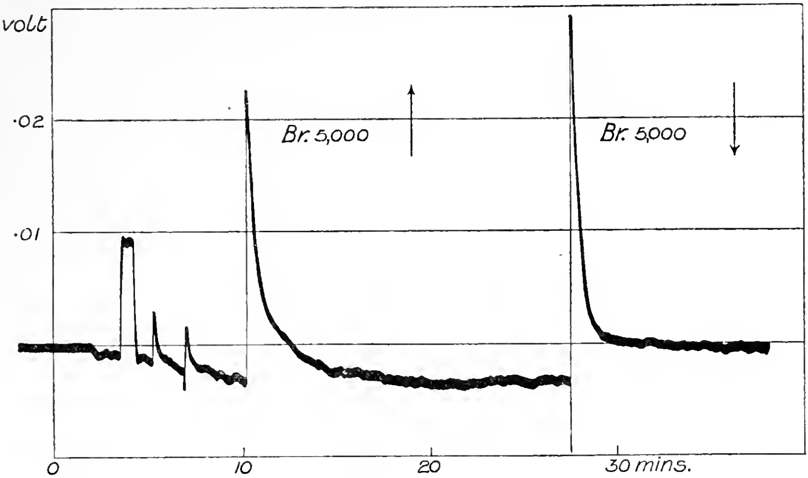

FIG. 30.—Frog's skin. Response to direct electrical excitation. The first deflection is by a standard voltage. The next two small deflections are in response to + and − break induced shocks with the coil at 1000 units. The last two large deflections are with the coil at 5000. (The principal "outgoing" effect is preceded by a brief ingoing effect in the case of ingoing excitation.)

And to complete the proof, I will kill the skin either with a few drops of mercuric chloride solution, or by plunging it into hot water, and now the skin gives no response at all to either direction of excitation. The spot does not stir. If I unshunted the galvanometer we might see the small polarisation effects that occur with any electrolyte. But this is an unessential point, and we will leave the galvanometer as it is for our further experiments, *i.e.*, with its scale to take in a range of about 0.05 volt.

§ 42. *Summation.*—The positive response of the skin is ordinarily of considerable duration; in general, the stronger the stimulus, the longer the response; five minutes has been a very ordinary duration in these experiments. If, then, a second stimulus is applied at the end of one or two minutes, before the first response has fully subsided, we shall obtain a second response superposed on the first, and so on for a third and fourth and nth response, which give a summation of effects by successive deflection remainders. Here is a record that will make this point clear.

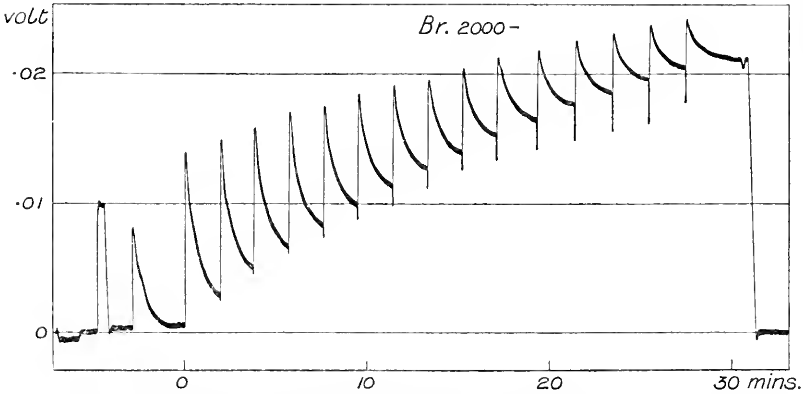

FIG. 31.—Frog's skin. Summating effect of excitation at intervals of 2 mins. (The first response is to a weaker excitation.)

With stimuli at shorter intervals, the summation is steeper, and the individual effects of which it is composed may be indistinguishable. There is a fusion of deflections analogous with the tetanic fusion of muscular contractions with which we are all familiar.

By reason of this summation, and of the fact that both directions of induction shock arouse response in one and the same (positive) direction, the rapidly alternating currents of an induction coil as ordinarily used for tetanisation give rise to a much larger (positive) response than does a single shock at the same strength of coil. This is a summation of effects. Moreover, if a strength of coil be taken so small as to produce no response with single shocks, tetanisation at the same strength will bring out an evident or even large positive response. Notice that, in making this experiment with tetanisation, I have taken the response immediately *after* and not *during* tetanisation. A similar effect can be brought out during tetanisation, and in cases (like the present) where there is a clear and manifest effect in one direction, we may without fear of fallacy demonstrate that effect during as well as after tetanisation. But in doubtful cases (p. 131) there is considerable difficulty in distinguishing a true blaze-current from the disturbance of the galvanometer by the necessarily strong currents used, and from the relatively large polarisation currents manifested during strong tetanisation. For this reason I have deliberately abstained from laying any stress upon the effects produced during tetanisation, and have limited myself to the information obtainable with and after single shocks, and after tetanisation.

§ 43. *The A B C plan.*—With a piece of skin arranged as shown in Fig. 32, an induction current passed through the skin in the positive direction from B to A has its anode at the lower surface B and its kathode at the upper surface A. A blaze-current is aroused in that same direction from B to A, and we put to ourselves the question whether that current depends upon an electro-positive state at B, or upon an electro-negative state at A, or upon both states. Or more familiarly put: is the B to A current by push of B, or by pull of A, or by both?

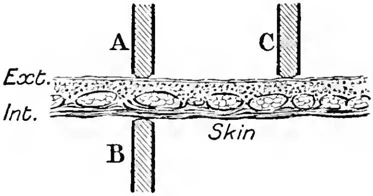

FIG. 32.

The question will be answered by the following plan of experiment, which will enable us to examine separately the two surfaces B and A by connecting first one, then the other, with an indifferent point C through the galvanometer. And having done this by a first pair of trials with excitation from B to A, we shall complete the experiment by a second pair of trials with excitation in the opposite direction from A to B, *i.e.*, A having been anodic, and B having been kathodic, and the blaze-current being as before in the outgoing direction from B to A.

Try to forecast the result *a priori*, as I did; I think you will probably guess wrong, as I did. I imagined at this stage that we had to do with something of the nature of so-called positive polarisation, which Hermann and Hering have shown to be in reality (in the cases of nerve and muscle) post-anodic action current. On this view, the positive effect in the first case was presumably due to a post-anodic "push" at B, and we should therefore expect current through the galvanometer from C to B (in the skin from B to C). But the positive effect in the second case could not be explained, post-anodic "push" should be in the negative direction, and the effect observed was evidently either by post-anodic "pull" or by post-kathodic "push" (through the skin).

So I gave up forecasting and proceeded to experiments, of which I hope you now see the interest.

We shall begin by a first pair of trials to localise the seat of electro-motive change in the case of the unequivocal blaze-current, positive response to positive shock. We shall examine the anodic surface B. Therefore, we have to compensate B with C (the indifferent point) through the galvanometer, then to send an induction shock through B A, then to reconnect B C with the galvanometer to observe the altered electrical state of B. All which we have now done, and find somewhat to our surprise that the spot does not stir, *i.e.*, that the electrical state at B has not been altered. You suspect, perhaps, as I did, that there is a break in the galvanometer circuit, so I throw a $\frac{1}{1000}$ volt into circuit, and you see by the movement of the spot that the circuit is all right.

We next examine the kathodic surface A, so I balance A with C (the indifferent point) through the galvanometer, send then an induction shock through B A, and finally reconnect A C with the galvanometer. There is a large deflection to your right, indicating current in the skin from C to A, *i.e.*, that A has been rendered electro-negative to C, an unaltered point, and to other unaltered points inclusive of B, which by the previous trial you saw to be unaltered. We infer from this first pair of trials that the outgoing (unequivocal) blaze B A depends upon post-kathodic "pull" under A at or near the outer surface.

Now reverse the direction of excitation, passing the induction shock through the skin in the negative direction from A to B.

First test the altered state of B, in the same way as before (balance B with C, excite through A B, connect B C with the galvanometer), there is no effect. Then test the altered state of A (balance A C, excite A B, connect A C), there is a large deflection to your right, *i.e.*, current in the skin from C to A, *i.e.*, A is electro-negative to unaltered points C and B, etc. We infer from this second pair of trials, that the outgoing (equivocal) blaze B A depends upon post-anodic "pull" under A at or near the external surface. And from both pairs of trials we infer the simple conclusion that the blaze-currents B A—unequivocal by excitation B A and equivocal by excitation A B—depend upon an electro-motive action aroused at or near the external surface. We must further infer, against all our preconceptions of the matter, that this electro-motive action is aroused by the kathode as well as by the anode of an exciting current (*i.e.*, is post-kathodic as well as post-anodic) and that in both cases it consists in an electro-negative state of the active part, *i.e.*, that this part is galvanometrically positive to inactive parts—the seat of an increased anionic solution-pressure.

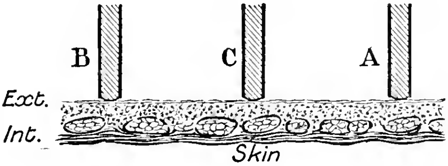

FIG. 33.

§ 44. *Intact external surface.*—We shall find in this A B C plan a ready means of testing an intact external surface, and of thereby learning what are the separate contributions of A and of B in any total reaction between A and B;

we shall do so by observing the separate partial reactions A C and B C. Both these reactions will be found to be outgoing at A and at B, being directed (in the skin) from C to A and from C to B.

§ 45. There has been one very striking feature in the foregoing experiments that must at once have attracted your attention, namely, the surprisingly strict and limited localisation of the reaction. With a layer of skin only a fraction of a millimetre thick between our exciting electrode A and B, we saw a great reaction when the external electrode A and an indifferent electrode C were connected with the galvanometer, but no reaction at all when the connection was with B and C; yet in this case also we had quite close above B an active area A that might have been expected to alter the potential of B.

J. S. MacDonald, to whom I had the pleasure of showing this experiment, said, "Oh, there must be a membrane." I think he is quite right, but I am unable to analyse the mode of action of this membrane.

This strictly local character of the response—which in the present case of electrodes A and B in close juxtaposition is as difficult to understand as it is easy to demonstrate—is a singularly favourable condition as regards the experimental application of the blaze test to skin and to other animal and vegetable tissues, in which there is little or no diffusion of the local polar effect of excitation. In the cases of muscle and of nerve these local effects are to some extent masked by the propagated distal effects of excitation, and require for their manifestation current strengths greatly in excess of those sufficient to give maximal propagated effects. In a piece of skin, or in a leaf or petal—provided they are alive, the excited and therefore blazing spot is limited as to depth and breadth, and the exhaustion of that spot by excessive stimulation does not sensibly modify the vitality of parts in its close proximity. Of course the result is a question of degree; the entire interpolar length of a tender shoot traversed longitudinally by violent currents is stunned (or killed) and may shrivel up and be obviously dead in a day or two; a flat leaf traversed by violent currents will exhibit changes outside the polar area in general accordance with ordinary current-diffusion. But for all moderate strengths the blaze reaction of a living skin or of a living leaf is strictly local.

These experiments have been troublesome to follow, as they have been troublesome to demonstrate, and we may perhaps find it a relief from a somewhat absorbing effort of attention, to turn to an academic discussion, touching the nomenclature of these phenomena, and their relation to other known phenomena, and their conceivable biological significance.

§ 46. I have been asked why I chose to designate the effects by the name of "blaze-currents" rather than "positive polarisation currents," or "post-anodic action currents." I think you will readily understand the answer to the negative parts of this question. Apart from the fact that the name "positive polarisation," as first used by du Bois-Reymond to designate certain homodrome effects observed by him in muscle, nerve, and electrical organs, has been adversely criticised by Hermann and Hering—shown by them, indeed, to be a misnomer inasmuch as the effects to which it was applied are demonstrably due to post-anodic action current—I think it is sufficient to refer to the equivocal or antidrome blaze as forbidding the use of the term "positive polarisation." The use of the term "post-anodic action currents" you have just seen to be altogether unjustified for these skin-currents; in one case the current is not post-anodic at all, and in the other it is post-anodic, but of opposite electrical sign to that of a post-anodic state. In muscle and in nerve a post-anodic spot is galvanometrically negative; in the skin it is galvanometrically positive. So that both these cumbersome expressions are happily inapplicable, and a new term is required. I have been led to adopt the term blaze-current, and I think you may now understand how it arose in the study of retinal effects, and how it serves to clearly earmark a natural group of phenomena of very definite physiological meaning.

A blaze-current is literally and strictly a "current of action"; but it is a particular kind of action current, and requires a distinctive name. The known phenomenon to which it bears most resemblance is the discharge of an electrical organ, and we shall not infrequently find the term "discharge" a convenient indicative word. But as a distinctive and specific name, the word "discharge" is insufficient, all the more so from the inconvenience that would arise when we have to refer to the blaze-currents aroused by the condenser discharge.

I have had another reason in my mind that has helped to make me use the expression blaze-current. The great mass of living things, whatever else they may give and take from their surroundings, take oxygen and give carbonic acid; they may live slowly or they may live quickly—sluggishly smoulder or suddenly blaze. A muscle at rest is smouldering, a muscle in its contraction is blazing; the consumption of carbohydrate and the production of CO_2, never absolutely in abeyance, even in the most profound state of rest, are sharply intensified when the living machine puts forth its full power; and there is then a sudden burst of heat, and an electrical discharge, by reason of an electro-positive state of the active muscle giving birth to a current of action which in effect you may, without great stretch of thought, regard as of the family of blaze-currents. So that in last resort we find that these striking electrical effects in living matter that we had hardly considered as electro-motive at all—in the eyeball, in its crystalline lens, in a bean or pea or leaf or flower—are, after all, intense local changes, significant of intense local action, that may be imagined and characterised as a blaze amid the smouldering state of living matter.

There is a certain similarity between a blaze-current and the discharge of an electrical organ—no very close and detailed resemblance indeed, yet one that cannot be ignored, and that may be of service to us towards a further comprehension of the electrical signs of life. But it will not be an easy matter to appreciate the connection, and in preparation for the attempt, I should advise you to read two papers by du Bois-Reymond, the first on "Secondary Electromotive Phenomena in Nerve, Muscle, and Electrical Organ," the second on "The Polarisation Phenomena caused by Constant Currents in the Electrical Organ of Torpedo."

And let me say in conclusion that I have not named these papers to you because either nerve or muscle or electrical tissue are favourable objects upon which to demonstrate blaze-currents —they are, in fact, among the least favourable objects for this purpose—but because their secondary electromotive action or response, as described by du Bois-Reymond, presents points of similarity with the currents that are now engrossing our attention.

Those of you who do not read German may refer to the *Translations of Foreign Biological Memoirs* (Oxford, 1887), edited by J. Burdon-Sanderson. And any one who is specially interested in the phenomena of electrical fishes should also read in the original the two memoirs by Gotch, published fifteen years ago in the *Philosophical Transactions*. For a student preparing for examination, the general summary by Gotch in Schäfer's *Text-book of Physiology* will be more than sufficient.

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GOTCH.—"The Electromotive Properties of the Electrical Organ of Torpedo Marmorata," *Phil. Trans. Roy. Soc.*, p. 487, 1887, and p. 329, 1888.

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LECTURE V

The Discharge of an Electrical Organ in Response to Direct Excitation—Du Bois-Reymond's Summary—Similarity between "Blaze-currents" of the Skin and "Discharges" of an Electrical Organ—Normal Direction of the Organ-current—A Speculation and some Experiments—Further Investigation of these Currents by the A B C Method—The Positive Polarisation of du Bois-Reymond—The Polar After-currents of Hering and of Biedermann—Ritter's Tetanus and the Post-anodic Action Currents.

§ 47. *Electrical organs.*—We shall take a point of departure from the diagram on p. 121 of the second paper by du Bois-Reymond,* where he gives a summary of the effects of direct electrical excitation of an excised portion of the electrical organ of torpedo marmorata.

The prefix "absolutely" in du Bois' terminology is used with reference to the organ discharge, the response being denoted as "absolutely positive" or "absolutely negative," according as it is in the same direction as the normal discharge, or of opposite direction.

The prefix "relatively" refers to the direction of response with reference to the exciting current, "relatively positive" and "relatively negative" signifying that the response is in the same and in the opposite direction to that of the exciting current. If you are puzzled by these expressions, or doubt my rendering of them, you should refer to the original paper. Negative polarisation is of contrary direction to that of the

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* *Archiv*, 1885.

exciting current; positive polarisation is in the same direction as the exciting current.

These four stages are reducible to two, by omission of Type II. (variety below Type I.) and of Type III. (variety above Type IV.). We thus have Type I. as the characteristic response of the living organ, and Type IV. as that of the dead organ. This—if you will carefully read du Bois' description, and clearly appreciate the significance of his terminology—is the essential pair of features that respectively characterise the living and dead states of an electrical organ—it discharges in a direction of its own while it is alive; after death, it exhibits the ordinary polarisation of a non-living electrolyte.

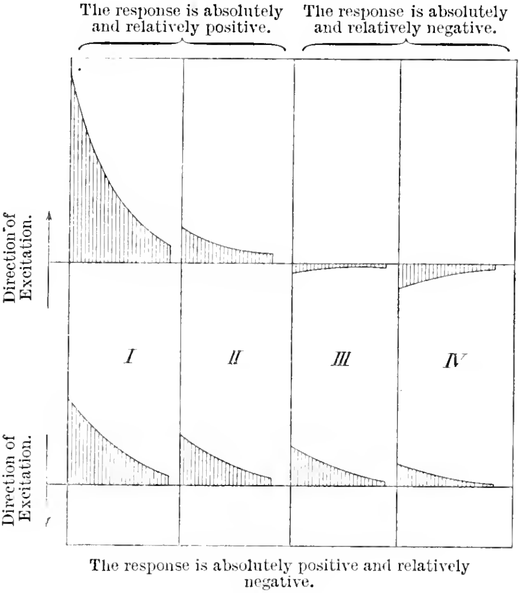

FIG. 34.—Du Bois-Reymond's diagram (*Archiv*, 1885, p. 121) to illustrate the electrical response to electrical excitation of a strip of the electrical organ of Torpedo. The direction of the normal organ-discharge is supposed to be upwards, so that the first two responses of the upper line are homodrome in relation to the exciting current; the next two responses and all four responses of the lower line are antidrome.

The response of skin is on a precisely similar schema, thus:—

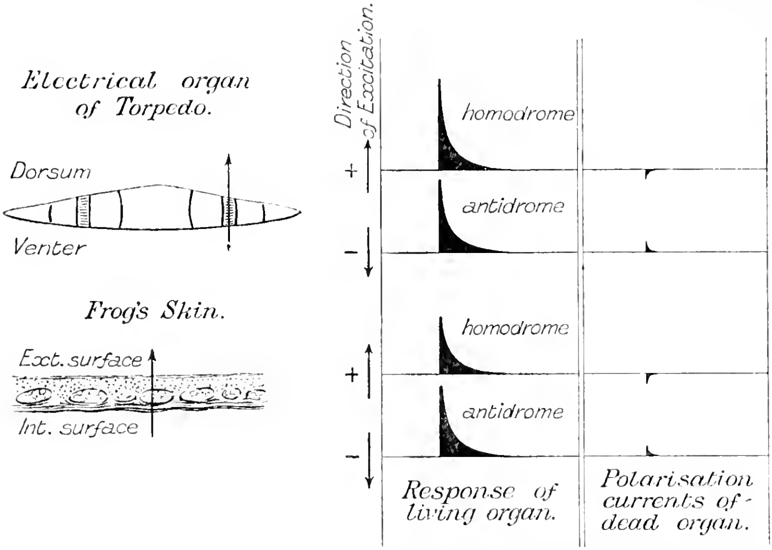

FIG. 35.—Diagram exhibiting the similarity between an electrical organ and the skin as regards their normal electrical responses during life (and the polarisation effects after death).

And as you see from the diagram (or from the experiment that is set up to reproduce it), we are justified in saying of the skin that it discharges in a direction of its own while it is alive, and exhibits after death the ordinary polarisation of a non-living electrolyte. It responds better, as you may notice, to an anti- than to a homodrome excitation, agreeing in this respect with the organ of Malapterurus (Gotch), but disagreeing, I may add, from that of Torpedo (du Bois-Reymond).

§ 48. *The organ-discharge.*—The essential component of an electrical organ is a disc, upon one surface of which a nerve twig ramifies, while the other surface is vascular. The electrical organ consists of piles of such discs, surface to surface, like the elements of an old-fashioned voltaic pile; its structure, as well as the great electro-motive force of the discharge, suggest that it actually is a battery of which the elements (discs) are disposed in series. Further, the direction of discharge, excepting in the somewhat doubtful case of Malapterurus, is always such that current passes (in the animal) from the nervous to the vascular surfaces of the discs. Thus, in Torpedo, where the nervous surface is ventral and the vascular surface dorsal, the discharge is from venter to dorsum. In Gymnotus the nervous surface is posterior, and the discharge is from tail to head. In Raia (the skate, which possesses a well-formed, if attenuated, pair of electrical organs) the nervous surface is anterior, and the discharge is from head to tail. This relation between position of nervous plate and direction of discharge is called after its discoverer "Pacini's law." The discharge is attributable to a sudden action of the nervous surfaces, which, while active, play the part of a series of zinc plates in a voltaic pile. The electro-motive force in the discharge of a single disc has been estimated to be 0.03 to 0.05 volt,* and it is by reason of their columnar arrangement and large number, that the high electro-motive values of the organ-discharge are reached—200 volts from a column of 500 plates is an E.M.F. estimated by Gotch and Burch in the case of Malapterurus.

The discharge can be brought about experimentally by indirect (reflex) and by direct excitation. If, as was first done by du Bois-Reymond, a longitudinal strip of organ be excised, placed between unpolarisable electrodes, and directly excited, it will respond to both directions of excitation by a discharge in one given direction, that namely of the normal discharge. This photographic record (Fig. 36) gives the responses (both in head to tail direction) to induction shocks in positive and negative directions, in the case of a portion of the rudimentary (or vestigial) organ of the skate. The similarity between these effects and the effects above described in the case of the eyeball and the skin, are sufficiently obvious, and you will readily understand how it has come about that I have compared the "blaze-currents" of the eyeball, and of the skin, and of other organs

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* Gotch, *Schäfer's Text-Book of Physiology*, vol ii., p. 584.

with the discharges of an electrical organ. I do not mean to say that eyeball or skin are specifically "electrical organs," for there are no structural features in common; but I think that the comparison goes some way towards generalising our notion of the electrical signs of life. It is at least remarkable that the electro-motive values of the discharge in the cases of the eyeball and of the skin are of the same order of magnitude as that calculated for a single plate of the electrical organ (0.03 to 0.05). According to a recent estimate by Gotch,* the E.M.F. of nerve in response to a single induction shock reaches a value not far short of this—viz., 0.03 volt. And the very points where the comparison is defective should serve to instigate further study. Thus the organs of Torpedo, Gymnotus and Raia are

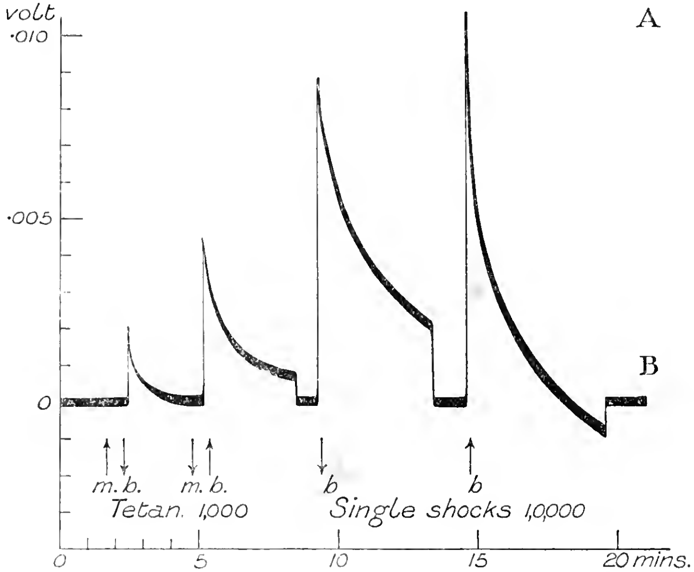

FIG. 36.—Normal (head to tail) discharges of a strip of the electrical organ of a skate (*Raia clavata*) in response to tetanisation and to strong single break induction shocks.

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* Gotch and Burch, *Proc. Roy. Soc.*, vol. 63, p. 300, 1898.

modifications of muscle.* The organ of Malapterurus (which does not follow Pacini's law) is a modification of cutaneous gland; we therefore want to examine that organ by the light of what we have learned of skin. Does the electrical case of Malapterurus give an outgoing current? Perhaps one of these days we shall have an opportunity of finding out.

Meanwhile let me warn you that our knowledge of even the most carefully studied of electrical organs—that of Torpedo, namely—is by no means exhaustive. Its discharge is of very short duration; one may feel an intense thrill from a discharge giving by no means an excessive effect upon a galvanometer; the organ itself while reacting perfectly well to indirect excitation, is peculiarly refractory to direct electrical excitation. This same peculiarity is exhibited by the excised organ or by strips of organ from even the most lively fish, and I have failed to obtain from such strips any well-marked response to single induction shocks; I had to use tetanising currents to bring out any regular venter-to-dorsum response; the organ was easily exhausted, and easily injured, by *e.g.*, removal of the skin, which is closely attached to it; obviously an effect obtained only in the presence of skin, and not obtained after its removal, might not straightway be set down as "organ-response"; I have indeed seen similar responses, of a value of +0.005 volt, with strips of fish that contained no electrical organ at all, but only muscle between two layers of skin.

So that on the whole the case of the electrical organ is a good deal less satisfactory than that of the skin, and in comparing the skin and the eyeball with an "electrical organ," we use the expression in a general rather than in a special sense. As regards blaze-currents, the skin of a frog is a far more efficient electrical organ than is the electrical organ of a Torpedo. And perhaps this is not so very unfortunate; you may easily control statements concerning the frog's skin, you would have to take

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* Developmentally, inasmuch as muscle and electrical organ come from the same muscle plates; and, in the skate, muscle shades into organ by gradual transition. Gotch considers the electrical organ to be a nerve-ending. But, in a sense, muscle itself is a nerve-ending.

a good deal of trouble if you wanted to control statements concerning the Torpedo.

§ 49. *Its direction.*—The direction of response to stimuli of both directions is an indication of the natural direction of organ response. The strip of organ discharges in the way determined by its structural and functional disposition. Can we trace any analogous disposition in the case of the analagous response of eye or skin? May we consider that the direction of a blaze-current is in any measure determined by structural and functional disposition of organ; or, otherwise expressed, have we any right to attribute an organ-current to such structures? I think there are reasons for and reasons against an affirmative answer. As regards the eye, we have positive response to light and positive response to both directions of electrical excitation. We also have negative response to light and negative response to both directions of electrical excitation. But here is no definite and fixed direction of organ-discharge, only a predominance, fluctuating with state of organ and kind of animal.

§ 50. *The skin-discharge.*—As regards the skin, we have positive response and negative response to indirect excitation, and almost exclusively positive (outgoing) response to direct electrical excitation of whatever direction. Here, again, is no definite and fixed direction of organ-discharge by the natural mode of action through nervous channels, but a marked predominance in one (the outgoing) direction in response to both directions of electrical excitation.

With direct excitation of the skin, we must suppose that all its living parts are aroused to action, gland cells and general epithelium alike, and we may not attribute the effect to any one kind of tissue element to the exclusion of others. We know by experiment, however, that the action proceeds from elements at or near the external surface; and we find further that with shavings of skin, including Malphigian layer and excluding the deeper situated glands, the direct response is obtained as before, while with shavings of cuticle only, no response whatever is obtained. Mercuric chloride, which, as you saw, abolished the direct response, is said by Bach and Oehler not to abolish the indirect excitability, which presumably depends on deeper parts. We therefore conclude that the main factor of the response is the general epithelial investment—its Malpighian layer in particular. Indirect excitation of the skin through nervous channels presumably arouses the cutaneous glands alone; the general epithelium is, as far as we know, as much outside the control of nerve fibres as are blood-corpuscles.

We cannot, therefore, in comparing the effects of direct and of indirect excitation, regard the comparison as a simple one, like that of direct and indirect excitation of muscle.

Thus, in frog's skin, the effect of indirect excitation is often negative (ingoing) when that of direct excitation is positive (outgoing). In cat's skin the effect of indirect excitation is always ingoing, that of direct excitation is at first ingoing, at last outgoing.

It would be interesting to see what effect, if any, the two forms of excitation exercise upon each other. I have not found time to do this, although obviously it would be an easy matter to take a regular series of indirect effects, interpolating in the series one or more direct excitations of some convenient duration and strength; or a regular series of direct effects, interpolating in the series one or more indirect excitations. Of course, it would be necessary to photograph the effects; I wonder what they would be? *

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* I have since tested this point, as regards the effect of direct upon indirect excitation, in the case of frog's skin, also in the case of the cat (*vide infra*, Lecture VI.), with the following results:—

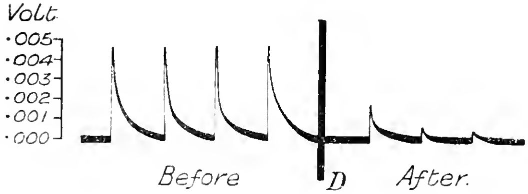


FIG. 37.—Indirect responses of frog's skin to tetanisation of the sciatic nerve before and after direct excitation of the skin itself by a single strong induction shock D.

[*For continuation of Note, see next page.*

So that, in sum, while pointing to the conclusion that there is, as regards the external cover of an animal body, an outgoing organ-current of action, the facts forbid us to rest content in an exclusive conclusion of such simplicity, and we are obliged to admit that a cutaneous organ-current, even if it really exists by reason of a general functional and structural organisation of the integument, is twisted and obscured by other accessory and complicating conditions.

Let us, however, imagine how things might have been. The fancy will, if nothing else, remind us of facts, and make us curious for further facts. The facts—let me reiterate them once more—are that the skin, when first placed on the electrodes, gives an ingoing current which increases, and that excitation of either direction gives an outgoing response which diminishes. The former is "current of rest," the latter "current of action."

§ 51. *A speculation.*—A lump of protoplasm, at rest and homogeneous throughout, is iso-electric throughout; let it be

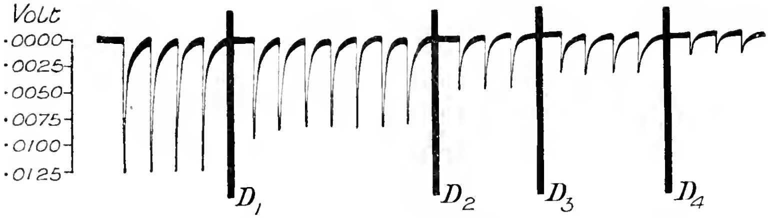
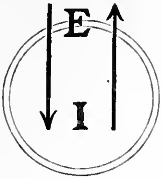


FIG. 38.—Indirect responses of a pad of a cat's paw to single induction shocks exciting the sciatic nerve, before and after :—

D_1 = direct excitation of the pad by one strong break shock.
D_2 = " " by two strong break shocks.
D_3 = " " by tetanisation for 5 seconds.
D_4 = " " by tetanisation for 15 seconds.

It is somewhat surprising that direct excitation should have produced a greater diminution of the indirect response in the frog than in the cat. But in the former case the indirect response was elicited by tetanisation of the nerve, while in the case of the cat, the nerve was excited by single strong shocks. The regular effects (on the skin glands) of such stimulation are in themselves sufficiently remarkable; their true physiological character was proved by the long interval between each excitation and response—about 3 seconds.

acted upon by its environment, any point of its surface E is chemically more active than any point of its mass I; E becomes electro-positive to I; there is therefore current from E to I, an ingoing current, the so-called "current of rest." Let the lump become active, any point I is chemically more active than any point E; there is current from I to E, outgoing current, the "normal organ-current of action." Now, the currents that we call "electrical" and actual currents of matter, streaming through a porous substance, generally occur in the same direction, so that there is an association of phenomena —(1) in the case of ingoing electrical current and centripetal current of matter (and of energy) from environment to living substance, and (2) in the case of outgoing electrical current and centrifugal current of matter (and of energy) from living substance to environment. *A priori*, therefore, we should expect the "skin" of living substance to be the channel of a double current, material and electrical—(1) of a current of rest or reception, ingoing and centripetal, subserving the synthetic accumulation of energy; (2) of a current of action or emission, outgoing and centrifugal, subserving the analytic expenditure of energy. If you are accustomed to think in terms of charged ions, you will imagine the kation as travelling from without inwards with a receipt of energy, from within outwards with a discharge of energy.



"Current of rest" from E to I.
"Current of action" from I to E.

And now consider further what kind of modifications we may expect and look for with the differentiations of function and of structure that have occurred in the external surface of plants and animals.

Consider, in first place, the principal difference of chemical direction in the main drift of vegetable and of animal metabolism. Vegetable protoplasm is in major degree an instrument of synthesis and accumulation, in minor degree the seat of analysis and emission. Animal protoplasm is in major degree an instrument of analysis and emission, in minor degree the seat of synthesis and accumulation. The vegetable, in most immediate contact with inert things, combines, organises, and accumulates. The animal, in less immediate contact with inert matter, disrupts, utilises, and dissipates in their fragments organic compounds that it has received ready-made from other animals and from plants. And quite early in its development the external surface of the animal is distinguishable into two parts: (1) a surface principally receptive of incoming matter, the digestive and absorbent surface; (2) a principally emissive surface, the external skin, through which the greater moiety of animal energy is dissipated. An "organ-current of action," if aroused in these surfaces, should, according to their several physiological habits and dispositions, be:—

Principally ingoing for the vegetable "skin."
Principally outgoing for the animal skin.
Principally ingoing for the animal mucosa.

§ 52. *Some experiments.*—And whatever the fate of our theoretical motive, it will have served to instigate a search for facts; but we must take due care to emancipate observation from expectation, and not merely see that which we expect or hope to see. Here is a piece of orange peel, chosen for our purpose not merely because it is a handy object, but because the "skin," presumably living, is easily separated from the "body" of the fruit by breaking through "subcutaneous tissue," presumably not-living. And in point of fact, you notice that the bit of orange peel, placed between unpolarisable electrodes, exhibits little or no current, unlike a paring of an apple or a potato that necessarily has an injured inner surface, and exhibits, therefore, a strong outgoing current of injury. I compensate precisely and then test in the way now familiar to you (plug the galvanometer, send an induction shock through skin, unplug the galvanometer), and you see that to both + and − directions of excitation the orange peel responds by a deflection to your left, signifying current of negative or ingoing direction.

§ 53. *Human skin.*—I next take a piece of human skin, twenty-four hours after excision, and test it in the same way by + and − break induction shocks. You see that to both directions of excitation the response has been a deflection to your right, signifying current of positive or outgoing direction.

§ 54. *Mucous membranes.*—These two experiments are in accord with our theoretical forecast, but that they prove that forecast to be a true guess, or even bear it out to any serious extent, I shall be the last to urge. The two facts (both of which are representative results based upon a sufficient number of trials) are, however, interesting in themselves, whether this or any other explanation be the true one. With regard to the digestive mucosa, I prefer, for lack of sufficient experience, not to show you any experiment at all, for I am at present by no means sure what is to be considered as a typical and what as an exceptional result. I have seen ingoing response more frequently than outgoing response, but I desire to study the conditions and magnitude of the response before coming to any conclusion as to which is the typical one.*

I would rather show you another pair of experiments, illustrating in a different way the apparent opposition of direction in the blaze-currents of vegetable and of animal "skins."

§ 55. *Intact surfaces.*—We want to test, *e.g.*, the skin of an animal, or of a vegetable, without previous injury of the surface. A very little reflection will convince us that this can only be done by applying what has already been alluded to above as the A B C method, viz., stimulating through A B, and leading off through either A or B and a third indifferent point C (p. 69).

The three electrodes, A B C, are applied to three separate external spots of a piece of frog's skin. I intend to test the

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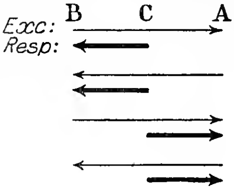
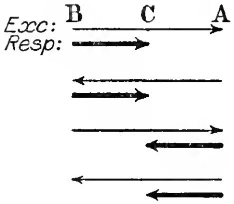
* From further observations made subsequently to the delivery of these lectures, I think the above statements may be considerably hardened. In the great majority of cases—so great that we may reckon an opposite result as exceptional—the mucosæ manifest ingoing response to both directions of excitation.

point B, so I compensate B C, then excite through A B, and then lead off B C to the galvanometer, as shown in Fig. 33. You note the deflection. I repeat the experiment with excitation in the reverse direction; again you note the deflection. I repeat a similar pair of trials upon another point A, merely to get a further pair of observations—compensating A C, exciting through A B, and leading off through A C. You have noted the deflections, both the B C deflections to your left, and the A C deflections to your right, thus:—signifying—as you will easily verify—in all four instances that the after-effect at A or at B, whether anode or kathode of the exciting current, has been *outgoing*.

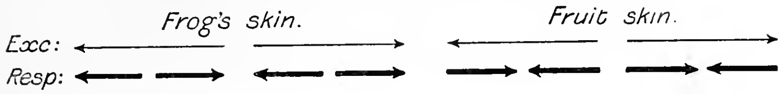


Repeating a similar series of four trials with an apple—a living apple of course—and noting the deflections as before, you find that they are in every case the other way round, viz., both B C deflections to your right, both A C deflections to your left, like this:—signifying in all four instances that the after-effect at A or at B, whether anode or kathode of the exciting current, has been *ingoing*.



Now, is not this an interesting result, and does it not come out very clearly on this system of notation? In my first attempts to examine one of two stimulated points by conjoining it through the galvanometer with a third indifferent point, I found it very troublesome to take notes correctly, very difficult to read notes when taken, and quite impossible to realise during an observation, what was the meaning of each individual deflection. But since I have followed and become familiar with this system of notation, all these drawbacks have disappeared, and we may read and compare at a glance "formulæ of response" of a great variety of living things.

I shall not enter into further explanations now; the method will be used again, and more fully explained in a future lecture, and then appreciated by you as a simplification, if meanwhile you will puzzle the thing out for yourselves. To save space, the formulæ, which to show order of individual trials have been set out as above, will sometimes be given thus:—



§ 56. *Positive polarisation.*—Let us now turn our attention to another related subject, that of positive polarisation, and of post-anodic (and post-kathodic) action-currents.

Du Bois-Reymond obtained his first inkling of “positive polarisation” in 1843, but it was not till 1883 that he published a full account of the subject. He introduces that account in the following terms, which clearly indicate the place held by the matter in his thoughts:—

> “I consider that the time has come to break the silence which I have preserved till now concerning certain electro-physiological experiments that have engaged my attention for nearly forty years, and to which I attribute very great importance.”

Taking the case of muscle, he studies the secondary polarisation effects produced by strong constant currents, tabulating his results in relation to current-strength and time of closure; and how laborious a task this was du Bois' own words will most vividly bring before you.

> “The preparation of such a table of data is a very wearisome undertaking. The secondary effects of currents that are at all strong or long, are for the most part so enduring that a fresh preparation is required for nearly each single experiment . . . each fresh preparation requires a fresh frog . . . to permit of comparison, the frogs must be as uniform as possible in size and health. . . . So that the completion of a table of data is the work of many weeks, and it will therefore hardly be matter for surprise that I have only twice accomplished the task, once in the autumn of 1855, once in the summer of 1882.”

Each such table comprised 200 successful observations, with currents of 1 Daniel to 40 Groves, and closure times of 0.006 sec. to 25 minutes. The polarisation currents were of two kinds:—*negative*, first visible after a current of 1 Daniel passed for a period of 1 sec.; *positive*, requiring at least 2 Groves with a closure time of 0.3 sec. The strongest negative polarisation occurred after a current of 1 Daniel passed for 10 minutes; the strongest positive polarisation after a current of 20 Groves passed for 0.075 sec.; in the latter case the E.M.F. appeared to be rather less than that of a muscle-current.

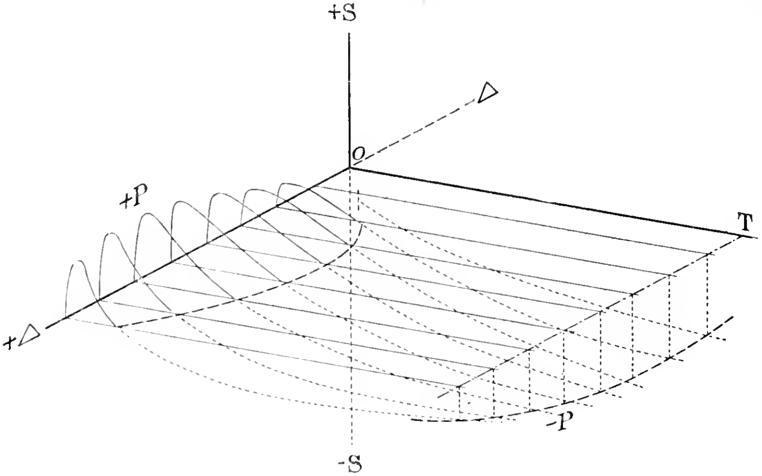


FIG. 39.—T is the time of closure, △ the density of the polarising current, ±S the strength of the secondary electromotive effect, so that the plane viewed in perspective is the T △ Plane. The individual ordinates S are not represented, but only the curves joining the ordinates belonging to given current density and given time (from du Bois-Reymond, *Archiv*, 1884, p. 15).

§ 57. *Two criticisms.*—Hermann—du Bois' former pupil and untiring critic—pounced at once—showing and saying in a paper of upwards of sixty closely printed pages of *Pflüger's Archiv* (vol. xxxiii.), that du Bois' positive polarisation current was in reality a post-anodic action-current. Hering also intervened, and said the same thing in two successive papers of the *Wiener Sitzungsberichte* (12th and 13th communications, 1883).

Both du Bois' critics confined themselves to a discussion of the interpretation to be placed upon du Bois' phenomenon, and proved that it was of post-anodic nature, and that the designation of positive polarisation was a very unhappy one. But the critics did not demur to or subtract from the fact itself, nor indeed did they add to or extend it. Indirectly, however, by the effect produced in the mind of his pupil Biedermann, Hering has "authorised" a very considerable extension of fact and still more of doctrine. Biedermann finds evidence of the existence not only of a positive anodic, but also of a negative kathodic after-current, and further of the counterpart of this first pair, viz., a negative anodic and a positive kathodic. The last pair of currents are, however, asked for by theory rather than offered by simple observation; Biedermann himself admits that of his four currents the positive kathodic is very doubtful, and it is clear that the negative anodic, being in the direction of ordinary polarisation, is also on a doubtful footing of fact. Nevertheless he considers theoretically the first pair as being of irritative origin, and the second pair as being of inhibitory origin. His quadrille of after-currents may be put together in the following schema:—

	Anode	+ $\xrightarrow{\text{Exciting or primary current.}}$ −	Kathode
Irritative or dissimilatory.	positive anodic	→	"the most certain"
	negative kathodic	←	[? polarisation]
Inhibitory or assimilatory.	negative anodic	←	[? polarisation]
	positive kathodic	→	the most uncertain

§ 58. *A demonstration.*—I should be sorry to attempt to demonstrate to you the existence of these four currents upon muscle or upon nerve, which are the tissues upon which Biedermann claims to have observed them; you must refer to Biedermann's own account for what in his opinion constitutes the evidence of their existence.

At most, I shall be able to show you the first and "most certain" of them, viz., the positive anodic or post-anodic action-current, and that only in a form that does not exclude a participation in the total effect of a positive kathodic factor. And I will show the experiment in a form intended to associate in your mind this post-anodic action-current with an irritative phenomenon long known to physiologists under the name of Ritter's tetanus.

Here is a nerve-muscle preparation, the nerve of which is laid across electrodes that are connected with the keyboard and galvanometer. There can also be led into the keyboard, by means of a double key, a strong battery-current which is to traverse the nerve in an ascending direction as figured (the galvanometer meanwhile being plugged). During the passage of the constant current, the muscle remains quiescent, but when I break the current, the muscle, as you see, contracts, and will contract for a longer or shorter period. Immediately after breaking the battery current, I unplug the galvanometer, when you witness a strong and permanent positive deflection, significant of an action-current in the nerve of the same direction as that of the previous battery-current. The deflection is not absolutely permanent, it is gradually falling, the muscle will not remain indefinitely contracted, it will relax sooner or later; the positive current in the nerve, and the contraction of the muscle, are associated effects of a state of local irritation or action in the previously anodic region of the nerve. You know that the current from an active to an inactive spot of nerve runs in the nerve from active to inactive (in the galvanometer from inactive to active, the latter *pole* being therefore called negative), and that the active spot acts like the zinc of a voltaic couple—is in brief a zincative spot. Therefore you know from the direction of this after-current that the active spot from which the irritation to the muscle proceeds is post-anodic as to its source in the nerve itself.

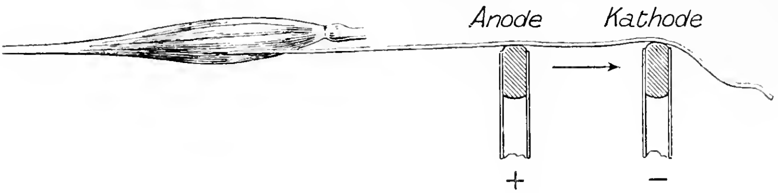


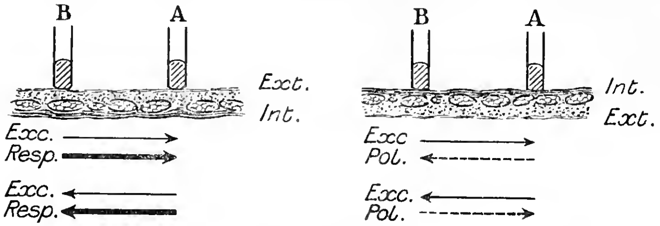
FIG. 40.—Nerve-muscle preparation; to demonstrate the muscular contractions associated with the positive anodic after-current in nerve.

§ 59. *Locality of reaction.*—Polar inequalities of effect have been alluded to above, and now demand our somewhat closer scrutiny. Is a blaze-current exclusively post-anodic or post-kathodic, or both, and if both, which is the more effective pole?

The question can be experimentally tested in three ways—the exciting current can be sent through the skin by two electrodes in contact with its two surfaces (Fig. 26), or through electrodes both of which are applied to the external surface, or with three electrodes A B C on the external surface (Fig. 33).

By the first of these three plans we have already seen that with both directions of excitation an outgoing response is provoked; we have seen farther (§ 43) that both these responses depend on an electro-negative state at or close to the external surface. Both poles produce this change, and the fact (illustrated by Fig. 30) that the antidrome is sometimes greater than the homodrome response, signifies at first sight that the anode is more efficacious than the kathode. But this conclusion is not confirmed by our next two experiments, and the inequality of response, which, indeed, I find on reference to my notes, is by no means invariable, may have been due to other causes, *e.g.*, to ordinary polarisation currents *against* homodrome and with the antidrome response, the true physiological response being greater in the homodrome sense.

The second plan of experiment, by two external electrodes, gives a result that can hardly consist with superiority of a post-anodic effect. The response in this case is always homodrome, and since it is the algebraic sum of two opposed outgoing currents at the two poles, this signifies that the kathode has been more efficacious than the anode. A homodrome post-anodic response would have been ingoing, but as we have seen, and shall see again, it is the post-anodic response which is antidrome and outgoing. This experiment exhibiting homodrome response with two external electrodes is easily repeated; the result is very constant and contrasts sharply with that obtained when the two electrodes are applied to the internal surface; this surface is ineffective, and gives only small antidrome deflections attributable to ordinary polarisation, whereas the external surface gave large homodrome deflections of which the physiological integrity of the skin is a necessary condition. With killed skin, both surfaces give only the small counter currents of ordinary polarisation. With three external electrodes, and proceeding on the A B C plan, to test the separate unipolar effects at A and at B (p. 69), the antidrome-anodic effect has sometimes exceeded and sometimes fallen short of the homodrome-kathodic effect. The first inequality proves nothing, as it might be an effect of ordinary polarisation; the second inequality proves, that under certain conditions, and in spite of ordinary polarisation, the kathode is the more effective pole.

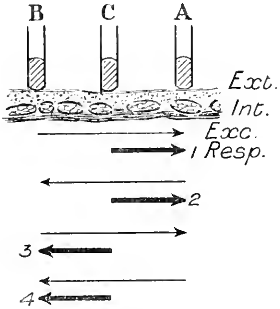


SKIN OF FROG.

Excited and led off by its external surface.

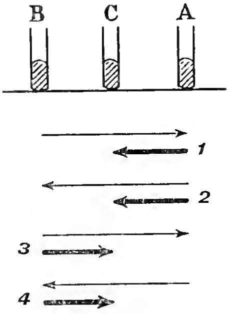
Excited and led off by its internal surface.

So that, in sum, we may conclude with certainty that both poles are effective, and with less certainty that the kathode is more effective than the anode. It is somewhat surprising



FROG'S SKIN.

All responses are outgoing. The homodrome kathodic currents 1 and 4 exceed the antidrome anodic currents 2 and 3.



VEGETABLE SKIN.

All responses are ingoing. The homodrome anodic currents 2 and 3 exceed the antidrome kathodic currents 1 and 4.

to have to admit that we have to do with a homodrome post-kathodic current. A homodrome post-anodic current would have seemed more familiar to us.

In all these experiments, it is remarkable how strictly the effects of excitation are limited to the directly excited spot. Outside the area of direct excitation, the excitability of the skin remains unaffected; we can locally exhaust the skin by strong excitation, and obtain good response from other spots of the same piece of skin.

This local independence of parts, characteristic of vegetable tissues as well as of the skin, is in marked contrast with the spread of disturbance that is peculiar to muscle and nerve where propagated effects are the salient feature. It is one of the reasons why a piece of skin or of a plant is a more favourable object than a muscle or a nerve for the demonstration of blaze-currents.

Plants, excited and led off by two points of their external surface, give, like the frog's skin, homodrome responses to both directions of excitation. But whereas in the case of frog's skin, the total homodrome effect between A B is the algebraic sum of the partial outgoing effects at A and B, in that of a vegetable skin it is the sum of two ingoing effects. The prepotent pole, in the case of the frog's skin, was the kathode, in that of the vegetable skin, it is the anode, as will be evident to you on careful consideration of the figure. It is not difficult in the case of vegetables to obtain measurements of the total and partial blaze-currents, showing quite clearly that the anode has been the prepotent pole, thus:—

Excitation from	B.........to.........A	
Total response from	B.........to.........A	+ 0.012 volt.
Partial response from	B...to...C	+ 0.035 ,,
Partial response	to C from A	− 0.021 ,,

Cut surfaces of fruits—*e.g.*, of apples and pears—have given ingoing currents at both poles after excitation, but smaller than the currents aroused at intact surfaces. Ripe orange peel has given ingoing effects at its external surface, and only small polarisation counter-currents at its internal surface, the former is "alive," the latter is "dead."

§ 60. Exposed muscle has given precisely the same formula as that of vegetables, *i.e.*, ingoing effects at both poles; while dead muscle gave only the small antidrome deflections due to ordinary polarisation.

A frog's sciatic nerve gave responses homodrome with excitation, larger on the anodic than on the kathodic side. But a detailed examination of blaze-currents in nerve and in muscle still remains to be made.

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LECTURE VI

A Representative Experiment—Effects of Indirect Excitation—Effects of Direct Excitation immediately after Death, and Later—How Long, after a Cat's Death, can a Cat's Foot continue to Exhibit Signs of Life?—More A B C—A Vegetable Surface—Surface against Surface—Anodic and Kathodic—Biedermann and the Frog's Tongue—A Warning.

§ 61. *Demonstration.*—This cat is dead, but its tissues are still alive. It was decapitated at 4.45; it is now 5.5, and I shall talk with my eye on the clock, as I wish to show you an experiment just half an hour after the death of the cat.

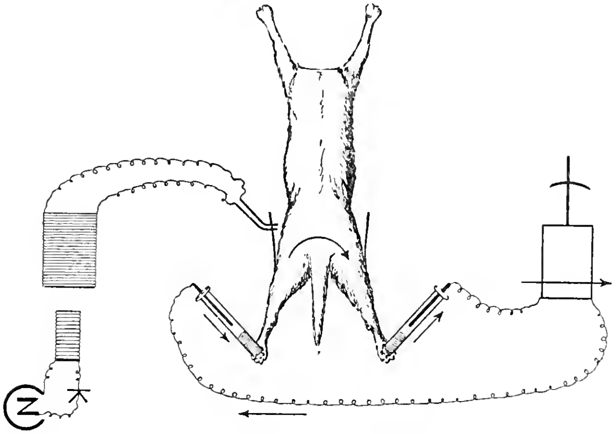

FIG. 41.—Diagram of experiment described in the text.

The story of the cat's skin, or, more properly speaking, of its foot-pad, commences from the observations of Hermann and Luchsinger, who showed that on the skin, as on glands, secreto-motor can be disentangled from vasomotor reactions. The experiment of Hermann and Luchsinger cannot be shown here. It is a vivisection of which preliminary No. 1 is the abolition of muscular movement by curare, and therefore preliminary No. 2 is artificial respiration.

It is now 5.10 P.M.; the cat has been dead twenty-five minutes. I have therefore five minutes time to further explain my meaning. The surviving tissues are dying; the junction between motor nerve fibre and muscular fibre is dying; the junction between secretomotor fibre and gland cell is also dying; but, according to my experience, the first will die in thirty, the second will die in sixty minutes. I have therefore a margin of thirty minutes during which excitation of that packet of nerve fibres called the sciatic nerve will not cause any movement of the limb (nor, therefore, any possible shifting of contacts or other disturbance), but will cause an activity of the cutaneous glands.*

You will find as a book datum (and as a printed datum it is a very satisfying datum) that the independence of secretomotor nerves is proved by the fact that after death (of the cat), when the circulation, and therefore vasomotor, effects are out of count, beads of sweat are made to appear on the carefully wiped pad by excitation of the sciatic nerve.

I have never succeeded in witnessing these beads of sweat, and will not therefore make the attempt to demonstrate them to you; but I shall show you by means of the galvanometer, within this margin between the thirtieth and sixtieth minute post-mortem, that the excitation of the sciatic nerve on one side (and on the other), causes a marked physical alteration in the skin of the pad, first on one side and then on the other. Cats differ, and I will not answer for my times to a minute, but it is now thirty-five minutes *post mortem felis*, and I am well within the margin. The two hind pads are connected with the two terminals of the galvanometer. I don't know which is which, so I test my connections with a bit of zinc, by touching the two terminals on the operation table with which the two galvanometer terminals are connected. Touching the terminal of the left pad with the bit of zinc, while my finger is on the

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* The longest period recorded in my notes has been 2 hrs. 15 mins., in the case of a particularly well-nourished cat.

terminal connected with the right pad, sends the spot off to your right; I know, therefore, that on excitation of the left sciatic, the spot will go to your right. I know that the skin under its control is rendered zincative (galvanometrically negative according to physiologists, electro-positive according to physicists—but in any case in the direction of the arrow on the black board—from outer to inner surface of that skin, *i.e.*, in an ingoing direction).

The spot has "flown off scale"—as Biedermann so often expresses it—to your right (I am giving a demonstration, and not making a measurement). In order to save time to make the converse experiment without undue delay, I bring the spot back by the counter current of a compensator. I have used .015 volt; that therefore has been the approximate electromotive value of the response—by no means an inconsiderable value.

I now apply similar excitation to the sciatic nerve of the right side. You think nothing happens, but before you have made up your mind that nothing happens, the spot flies off to the left. Opposite side—opposite direction of course. Ingoing current in the right side gives deflection to the left, just as ingoing current in the left side gave deflection to the right; and the pause perceptible to most of you at the second observation, but not at the first, was the latent period between cause and effect, between excitation of the sciatic nerve and response of the cutaneous gland-cell. I guess it to be about three seconds, but we will measure it presently.

This obvious delay between excitation and response should make its mark upon your memory. It is a sure and reassuring sign that we are dealing with a true physiological response, outside all possibility of coarse physical fallacy. The response—I mean the indirect response of the skin to excitation of the nerve—can be elicited by a single induction shock. This in itself is rather curious; we should have expected a visceral (sudo-motor) nerve to need prolonged or summating stimuli for its effective excitation; you see for yourselves, however, that a single shock causes an unmistakably delayed, well-marked and somewhat prolonged response.

The nerve-skin response, now before your eyes, is a very good case to use for familiarising you with some of our apparatus.

We guessed the lost time at three seconds, we will now make a rather more accurate measurement by photographing a galvanometric deflection, and finally we will control our measurement by taking an electrometer photograph. (*Vide infra*, p. 105.)

Two galvanometers are in circuit in series (as described in the Appendix, p. 156); the recording galvanometer or galvanograph will take on the sensitive plate a *replica* of the indication witnessed by you on the demonstrating galvanometer, and it will be rather interesting to you, perhaps, to see whether the impression on your mind is borne out by the impression on the photographic plate. The plate is set to fall at the rate of about 2.5 mm. per second (or an inch in 10 seconds), and the instant of stimulation is signalled on the plate by a device that you can examine afterwards. I start the clockwork, and 2 or 3 seconds after you have heard the commencement of excitation (of the nerve), you see the deflection caused by the electrical change that has taken place in the skin. When the plate has got to the end—*i.e.*, after 40 seconds—it is shut up in its carrier and sent to the developing-room, from which it will be brought back in a few minutes, and placed in the projecting lantern (Fig. 43).

Meanwhile let us examine the response by means of another instrument—the capillary electrometer—put into the circuit instead of the galvanometers (Appendix, p. 162). The magnified image (× about 1500 diameters) of the mercury column, projected on the transparent screen, looks to you like a large manometer—and, in point of fact, it is an electrical manometer, as you see at once if I raise or lower the electrical pressure in circuit by, *e.g.*, thousandths of a volt. Having verified that the connections are such that movement of the mercury upwards on the screen signifies outgoing current, and downwards the reverse, we may proceed to excite the sciatic nerve as before and watch the electrometer image on the screen. It reacts perfectly well—by a downward movement each time I excite the sciatic nerve—and my impulse is to exclaim on seeing these responses on the screen—"What a splendid cat!" For they are, as you may have noticed, responses to single break induction shocks. And notice also the delay, about 2 seconds—with an electrometer this time.* But we must photograph this, which will be easily and expeditiously done on the lecture-table by slipping in a recording instrument, so as to receive the image of the mercury column. This is now done; the plate travels horizontally at a rate of about 3 mm. per second; the record is completed in 40 seconds, and in a few minutes you will be able to compare it with that previously taken by the recording galvanometer, and with your own memory-image (Fig. 44).

I repeat the two experiments to make sure that the effects of indirect excitation are clear to you, and turn to the results of direct excitation. I have no history to give you in this connection, nor list of German names. You must be satisfied with the story of the thing as given by the thing itself—not a complete story indeed, but a fragment, a word or two.

§ 62. *Direct excitation.*—A pad of the cat's foot is cut off and placed between electrodes on a bit of ebonite with a central perforation, to ensure normal passage of the excitation current. Excitation, compensation, etc., are applied as you now well understand from previous lectures, in accordance with the diagram now fully familiar to you (p. 152). I compensate exactly, so that the galvanometer may be plugged and unplugged without disturbance (notice in passing that the current to be compensated has been from surface to section, *i.e.*, ingoing through the skin; it cannot therefore be current of injury, for such current should be from section to surface, *i.e.*, outgoing through the skin); I excite the pad by a break induction shock in the ingoing direction, and on unplugging the

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* In another case a series of electrometer records came out:—

Time post mortem . .	30	40	48	55	65	minutes.
Voltage of response . .	12	10	8	5	2	millivolts.
Period of latency . .	1.4	1.6	1.7	1.8	2.0	seconds.

There was no appreciable lost time with direct excitation, nor excessive delay of transmission in the nerve itself; the delay was exclusively "junctional."

galvanometer you see an effect (or after-effect) in that same direction. I turn over the reverser of the exciting current, I apply a similar induction shock in the outgoing direction; the response (or after-affect) as you see, is again to your left, in the ingoing direction, and it is larger than the previous one; there is perhaps a polarisation factor (ingoing after outgoing) that makes this ingoing response larger than in the previous case, where the polarisation factor (outgoing after ingoing) was opposite to the main physiological ingoing effect—but that is a detail. The principal point is, that the effects of electrical excitation of whatever direction have been ingoing, or as I choose to call it—"negative."

The effects of excitation in either direction being ingoing, it is clear that a series of currents of alternating directions will produce an ingoing effect. Tetanisation, *i.e.*, a series of make-and-break current in rapid succession, will therefore produce an ingoing effect; and as you now see, that ingoing effect is off scale to your left; there has been a summation of separate stimuli forming the tetanising series.

I reverse the direction of the tetanising currents, and as before, you see the spot flying off scale to your left, indicating response (or more precisely after-effect) through the directly excited pad in the ingoing direction.

This has been a single experiment. I do not remember having ever seen better marked ingoing effects of excitation; but the pad was very fresh, and I did not use very strong tetanisation, which two conditions have been shown by previous experiments to be favourable as regards the demonstration of ingoing effects of direct excitation. In previous experiments I have indeed observed precisely the reverse effects, viz., outgoing effects by direct excitation; but I was then following out the effects day by day, and using excitation of full strength, in order to learn how long after the death of a cat this sign of life was observable on one of its feet.

Such a pad has now been set up, taken from a cat twenty-four hours after death, and you see as a matter of fact that it gives large outgoing effects (deflections to your right) after both directions of strong tetanisation.

It is an easy matter in the case of an animal like the cat, to test the skin *in situ.* Two or three hours after death, when the muscles are no longer inconveniently excitable, a pad is cut off, and one electrode is applied to the wounded surface; the other electrode is applied to an intact pad. The accidental current (which is not an "injury current," since its direction in the cat is from intact to injured spot, but the normal and accidental ingoing current at the uninjured spot) is compensated, and the blaze test applied in the usual way. Both responses are in the same direction as that of the accidental current, from intact to wounded spot, ingoing through the intact skin. These are evidently not negative variations of any injury current.

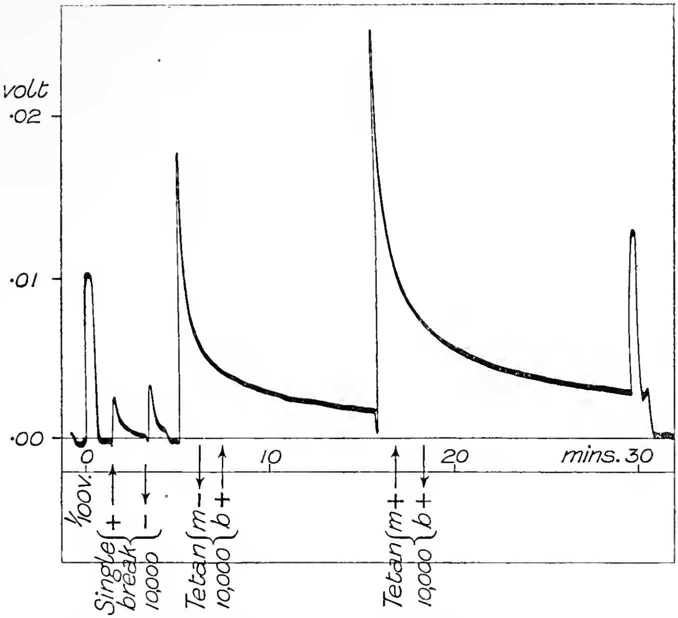

FIG. 42. (4219.)—Outgoing responses of the pad of a cat's foot, directly excited by single break induction shocks in both directions, and by tetanising currents in both pairs of directions.

We may provisionally infer from the absence of obvious injury current that the subcutaneous connective tissue is of very inert character, and that an unpolarisable electrode applied to subcutaneous tissue will serve us as an indifferent electrode, under which little or no local response to excitation need be expected. But we must take care that the wound does not involve injured or exposed muscle, we need only transfer our "indifferent" electrode to an injured muscle (or to an injured nerve) to be convinced that the latter is strongly electromotive in the usual (zincative) sense. The hint may, perhaps, prove of some service to us; we may one day want to make use of an indifferent electrode for the further investigation of the electrical reactions of undisturbed skin or mucous membrane. Reflect for an instant—we must always get a resultant of two factors, if our circuit includes two active surfaces, whether both be of skin, or both mucous or one skin and one mucous. So that to get at the reaction of one spot of skin *in situ* or of mucosa *in situ*, it will greatly simplify our task if the subcutaneous tissue may be treated as electrically indifferent and non-responsive.

§ 63. *Review.*—We have gone over the whole ground, and rather more rapidly than I expected. These three experiments—exhibiting, first, the ingoing current aroused by indirect excitation; second, the ingoing current aroused by not too strong direct excitation of a fresh pad; third, the outgoing current aroused by strong direct excitation of a twenty-four hour pad—very fairly summarise all I have learned about these currents during the last few months. Some few details may, indeed, be added—the lost time of indirect excitation for instance, and the rapid exhaustion of the indirect effect by repeated stimuli; but these will be best shown to you by projecting on the screen the actual records of these phenomena. And I may mention that in one experiment directed to the point, it was found that no effect was produced by excitation post-mortem of the sciatic nerve of a previously atropinised cat, and that in another experiment the same state was found on a cat killed by chloroform *; in both these experiments the effects of direct excitation were found to be normal. One other point—in both

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* In other cats, chloroformed and killed, the indirect effects have always been normal; the instance quoted in the text was exceptional.

excised pads that we tested by direct excitation, the "normal current" was ingoing—in precisely the opposite direction to what might have been expected in a piece of living tissue with an artificial section—in one pad the effects of excitation were ingoing, increments of the normal current; in the other they were outgoing, decrements of the "normal current."

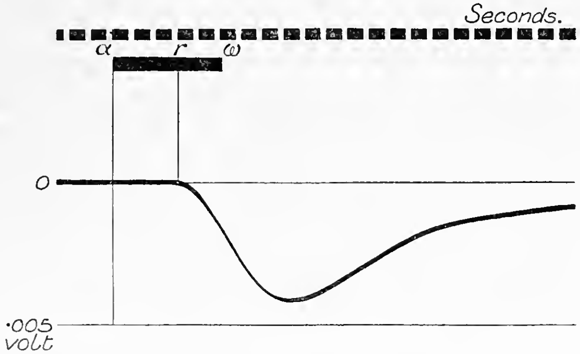


FIG 43.—Cat. Ingoing response of pad of foot aroused by excitation of the sciatic nerve. Berne coil at 1000 units. The latent period is 3 seconds. (Galvanometer record.)

Here are the records you saw taken a few minutes ago (p. 100), showing the lost time and the course of the indirect effect, on the galvanometer and on the electrometer. Compar-

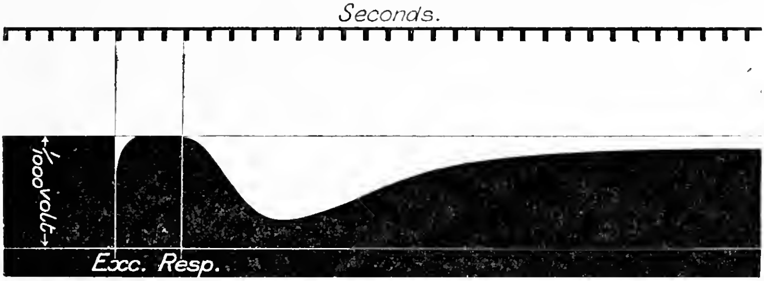


FIG. 44.—Electrometer-record. Indirect response (ingoing) of cat's foot-pad to single break induction shock through sciatic nerve. Lost time = 3 seconds.

ing the two curves, you see that they have very similar time-relations, and there does not seem to be much to choose between the two instruments. This, however, is merely due to the fact that the phenomenon is comparatively slow and prolonged, so that it can be followed and observed by galvanometer almost as well as by electrometer; the former instrument has indeed inertia and "lost time," but these are not considerable in comparison with the physiological inertia and lost time of the change observed; this particular galvanometer has a lost time of about 0.3 second, *i.e.*, only one-tenth that of the physiological lost time under observation; the electrometer has no appreciable lost time, which of course, is an advantage.

The voltage of the response is greater in the galvanometric than in the electrometric curve, but that is only incidental to the fact that in the former case the response was taken to tetanisation, and in the latter to a single induction shock; perhaps also the nerve-skin was becoming fatigued. Such fatigue, in consequence of repeated action, does in fact always appear in more or less pronounced degree. Here is an instance in which it is very well marked.

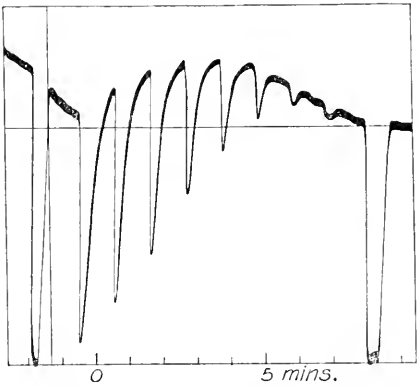
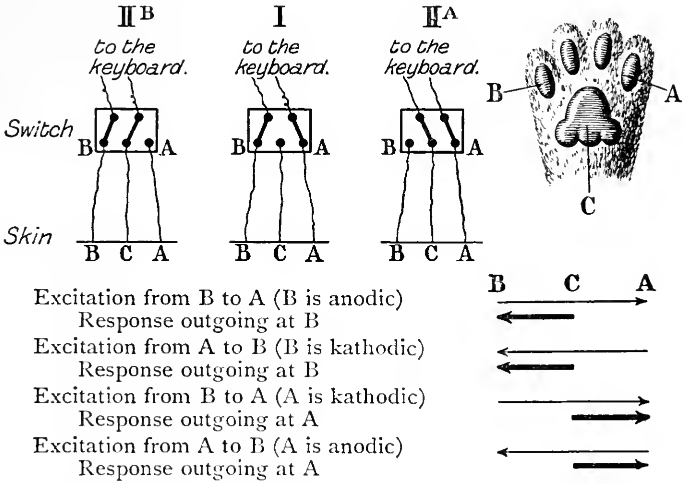


FIG. 45.—Cat. Response of skin to tetanisation of the sciatic nerve, repeated at 1 minute intervals, and lasting for about 5 seconds. The deflections at the beginning and at the end of the record are standardising deflections by $\frac{1}{100}$th volt.

The direct (blaze) effects that persist for hours or days after the indirect excitability of the skin and the indirect and direct excitability of muscle have disappeared. I am here referring to the direct and indirect excitability of muscle in the usual acceptation of these terms; I have not yet studied in detail the direct (blaze) effects in either muscle or nerve, but only in the skin. The question, "How long does a cat's foot live?" is, I believe, to be answered by reference to the blaze-currents of the skin, which I have found in a favourable case as long as a week post-mortem, when no other sign of life on any other tissue could be detected. And by a favourable case I mean that of a strong, well-nourished cat—the half-starved derelicts that sometimes find their way into a physiological laboratory have a dead skin two or three days post-mortem.

§ 64. *More A B C.*—Our second half-hour will have been well employed if the application of what in the last lecture was entitled the A B C method can be made absolutely plain. We shall follow the system of notation that I then recommended to your attention, and work through the four tests on a cat's foot in accordance with the following diagram, which gives the A B C switch in its several positions and the manner of its connection with the keyboard and galvanometer. You will see, if you trace out the connections, that, with the switch in the first position, deflection to your right means current from B to A, that in the position II^B it means current from B to C, and that in the position II^A it means current from C to A. By a glance at the switch and reverser, you can therefore recognise the direction of excitation and the direction of response at B or at A; and it will be a perfectly simple matter to work through the four tests

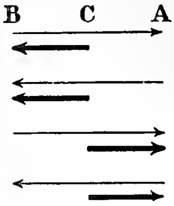


Excitation from B to A (B is anodic)
Response outgoing at B
Excitation from A to B (B is kathodic)
Response outgoing at B
Excitation from B to A (A is kathodic)
Response outgoing at A
Excitation from A to B (A is anodic)
Response outgoing at A

FIG. 46.—Cat's paw (24 hours post-mortem), A, B, C, as indicated above. Excitation by tetanising currents. Berne coil. Two Leclanchés. 10,000 units. The response is always of the nature of an outgoing current at A, and at B for both directions of excitation.

to verify the following formula, which previous experiments have shown to be that of the responses of a cat's paw twenty-four hours after death :—

Excitation from B to A (B is anodic)
Response outgoing at B
Excitation from A to B (B is kathodic)
Response outgoing at B
Excitation from B to A (A is kathodic)
Response outgoing at A
Excitation from A to B (A is anodic)
Response outgoing at A



And now, if I have succeeded in making clear to you that the deflections seen on the scale indicate current in the object towards B (*i.e.*, out at B), or towards A (out at A), or from B (in at B), or from A (in at A)—the results of the experiment will be clear to you as it progresses.

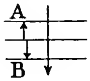
I intend to examine B; I therefore compensate the points B C with the switch in the position II . Then I plug the galvanometer at the keyboard, move the switch to the first position, and send a break induction shock through the paw from B to A. I turn back the switch to the old position, II^{B}, and unplug the galvanometer. The deflection is to your left as figured, signifying that there is now current from C to B (the previous anode), which is outgoing at B. It is what in Biedermann's terminology is called a negative anodic current—*i.e.*, "negative" to the original current.

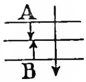
I repeat a second trial in precisely the same way, but with a reversed direction of excitation, so that B is now its kathode. The deflection is again to your left, outgoing at B; it is a positive, kathodic current—*i.e.*, "positive" to the original current.

And in precisely the same way, as a confirmatory pair of trials, I repeat on the A C side; only, perhaps, especially if the previous trials have been made with strong currents, it may be prudent to shift the electrode A to a fresh pad. Both the trials give deflection to your right, outgoing at A, positive kathodic after excitation from B to A, negative anodic after excitation from A to B. So that the formula previously sketched has been precisely fulfilled; all the responses have been outgoing.

§ 65. *A vegetable surface.*—In contrast with the preceding, let me now show you another group of four trials—on a vegetable surface—of which the formula has been drawn up beforehand, to be verified presently. I have chosen a geranium leaf.

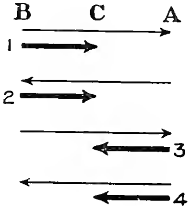
But let us pause a moment to reflect upon the conditions of experiment if we were limited to the use of two electrodes, and had no previous knowledge of the direction in which the response takes place. We should be obliged to apply our electrodes to two external points of the leaf, the deflection would be the sum or the difference between two opposed responses, and we could not tell which was the greater of the two. Suppose, *e.g.*, that we applied the two electrodes to opposite points on the upper and lower surfaces, and observed a response directed from upper to lower surface; this might result either from two outgoing currents that at B exceeding that at A : or from two ingoing currents, that at A exceeding that at B : and until we know whether the effects are ingoing or outgoing, we could not decide between the two alternatives. We are obliged to use three electrodes to enable us to test separately the point A and the point B, by connecting first one and then the other point through the galvanometer with an indifferent point C.





We proceed then with the experiment, having clearly realised the simplicity and necessity of its apparent complication. The results, as you see, come out precisely as figured in the diagram before you :

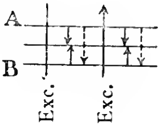
All four reactions are ingoing; Nos. 1 and 4 are homodrome post-anodic; Nos. 2 and 3 are antidrome post-kathodic.



§ 66. *Surface against surface.*—And now, having learned that the reactions of the external surface of a leaf are ingoing, we may make use of the resultant effect when only two electrodes are used, to learn whether one of two points or of two surfaces acts more powerfully than the other. Is, *e.g.*, the ingoing blaze of the upper or of the lower surface predominant when points of both surfaces act against each other through the galvanometer? If to both directions of excitation, the resultant is in one, say, a descending direction, we may be pretty sure that the upper surface reacts more powerfully than the lower surface; but to make quite sure, it is better to take two pairs of tests, reversing the order of direction in each pair, *i.e.*, to take the responses after excitations B to A, A to B, and after excitations A to B then B to A, because it may well happen with excitations of any considerable strength that the first is greater than a second excitation, and we are not assured that a difference thus caused might not disturb a comparison.

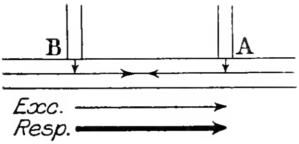
Homodrome post-anodic of upper surface greater than
Antidrome post-kathodic of lower surface; therefore
Homodrome descending response A to B.

Antidrome post-kathodic of upper surface greater than
Homodrome post-anodic of lower surface; therefore
Antidrome descending response A to B.

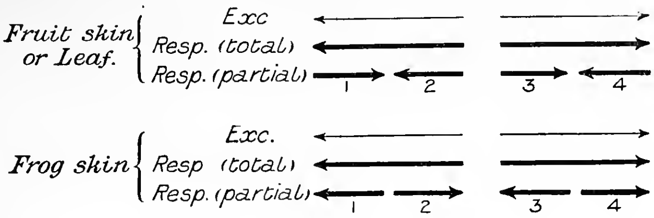


A result of this character clearly proves that the blaze of the upper surface of a leaf (beside geranium I have also tested lilac and violet leaves) predominates over the blaze of its lower surface. The ingoing current of the upper surface, whether anodic or kathodic, has exceeded the ingoing current of the lower surface, whether kathodic or anodic. We must be careful, however, to secure equal areæ of the two exciting electrodes (see § 69).

§ 67. *Anodic versus Kathodic blaze.*—You ask again, whether, *cæteris paribus*, an anodic or a kathodic blaze is the greater. To answer this question, you only require to make a sufficient number of trials in which the two currents are opposed to each other from points on one surface. You apply, *e.g.*, your two electrodes to the upper surface (or to the lower surface), and find that the after-effect is homodrome with the exciting current. You conclude that normally the post-anodic ingoing homodrome blaze exceeds the post-kathodic ingoing antidrome blaze.



The frog's skin gives—with two electrodes applied to its external surface—a similar positive effect; but in this instance we found, by analysing its polar factors, that the after-effect is homodrome with the exciting current by reason of an excess of post-kathodic outgoing homodrome over post-anodic outgoing antidrome blaze. The complete formulæ in the two cases run as follows:—



§ 68. *Tongue surfaces.*—The frog's tongue, examined in the usual way by the electrodes applied to the upper and lower surfaces, presents an analogous case to that of a leaf; its response, when stimulated, is the resultant of two effects at the two opposite poles. The tongue, as it lies on the floor of the mouth, gives an ascending resultant, which, if we might be sure that the effects were outgoing at the two surfaces, indicates that the upper surface of the tongue acts more powerfully than the lower surface. The current of rest is descending, and if we may admit as proved that the upper is the more effective surface, this descending resultant indicates an ingoing current of rest.

But the detailed study of the frog's tongue belongs to the intricate and theoretically important subject of mucous currents, which has been treated of at a considerable length by Biedermann. I hope to discuss the whole question of mucous currents in a more complete manner than is possible to-day. Any one who is curious in the matter should refer to Biedermann's papers or to the full account in his *Electro-physiology*. You will find there that he attributes great importance to the positive and negative responses of the tongue in connection with the theory of assimilatory and dissimilatory phenomena. You may very probably think, as I do, that an organ with *two* effective epithelial layers, even if one of these layers is greatly more effective than the other, is not the most suitable object to afford contrary electrical effects significant of contrary chemical changes. It would have been preferable if Biedermann had based his case upon contrary electrical effects of a single mucous surface. And I think that when you have reflected upon the conditions of the problem, you will realise as a clear economy of labour and an escape from much perplexity, to methodically follow the A B C plan for the separate examination of the single points A and B of a simple mucous surface. I have done so to some extent, but by no means sufficiently. As far as I have gone, I find that the electrical response of a mucous surface may be ingoing or outgoing, but that it is usually the former. Here, *e.g.*, is the record of a series of ingoing responses of a frog's stomach:—

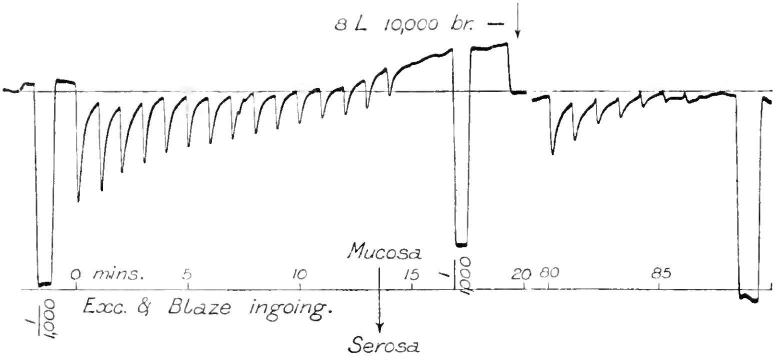


FIG. 47.—Frog. Stomach. Two series of ingoing responses to ingoing single break induction shocks at one minute intervals. Interval of one hour between the first and second series.

§ 69. *A warning.*—Let me here put you on your guard against a fallacy to which I was myself hardly alive in the first comparisons of anode *versus* kathode, and surface against surface. It is important that the area of contact between surface and electrode shall, as far as possible, be equal on both sides and not accidentally extended by excess of clay or by fluid used to moisten the electrodes. As a matter of fact, it generally happened that this necessary condition obtained in my earliest experiments, for the tubes of both electrodes were of equal bore, and any excess of fluid around them was removed by filter paper. But failing this precaution, we should be liable to have unequal effects, due to unequal current densities at the two poles. If the inequality is very marked, we shall obtain greater response from the pole of smaller area (*i.e.*, where current density is greater), whether that pole be anode or kathode. The fact deserves to be illustrated by an experiment *ad hoc*. Here then is a living surface—it happens to be a vegetable surface—to which two electrodes of different area are applied; the excitation is applied first in one then in the other direction, and as you see, both the responses are in the same direction, ingoing at the pointed electrode, whether that electrode has been anodic or kathodic.

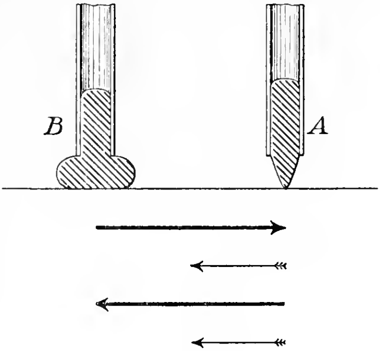


FIG. 48.

Will some one be good enough to repeat this experiment on a piece of frog's skin? I should expect him to find both responses to be outgoing at the pointed electrode, instead of ingoing as in the vegetable surface.*

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* This has since been verified by Dr Alcock.

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LECTURE VII

Observations on the Human Skin—Du Bois-Reymond's Experiments—Tarchanoff's Observations—Sweat-prints—Introduction of Ions through the Skin.

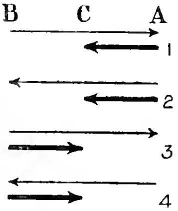
EXPERIMENTS by which electro-motive reactions are sought to be demonstrated on the human subject are full of pitfalls, and beset with fallacies. I do not consider that any one of the three principal experiments I am about to show you ought to be regarded as convincing or conclusive, and it is mainly as an exercise in criticism that they have been prepared for demonstration.

A monotonous series of successful experiments is against all nature; lecture-table discoveries are never as easy as they are made to appear; there is often more real instruction in "failure" than in "success."

§ 70. *A fruitless "experiment."* — More than one person, on learning that a blaze-current is a characteristic sign of life, has said this: "Will my finger give a blaze-current if I place it between those electrodes: it is alive I suppose?" To which question the obvious reply is, "Try it." In some cases the "student" has said, "Oh, I don't like electric shocks," and his research has terminated at this point. But if of a more inquiring type, he has perhaps placed a finger between the electrodes, and thereby experienced a first difficulty in this simple-looking experiment. He cannot keep his finger absolutely still between the electrodes, and the galvanometer spot wanders aimlessly to and fro on the scale. The "research" may stop here; the "student" has to catch a train; his scientific curiosity is satisfied. A third student having cleared the first (imaginary) and second very real and most obstructive fence, keeps his finger fairly quiet between the electrodes, so that it is possible to neutralise the accidental effects occurring between electrodes and skin, and get the galvanometer spot fairly steady at or near its zero point. An induction shock may now be passed through the finger. This is the third fence; for take the shock as weak as you like, and you may be sure that the patient will jump, shift contact, disturb compensation, and have to begin over again many times, before he is able to keep his finger quiet while a sufficiently strong shock is passed through it. But let us say that he has reached this point, and that his finger is in circuit, steady and currentless, and unmoved when a shock is passed. You would find, even now, that the response is uncertain, irregular, and capricious, always open to the objection that contact between skin and electrodes has been altered during experiment. And if you reflect upon the conditions of experiment, I think you may fairly abandon it at this point. For you have at best the resultant of two opposite effects at the two electrodes, which resultant will depend upon at least two or three unknown variables. You do not know what is the normal direction of skin response, nor whether one or other portion of skin is physiologically more or less effective, nor whether there are polar differences when one or other portion is anodic or kathodic. The original question cannot be answered by this apparently simple, but in reality most objectionable and complicated experiment.

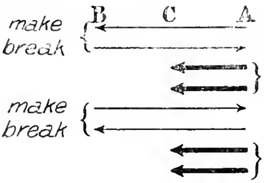
I am not sure yet, in spite of several trials of the point, whether or no a conclusive answer is to be obtained as to the nature and direction of excitatory currents in the intact human skin. I am, however, quite sure that no such answer is to be got with a single pair of electrodes, and that we must first study the separate polar effects by the A B C method, exciting through A B, leading off through A C or B C after previous compensation.

I did this two years ago, obtaining what then appeared to me to be sufficiently constant and regular effects; the formula of skin response was thus—



The responses Nos. 1 and 4, being antidrome to the exciting current, I regarded as equivocal; Nos. 2 and 3, being homodrome to the exciting current, as unequivocal. All the responses were "ingoing" at the excited spot, a direction that is generally assumed to be the normal direction of skin-current in the cat and in man. But there was the principal and unavoidable defect in these trials, that they have not and cannot be repeated on the same skin after death; so that we cannot feel certain that the so-called unequivocal responses have not been due to anomalous polarisation, which with the form of electrodes employed was found liable to occur. Amalgamated zinc plates covered with chamois leather soaked in zinc sulphate are rarely free of polarisation currents, ordinary kathodic antidrome as well as anomalous anodic homodrome, and with tetanisation they give a formula in all points similar to that given above. I do not therefore regard the results as being conclusive until repeated with more perfect electrodes.

The fallacy caused by anomalous polarisation of imperfect electrodes—so far from being avoided by the use of tetanising currents—is favoured, for we then have to do with antidrome kathodic polarisation by one current *plus* homodrome anodic polarisation by the opposite current.



§ 71. *A fruitful experiment.*—Allusion has been made above to the "blaze-currents" of excised human skin (§ 53, p. 86), and I should like to bring the point once more under your notice, as it has been for the last few weeks under my close observation. I wanted to know how long after death this sign of life can be detected in the skin itself, and whether the duration of survival is found to vary after various modes of death. The skin is a tissue of quite remarkable vitality; it seems as if it had learned to resist injury from its surroundings, and to have become tough and hardy of habit. You may have noticed in your rambles logs by the wayside from which young shoots have sprung from surviving subcortical tissues; perhaps you have heard that on Napoleon I.'s removal from St Helena to the Invalides, his toe-nails were found to have grown through his boots—a sign of the extraordinary vitality of the cells of the nail-matrix, or of the perishable quality of boot-leather — nearly twenty years had elapsed between burial and exhumation. There is no doubt whatever that the hair grows after death.

In surgical practice it is a very common proceeding to accelerate the recovering of a raw surface by "skin-grafting." It is essential that such grafts should include cells of the malpighian layer.

All these things point to an exceptional vitality of cutaneous or rather subcutaneous malpighian elements.

I find that in the skin of persons dying suddenly in otherwise good health, the cutaneous blaze-currents persist for several days, whereas the skin taken from ordinary post-mortem room subjects, having died gradually and completely, exhibits little or none of this sign of life twenty-four and forty-eight hours *post mortem.*

Let me remind you of the nature of this sign, for the questions to which it may serve as an indicator are by no means exhausted. A piece of living skin set up between electrodes, and tested in the usual way by induction currents of both directions, responds by blaze-current in one—the outgoing direction. A piece of dead skin does nothing of the kind, but gives, if anything, small polarisation counter-currents. And since living skin responds in one direction to both directions of excitation, you may (observing due reservation and precaution) obtain outgoing blaze-currents after tetanisation by alternating currents in both pairs of directions. Here are galvanometric records of the electrical responses of surviving human skin, and of the same skin, killed by heat.

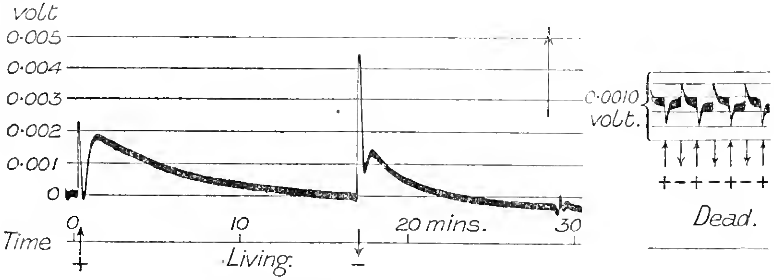


FIG. 49 (4201).—Skin of breast 8 hours after amputation. *Living.*—Two + responses to single break induction shocks in + and − directions. 8 L. 10,000. *Dead.*—Several − and + effects to + and − shocks, *i.e.*, polarisation. Resistance diminished.

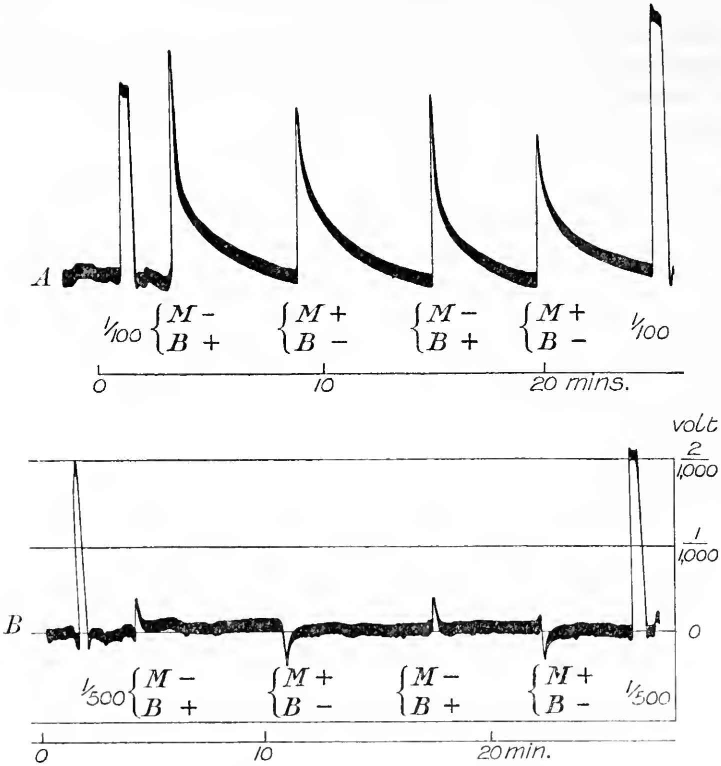


FIG. 50 (Nos. 4199-4200).—Skin of breast 5 hours after amputation. Tested by tetanising currents for periods of 5 seconds each from a Berne coil at 5000 units, supplied by 8 Leclanché cells. Conductance at outset of experiment = 5, and calculated resistance = 520,000 ohms. After tetanisation the conductance was raised to 12.5 (= 196,000 ohms); after further tetanisation it rose further to 25 (= 88,000 ohms), when the record commenced. The resistance of the galvanometer and electrodes = 20,000 ohms. The deflection by $\frac{1}{10}$th volt through 1 megohm = 27.

A, *living*.—Conductance at outset . . . . = 25
1st response to tetan., m. −, br. +, = +0.0120 volt.
2nd " " m. +, br. −, = +0.0092 "
3rd " " m. −, br. +, = +0.0100 "
4th " " m. +, br. −, = +0.0076 "
Conductance at end . . . . . . = 35

B, *boiled*.—Conductance . . . . = 115
1st response to tetan., m. −, br. +, = +0.0004 volt.
2nd " " m. +, br. −, = −0.0004 "
3rd " " m. −, br. +, = +0.0004 "
4th " " m. +, br. −, = −0.0004 "
Conductance . . . . = 115

One more point to conclude this matter of the surviving human skin. If a piece of living skin, placed between electrodes and connected with a galvanometer in the usual way, is gradually cooled in a freezing-box, we shall notice, at a given temperature of about – 5°, a sudden deflection of the galvanometric spot indicative of a sudden electromotive change. The effect is due to the sudden congelation of the under-cooled tissue. This "congelation blaze," which is manifested by vegetable as well as by animal tissues, is in general their last sign of life; if the frozen tissue is thawed, and then cooled a second time, there is little or no second blaze according as the tissue has been more or less completely killed by the first proceeding. In the present case, that of the human skin, the congelation blaze-current is of outgoing direction.

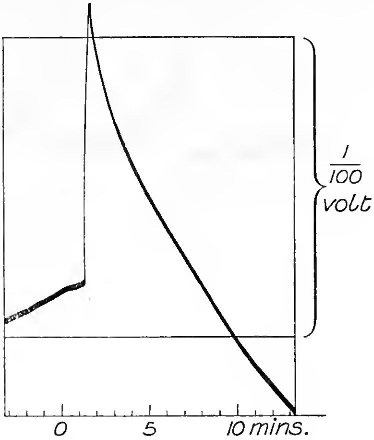


FIG. 51 (4209).—Skin of man. 2nd day after excision. Skin gradually cooled by surrounding the skin-chamber with a freezing mixture. Sudden electromotive discharge (outgoing current) at a temperature of – 6° inside the skin-chamber. Before freezing the + responses to + and – single induction shocks were +0.004 and +0.008 volt. After freezing, the + responses were absent, being replaced by small – and + polarisation effects. On recongelation no second discharge was observed.

Alterations of electrical resistance occur in marked degree in connection with the electromotive effects that first attract our attention. Surviving skin as it dies exhibits a fall of resistance. There is a well-marked diminution of resistance as the immediate consequence of electrical excitation; Fig. 50 incidentally shows this. And in the course of cooling, there is first a gradually increasing resistance, then at the point of congelation a sudden increase of resistance, which in some instances is preceded by a small and evanescent diminution, not unlike a congelation blaze, which, however, I have reason to attribute to a slight rise of temperature and of conductivity occurring when the under-cooled tissue juices pass from the liquid to the solid state. But the details of this effect require closer investigation than I have yet found time to give to them. Thawed skin, subsequent to congelation, has a greatly diminished resistance —*e.g.*, a diminution to 50,000 ohms from an original resistance of 150,000 ohms.

Vegetable tissues likewise exhibit a very marked diminution of resistance in consequence of excitation, and the diminution is not solely a diminution of "contact resistance" at the electrodes. It is internal or interpolar as well, owing probably to a multiplication of electrolytes, possibly also to an actual rupture of cell membranes. A very simple experiment will serve to show you that the augmented conductivity is interpolar as well as polar. A flower stalk is laid across four unpolarisable electrodes, E I I E, at 5 cm. intervals; a tenth of a volt is allowed to act upon the galvanometer through the entire length of stalk E E, and through an intermediate portion I I. The deflections indicate the current strength, and therefore the conductance of the corresponding lengths of stem. Noting their values before and after tetanisation of the whole stem through the terminal electrodes E E, you will find that the conductance is augmented in the intermediate part I I, showing that the alteration is not restricted to the contacts E E. The conductance of I I, which was 0.8 γ before the excitation through E E, is raised to 2.0 γ; in E E itself, it has been raised from 0.4 γ to 1.6 γ.*

§ 72. *Du Bois' experiment.*—The galvanometer is in its usual position, with its magnets pointing N and S, and the scale correspondingly arranged N and S; you may consider that the two ends of the scale represent the two terminals of the galvanometer. I am seated facing you below the scale, with my

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* The symbol γ denotes our unit of conductivity. (See Appendix, p. 169.) The conductance and resistance in the above experiment are :—

of I I before	0.8 γ	1.25 Ω.
after	2.0 ,,	0.5 ,,
E E before	0.4 ,,	2.5 ,,
after	1.6 ,,	0.625 ,,

left hand connected with the S terminal, and my right hand with the N. The forefinger of each hand dips in salt solution, there is little or no difference of potential between my two hands, and the spot is at rest.

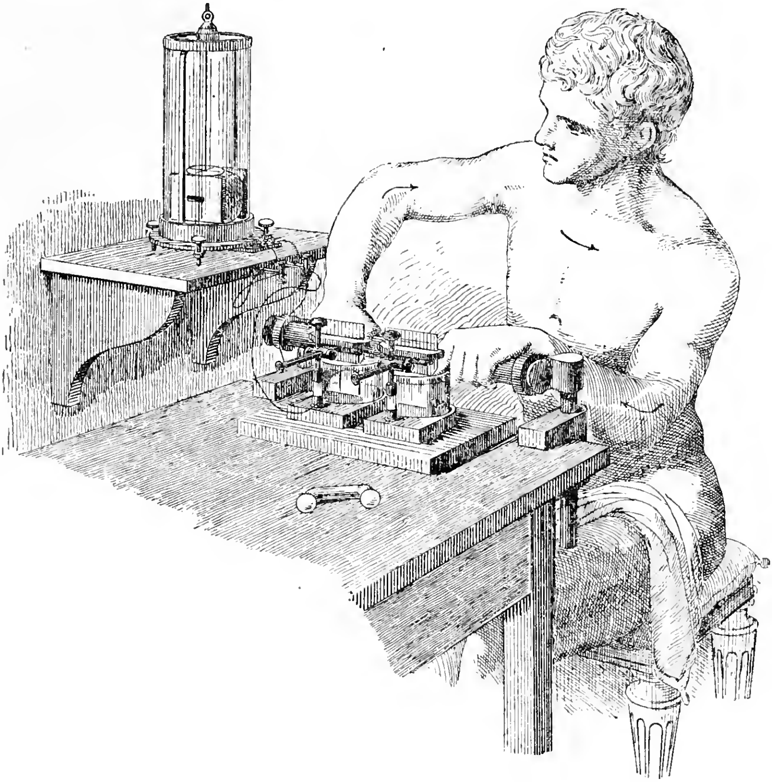

FIG. 52.—Du Bois-Reymond's "Willkürversuch," to demonstrate a negative variation during voluntary muscular contraction. The current is ascending in the active arm. (From du Bois-Reymond's *Thierische Elektricität*).

I now firmly contract the muscles of my right forearm; the spot moves to my right (your left), or clockwise in the circuit, or in my body from right to left. The spot is "pulled."

Now I contract the muscles of my left forearm, and everything is reversed. You have witnessed du Bois-Reymond's celebrated "willkürversuch," by which he considered that he had demonstrated on the normal human subject the electrical effects of voluntary muscular contraction, and I think you may be interested to see the actual figure by which he illustrated the experiment (Fig. 52).

The usual criticism quoted of this experiment is that of Hermann, who explains the deflection observed in du Bois-Reymond's experiment as being the effect of a secretion current provoked in the skin of the contracting side. He says that in the skin of that side such current will be directed from without inwards, giving current ascending in the active arm.

This criticism is based upon observations by Hermann and Luchsinger concerning the effects of atropine on the sweat currents of cats, and he expresses himself as follows:—"A curarised man could give the du Bois current in the absence of muscular contraction. In the case of an atropinised man it would be absent, in spite of the presence of muscular contraction."*

I do not myself think that the alternative explanation is necessary. To my mind, du Bois-Reymond's experiment does not demonstrate the existence of contraction currents on man; nor do Hermann's experiments on cats show that du Bois' currents on man are secretion currents. Neither the contraction current nor the secretion current has been separately obtained on man; the currents that we have witnessed are susceptible of a far simpler explanation.

I think they are simply capillary currents arising at the surface of separation between salt solution and skin. Let me show you a couple of experiments in point.

Instead of dipping the two fingers simultaneously, I will dip them successively, so that the skin of one finger may be pretty completely soaked when the skin of the second finger commences to be moistened. There is no deflection so long as only one finger is introduced, but on introduction of the second finger there is current through the galvanometer from the first to the second finger, therefore through the body from the second

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* Hermann, *Handbuch*, vol. i., p. 225.

to the first. The spot is "pulled by the ingoing capillary soakage."

Here, now, is a counter experiment:—

Both fingers are resting against the bottom of the vessels, as indeed was recommended by du Bois-Reymond in order to avoid the fallacy that I have just mentioned, and when the spot is at rest I squeeze one of my fingers, say, of the left hand, against the bottom of the vessel. The current through the galvanometer is now from the compressed skin. The spot is "pushed." In case you should object to the possible muscular or secretory origin of the current by reason of the voluntary action on that side used to effect the compression, I will remain perfectly passive, and have the compression effected by a second person without any act of mine. The effect follows as before.

While I am on this subject, let me show you one more surface experiment. You have seen that contraction pulls the spot, that soaking skin pulls the spot, that squeezed skin pushes. I want to dry a wet finger in order to dip it in dry, I naturally rub it, and then proceed to show that on soaking it again the spot is pulled. But now, as you see, the effect is reversed, the spot is pushed; dry *rubbed* skin pushes the spot.

And so we may use for our memorandum, that if zinc *pulls* the spot, last-dipped and therefore soaking skin *pulls*, that squeezed skin *pushes*, and that recently rubbed skin *pushes*. Neither du Bois-Reymond's contraction current, nor Hermann's secretion current are above suspicion in presence of those unavoidable capillary currents. And for my part I find it quite impossible to contract the muscles of my forearm without moving a finger or pressing it against something.

§ 73. *Tarchanoff's experiment.*—Over ten years ago, Tarchanoff published an account of observations on the skin-currents of the human subject, in which he considered that he had obtained evidence of their reflex causation by all kinds of peripheral stimuli—by tickling, by induction shocks, by pricking with a pin, by hot and cold water, by sudden sound, sight, taste, and smell. He assures us, further, that imaginary sensations, intellectual effort, or strained attention bring about similar effects—"always, of course, during complete immobility of the subject." Voluntary movement of any part of the body, during absolute quiescence of the part connected with the galvanometer, gives a skin current the strength of which is dependent on the strength of the voluntary effort. He says that parts in which sweat-glands are most abundant (palm of hand, toes, axilla, etc.) become negative to parts containing few glands (back, nates, external surface of thigh and arm), and considers, therefore, that the active state of the nervous system gives rise to an ingoing secretion current similar to that shown by Hermann in the case of the frog's skin, by excitation of its cutaneous nerves.

Tarchanoff further assures us that he used a sensitive, almost completely aperiodic, galvanometer, giving with the nerve current of a frog's sciatic a deflection "off scale" (*i.e.*, greater than 50 divisions); the skin effects he observed also gave deflections "off scale," had a latent period of one to three seconds, outlasted the stimulus by several minutes, and returned gradually but irregularly to rest. Connection with the skin was made from unpolarisable electrodes of the usual type by strips of hygroscopic wool (10 to 15 cm. long) soaked in normal saline, brought in contact with pads of the same material previously applied to the skin. These pads were of an area of 10 to 15 cm. The currents of rest were previously compensated. In the case of the hand, the effect of gentle tickling was generally such that "die Basis der Finger in der Mehrzahl der Fälle negative, der Thenar dagegen positive elektrische Spannung besitzt." Imaginary sensation gave deflections of 10 to 15 divisions.

Now these things are clearly of considerable interest, if a true physiological effect regularly coincident with nervous activity can be demonstrated; and I have somewhat minutely described to you the conditions of observation, in case any one should be inclined to make fair and patient test of the statements. I must confess, however, that for my own part I am not convinced that the deflections have been anything more than rather unduly pronounced galvanometric vagaries occurring with shifting contacts. We all know how difficult it is to preserve a limb absolutely quiet, and that even when we think that our muscles are completely at rest, a "thought-reader" can obtain information from our unconscious movements. It is no easy matter to have a loose pad immobile against the skin, and if it be fixed by a band, the least swelling or movement will alter its pressure against the skin; and I cannot say that I have succeeded in satisfying myself that the irregular deflections that certainly do occur with a subject keeping as quiet as possible, and more markedly when the subject is anywise startled or stimulated, have been anything else than the effects of accidents of surface contact. I am willing to admit that they *might* be accidents of nervous tension giving true alterations of skin-currents, but I cannot admit that this possibility has been proved to the exclusion of the coarser fallacy. Will any one undertake to clear up this point? If so, perhaps it may be worth while to mention that the skin can be locally atropinised * by means of a belladonna plaster, and that obviously a locally atropinised skin should show no effect of glandular action, but the usual effects of accidents of contact.

I do not think that these observations on the human subject are particularly satisfactory, and shall not dwell upon them any longer. I will use the remainder of the hour to place before you certain facts relating to the transport of medicaments into the human body under the influence of the galvanic current.

§ 74. *Importation of ions.*—All such facts are illustrations of the principles of electrolytic conduction. If a sufficiently strong current is passed through a saline solution, or, as I am about to show you, through a porous electrode soaked in a saline solution, the electro-positive kations of the salt travel with the current from the anode to the kathode, while the electro-negative anions travel against the current from the kathode to the anode. Taking, *e.g.*, the case of NaCl, the Na travels with the current, the Cl against the current. You may for the present purpose

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* Aubert, "Sweat-prints," *Ann. de Dermatologie*, 1877-8; Article "Sueur," (by François Franc) in *Dict. Encycl. des Sciences Médicales*, xiii.

regard the tissues as represented by a sponge of such NaCl solution; if you pass the current into the body by porous electrodes soaked in some other salt—and for this purpose we shall take permanganate of potash—you will, after a few minutes, observe a visible sign of the transfer of the anion from electrode to body in the form of a discoloration of the skin at the spot where the anions have travelled against the direction of current from kathode to anode. I chose permanganate of potash because it has a coloured ion, in this case the anion. If I had taken copper sulphate, where it is the kation copper that is coloured, I should have made the anodic spot the more apparent since the metal travels *with* the current and is carried into the body at the anode.

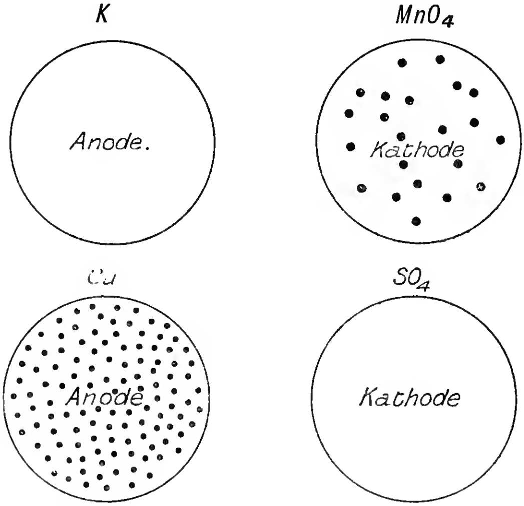

FIG. 53.—Circular areæ of skin of the forearm that have served as electrodes to a constant current for a few minutes. In the upper pair of circles the two electrodes in contact with the skin were a solution of permanganate of potash; the coloured ion was the anion MnO_4, which travels up stream and enters the body at the kathode. In the lower pair of circles, the two electrodes in contact with the skin were a solution of copper sulphate; the coloured ion was the kation Cu, which travels down stream and enters the body at the anode.

Two electrodes—one-inch glass tubes half full of permanganate of potash—are strapped to the front of my forearm, and perpendicular to it. The electrodes are connected with the house current, which is at 110 volts. Out of caution for my own comfort, I have means of taking any desired fraction of the whole current; and to tell what current I am taking, there is a milliamperemeter in circuit with my arm. The electrodes have areæ of about seven square centimetres, and a current of between two and three milliamperes should produce a distinct result in about five minutes. The kathode is, I believe, nearer to the wrist, the anode above it; but we shall soon see, for it is at the kathode that we shall find evidence of penetration of the coloured anion, MnO_4.

The trial is over; and after washing the forearm under the tap, you see a number of indelible brown spots over the previously kathodic area of the skin, which are due to its penetration by the coloured anion, which you remember travels *against* the current, and therefore gets into the body where the current leaves it. Notice their clearly defined punctiform appearance; this signifies that the path of current has been chiefly, if not entirely, by way of the sweat-ducts, hardly or not at all through the general epidermic investment.

A similar principle of transport holds good in the case of other electrolytes, and it is interesting to note, in the case of poisonous salts, whether it is the anode or the kathode that acts as the channel of introduction. In most cases, *e.g.*, in that of strychnine sulphate, the poisonous property belongs to the base, the kation, which penetrates at the anode; in others, *e.g.*, in that of cyanide of potassium, it belongs to the acidic moiety, the anion, which penetrates by the kathode. In the first case the anode is the poison carrier, the kathode being innocuous; in the second case it is the kathode that kills. If, following the example of Leduc, I should place two rabbits side by side, connecting them by a couple of electrodes of indifferent nature, *i.e.*, soaked in NaCl, and then run a current through both rabbits in series, by means of electrodes moistened with strychnine sulphate, I should put the anodic rabbit into strychnine convulsions by reason of penetration of the kation, while the kathodic rabbit, taking in only the non-toxic anion, would remain quite unaffected.

§ 75. *A supplementary experiment.*—Let us take advantage, of the altered area of skin of our $KMnO_4$ experiment to make a further trial. Its sweat-ducts are choked with MnO_4—*i.e.*, with a non-living electrolyte that may serve us as a conductor to the inner aspect of the skin. I should like to take this altered area of skin and an unaltered area of intact skin into circuit with an induction coil and a galvanometer, to be tested in the usual way. This is now done by tubes of zinc sulphate, and the first point you notice is that there is a considerable current directed in the body from the irritated to the intact spot, or ingoing through the former and outgoing through the latter. This current being compensated and the galvanometer plugged out, I apply excitation in the usual way by induction shocks and by tetanisation, and look for the after-currents that may be aroused. In accordance with your expectation, they are in every case opposed to the current of injury—*i.e.*, ingoing at the intact skin and outgoing at the manganised skin. This result, as far as it goes, agrees with the conclusion that the normal irritated skin of man is the seat of an ingoing current; but I should be sorry to lay much stress on the result of an isolated experiment, the point deserves further investigation.

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LECTURE VIII

The Fallacy of the Electrodes—Water Transport at Anode or Kathode—Alteration of Resistance at Anode or Kathode.

§ 76. *Review.*—This lecture is to be partly retrospective, partly prospective. We shall pass under a rapid review the principal steps of our investigation, inspecting with most care what may appear to us to be weak points, finding perhaps in those very weak points, points of attraction to further investigation.

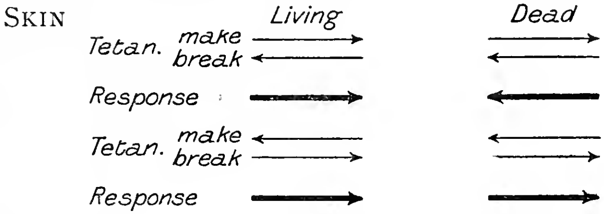
The main principle and "motif" running through the investigation has been that the electrical responses to electrical stimulation are a token and measure of vitality in the objects selected for examination—in the retina, in the entire eyeball, in its crystalline lens, in the skin of animals, in the "skin" of plants, in all the living tissues of plants, in living tissues of animals; and in my last lecture, when I tried to show you how slowly and gradually the vitality of human skin is lost, I ventured to touch upon a fallacy that becomes specially apparent when one undertakes to follow the sign to its last discernible trace. It was lost to sight among accessory physical reactions, fortunately small as compared with the physiological reactions of full vigour, but quite unavoidable, since they are inherent to the apparatus we have to use, I mean the electrodes. And although I call your special attention to the "Fallacy of the Electrodes" at this last stage, I should like to assure you that it has been carefully excluded in all the experiments you have witnessed, and that from the very outset of the investigation the possible simulation of a blaze-current by a polarisation at the electrodes has been considered and excluded. You remember, no doubt, that we hardly ever omitted to control the result observed on the living thing by the identical test applied to the same thing killed.

§ 77. *Fallacies.* — Fallacy of the electrodes arises from polarisation; our "unpolarisable" electrodes are not absolutely unpolarisable, and may accidentally be quite sensibly polarisable. Their polarisation currents, anomalous or positive, as well as normal or negative, are most manifest with a constant current, much less so, but still sensibly so, with induced currents. We have made use of induced currents only, and shall therefore restrict our attention to these.

With single shocks I do not think there is any liability to fallacy; an unequivocal or homodrome blaze-current cannot be simulated by anomalous polarisation, which is a rare and feeble effect manifested by a defective electrode, and quite absent from a properly prepared electrode. An equivocal or antidrome blaze-current might at first sight be taken as being due to ordinary polarisation, since it is of the same direction; but the magnitude of the response, its absence from the electrodes themselves when joined, and from the tissue itself when killed, will leave us in no doubt as to the physiological character of the reaction. It is only in the cases where single shocks having proved to be ineffective, we have recourse to the further test of tetanisation by alternating currents, in order to bring out a summated effect (p. 68), that there is any real possibility of deception. Distinguish between the two cases: (1) that in which the alternating currents are passed through the galvanometer and test-object; (2) that in which they are passed through the test object only while the galvanometer is short-circuited. The first of these two dispositions reproduces an arrangement that was first adopted by V. Fleischl in the case of nerve, and that I have already considered at some length in that connection. The opposed make-and-break currents are supposed to neutralise each other through the galvanometer, and such deflection as occurs is attributed to an electro-motive action of the test-object. This deflection occurs in the direction of the break current, *i.e.*, is such as would be produced by a physiological reaction in that direction, or as a physical reaction—the sum of counter-currents at make exceeding the sum of counter-currents at break. A closer scrutiny of the conditions of the reaction shows that both factors are, or may be, effective, *i.e.*, a physiological reaction in the direction of break can occur by reason of post-anodic action-current, and a physical reaction in that same direction can be due to an algebraic sum of ordinary polarisation currents.*

It is not quite easy to clearly demonstrate the physiological factor even in a favourable case, and practically impossible to do so in an unfavourable case; I have therefore not made systematic use of this first disposition of test.

The second disposition, by which only the after-effect of tetanisation is observed on the galvanometer, is, in my experience, less liable to be misleading than the first. But the case to which I systematically applied it, viz., the human skin, has been a somewhat favourable one to follow out, since by reason of its physiological disposition the skin gives sign of life by an outgoing response to all directions of induction currents. Tetanisation by such alternating currents provokes, first, a summation of physiological (outgoing) effects; second, a resultant of alternated polarisation effects which is in the



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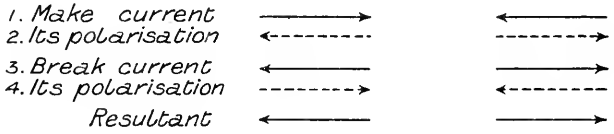
* Von Fleischl's deflection is discussed at some length in *Animal Electricity*, pp. 115-119, 1897. The superior polarisation by make there alluded to is shown in a paper to the Physiological Society (12th Nov. 1898), on the "Influence of Polarisation on the Electrical Resistance of Nerve." A deflection in the direction of break, during the passage of alternating induction shocks, might also be due to an irreciprocal resistance, smaller to the break than to the make shock, as occurs in the passage of alternating currents through a vacuum tube. I have not undertaken the physical analysis of these possible factors, and have simply abstained from using von Fleischl's deflection as a sign of life.

direction of the break current. Therefore, if to both pairs of directions of tetanisation the after-effect is in one (positive or outgoing) direction, we have proof that the skin is alive; if to both pairs of directions it is in the direction of the break, we have proof that it is dead.

I found it at first not a little confusing that a deflection in the direction of the break current—which in V. Fleischl's experiment on nerve is generally considered as a sign of life—should on skin (and on other killed tissues) be a sign of death. But evidently the deflection in question is, by reason of the physical factor mentioned above, a balance of ordinary polarisation in the direction of break. Here is the analysis of this physical resultant for the two pairs of tetanisation directions:—



the resultant in each case being due to the summated effects, No. 2 being greater than the summated effects No. 4.[*] You ask, perhaps—if you have followed the argument so far—why it should be preferable to observe an after-effect of tetanisation rather than an effect during tetanisation. Ought not a positive outgoing effect to manifest itself during as well as after tetanisation? So it does, with a lively skin, that will respond to strengths of tetanisation that can be passed through the galvanometer; such a skin will, however, also respond to the simpler question of single induction shocks; a skin so little

[*] This result may be observed; with strong tetanisation the resultant may be in the direction of make, the after-effect of the summated effects No. 4 being greater than that of the summated effects No. 2. Yet even in this case the effect *during* tetanisation is in the direction of the break. I am not certain whether the after-deflection in the direction of the make is physiological or purely physical. I place no reliance whatever upon the deflections obtained *during* strong tetanisation. They can happen by alterations of the galvanometer magnets by the opposed long and short currents, or by reason of asymmetry of the magnetic field in the absence of any electrolyte at all in circuit, or by reason of irreciprocal resistance.

alive as to require a series of shocks to bring about summation of effects, must be tested by tetanisation that cannot be passed through the galvanometer, which, therefore, must be short circuited during the process.

There is one more shape in which the fallacy of the electrodes may appear, which, under certain conditions, may be very deceptive indeed. The state of the electrodes, especially if they have been long put up, may be such that anomalous polarisation of one electrode may be present, with ordinary polarisation of the other electrode. The seat of such polarisation may be between zinc and zinc sulphate, or between zinc sulphate and saline clay. The deflection may be in one and the same direction for both pairs of directions of tetanisation, thus simulating the formula given above as characterising the living state. Electrodes of this nature must not be used. Electrodes prepared with ordinary care do not exhibit the fallacy.

§ 78. *A future preliminary.*—A methodical examination by the A B C method, of the polarisation effects produced by constant and by induced currents passed through various electrodes and electrolytes, would form a very useful preliminary exercise introductory to the study of physiological polarisation. You would find that some combinations are polarisable at both poles, that others give only anodic or only kathodic polarisation, and prominent among these purely physical effects you would find that by reason of anomalous polarisation the chief physiological after-current—the positive post-anodic action current—is exactly imitated, which things should not lead you to imagine that the physiological effects are "merely physical," but invite you rather to the further physical analysis of physiological phenomena.

§ 79. *Quinke currents.*—Currents of liquid through a porous partition, *e.g.*, a membrane through which osmose is taking place, arouse electrical currents in the direction of the water movement. Conversely, an electrical current passed through a porous partition between two electrolytes causes a flow of water in its own direction. This water transport, from anode towards kathode—kataphoresis—is a chief factor in the electrical osmose first made known to us by the investigations of Quinke.

Our attention is naturally directed to the question of such water transport through porous bodies by a very remarkable diminution of resistance that occurs—in skin, in leaves, etc.—as a consequence of the passage of induction shocks. This diminution of resistance, or augmentation of conductivity, is far more pronounced in living than in dead matter, and a diminution of resistance in consequence of molecular dissociation of active stuff must therefore be thought of.

I think it probable that both factors contribute to the result; their experimental distinction and separate examination appears very desirable, but very difficult.

It is indeed easy enough to witness what must be an effect of kataphoric water movement on an inert object, such as an eggshell; it is the distinction between effects of kataphoresis and a dissociation on a living object that is difficult. The best thing that can be hoped for, is to find cases where one factor is predominant and the other insignificant. In a muscle, *e.g.*, we may expect to get most distinct evidence of dissociation; Loeb* has, in fact, shown that the osmotic pressure of muscle is considerably augmented by tetanisation, resting muscle being isotonic with a 0.6 per cent. NaCl solution, tetanised muscle with a 1.0 per cent. solution. We should accordingly expect to find an increased conductivity in active muscle, perhaps also in active nerve—as was supposed to be the case by Grünhagen. I have not yet found time to carry out such experiments; perhaps someone among my present hearers will take them in hand.

The following experiment has been put up to show this purely physical effect of kataphoresis; it will at the same time serve to illustrate another of the fallacies that might deceive an inexperienced observer.

An eggshell (with its membrane) has been set up between the exploring electrodes to be examined in the usual way. From a compensator I pass $\frac{1}{100}$ volt through the shell and galvanometer; the deflection is $\frac{1}{2}$ degree of scale. I pass

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* Loeb, "Physiologische Untersuchungen über Ionenwirkungen (I Versuche am Muskel)," *Pflüger's Archiv*, lxix., p. 1, 1898, and lxxi., p. 457.

strong alternating induction currents through the eggshell (plugging out the galvanometer meanwhile), and then again pass $\frac{1}{100}$ volt through the eggshell and galvanometer. The deflection is now 20 degrees of scale, *i.e.*, the conductivity, by reason of water transport from electrodes to shell, has been increased more than fortyfold.

A propulsion of water, through capillary pores, by an electrical current, might conceivably outlast its original cause. And since a capillary current can give rise to an electrical current in its own direction, it is conceivable that a homodrome after-current might be thus brought about. I have at various times made a good many trials of this point, with porous septa of various kinds between saline solutions of various strengths, without ever observing anything at all comparable with an unequivocal blaze-current of a living object. Here is an ordinary dialysing tube containing a strong solution of zinc sulphate, and surrounded by a weaker solution; two amalgamated zinc rods dipping in the fluid on each side of the septum, serve as electrodes; the dialysing cell, compensator, induction coil and galvanometer are connected to the keyboard in the usual way. Notice, in the first place, the normal current—from less concentrated to more concentrated solution in the dialysing cell, *i.e.*, "with" the water current, and from more to less through the galvanometer. And now, with this concentration current compensated, I send a strong break shock through the dialyser first from B to A, when you see a polarisation deflection from A to B; then from A to B, when you see a polarisation deflection from B to A. And I do not stop to inquire whether these polarisation counter-currents are at the electrodes or at the interface of the two solutions; for they are antidrome effects, and we are now looking for homodrome effects.

So we find that although no doubt water transport through pores occurs in living as well as in dead matter, and contributes no doubt to augmented conductivity caused by electrical currents, it cannot be made responsible for the currents now familiar to us as blaze-currents; the *sine qua non* of these currents, whatever their chemico-physical mechanism may ultimately prove to be, is the living state.

And yet, while we find reason to reject an appeal to water currents (or "concentration currents"), as being the original source of electrical effects that arise or are provoked in living matter, we should be careful to remember that water currents must actually play an important, if secondary part, in the complicated molecular play of physiological action. Local action implies local disintegration, raised osmotic pressure, attraction of water, and electrical current. The water current is towards the active spot; the electrical current is from that spot; we must imagine it as a kationic current.

§ 80. *Evaporation current.*—This first experiment should serve as reminder to you that gradual shiftings of the galvanometer spot may, among other causes, be due to evaporation of water, and to capillary currents thereby produced. The circuit contains nothing but the galvanometer, and a pair of unpolaris-

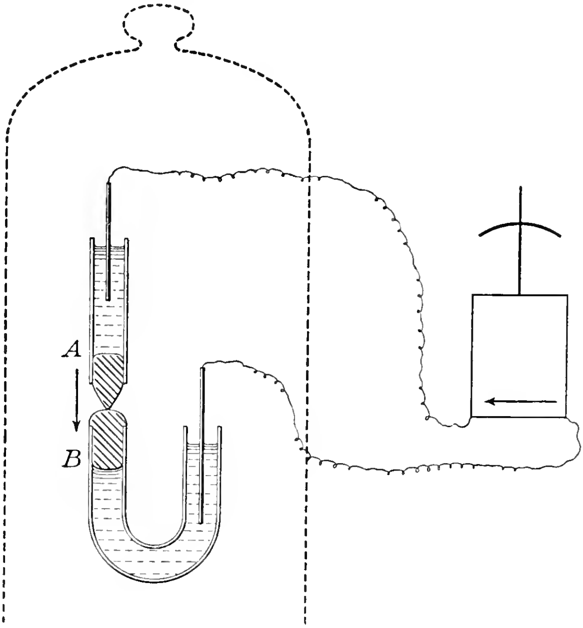

FIG. 54.—To illustrate evaporation currents.

able electrodes, the clay of which has been so shaped as to give dissimilar surfaces of evaporation. The clay is moist, the air of the room is dry, B is giving off water more quickly than A, and is sucking water from A, so the electrode current is to your left, as figured. I now bring down over the electrodes a bell-jar with a bit of wet blotting paper sticking inside it, *i.e.*, containing wet air. The galvanometer spot is sharply deflected to your right (by the checked or reversed water current). On removal of the bell-jar the spot is sharply deflected to the left (evaporation current to room air), and finally, when the evaporation and deflection have become steady, I cover the electrodes with a dry heated bell-jar, which at once, by accelerating the evaporation, causes a sharp deflection to the left. And for the present I am not concerned to know whether or no the concentration of saline solution plays a part in these evaporation effects; all I want to do is to show you that trifling alterations of evaporation can give quite considerable electrical effects.

§ 81. *Concentration current.*—The next experiment is intended to remind you of the usual direction of a concentration current —a point which in most text-books and monographs appears to be considered as too self-evident to be worth specifying. Two amalgamated zinc rods dip into a 25 per cent. solution of zinc sulphate, and are connected with the galvanometer.

A drop of distilled water allowed to run down B into the solution gives deflection to your right (current from B to A). A drop of saturated zinc sulphate to B gives deflection to your left (current from A to B).

And of course dilution at A gives deflection to the left, concentration at A gives deflection to the right. In terms of the ionic movements, this happens by reason of greater velocity of the anion (which travels from the more concentrated to the less concentrated solution, giving therefore current in the reverse direction). With acids, *e.g.*, HCl, and complex organic salts, *e.g.*, CH_3COOK, in which the kation travels faster than the anion, the current is from more to less concentrated solution. But with all our ordinary neutral salts, and with alkalies, the current is from dilute to concentrated, *i.e.*, *with* the water current.

The direction of electrical current between two unequally concentrated solutions of any electrolyte depends upon the relative velocities of the two ions, both of which are of course travelling from concentrated to dilute solution. If the anion is of higher velocity, as is the case with alkalies and most salts, the current is from dilute to concentrated; if the kation is of higher velocity, as is the case with acids and some salts, the current is from concentrated to dilute. (See Fig. 55.) You may be disposed to admit provisionally, as I do, that the latter condition obtains in the case of the complex organic compounds that take part in the dance of life; current of action proceeding from the spot of greatest "livingness," where solution pressure is increased — and dissociation — and ionic concentration — and osmotic pressure.

SOME RELATIVE IONIC VELOCITIES.

	Kation +		Anion −	
NaCl	Sodium	37	Chloride	63
HCl	Hydrogen	80	Chloride	20
NaOH	Sodium	20	Hydrate	80
CH_3COOK	Potassium	68	Acetate	32

SOME ABSOLUTE IONIC VELOCITIES.

(At P.D. of 1 volt per 1 cm., and Temp. of 18° C.)

		In cm. per sec.	In mm. per hour.
Hydrogen	H +	0.00320	115
Hydroxyl	OH −	0.00182	65
Sodium	Na +	0.00045	16
Chlorine	Cl −	0.00069	25
Potassium	K +	0.00066	24
Acetyl	CH_3COO −	0.00036	13

Engelmann in the course of his investigation of skin currents, and Biedermann in his examination of mucous currents, paid particular attention to the effects of water, and of saline solutions on the normal current. Neither of these authors explicitly distinguishes the physical imbibition current, which must evidently have been a considerable, if not the chief or sole efficient cause of the effects. If you refer to the detailed accounts given by Engelmann,* and by Biedermann,† you will

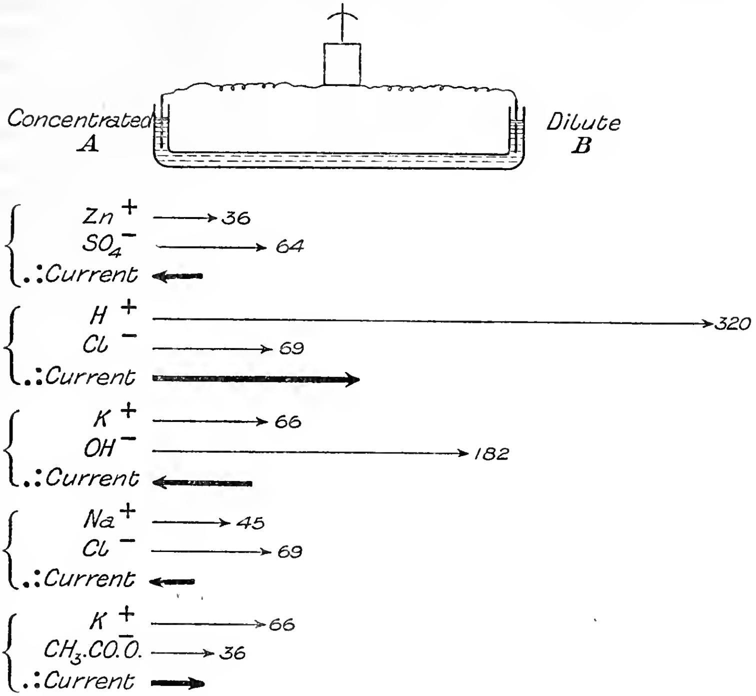

FIG. 55.—To illustrate concentration currents. The thin arrows indicate direction of ions from concentrated to dilute side of an electrolyte. The thick arrow in each case indicates the resultant current—from dilute to concentrated where the anionic is higher than the kationic velocity; from concentrated to dilute where the kationic is higher than the anionic velocity. (The relative ionic velocities are indicated by the numbers at the arrow-heads.)

N.B.—With the kation travelling from left to right, there is current from left to right, and *vice versa.*

With the anion travelling from left to right, there is current from right to left, and *vice versa.*

find that a large ingoing effect was generally produced by water or weak saline, a large outgoing effect by strong saline. The

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* Engelmann, *P. A.*, vi., p. 110.

† Biedermann, *Elektrophysiologie*, p. 401.

former is such as would be produced by an ingoing current of water through the skin, the latter by an outgoing current of water. The effects appear to be similar in character to those more recently pointed out by MacDonald, as regards the injury current of nerve—which he considers as being essentially a concentration current—viz., augmentation by water or by dilute salt solution, diminution or abolition by strong salt solution.

§ 82. *A limitation.*—While it is perfectly true that blaze is a sign of life, it is equally true that many assuredly living things do not blaze. But at this stage, without a fuller and more exhaustive examination of all sorts and conditions of living matter, it would be hazardous to propound any absolute and unrestricted negation. In the more familiar case of the evolution of CO_2, we know that the phenomenon is a sign of life; but we also know that many assuredly living things do not demonstrably discharge CO_2, and that the same living things may comport themselves very differently under different conditions. The low resistance of organs like the liver and kidney, the absence of a definite membrane between our electrodes enabling living cells to exercise the osmotic pressure that underlies ionic transfer, are conditions obviously unfavourable to the delivery of blaze-currents into an external circuit.

Many assuredly living things have not, to such examination as we have as yet made, manifested the clear and typical effects familiar to us in the case of the eye, and the skin and vegetable tissues. Muscle and nerves give comparatively small effects, and I have even failed to obtain any trace of response—under similar conditions of experiment—from the recently excised organ of torpedo which a few moments before, in the animal itself, gave me the well-known thrill characteristic of the discharge. I have witnessed well-marked effects in frog's spawn at one time, and have failed to obtain any effect at all in other spawn at a different stage of development. I do not conclude from this that blaze is not a sign of life; indeed, I should be reluctant, without further and closer examination—by the A B C method, and with shortest possible transfer time—to state absolutely that any given object exhibits no blaze at all. The internal organs certainly do not blaze like the skin, or even like nerve, the failure is in itself of interest, and the cause of difference matter for investigation, and we shall have to learn what is the determinant factor between a living tissue that manifests blaze, and another living tissue that does not. Durig thinks that the effect is peculiar to epithelial tissues, and it is certainly the case that epithelial tissues do give it better than other tissues—witness the case of the crystalline lens. But I do not think it is confined to epithelia, for it occurs in muscle, and in vegetable tissues which can scarcely be classed as epithelial.

I am unwilling to express any opinion at all. I have witnessed it in muscle; witnessed it in some frog's spawn, and failed to witness it in other frog's spawn. Does it depend upon some regular orientation of cells? Is their regular arrangement on a basement membrane a favouring condition of things? What part do membranes play in the effect? These are questions all of which I must leave unanswered now.

In two successive years I took occasion to examine seaweeds, with the object of comparing their reactions with those of land plants. To my considerable surprise, they gave little or no reaction, and I left the seaside on the first occasion without having been able to satisfy myself of the physiological nature of such small reactions as were occasionally witnessed. The "weeds" —obtained in the Channel Islands in an obviously living state during the month of August—always gave small antidrome after-currents at both poles to single shocks as if by ordinary polarisation. But the effects were abolished by boiling. This was a puzzle, and I cannot yet explain it. The elements of the problem are: deflections antidrome throughout, therefore apparently ordinary polarisation; but abolished by boiling, therefore apparently of a physiological character.

Pieces of apple gave a similar puzzle, viz., antidrome effects abolished by boiling, and it is possible in such cases that we have to do with a mere physical effect of altered structure or altered composition, possessing no physiological significance.

On the second occasion after several trials with negative results, I excited the cupidity of my children by the offer of a reward for a blazing seaweed, and was myself rewarded by their discovery of a long, narrow seaweed, called "boot laces" by the fishermen—*chorda filum* by its museum name—that gave typical homodrome effects of more than 0.02 volt to both directions of excitation, and therefore saved me from saying that sea-plants unlike land-plants do not blaze. The difference between the two kinds of vegetable is indeed very marked, but it is one of degree rather than of kind, and one of the chief conditions of the difference is that the former are bad and the latter good conductors. Evidently, if the resistance of the inactive stuff between our electrodes is so low as to afford great internal shunting, an electromotive change, unless very large, will not give much current to a high resistance galvanometer.

The common animals of the sea shore—limpets, anemones, jelly-fish, etc.—afforded little or no response to the usual test of single and of tetanising induction shocks. The eyes and the muscles of crabs and lobsters, the eyes and the skin of fishes (whiting, sand eel), gave very well-marked effects.

But we should not hastily conclude that the absence or smallness of blaze-currents depends on conductivity alone. Absence of blaze depends, also, I think, upon the relatively small amount of active living electromotive stuff in the mass of indifferent stuff that is its habitation. Low-class living matter, pervaded and diluted by the medium in which it lives, cannot be expected to exhibit any very intense sign of life; we do not expect it to blaze much. The mass of a jelly-fish or of a seaweed is in chief part sea-water; its living stuff has not the power to emancipate itself from the external medium, nor to create an internal medium, different and distinct from the general environment. It is practically isotonic with sea-water; its freezing point, and that of sea-water, are both about $-2°$. Like sea-water, it contains over 3 per cent. of salts, and its conductivity is at least fifty-fold that of land-plants. This no doubt is an unfavourable condition to the production as well as to the manifestation of a local alteration of potential.

But we may hardly proceed further on these lines of argument without further information concerning the exact freezing points and the relative conductivities of various animal and vegetable tissues, and to obtain such information means engaging in a new investigation, for which new methods have to be elaborated.

§ 83. *A question.*—It has probably occurred to some of us to ask what relation, if any, exists between the normal current and a blaze-current. Is not the normal current itself a sign of life, and in certain cases of obviously identical nature with a blaze?

To some extent these questions have been incidentally answered in previous lectures, but not formally and explicitly.

Indeed it is difficult to frame a formal and explicit answer, and I should prefer to avoid giving such an answer otherwise than with much reservation. For the facts of the case are by no means as clear as they seem to be at first sight. As regards the first question, we can make, with about equal probability, the two apparently contradictory statements that in some cases there is an evident relation between normal and blaze-currents, in other cases there is evidently no relation at all between the two currents. And on reflection it will appear that our first question should logically be preceded by our second as to whether normal current is or is not a sign of life, which amounts to asking what view we take of the nature of normal currents.

Now, I think you may take as granted that normal current is always injury current or excitation current; but I do not think you may take as granted that injury current is always excitation current.

The question of the nature of injury current has largely turned of late years upon the demarcation current of medullated nerve; in opposition to the view of Gotch, who assumes that this current is wholly an excitation current, MacDonald urges that it is a concentration current dependent upon the electrolytes of nerve. He regards nerve as a concentration cell in which the sheath is the dilute solution (= 0.9 per cent. KCl), the axis-cylinder the concentrated solution (= 10 per cent. KCl), and the current determined by the physico-physiological state of a membrane between sheath and axis. It would lead us too far to discuss this theory in all its details. My own opinion of the matter is that MacDonald has sufficiently proved the reality of the concentration currents of nerve by the annulling effects of strong salt solutions and by the recuperative effects of weak salt solutions, but that he has not disproved the irritative factor. I think both factors are concerned in the current, and if called upon to put a figure upon their value, should guess that in a fresh demarcation current of say 0.05 volt something like 0.04 is by concentration, and 0.01, or less, by irritation.

To return to the first question, stated at the outset of this paragraph, I should tentatively answer that, in so far as an "injury current" is irritation current, blaze-current bears relation to it, but that in the absence of irritation current, or in so far as "injury current" is of mere physical origin, blaze-current is quite an independent phenomenon.

I think that, on this view, we may now reconcile with each other these several facts, of which the first three are affirmative as regards a relation between blaze-current and injury current, the last negative.

1st. That a blaze-current is in general antidrome to an injury current.

2nd. That it is always antidrome to a previous (maximal) blaze-current.

3rd. That a (polarising) constant current favours homodrome and disfavours antidrome blaze-current.

4th. That in some cases blaze-current may be homodrome with injury current.

5th. That in many cases—eyeball, skin, and electrical organ—there is no discernible relation between the direction and magnitude of normal current and of blaze-current.

The fact that a blaze-current, antidrome to an injury current, is aroused by both directions of excitation, proves of itself, what is more clearly proved by the A B C method, viz., that the response may be post-kathodic as well as post-anodic, or, in Biedermann's phrase, negative-kathodic as well as positive-anodic. In either case it is the analogue of the "negative variation" of a demarcation current of muscle or of nerve, where it is known to us as a transmitted excitatory effect, whereas the "blaze" is a direct excitatory effect.

The fact that a blaze-current homodrome with its exciting current, is obtained between two uninjured and iso-electric points, signifies that in general the post-anodic homodrome is greater than the post-kathodic antidrome current. There is an excitatory state at *both* poles, greater at anode than at kathode, and if the excitation be reversed, there is as before a homodrome effect, but reversed with the reversal of excitation. If, before applying the second stimulus, we shift one of the electrodes that have served for the first stimulus and blaze, to a fresh spot (or, better, if by the A B C plan we transfer the A or B connections to a third indifferent point C), we shall find (on muscle, on vegetables) that both A and B—*i.e.*, post-kathodic and post-anodic points—are zincative (electro-positive) to C. And if, now, having compensated, we stimulate in either direction through these points A C or B C, *i.e.*, through one active point A or B, and one passive point C, we shall arouse blaze in the tissue from C to A or B. The first excitation has given blaze of A and B, which are zincative (electro-positive) to C. The second excitation has given a second blaze of either A or B, which is opposed and greatly exceeded by the first blaze of the previously untouched C. We may regard the first current from A or B to C as an injury current, and the second current from C to A or B as its negative variation.

So that in sum total we assimilate, as belonging to one class, what has been variously designated blaze-current, injury current (in so far as it is an irritation current), and action current. The fact that a blaze-current is augmented where it occurs in the same direction as a polarising current, is essentially similar with the phenomenon known to you in nerve-physiology as the polarisation increment. In the latter case, an active state sweeping wave-like along a nerve undergoes a sudden increment on reaching an anodic region, and the polarising current is increased; the anodic region, in which action is lowered, is capable of great increase of action when it is aroused by the transmitted excitation. It is more "zincable." In our case, also, the anodic region of a polarising current is more "zincable," *i.e.*, more capable of that electro-positive change which is the essential factor of a blaze-current, and is aroused to action by the direct stimulus of an induction shock whatever its direction.

§ 84. *Solution-pressure.*—I will bring these lectures to a conclusion with certain theoretical views to which slight allusion was made in the first lecture (p. 16).

I there attempted to account in some measure for the use of the term "zincative," and promised, when an opportunity should present itself, to formulate on similar lines a view of the mechanism of excitatory phenomena in general.

You are familiar with the idea that active tissue gives off electro-positive ions to its lymph bath, that in the tissue itself there is current of action from active to resting spot, that active tissue is zincative. You also know that in the electrical excitation of nerve and of muscle, the effective pole is the kathode, when current is made, the anode when current is broken. And you know that while a constant current is passing there is augmented excitability by the kathode, diminished excitability by the anode.

I take the case of medullated nerve, since the results are typical. Moreover, its coarse structure of central core as the essential part and surrounding sheath as the accessory part, which is a familiar image in everyone's mind, will help us to form a clear picture of what can be imagined as the actual movements of ions between any core of living stuff and any surrounding medium. (A word of warning, however—this is only a coarse picture, there is no doubt a peculiar commerce of ions between axis-cylinder and medullary sheath of a nerve-fibre, but there is probably a further and more refined commerce of ions between fibrils and fluid within the axis-cylinder itself.)

Consider then a core of living stuff, bring it in contact with an electrode, and let the latter be suddenly made kathodic by closure of a contact key in the circuit. The core of living stuff has been aroused to action. What have been the movements of ions when the electrode was made kathodic?

Clearly, there must have been movement of kations towards the kathode, of anions from the kathode—viz., attraction of the former, repulsion of the latter, as regards the surface of separation between core and bath.

The attraction of the kation to the surface of the core is in this view of the matter to be regarded as the essential factor of excitation (and of increased excitability), inasmuch as such attraction is equivalent to an increased "solution-pressure" of kations. The living core, under the influence of the kathode, is rendered more active and discharges into the surrounding solution a greater number of electro-positive ions since the pressure-difference of such ions in the core and in the solution is increased. As mentioned in a previous lecture, this is the state of things that I conceive to exist when I make use of the expression that active (or excited) living matter is "zincative" to resting living matter. I imagine "current of action" as being conditioned by the discharge from active stuff of free kations, and I choose zinc by name as the representative kation.

But, you say perhaps, why have you specified the kation rather than the anion as the effective agent in the production of an action current? Is not current from an excited to an unexcited spot accounted for by a transport of negative electricity by anions towards an excited spot, as well as by a transport of positive electricity by kations away from an excited spot?

Or again, you definitely object that it is wrong to think of kations as travelling against current, or anions with current. To the second of these possible objections in your mind, I answer at once that we are not considering simple passage of the exciting current through the electrolyte, but the excited current arising at the exciting pole of the former—viz., at the kathode. And, if you are in any doubt about this kathodic action current produced during the passage of the exciting current, perhaps you had better consider on similar lines the post-anodic action current that is witnessed after an exciting current has been stopped. In this case we clearly have to do with a sudden release of kationic pressure, as the repellant influence of the anode terminates.

To the first point—I have to offer you at least two considerations in support of my choice of the kation rather than the anion as the principal carrier in the case of an action current.

We have regarded the tension and solution-pressure of metallic, basic, *positive* sign as increased at the surface of the living core under the influence of the negative pole.

Under this same influence we should also have a decreased tension and solution pressure of non-metallic, acidic, *negative* sign.

This second mode of transport seems to me to imply necessarily the diminution of a pre-existing state of difference; whereas the kationic nature of an action current does not necessarily imply any pre-existing state of difference. No doubt, as a rule, all living matter is at least sub-active at low pressure within its internal medium, the lymph. But that is "pre-existing difference" of very different order to a pre-existing difference great enough to permit of the great diminutions of difference that should be caused by great augmentation of activity and of pressure.

On these general grounds, therefore, without wholly disregarding the possibilities of anionic transport, I have chosen to consider action currents as effected by kationic transport from the seat of action rather than by anionic transport towards the seat of action. And I say again on these grounds, as well as for reasons given in a previous lecture, that *active living matter is zincative.*

One further reason for this preference of the kationic to the anionic view of action currents (vegetable as well as animal, I may remark) may be briefly mentioned now, in anticipation of evidence that I hope to more fully place before you at some future occasion.

You know that, according to modern theory, the molecules of a neutral salt, such as, *e.g.*, NaCl in aqueous solution, exist not solely as non-electrical molecules of NaCl, but also (and in dilute solutions chiefly) as charged ions Na+ and Cl−. In, *e.g.*, what we ordinarily call "normal saline" in the laboratory, made up to contain $\frac{1}{10}$ grammolecule per litre of water, *i.e.*, 5.84 grammes per litre, $\frac{9}{10}$ of the amount of salt is present in the dissociated or ionised state as Na+ and Cl−, and the only uniting force between these dissociated ions is the mutual attraction of their + and - charges. Chlorides, bromides, and iodides, etc., of sodium, potassium, and ammonium, etc., in dilute solution—and decimolecular solutions such as we find it convenient to use in the physiological laboratory are in this connection "dilute"—exist in this active state of ionisation as positively charged kations and negatively charged anions. I said this *active* state of ionisation, since it is to this state of ionisation that their chief chemical and physical actions are due, and among these actions no doubt we must reckon their action upon living matter.

Now, if we take a number of salts, such as those just named, in dilute equimolecular (or, better, in isosmotic) solution, and systematically compare their respective effects upon some convenient physiological reaction of living matter, we shall find that differences of the kation produce far greater differences of reaction than do differences of the anion.

I do not pretend that this is in itself any proof that action and action currents are essentially characterised by increased solution-pressure and actual discharge into solution of electro-positive ions. But I think we may provisionally conclude that in the action of dilute saline solutions upon living matter, it is the electro-positive kation that takes the lead, acting presumably in the sense that we should anticipate, viz., increasing the kationic pressure of the lymph bath, and decreasing, therefore, the difference between that pressure and the kationic solution-pressure of the living matter.

The state of things under the influence of the anode must be regarded as the converse to that just pictured as obtaining under that of the kathode. Anions are attracted, kations are repelled; the solution-pressure of the latter must be lowered, and the surface of living matter must be rendered less zincative, less easily made to discharge kations; and, if forced to such discharge by adequate excitation, manifesting greater effect than when the initial pressure was higher.

The post-anodic action current, which makes its appearance at the moment of cessation of an exciting (or polarising) current, is very easily accounted for. The kationic solution-pressure, depressed under the influence of the anode, is suddenly released when that influence is removed, and manifests itself in a kationic discharge from the previously anodic surface. Thus we have a post-anodic action current which is of the same direction as that of the previous (polarising) current.

Blaze-currents—of which such frequent mention has been made in these lectures—are an effect of local intensifications of electrolytic solution-pressure—of kationic pressure when their direction is *from* the excited spot; of anionic pressure when their direction is *towards* the excited spot.

This is hypothesis which, whether or no it "explains" all the known facts, at least neither contradicts nor obscures them; it seems to me to bring them under a common denomination, and to invite us to their further investigation. Hypothesis is the mother of experiment.

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APPENDIX

The Normal Circuit—Galvanometer, Coil, Compensator, Electrodes, and Keyboard—Photographic Recording—Lippmann's Capillary Electrometer—Special Keys—Units of Resistance and of Conductance.

In a physiological laboratory the galvanometer may be used either for special electro-physiological research, or in the course of research work where electro-physiology is of secondary interest—the galvanometer playing the part of a balance, to indicate physico-chemical differences between any two different points.

The following remarks are more especially directed to meet this latter case. The galvanometer may be looked upon either as a manometer, measuring electrical pressures just as one measures blood-pressure, or as a chemical balance, by means of which one can compare numerically the energy values of physiological phenomena capable of an electrical expression. In many cases it will be found convenient, or even necessary, to record the indications of the galvanometer photographically.

The requisite apparatus consist of: (I) the galvanometer; (II) the compensator; to these must be added various accessories; (III) the exciting apparatus; (IV) the electrodes; and (V) the keyboard, by means of which the constituent pieces of apparatus will be connected together to form what may be termed the normal circuit. (The arrangement for taking photographic records is a further accessory described below, p. 156.)

The galvanometer.—The style of instrument matters very little so long as its sensibility can easily be ascertained and adjusted.

The delicacy of the galvanometer should be such that 0.001 volt through a megohm gives a deflection of 10 cms. at a distance of 2 metres. Thus a deflection of 1 cm. corresponds in such a circuit to a current of 10^{-10} ampere.

It is advisable to fit up a galvanometer once and for all in one particular place. The best position for the instrument, and one in which it will always be ready to work, is either a recess or small cupboard built in the thickness of a perfectly firm wall. Failing this, a firm bracket or shelf, not connected with the floor, is sufficient.

Whether the instrument is being used for purposes of demonstration or for actual measurement, the objective method must be used. This consists in the projection of a beam of light either on to a transparent and graduated scale or upon a photographic plate. The most convenient light for either purpose is the image of the filament of an incandescent lamp. When photographic records are required, it is very desirable, indeed almost indispensable, to work with two galvanometers in series, one for purposes of observation, the other as recording instrument.

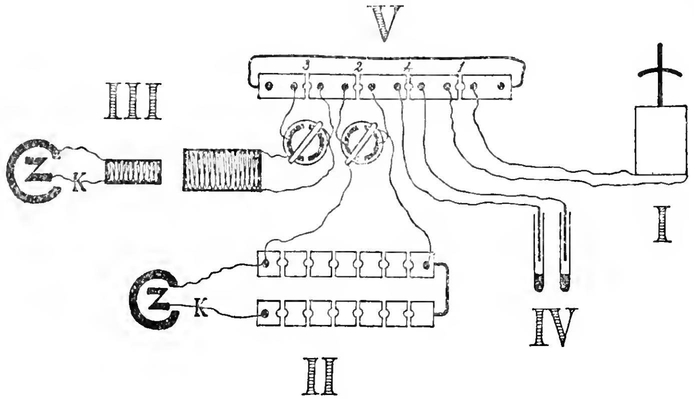

FIG. 56.—Normal circuit described in the text. (The secondary coil is figured as if for direct excitation of a given object, IV. Obviously, if we have to apply indirect excitation, the wires are removed from the keyboard, and the plug hole is filled to complete the keyboard circuit.)

Calibration of the galvanometer, and choice of a convenient scale.—The deviations of the same galvanometer have not always a constant value, seeing that the resistance of the circuit varies according to the resistance of the object under examination and of the unpolarisable electrodes.

The quickest way to calibrate a galvanometer is to observe or photograph the deflection of the spot when a current of known voltage from the compensator is allowed to flow in the circuit, which must be of known resistance (Fig. 59). It is convenient to use a carbon megohm for calibration (*vide infra* p. 169).

In those cases where an alteration of resistance actually occurs during the course of the experiment, the value of the standard voltage must be taken before and after.

Note.—In early trial experiments the deflections obtained will probably be too large to be kept well within the scale limits. The best way to obtain a readable deflection is to shunt the galvanometer, thus sending only a convenient fraction of the total current through the instrument.

The compensator or potentiometer is a means (1) of supplying a standard voltage, and (2) of compensating and so measuring P.D. currents derived from the object under examination. Further, the compensating current affords the quickest means of verifying the integrity of the general circuit and of the galvanometer.

In its simplest, and for all ordinary purposes, sufficiently accurate form, the compensating arrangement consists of a Leclanché cell, joined up with two resistance-boxes, which act as numerator and denominator of any convenient fraction of a volt.

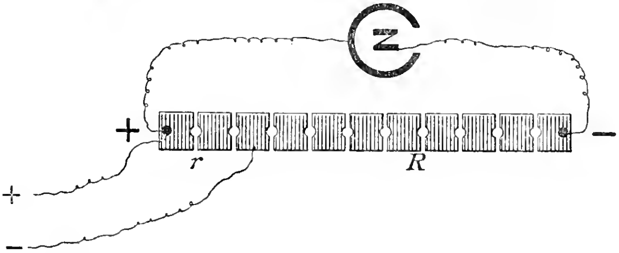

FIG. 57.—To illustrate the principle on which a compensator is constructed; with a battery of 1 volt, R = 1000 ohms and $r = 1$ ohm, the P.D. at the ends + and − would be approximately $\frac{1}{1000}$ volt; the same P.D. would obtain with a battery of 1.4 volt and R = 1400 ohms. Compensation is established by varying r.

Taking the voltage of the cell as 1.4, and the resistance (R) of the denominator to be 14,000 ohms, than the resistance (r) of the numerator reckoned in ohms will give a voltage in ten-thousandths at the electrodes—*e.g.*, if $r = 10$ ohms, the voltage obtained = .001; if $r = 100$, voltage = .01, *Note.*—Obviously this yields only approximate results, since the voltage of a Leclanché is never quite 1.4 volt, and the fraction of the voltage taken is not $\frac{r}{R}$ but $\frac{r}{R+r}$. Further, the internal resistance of the cell is not taken into account. The method is, however, sufficiently accurate, seeing that the principal error is a constant one and the variable error is negligible.

In actual experiments it is advisable to have a standard compensator which will give values of .01, .001, .0001 volt, independently of the compensator proper.

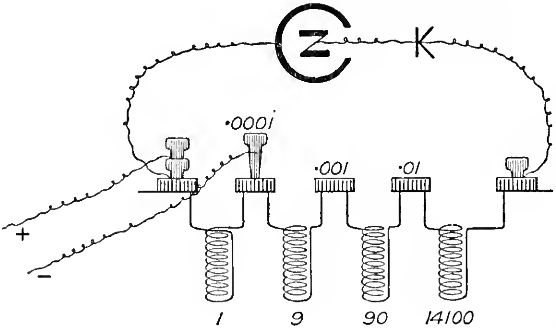

FIG. 57 A. Compensator to deliver $\frac{1}{10000}$th, $\frac{1}{1000}$th, or $\frac{1}{100}$th of a volt from a Leclanché cell (of 1.42 volt).

The comparison between experimental deflections and the standard deflection of known external voltage is not calculated to give the absolute value of internal E.M.F. of active tissue. The external circuit and galvanometer receive only a fraction of the total internal electromotive difference, which produces current partly through the internal conducting tissues, partly through the external (galvanometric) arc. Moreover, the time-relations of physiological action are generally such that internal effects of brief duration produce small external effects that cannot be standardised by a prolonged external voltage.

Thus, *e.g.*, a nervous impulse with a duration of say 0.005 sec. might, on a given instrument, produce the same deflection as a constant current from an E.M.F. of 0.001 volt, but this would not indicate electromotive value of the nervous impulse. A closer approximation would be arrived at by making the comparison with an external voltage effective for only 0.005 sec.; in this manner Gotch and Burch have assigned 0.03 volt as the electromotive value of a single nervous impulse. And this is not yet a true value, by reason of the internal derivation alluded to above.

The principal object of a standard voltage at the commencement and termination of experiment is (1) to indicate that the resistance has or has not sensibly altered during experiment; and (2) to indicate the sensibility of instruments employed. It does not afford in itself satisfactory data for a comparison between electromotive values of response of different tissues, and it is only with reservation (*i.e.*, after control of altered resistance and altered duration of action) that it can be utilised for the detection and estimation of altered electromotive values during any one observation.

Bearing these reservations in mind, we may, however, be allowed to speak of the "voltage" of an injury current as "measured" by that of a compensation current,* and to indicate by reference to standard deflections the scale of voltage in which blaze-currents are externally manifested.

The exciting apparatus.—In the great proportion of experiments the du Bois-Reymond induction coil (Berne model) is used. This coil has its graduation in arithmetical progression.

In those experiments where it is necessary to estimate the quantity or energy of the discharge, a condenser must be used. In either case there are two possible methods of excitation:—(1) the excitation is sent through object and galvanometer in series, and (2) the galvanometer is short-circuited during excitation, and put into circuit after a given short interval of time.

Electrodes.—It is absolutely essential that the electrodes should be unpolarisable. Du Bois-Reymond's combination (zinc and sulphate of zinc) has, in my experience, given better electrodes than those recently introduced—*e.g.*, silver and silver chloride, or mercury and calomel.

Keyboard.—In the constant use of a galvanometer as a measuring instrument, the circuit should be set up in such a manner that the direction of exciting and reaction currents may be quickly determined.

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* The instrument by which this is done is a *compensator*; it is not strictly speaking a *potentiometer*.

The simplest way of obtaining this arrangement is to have a keyboard with several pairs of terminals, to which are connected the various parts of apparatus, making up what has already been called the normal circuit. Each particular piece of apparatus is controlled by a plug, opening or closing the interval between the two terminals to which each pair of wires is connected. Two commutators, one in the exciting circuit and the other in the compensator circuit, allow the current to be sent in the direction desired. An ordinary key interrupts the principal circuit of the compensator.

Note.—It much simplifies matters to arrange the circuit permanently, or at least at the beginning of each experiment, so that a positive or negative current may be in conventional directions, *i.e.*, positive to the right and negative to the left. The quickest way of determining the direction of a current is to touch one of the terminals with a piece of metal (*e.g.*, zinc) held in one hand, while a finger of the other hand makes contact with the other terminal. The terminal touched by the zinc "pulls" through the galvanometer, and if the previous deflection has been in the same or in the opposite direction, we know that the spot in connection with the same terminal was then zincative or counter-zincative, *i.e.*, electro-positive or electro-negative.

Photogaphic recording.—If necessary, it is possible to photograph and to take readings at one and the same time. To this end the transparent scale must be replaced by a vertical opaque screen, with a narrow horizontal slit, behind which a photographic plate is let down by clockwork.

The use of two galvanometers in series so simplifies matters, however, that it is preferable to use a second instrument for taking graphic records. One of the galvanometers stands in the laboratory, with its transparent scale in front of the observer, while the second is some distance away in a dark (and non-vibrating) room. The former exhibits and the latter registers the currents under observation.

The graduation of the recording galvanometer should be to a smaller scale than that of the indicating galvanometer. A convenient relation between the two scales is 1 to 10, so that each centimetre deflection of the indicator is represented by a millimetre on the recorder. The relation is, if necessary, adjusted by shunting one or other of the two galvanometers ; and once established, we may, if desired further, shunt both galvanometers, so as to reduce both deflections in the same proportion. For this reduction, the common shunt is to be connected with the terminals on each side of plug No. 1.

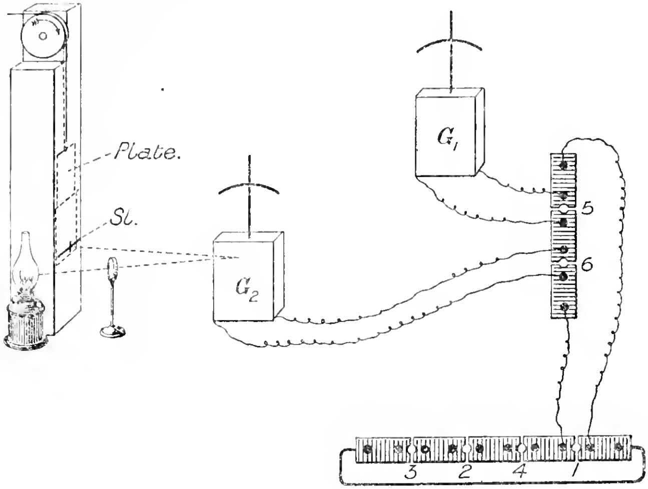

FIG. 58.—Galvanograph.

The most convenient arrangement of the two galvanometers is shown in Fig. 58, in which G_1 is the indicator and G_2 the recorder. The two galvanometers are controlled simultaneously by plug No. 1, separately and individually by plugs No. 5 and 6 of a secondary keyboard. We are therefore able to adjust compensation and make any necessary preliminary adjustments with the photographing galvanometer short-circuited at No. 6, and therefore undisturbed by manipulations in the remainder of circuit, where we are guided by the indicating galvanometer. For an observation of any duration, both galvanometers are in circuit and simultaneously controlled by plug No. 1, and the general progress of a record on G_2 in the dark room, can be followed on the scale of G_1 placed in front of the work-table.

The accessory apparatus, containing the sensitive plate, consists in a box, $\frac{1}{2}$ metre in height, which carries the scale, and the horizontal slit, $\frac{1}{2}$ mm. in width, upon its anterior surface. The plate, which is

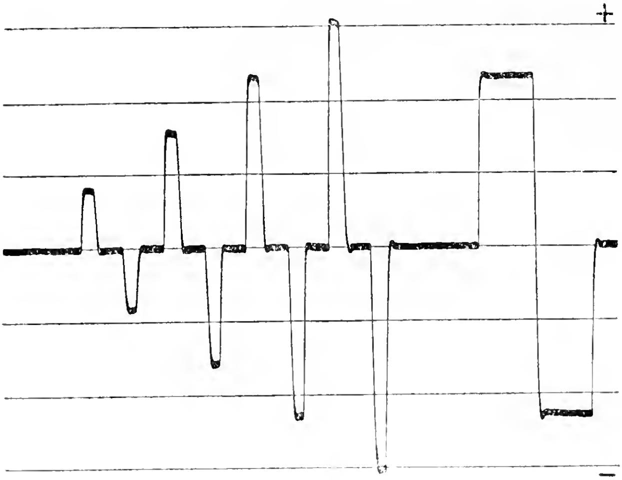

FIG. 59.—Photographic record of the galvanometric deflections in + and – directions, caused by (approximate) voltages of 0.01, 0.02, 0.03, 0.04, and again 0.03, through a circuit of (approximately) one Megohm (= 1000000 ohms).

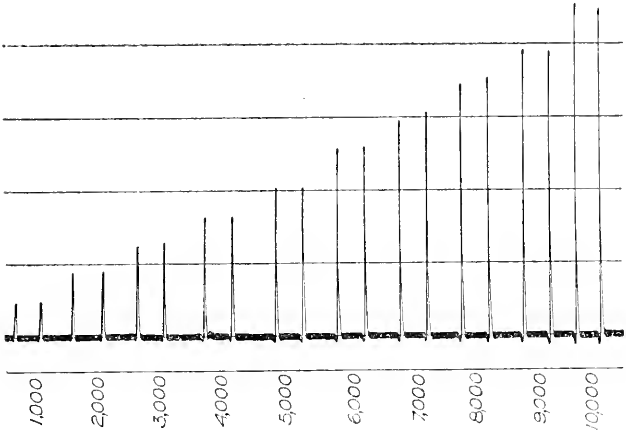

FIG. 60.—Photographic record of the deflections caused by break induction shocks of a Berne coil. Two trials at each strength.

in a photographic carrier suspended by a thread from a wheel revolving by clockwork, descends vertically. The deflections of the galvanometer spot are recorded laterally upon the line of the horizontal slit. An electric bell gives warning when the plate has completed its descent. If necessary, a chronograph, and a signal to mark the beginning and close of excitation, are easily added when required.

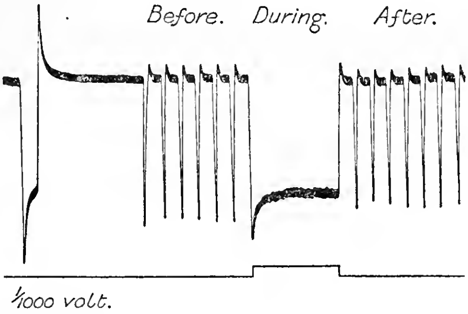

FIG. 61.—Response of an oxydised copper plate, illuminated for seven seconds at one minute intervals. A prolonged illumination was made in the middle of the series to see whether any sign of expenditure would be elicited. (The first deflection by $\frac{1}{1000}$ volt turned into circuit exhibits signs of ordinary polarisation.)

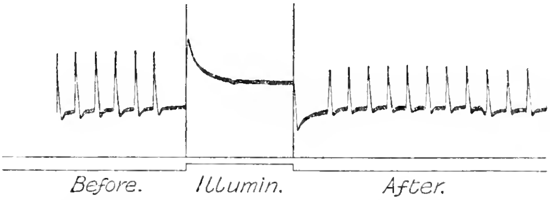

FIG. 62.—Similar observation on a chlorinated silver plate. In consequence of prolonged illumination there is well-marked evidence of alteration.

Speed of registration.—By reason of the inertia of the suspended magnets and mirror of the galvanometer, we must content ourselves with registering phenomena that are, comparatively speaking, prolonged, or repeated at regular intervals. The method is not adapted to record phenomena that require a speed of recording surface greater than 5 mm. per second. It is best adapted to the recording of phenomena of long duration, or to reactions that are repeated at regular intervals. In this class of observations, a speed of 2½ to 5 mm. per minute is usually sufficient. The "lost time" of nerve-skin reaction is a good instance of a phenomenon fitted for the galvanometric record, *e.g.*, Figs. 28 and 43.

It is convenient to adopt a standard size of recording plate; the "quarter plate" in England, and the 9 by 12 on the Continent, answer all ordinary purposes. These dimensions enable us to record a series of deflections with an amplitude varying from 1 to 5 cm., and a length of at least 10 cm. The speeds named give records lasting 40 and 20 minutes; 5 mm. per second gives a 20 seconds record. For speeds above 5 mm. per second a recording electrometer should be used.

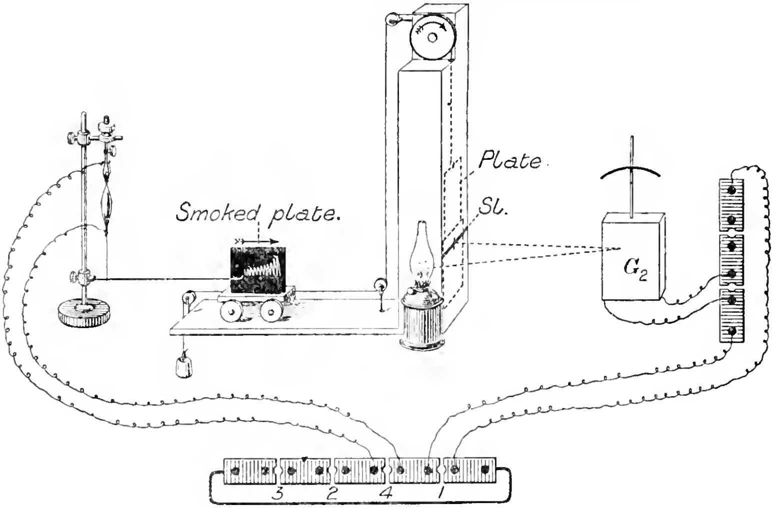

Fig. 63.—Galvanograph and Railway Myograph.

Simultaneous records.—In certain cases it is desirable to obtain the simultaneous record of a series of electrical reactions and of the corresponding series of muscular contractions.

For this purpose, a truck carrying a smoked plate, and connected with the suspended carrier that holds the photographic plate, is added to the apparatus. The thread by which the carrier is suspended passes round the axis of the motor and over two small pulleys, and is fastened to the carrier of the smoked plate, which accordingly moves in a horizontal direction, corresponding with the vertical descent of the sensitive plate. In this manner a simultaneous record may be obtained, *e.g.*, of a series of muscular contractions along with the negative variations of the muscle-current; or, again, of contraction and heat (by means of a thermo-galvanometer); or of the contractions of a muscle and the negative variations of its nerve; etc., etc.

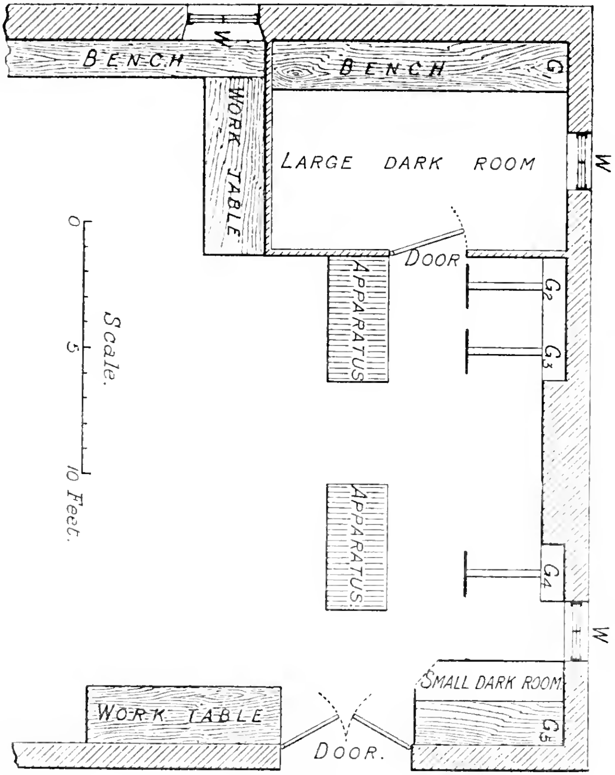

FIG. 64.

In the Physiological Laboratory of the University of London the apparatus described above is disposed according to the following plan, so as to afford two complete working tables with two pairs of galvanometers and accessory apparatus :—

The galvanometers G_1 to G_5 are placed on brackets along one side of the general laboratory as figured. (The extra galvanometer, G_3 is a separate low-resistance instrument, for use with either table, to give thermo-electric readings of temperature ; it is worked by a constantan-iron junction, the varying E.M.F. of which is balanced by compensation ; the compensator is graduated so that a known length has a known temperature value.)

Each pair of galvanometers, G_1 and G_2, G_4 and G_5 is intended to be used as described above ; for ordinary work, only the observation galvanometer G_2, or G_4, is used ; when a phenomenon deserving to be recorded presents itself, the recording galvanometer G_1, or G_5, is unplugged, and the recording surface is set in motion.

The apparatus is thus utilised in the general laboratory without suffering any disturbance from other work in progress in the same room.

Lippmann's Capillary Electrometer, like the galvanometer, can be used (1) as a refined instrument of research for the special purposes of electro-physiology, in which case its photographed indications must be mathematically analysed ; or (2) as an ordinary laboratory instrument for the summary inspection and the convenient demonstration of electrical changes that are too brief or in too rapid succession to be readable by galvanometer—*e.g.*, the electrical changes accompanying the beat of the heart. By means of very simple recording apparatus, the value of the electrometer as an ordinary instrument of inspection and demonstration is greatly enhanced. In this laboratory a capillary electrometer is currently used in place of a demonstrating galvanometer. The image of the capillary in the projection microscope, with $\frac{1}{2}$ to $\frac{1}{10}$ objective, is first thrown upon a transparent screen, where the movements of the column of mercury are shown. An opaque screen with a narrow vertical slit, behind which a vertical photographic plate travels horizontally, is then placed on the lecture-table, so as to receive the image of the moving column of mercury, which is thus photographed. And lastly, the developed photograph is exhibited in the ordinary projection-lantern. Thus the record of movements that have just been seen, is exhibited and examined. In this manner there is no difficulty in demonstrating in the course of a quarter of an hour 1st, the electroscopic indications of, *e.g.*, a frog's heart ; 2nd, the photographed records of such indications.

The diameter of the capillary column of mercury is, *e.g.*, 25 μ.

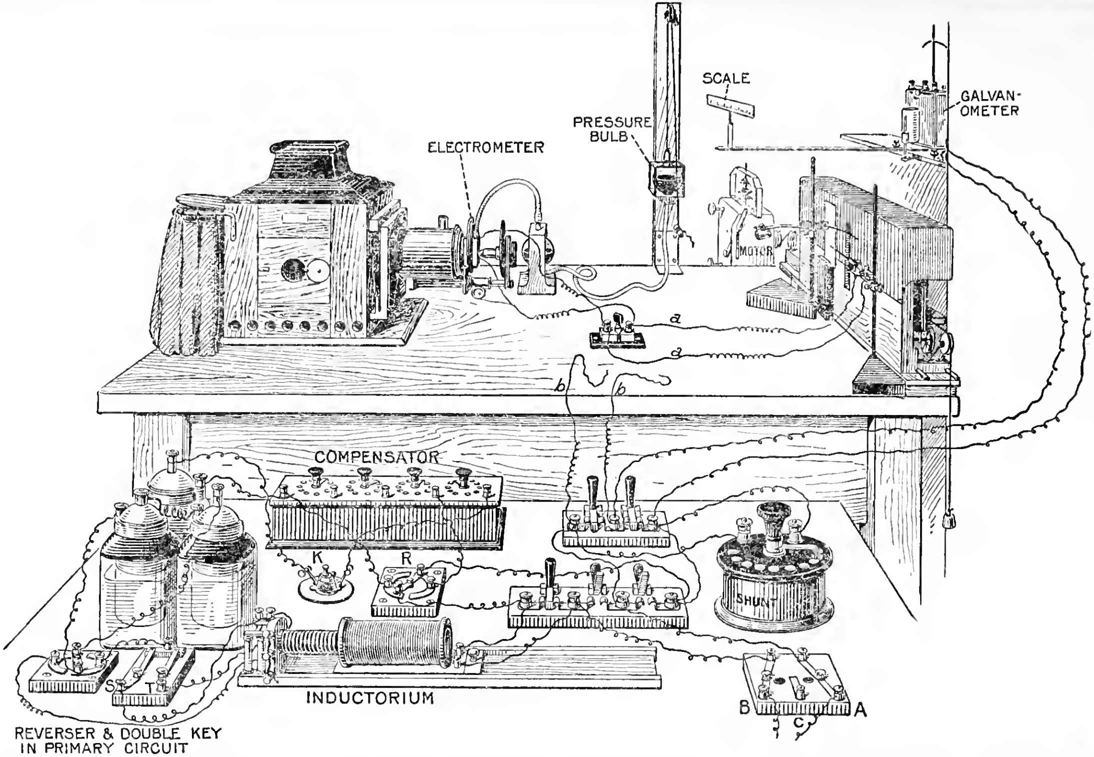

FIG. 65.—Disposition of tables in connection with an Electrometer and with a Galvanometer. The apparatus belonging to the electrometer is disposed on the upper table, the accessories—keys, compensator, shunt, coil, etc., are arranged on the lower table. The galvanometer and scale are shown in the background. The image of the electrometer is projected upon the vertical slit of the recording apparatus. Levers of a time marker and of, *e.g.*, a cardiograph, cast shadows across the same slit. The heart or other electromotive tissue is connected to the poles of the electrometer through a plug-key, shown in the middle of the table. The accessory apparatus on the lower table can be connected to the electrometer by means of a pair of wires *bb* from the double key put in place of the wires *aa*. The lower table shows in perspective the essential parts of the apparatus, shown in diagrammatic plan in Fig. 56. The primary coil of the inductorium is fed by two Leclanchés through a reverser and a double key. The purpose of the double key is to have at will single shocks (S) or tetanising currents (T). A third Leclanché cell, shown behind the previous two, supplies the compensator. Its key (K) is in the principal circuit; its reverser (R) is in the branch circuit which terminates at the two ends of the three-way key, of which the three possible pairs of passes are shown connected:—(1) to the secondary coil; (2) to the A B C key; and (3) with the two-way key, from which wires pass on to the galvanometer, or by *bb*, when desired, to the electrometer. Finally, the preparation is connected to the two terminals A B of the A B C key; the central terminal is not shown in use.

On the screen, at a distance of 8 to 12 feet the magnification of the image given by the $\frac{1}{10}$ inch objective is 1000 to 1500 diameters, *i.e.*, the column has an apparent diameter of 25 to 37.5 mm.—an inch to an inch and a half. On the photographic plate, at a distance of 2 feet, the apparent diameter is upwards of 6 mm.—far more than is sufficient to certainly cover the vertical slit, the breadth of which is less than $\frac{1}{4}$ mm. For the frog's heart, a lower magnification is generally sufficient. For the human heart, as high a magnification as practicable should be employed.

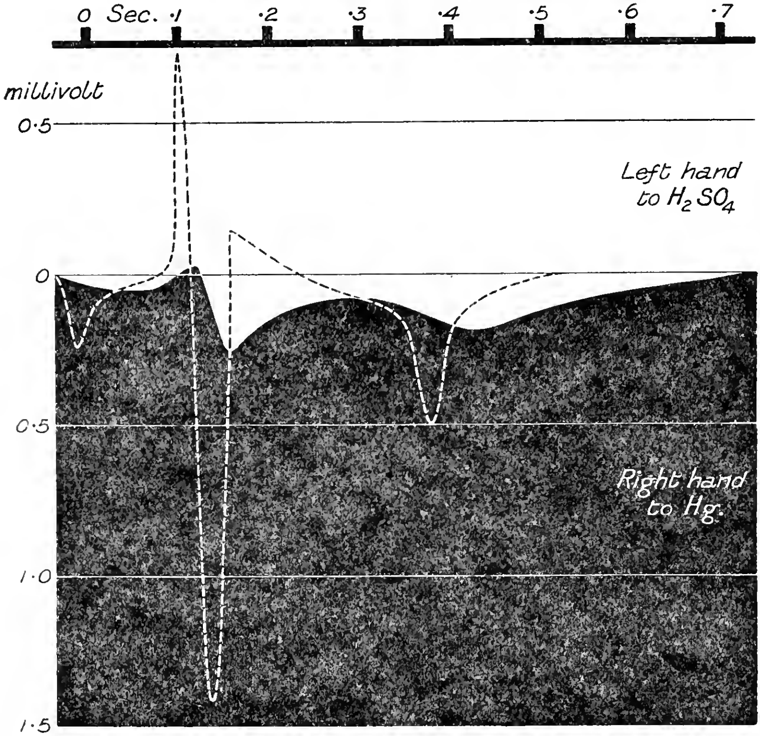

FIG. 66.—An electrometer-curve of the electrical variation of the human heart; the values calculated from the record of the mercury level are given as a dotted line. (From Einthoven, *Pflüger's Archiv*, vol. 60, 1895.)

The principle upon which electrometer values are obtained from such electroscopic records is readily illustrated by demonstrating the excursions and records caused by different voltages acting for equal times, and by a given voltage acting for different times.

The voltage actually indicated by any given curve or portion of a curve is most readily ascertained by superposing the record upon the record of a "normal curve," *i.e.*, of the curve described by a known constant P.D. taken under similar conditions. The two plates are slipped over each other, with abscissæ kept parallel until portions of the curve under examination coincide with portions of the normal curve at known voltage. Such coinciding parts are equipotential, so that the value on the normal curve gives the value on the curve under inspection.

For the more minute analysis of electrometric curves, the student should consult the papers of Burch, Einthoven, and Garten. In many instances the calculated curve appears very different from the original record of the curve described by the mercury column, *e.g.*, Fig. 66.

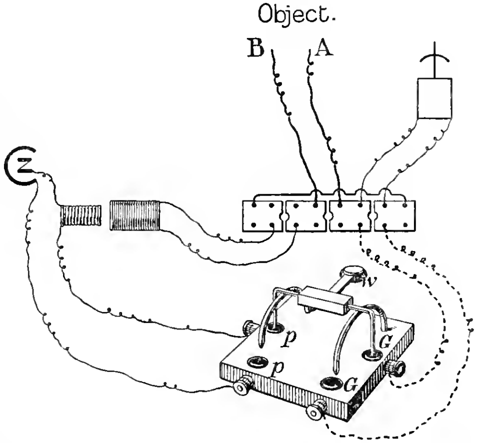

FIG. 67.—The primary circuit of the inductorium is completed through the pools *p p*. The galvanometer is short-circuited through the other pair of pools *G G*. The level of mercury in the lateral pool, and the length of the semicircular wires, are adjusted so that circuit is completed at *G G* (*i.e.*, the galvanometer is short-circuited) before circuit is completed at *p p*. On releasing the commutator cradle the weight, *W*, lifts the two wires from the mercury, breaking first the primary circuit, and subsequently the galvanometer short-circuit. The time of transfer is thus kept constant.

Keys.—For the study of blaze-currents, occasional use has been made of two special keys, modified from the well-known model of the Pohl's commutator, for the purpose of automatically (1) breaking the primary circuit, and (2) opening the galvanometer circuit, in quick and regular succession.

This is very simply effected in the first of these keys by making

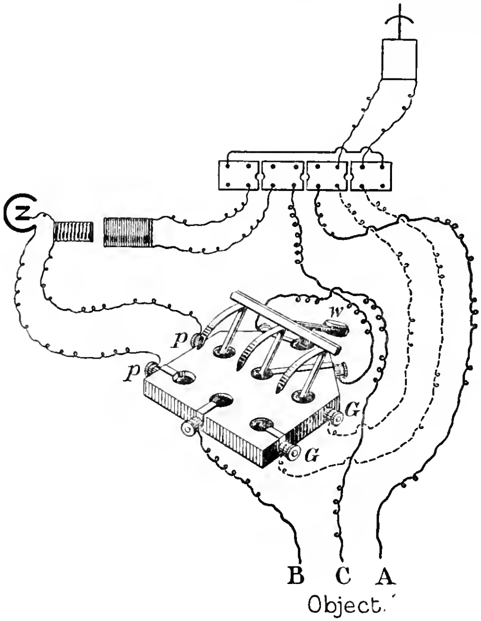

FIG. 68.—A B C Key. The primary circuit of the inductorium is completed through the pools *p p*. Connection between *G G* short-circuits the galvanometer. Of the three pools in the centre of the key, the middle is connected to A, *via* the keyboard and galvanometer, the pool under *W* to C, and the remaining pool to B. The three arms of the rocker are of unequal length, that connecting *G G* being a little longer than the centre arm, and this again longer than the connection between *p p*. On rocking the arms to the left, and then letting go the weight, the following events take place in order :—

(*a*) The circuit *p p* is broken, and an induction current passes through B A.
(*b*) ,, ,, B A is broken.
(*c*) ,, ,, A C is made.
(*d*) ,, ,, G G is broken, and any potential difference between A and C acts upon the galvanometer.

Thus the induction shock caused by breaking *p p* passes through A B, A is then connected to C, and not till then is the galvanometer short-circuit *G G* broken, and the current from A C allowed to pass. To take the current from B C, the connections A and B are transposed.

the curved wire in the galvanometer short-circuit a little longer than that in the primary circuit, so that the break shock takes place a little before the galvanometer is un-short-circuited. The removal of the two curved wires from their respective mercury pools is maintained at a regular interval by the use of a weight. This key is used to demonstrate the total effect between two points, A B, after excitation of these same points.

The second key is a little more complicated, and serves to demonstrate a partial effect A C or B C after excitation of two points A B.

Units of Resistance and of Conductance.[*]—The units of resistance are the ohm and the megohm (= 1,000,000 ohms). The corresponding units of conductance are the mho and the gemmho, which are the reciprocals of the ohm and megohm.

A substance having a resistance of one megohm (Ω) has a conductance of 1 gemmho or 1 γ.

$$1\ \gamma = \frac{1}{\Omega}.$$

The conductances of, *e.g.*, the skin in the experiment illustrated by Fig. 50 are accordingly :—

	Deflection by 0·01 volt	Resistance − 20,000 ohms	Conductance
At outset	5	520,000 ohms	1.92 γ.
After 1st tetanisation . .	12.5	196,000 ,,	5.67 ,,
,, 2nd ,, . .	25	88,000 ,,	11.35 ,,
,, 3rd ,, . .	35	57,143 ,,	17.50 ,,
After boiling	115	3,478 ,,	288.90 ,,
,, 4th tetanisation . .	115	3,478 ,,	288.90 ,,
Standard deflection through 1 megohm, or 1 γ.	2.7	1,000,000 ohms	1.00 γ.

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[*] I am indebted to Professor Ayrton for the suggestion of the reciprocal megohm as a convenient unit of conductance, and for the further suggestion of "gemmho" or γ as its convenient name and symbol, thus utilising Lord Kelvin's proposal to take resistance names written backwards to denote their conductance reciprocals. Kohlrausch's unit of conductivity 1 κ is the same as Kelvin's "mho," and is equal to 1,000,000 γ. I have also to acknowledge the kind assistance of Dr T. Martin Lowry in connection with conductivity measurements.

From which it is evident that where the resistance of the object examined is great as compared with the resistance of the galvanometer and electrodes (20,000 ohms in this instance), we may regard alterations of deflection as indicating alterations of conductance. Whereas, if the resistance of the object be relatively small, we must calculate the conductance after subtracting from the total resistance in circuit the resistance of the galvanometer and electrodes.

For many purposes—*e.g.*, for comparing the resistance (or conductance) of various objects—it will evidently be necessary to reduce our results to a common denomination, *i.e.*, to the resistance (or conductance) of a cube of 1 centimetre. Thus, *e.g.*, a stem 10 cm. long with a sectional area of 10 square millimetres, having a resistance of say 200,000 ohms (=a conductance of $5\,\gamma$) has a resistivity $= \frac{200000}{10 \times 10}$ and a conductivity $= 5 \times 10 \times 10$. The reduction to the cube of 1 cm. is in conformity with the practice of modern physical chemistry. The conductivity of 1 megohm, or $1\,\gamma$, $= 1.10^{-15}$ C.G.S. unit, that of 1 ohm, or $10^6\gamma$ being 1.10^{-9}.

Electrolytes in general are increased in conductivity by rise of temperature, the co-efficient of increase being approximately 2 per cent. per degree.

	Resistivity (in ohms)	*Conductivity* (in reciprocal megohms)
Mercury	0.000,094	10,630,000,000
Sulphuric acid, 30 % at 40°	1	1,000,000
Sodium chloride, sat. sol. at 18°, 26.4 %	4.627	216,100
,, ,, mol. sol. at 18°, 5.62 %	13.45	74,400
,, ,, $\frac{m}{10}$ sol. at 18°, 0.58 %	108	9,250
Sea-water, at 15°	20	50,000
Seaweeds	80	12,500
Urine	50	20,000
Blood serum	125	8,000
Defibrinated blood	250	4,000
Muscle and Nerve (longitudinally)	200	5,000
Grape-juice	500	2,000
Vegetables and Fruits	2,000	500
Ordinary tap-water	2,500	400
Ordinary distilled water	100,000	10
Good ,, ,,	1,000,000	1
Kohlrausch ,, ,,	25,000,000	0.04

Measurements of resistance (and of conductance) are best taken by means of a Wheatstone bridge, preferably by Kohlrausch's method, but for many purposes where polarisation of electrodes and of tissue may be disregarded, it is convenient and sufficient to estimate conductance directly from the galvanometric deflection. In the case of plants the resistance is generally so great that it is allowable to disregard that of the galvanometer and electrodes, and to at once express deflections in terms of conductance. A carbon megohm (= 1,000,000 ohms) attached to the keyboard is a convenient standard of reference, giving at once on the scale or photograph the value of our unit of conductance, 1 γ.

Correction for the resistance of the galvanometer and electrodes is to be made, when required, as follows :—

Let r_1 and d_1 be the resistance of the galvanometer + megohm, and the deflection by any convenient voltage.

r_2 and d_2 the resistance of the galvanometer + electrodes, and the deflection by the same voltage (practically we must take $\frac{1}{10}$th or $\frac{1}{100}$th that voltage and multiply by 10 or 100).

r_3 and d_3 the resistance of the galvanometer + electrodes + object of experiment, and the deflection by the same voltage.

The required resistance, r_4, of the object examined $= r_3 - r_2$,

and since $$\frac{r_1}{r_2} = \frac{d_2}{d_1}, \text{ and } \frac{r_1}{r_3} = \frac{d_3}{d_1}$$

$$r_2 = \frac{r_1 d_1}{d_2}, \text{ and } r_3 = \frac{r_1 d_1}{d_3}$$

the required resistance $$r_4 = \frac{r_1 d_1}{d_3} - \frac{r_1 d_1}{d_2}$$

$$= \frac{r_1 d_1 (d_2 - d_1)}{d_2 d_3}$$

and the corresponding conductance $$= \frac{d_2 d_3}{r_1 d_1 (d_2 - d_1)}.$$

If the galvanometer resistance is known, it is, although convenient, not necessary to take a megohm into circuit.

Kohlrausch's method is used in this laboratory for the rapid testing of distilled water, of dilute saline solutions, and of blood, serum, urine, etc.

The electrodes (of platinised platinum) are adjusted to a suitable "resistance capacity" (about $\frac{1}{10}$ for water, 1 for dilute saline, serum, and blood, and 10 for solutions of higher conductivity) so that the resistance under observation shall fall between the limits of 100 and 1000 ohms. The electrodes, forming the *x* arm of a Wheatstone bridge, are plunged into the fluid under examination ; a telephone is in the bridge in place of a galvanometer ; the testing currents come from a small induction coil, and the silence point (or its equal "to much" and "too little") is sought for by alteration of the variable resistance. Readings of resistance are thus easily obtained within an error of ± 1 per 100, with the normal temperature = 18°. A correction of ± 2 per 100 of the reading is to be made per ± 1°.

$$\text{The } \textit{specific conductivity} = \frac{\textit{Resistance Capacity}}{\textit{Observed Resistance}}$$

The resistance capacity of a given pair of electrodes in a given vessel is ascertained by taking a measurement of resistance through a standard solution of known conductivity. *E.g.*, a pair of electrodes in decinormal KCl at 18° is found to have a resistance = 200 ohms. The resistance capacity = 200 × 0.01119 = 2.238 (*Resistance* × *Conductivity* = *Capacity*).

With the same pair of electrodes the resistance of a specimen of serum is found to be 320 ohms. Its specific conductivity = $\frac{2.238}{320}$ = 0.006994 mho or 6994 γ.

The necessary data are given in Kohlrausch and Holborn's tables, from which the following useful empirical rule is taken :—

For weak saline solutions $\left(\frac{n}{10} \text{ and under}\right)$ the specific conductivity (in mhos) × 10 = the number of gramequivalents per litre, and – the specific conductivity × molecular weight = the percentage of salt in solution.

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