UBAKER

ELECTRO-PHYSIOLOGY.

BY

ALBERT P. BRUBAKER, A.M., M.D.,
PHILADELPHIA,
Demonstrator of Physiology at the Jefferson Medical College; Professor of Physiology in the Pennsylvania College of Dental Surgery, etc.

Reprinted from "The International System of Electro-Therapeutics." Published by The F. A. Davis Co., Philadelphia. See announcement on last page of cover.

ELECTRO-PHYSIOLOGY.

By ALBERT P. BRUBAKER, A.M., M.D.,
PHILADELPHIA, PA.

Historical Introduction.

One of the most interesting chapters in the history of physiological science is that relating to the origin and development of the electrical phenomena of muscles and nerves. Here, if anywhere, we have a striking illustration of the fact that new discoveries are not always the result of logical thought and a correct interpretation of phenomena. On the contrary, the history of electro-physiology clearly shows that often the new discoveries were dependent upon faulty observations, imperfect deductions, and bitter controversies; for, had Galvani's explanation of the first observed contraction been the correct one, it is quite possible that the phenomenon would have aroused but slight interest, and the development of electricity and physiology would have been retarded for many years.

Luigi Galvani, a professor of anatomy and physiology in Bologna, while making some experiments with a frictional apparatus, had his attention drawn to the fact that a recently-dissected frog's leg was thrown into a violent contraction whenever it was touched with a scalpel held in the hand of his assistant. Further investigations revealed, moreover, that the contractions occurred only when a spark was emitted from the frictional machine, and then only when the metallic substance was in contact with the preparation. Galvani was unable to offer any explanation of this phenomenon, as there was apparently no connection between the electrical machine and the frog's leg, by which the electrical spark could be conducted. The exact time of this observation is not known, but it is quite certain, from the evidence gathered by Prof. du Bois-Reymond ("Untersuchungen über thierische Electricität," Bd. i, S. 31), that it was prior to the year 1786, the date usually given in text-books. It is quite probable, from notes and dates upon the margins of his manuscripts, that Galvani began his investigations as far back as November, 1780. From this period he continued his observations and experiments up to the year 1786, when it occurred to him to determine whether the effects of atmospheric electricity upon the frog's muscles would be the same as that from the frictional apparatus. This supposition was confirmed by a series of experiments made during the year 1786, from the 26th of April to the 17th of August, for every flash of lightning was immediately followed by a contraction of the muscles. While yet occupied with these investigations, another observation was accidentally made by Galvani, which became the real starting-point for the development of the new science of electricity; for hitherto his observations had disclosed no new principle, although Galvani himself believed that only a new principle—animal electricity—could account for the phenomena. The effect of the electrical returning-stroke, however, which had been described by Lord Mahon, in 1779, in his "Principles of Electricity," offers, indeed, and was so held by Volta, a sufficient explanation for all the phenomena so far observed. On the evening of September 20, 1786, Galvani prepared and suspended three frogs to the iron trellis-work of his house by means of iron and, subsequently, of copper hooks, and observed that whenever the wind brought them into contact with the iron violent contractions took place. These movements Galvani also, at first, attributed to atmospheric electricity; but when it was afterward observed that the same phenomena occurred independently of variations in the electrical conditions of the atmosphere, and even in closed rooms, he arrived at the conclusion that the metallic arc, composed of either similar or dissimilar metals, was one of the conditions necessary for the production of contractions. That Galvani had, therefore, a true but slight perception of the cause of the contractions in these experiments is evident from the title of his paper, "Esperimenta circa l'Elettricita di metalli." He soon abandoned this view, however, and, from many other experiments, arrived at the conclusion that the electricity was developed within the animal tissues themselves, and that the metallic arc merely conducted the electricity from one part to another. These observations and conclusions were published in 1791, in the celebrated "De viribus Electricitatis in motu musculari commentarius."

With the publication of this paper, the attention of the whole scientific world was directed to Galvani's experiments. They were repeated again and again, wherever frogs were to be found and dissimilar metals procured, by all those who wished to familiarize themselves with these remarkable phenomena. Among the many distinguished men who became interested in this subject there was one who, by a series of delicate electrical experiments with Wilcke's electrophorus and the condenser, had made himself a recognized master in the field of electricity. Alexander Volta, a physicist, and professor of natural philosophy in the University of Pavia, repeated Galvani's experiments, and at first entered fully into the views of his countryman. But his calm and philosophic mind soon observed the important part which the arc played in the production of contractions; for, as he was unable to excite contractions except by a combination of heterogeneous metals, he soon dissented from the interpretation of Galvani, although the latter had already perceived and stated that the contractions were stronger when the arc consisted of two dissimilar metals than when composed of a single homogeneous metal. Volta then endeavored to produce muscular contractions in the tongue by placing on its upper surface a layer of tin-foil and on its under surface a silver spoon. When the circuit was closed, to his astonishment, he experienced, instead of the expected muscular contraction, a strange sensation of taste, and perceived that this sensation persisted as long as the two metals were in contact with each other and the two surfaces of the tongue. This experiment had been made by Sulzer in 1754, and recorded simply as a curious fact; but to Volta's mind it became a potent argument for his view, that the electricity which produced the contractions was not resident in the animal tissues, but was developed by the contact of two dissimilar metals with moist tissues. Subsequently he proved by physical apparatus that electricity was developed by the contact of two dissimilar metals with a moist conductor, independent of any animal tissue. Sulzer's experiment thus gave birth to voltaic electricity, the greatest discovery of the eighteenth century.

In support of his position Galvani asserted, and apparently demonstrated, that it was possible to excite contractions, though perhaps feeble ones, by contact of homogeneous metals; but Volta replied that, when metals were believed to be perfectly homogeneous, there were on their surfaces slight differences in temperature, hardness, polish, etc., which were sufficient to produce the electricity. Galvani then employed mercury as a metallic conductor, to which he thought the objections of Volta could not apply; by dipping the limb into the mercurial trough contractions at once resulted. To this experiment Volta replied that the surface of mercury was wanting in perfect homogeneity from the contact of air and moisture, and, therefore, capable of developing electricity.

Galvani's position thus seemed to be completely controverted by these experiments. It now remained for him to show that contractions could be produced without the contact of metals at all, and, in 1793, he offered what he believed to be the *experimentum crucis* in support of his theory, and which would establish it upon a firm and enduring basis. The leg of the frog was denuded and the sciatic nerve dissected out and its upper end cut off close to the spine; then, by means of non-conductors and without subjecting the nerve to any influence which could produce change in it, he gently brought its cut end in contact with the muscle. At once a distinct pulsation ensued. Similar pulsations were caused by allowing the nerve to fall upon a piece of abdominal muscle which was lying on a glass plate, and which had no connection with the frog. Galvani had thus apparently proved his case. Volta, however, did not admit his conclusions, and endeavored to refute them by declaring that the contractions so caused were extremely weak in comparison with those caused by the contact of heterogeneous metals, and that they were due to mechanical irritations incidental to the manipulations of the nerve. Subsequently he retracted these statements, and offered as an explanation that the electricity in these experiments was developed from contact of dissimilar fluids and tissues: a view which was readily accepted, as even Galvani and his followers had recognized that, after the contractions had become feeble or had entirely ceased, it was only necessary to moisten the muscle and nerve with blood, saliva, or some alkaline or acid fluid to again excite contractions. Thus again did Volta's marvelous dexterity convert Galvani's victory into an apparent defeat.

From this brief sketch of the long controversy between these two distinguished investigators, it is clear that the assertions of both are correct in many respects, and their denials equally incorrect. In all these experiments Galvani maintained the presence of electricity in animal tissues, but denied its development by the contact of metals; Volta maintained that the electricity was only of metallic origin, and denied its existence in the animal tissues.

In the next few years Galvani tried repeatedly, but unsuccessfully, to refute his great antagonist; even Alexander von Humboldt's remarkable experiments, in which all the extraneous influences objected to by Volta were carefully avoided, were of no avail. Humboldt recognized and stated the true position in the following words: "It is indisputably true, and first demonstrated by the observations of the great Ticinian philosopher, that when animals are not convulsed by homogeneous metals they will be so affected when the metals are made heterogeneous by the slightest change in their composition, polish, hardness, form, or temperature. This is the result, it appears to me, of Volta's experiments, and not that muscular contractions can only occur when the metals are heterogeneous."

Owing, however, to Volta's growing influence, Galvani's theory began to lose its adherents. Galvani himself died on December 4, 1798; happily for him, as, in the succeeding year, Volta discovered the pile, which enabled him to triumph over his adversary and to cause almost a total destruction of his theory. For the space of twenty-seven years animal electricity was almost lost sight of, although a few distinguished men, like Humboldt, Erman. and Pfaff, defended it, and Johannes Müller admitted its possibility. Voltaism developed from year to year, and by its aid brilliant discoveries were made in chemistry and physics, foreshadowing the great electrical discoveries and appliances of the present day. Nevertheless, it was this highly-developed voltaism which was destined to show the error in Volta's denial of the existence of animal electricity, though he himself did not live to witness the refutation of his erroneous statements.

In 1820, six years before Volta's death, the Danish philosopher, Oersted, discovered electro-magnetism. He found that an electric current, passing above or below a magnetic needle, immediately deflected it from the meridian. This discovery, in the hands of Schweigger and Poggendorff, led to the construction of the sensitive multiplicator, which in 1825 was rendered still more sensitive by the addition by Nobili of Ampère's astatic needles. By thus giving birth to this delicate and refined apparatus, "metallic electricity," in the words of du Bois-Reymond, "was to atone for the wrong she had done to her more delicate twin sister, animal electricity, in their earlier years."

After the lapse of twenty-eight years, Nobili was the first to again take up the subject of animal electricity in a scientific spirit. The first use he made of his galvanometer was to seek for the electrical currents in muscles and nerves,—in which, however, he was unsuccessful. The method he adopted was as follows: The spinal column and feet of the frog were dipped into two vessels containing a solution of salt and the multiplicator included in the circuit. As soon as it was closed the limbs were convulsed, but the needle remained stationary. With a new and more sensitive multiplicator, Nobili was enabled to obtain a deflection of twenty and even thirty degrees, and always in a direction which indicated the passage of a current, in the frog, from the feet to the head. This current he called "la corrente propria de la rana," which, later, du Bois-Reymond termed the "frog-current." Of this current, Nobili demonstrated that it is not only present at the moment of closure, but that it is constant, and that its power increases with the number of frogs employed. While he thus discovered the existence of the frog-current, he was led into the error of supposing it was independent of physiological processes, and thermo-electric in origin,—an opinion which was also shared by de la Rive and Magendie.

A few years later, Carlo Matteuçci began his investigations in the field of electro-physiology. He started with the endeavor to bring all physiological phenomena into some connection with electrical forces, which necessarily vitiated many of his conclusions and experiments. Nevertheless, he was the first to show, in 1838, by a series of experiments, that the electro-motive action upon which the frog-current depends is independent of the contact of nerve and muscle; that it is not necessary to prepare the frog according to Galvani's method, but that it sufficed to connect any two points of the frog's body—the back and leg, for example—to obtain a marked deflection of the needle. In 1841 he formulated the following law: The interior of a muscle, placed in connection with any part whatever of the same animal, such as nerve, surface of muscle, skin, etc., produces a current which goes, in the animal, from the muscular part to that which is not so.

In the spring of 1841, Emil du Bois-Reymond, at the suggestion of Johannes Müller, repeated and extended Matteucci's experiments contained in his "Essai sur les phénomenes électriques des animaux" (Paris, 1840). This investigator soon discovered the fact that all muscles and nerves are the seats of electrical currents, which differ in intensity and direction, and that the frog-current is but the resultant of individual currents, whose direction from the foot to the head is merely accidental and not essential. The first results of his investigations were embodied in his paper entitled "Vorläufiger Abriss einer Untersuchung über den sogenanaten Froschstrom und über die electromotorischen Fische," published in Poggendorff's *Annalen der Physik und Chemie*, January, 1842. With the aid of improved galvanometers, and various forms of apparatus devised by himself, du Bois-Reymond was enabled to accurately determine and formulate the laws relating to the electrical phenomena of muscles and nerves. The result of these laborious investigations was published in his great work, "Untersuchungen über thierische Electricität," 1848, from which year it may be said that electro-physiology took rank as a distinct science.

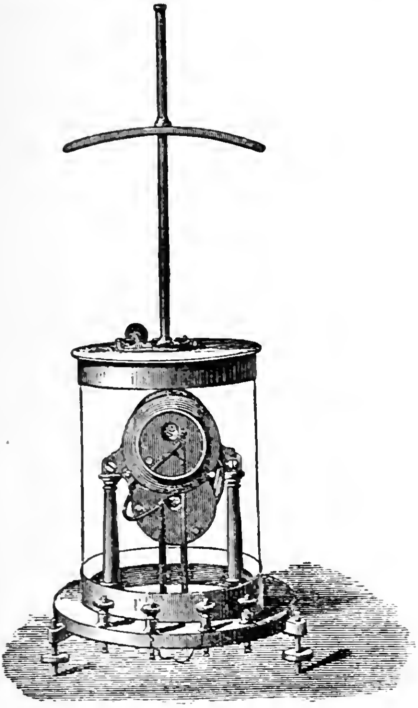

Fig. 1.—Thompson's Galvanometer.

Methods of Investigation.

Galvanometer.—In the investigation of the electrical currents of muscles and nerves the physiologist is limited practically to the galvanometer, though in recent years the capillary electrometer has afforded valuable assistance. The essential requisites of any galvanometer used for physiological purposes are that it possesses a high degree of sensitiveness, responding quickly to the influence of extremely-weak currents. These conditions have been realized by the use of small, light needles; the adoption of the astatic system, as suggested by Ampère and Nobili, by which the directive influence of the earth's magnetism is eliminated; and multiplication of the number of turns of the wire by which the needles are surrounded; this latter arrangement, within certain limits, increases the effect of feeble currents with which we have to deal upon the needle. One of the best galvanometers is that of Sir Wm. Thompson (Fig. 1). The principle upon which this instrument is constructed is the same as that of the ordinary galvanometer. Its superiority as an apparatus for refined physiological research lies in the fact that the needles, of which there are two sets, an upper and a lower, are very small and light, not measuring more than an eighth of an inch in length. They are united by a rod of aluminium and arranged astatically. To the upper set of needles there is attached a small, slightly-concave mirror, about six millimetres in diameter. The system of needles and mirrors, so slight and delicate that it hardly weighs more than a grain, is suspended by a single fibre of silk from the vulcanite frame of the wire coil. Around each set of needles is arranged a coil of fine wire, the upper of which is wound in a direction opposite to that of the lower coil. The terminals of these wires are attached to four binding-screws on the vulcanite disk. The coils are supported by brass uprights, covered by a glass shade, brass bound, which rests upon the vulcanite base, the whole being leveled by three screws. From the centre of the brass disk covering this shade rises a brass rod which carries a movable, curved magnet, slightly magnetized, by which it is possible, by moving it up and down, not only to neutralize the earth's magnetism, but to create an artificial meridian in any direction. For observing the deflections of the needles, a lamp and scale arrangement, such as shown in Figs. 2 and 3, is used, which is placed about three feet from the galvanometer. A small slit in the frame beneath the scale permits a narrow beam of light to pass to the mirror and by it is reflected to the scale. The image is brought to the zero-point by shifting the position of the magnet by fine adjusting-screws. When the electrodes are connected with the two outer of the four binding-screws, and the two inner ones joined together, the current to be investigated will pass through both coils; by removing the connecting wire between the two inner screws, the instrument may be converted into a differential galvanometer, and the relative intensities of two currents easily determined. The particular galvanometer which is used in the physiological laboratory of the Jefferson Medical College has a resistance of 6821 ohms at a temperature of 18° C. A single Daniell element produces through a circuit of 204,660,000 ohms resistance a deflection of 180 degrees on the scale, or a deflection of 1 division through a circuit of 36,838,800,000 ohms resistance. Owing to the extreme delicacy of this instrument it is provided with a shunt, by means of which a fractional part only of the current to be investigated is permitted to pass into the galvanometer. The coils of wire of which the shunt is composed are of varying lengths, and so arranged that they can be united by brass plugs. The resistance of the coils is so graduated, with reference to the resistance of the galva-

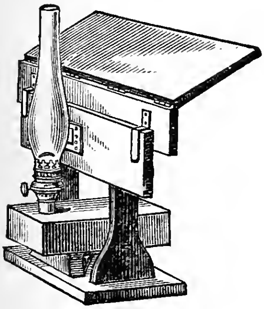
FIG. 2.

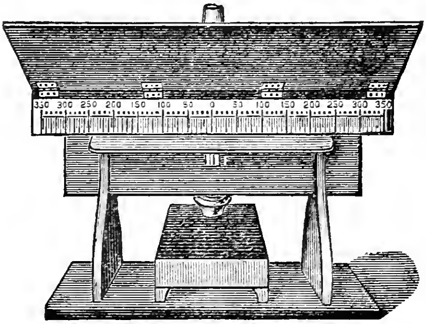

FIG. 3.

nometer, that it is possible to permit $\frac{1}{10}$, $\frac{1}{100}$, or $\frac{1}{1000}$ of the total current to influence the needle.

The tangent galvanometer, or *boussole*, as constructed by Wiedemann, is the form most generally employed in physiological investigations (Fig. 4). It consists primarily of a thick copper cylinder, through which a tunnel has been bored. Within this tunnel is suspended a magnetized ring, just large enough to swing clear of the sides of the chamber. The object of making the magnet ring-shaped is to increase its strength in proportion to its size, and to get rid of the central inactive part. Connected with and passing upward from the magnetized ring through the copper cylinder is an aluminium rod, surmounted by a circular plane mirror. Above the mirror rises a glass tube, which carries on top, on an ebonite support a little windlass, capable of being centred by three small screws. On the windlass is wound a single filament of silk, which passes down the tube and is attached to the mirror. The magnet can, by this contrivance, be raised or lowered and centred in the copper chamber. Deflections of the mirror from currents of air are prevented by inclosing it with a brass cover provided with a glass window. The coils are placed on each side of the copper chamber, and supported by a rod, on which they slide. By this arrangement they can be approximated until they meet and completely conceal the cylinder. By varying the position of the coils the influence of the current upon the needle can be increased or diminished. An advantage which this galvanometer possesses is the damping of the oscillation of the needle, so that it quickly comes to rest after deflection. This is accomplished by the development of induction currents in the copper cylinder, whose direction is opposite to that of the movement of the needle. The in-

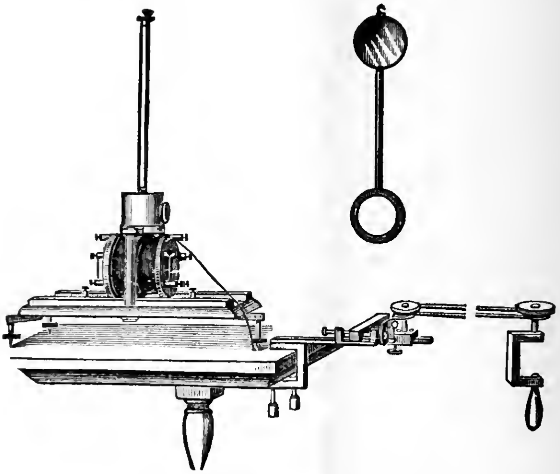

Fig. 4.—Wiedemann's Boussole.

strument, therefore, is aperiodic,—that is to say, that when the needle is influenced by a current it moves comparatively slowly until the maximum deflection is reached, when it comes to rest without oscillations. When the circuit is broken, the needle swings slowly back to zero, and again comes to rest without oscillations.

Inasmuch as the needle is not astatic, it is rendered so by the use of an accessory magnet,—the so-called Hauy's bar. This magnet, supported by a rod directed perpendicular to the coils, is placed in the magnetic meridian, horizontal to the needle, with its north pole pointing north. By sliding the magnet toward the needle the directive influence of the earth's magnetism is gradually diminished, and when it is reduced to a minimum the needle acquires its highest degree of instability. By means of a pulley an angular movement can be imparted to the end of the accessory magnet in the direction of the magnetic meridian, which serves to keep the needle on the zero of the scale. The deflections of the needle are observed by means of an astronomical telescope, above which is placed a scale divided into centimetres and millimetres, and distant from the galvanometer about six or eight feet. As the numbers on the scale are reversed they will be seen in the mirror in their natural position, and with the deflection of the needle the numbers will appear as if drawn across the mirror. The extent of the deflection is readily determined when the needle comes to rest.

The Capillary Electrometer.—Notwithstanding the extreme sensitiveness of the modern galvanometer, it has been found desirable, in the investigation of many physiological processes, to possess some means which would respond even more promptly to slight variations in electromotive force. This has been realized in the construction by Lippmann of the capillary electrometer. The principle of this apparatus rests upon the fact that the capillary constant or the surface-tension of mercury undergoes a change upon the passage of an electrical current, in consequence of a polarization by hydrogen taking place at its surface. If a capillary glass tube be filled with mercury and its lower end inserted into a solution of sulphuric acid, and the former connected with the positive and the latter with the negative electrode, it will be observed, upon the passage of the current, that a definite movement of the mercury takes place, in the direction of the negative electrode, in consequence of the diminution of its capillary constant or the tension of its surface in contact with the acid. As a reverse movement follows a cessation of the current, a series of oscillations will follow a rapid making and breaking of the current. If the direction of the current is reversed, the capillary constant is increased and the mercury ascends the tube toward the negative pole. From facts such as these Lippmann constructed the capillary electrometer, a convenient modification of which, devised by M. v. Frey, is shown in Fig. 5. This consists of a glass tube, *A*, forty millimetres in length, three millimetres in diameter, the lower end of which is drawn out to a fine capillary point. The tube is filled with mercury and its capillary point immersed in a 10-per-cent. solution of sulphuric acid. The vessel containing the acid is filled to the extent of several millimetres with mercury also. The mercury in the tube is put in connection with a platinum wire (*a*), and the acid in the vessel with a second wire (*b*). When a constant current passes into the apparatus in the direction from *b* to *a* the mercury is pushed up the tube, and, upon the breaking of the current, it may or may not return to the zero-point. For the purpose of measuring in millimetres of mercury the pressure necessary to compensate this change in the capillary constant produced by the electro-motive force of polarization, the apparatus is provided with a pressure-vessel, *H*, and a manometer, *B*. This electrometer can be applied to any microscope having a reversible stage. The oscillations of the mercury can then be observed with the microscope provided with an ocular micrometer. The special advantage of the electrometer is, that it will respond instantly to any variation in the electro-motive force, and indicate a difference of potential, according to Lippmann's observation, as slight as the $\frac{1}{10080}$ of a Daniell. These rapid oscillations can be recorded by photographic methods.

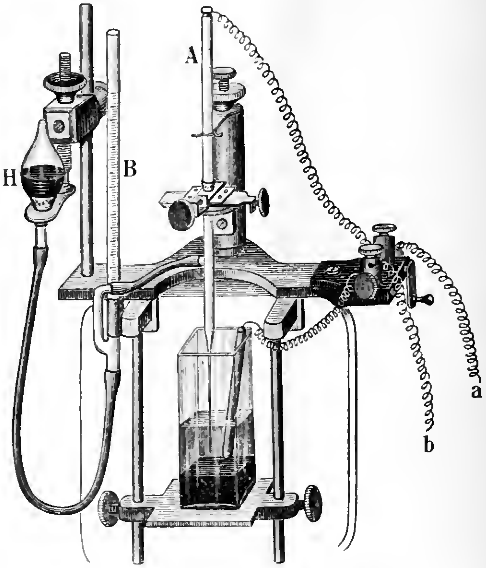

FIG. 5.—CAPILLARY ELECTROMETER.

Electrodes.—It is essential, in the detection of weak electrical currents with highly-sensitive galvanometers, that the electrodes, which are placed in contact with the tissues, should not only be absolutely homogeneous, as the slightest difference between them will develop a current upon the closure of the circuit, but that they should also be incapable of producing chemical changes in the tissues which would, in time, lead to a polarization of the electrodes. Should this condition be established, it would give rise to a current in an opposite direction, which would tend to weaken or neutralize the original current, whether artificial or natural. All these difficulties have been overcome by du Bois-Reymond in the construction of what he has termed non-polarizable electrodes, which are also absolutely homogeneous if correctly prepared. Du Bois-Reymond, availing himself of the discoveries of Regnauld, in 1854, that a strip of chemically-pure zinc immersed in a saturated solution of neutral sulphate of zinc, and of Matteucci, in 1856, that ordinary zinc amalgamated and immersed in the same solution, exhibited no polarization, constructed two forms of electrodes, known as diverting vessels and diverting tubes, which are of very general applicability.

The diverting vessel (Fig. 6) consists of a zinc trough insulated by a base of vulcanite, provided with a handle and a binding-screw for the attachment of wires. The inner surface of the vessel is carefully amalgamated, and the outer surface covered with a layer of black varnish. The cavity of the vessel is filled up with the deriving cushions, composed of a series of layers of Swedish filtering-paper, which are bent over the edge of the vessel. These layers are stitched together, and a clean, perpendicular edge obtained with a razor. Before using, they should be saturated with the zinc solution, and when placed in the vessel they are held in position by a strip of ebonite and a rubber band. The trough is then filled with the zinc solution. To prevent the corrosive action of the zinc solution upon the tissues to be examined, a thin clay guard is placed upon the deriving cushion. This guard consists of china-clay worked up into a soft mass with a $\frac{1}{2}$-per-cent. solution of sodium chloride. The guard not only prevents corrosion, but, from the presence of the salt, the secondary resistance which would arise between the liquid conductor and the tissues, and thus diminish the current-strength, is avoided. The diverting cylinder (Fig. 7) consists of a flattened glass tube attached to a universal joint and supported by an insulated brass stand. The lower end of the tube is closed by moistened china-clay, which can be molded into any desired shape. The interior of the tube is filled with

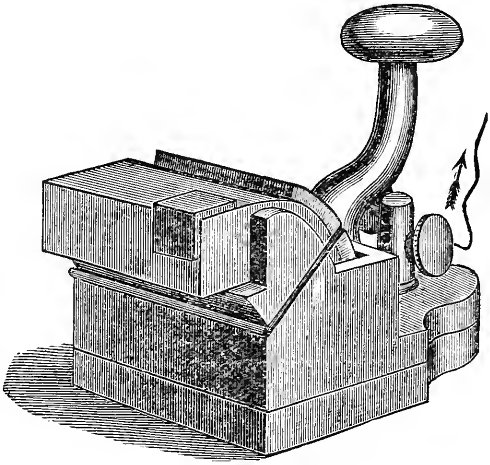

FIG. 6.—DIVERTING VESSEL.

the zinc solution, in which is immersed a slip of amalgamated zinc, the upper portion of which is lacquered. Electrodes of this form are not only serviceable for leading off currents from particular points of muscle and nerve, but are equally well adapted for purposes of electrical stimulation.

THE ELECTRICAL PROPERTIES OF INJURED MUSCLES.

Individual muscle-fibres, owing to their small size, are not well adapted for experimental investigation, and present many obstacles to a study of their electro-motive properties. Research is, therefore, limited to groups of fibres as they are found in any given muscle. A complex organ, like a muscle, whose fibres are arranged in a parallel manner, furnishes results which are sufficiently accurate for the formation of definite conclusions. As the primitive bundles of fibres into which a muscle may be divided also exhibit corresponding properties, it is highly probable that individual fibres are similarly endowed, and that the electromotive properties of a muscle are the resultant of those of its component fibres.

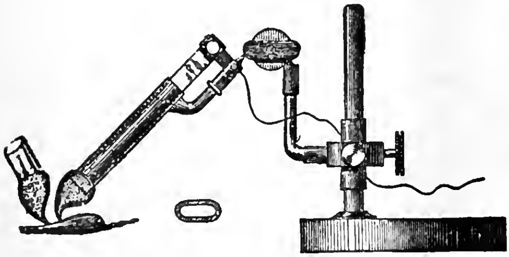

FIG. 7.—DIVERTING CYLINDER

The demonstration of the fundamental facts of the electrical properties of muscle is most conveniently made with single muscles, and, moreover, with those the arrangement of whose fibres is parallel, *e.g.*, the sartorius, the gracilis, or semimembranosus of the frog. Inasmuch as du Bois-Reymond discovered that the body-current is only the resultant of the currents of individual muscles, experimentation with the entire body, or even with a single limb, is wholly unnecessary.

Muscle-Prism.—If the tendinous ends of one of the above-mentioned cylindrical or oval muscles be removed by a section made at right angles to the longitudinal direction of its fibres, a muscle-prism is obtained, which presents a natural longitudinal surface and two artificial transverse surfaces. A line drawn upon the surface of such a muscle-prism, at a point lying midway between the two transverse sections, constitutes the equator. When the natural longitudinal and artificial transverse sections of a muscle-prism are brought into connection with the wires of a galvanometer whose terminals are provided with non-polarizable electrodes, an electrical current at once develops, the intensity and direction of which are indicated by the deflections of the galvanometer-needle. In all instances it is shown that the current passes from the longitudinal surface through the galvanometer to the transverse section, and then through the muscle to the original point of departure; in other words, the former surface is electrically positive to the latter, which is electrically negative. The two points exhibiting the greatest difference of potential, and, consequently, giving rise to the most powerful current, lie in the equator and in the centre of the transverse section. Currents of gradually-diminishing intensity are obtained when the electrode placed on the longitudinal surface is removed from the equator toward either extremity. Feeble currents are developed when two points, situated at unequal distances, either on corresponding or opposite sides of the equator, are connected; in either case, the current flows from the point lying nearest the equator to the point farthest from it. Similar currents are obtained when two points on the cross-section, situated at unequal distances from the central axis, are united, in which case the direction of the current will be from the point lying nearest the periphery toward the central axis, or from the less negative to the more negative point. On the contrary, no current is generated when two points on the longitudinal surface equally distant from the equator, or two points on the transverse surface equally distant from the central axis, are united; such points are said to be iso-electrical. These conditions are shown in Fig. 8.

From these facts it is evident that the muscle-prism may be looked upon as presenting, on its longitudinal surface, a series of tension-curves, which surround the prism in a concentric manner, and in a direction at right angles to that of its fibres. At the equator the greatest positive tension prevails, and from this point it gradually diminishes until zero is reached, at the junction of the longitudinal and transverse surfaces. In the same way the transverse section presents a series of tension-curves, all of which are negative with reference to the longitudinal surface; but, in passing from the periphery toward the centre, if the muscle be circular, the negativity gradually increases until it reaches its maximum, at the centre.

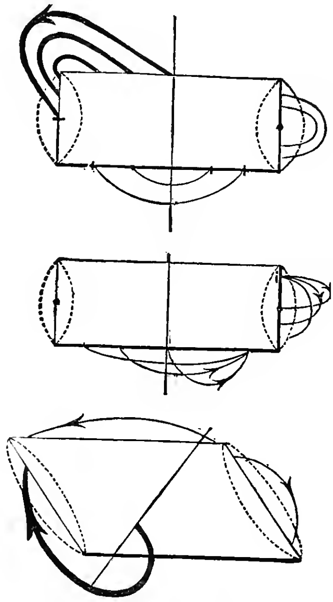

FIG. 8.—DIAGRAM TO ILLUSTRATE THE CURRENTS IN MUSCLE.

The arrow-heads indicate the direction and the thickness of the lines the strength of the currents.

The Muscle-Rhomb.—The regularity in the position of points of unequal tension, and the simplicity of the currents when such points are connected by an arch, hold true only for regularly-constructed muscles, as represented by the muscle-prism. Deviations from this assumed normal condition, both in the position of the points of positive and negative tensions, with reference to the longitudinal and transverse sections, and in the direction of the currents, become apparent when muscles whose fibres are irregularly arranged are subjected to galvanometric investigations. It is oftentimes very difficult to locate definitely in such muscles the positions of the points of opposite and similar potential. As an illustration of the shifting of the cardinal points, it is only necessary to examine a regular muscle-rhomb, constructed by dividing the two extremities of a regularly-constructed muscle in such a manner that the transverse sections are parallel and directed obliquely to the long axis of the fibres. In such a rhomb the fundamental law—that the longitudinal surface is everywhere positive toward the transverse surface, which is everywhere negative—holds true; but the position of the greatest positive electrical potential is no longer on the equator, but situated near the obtuse angle, from which the tension gradually declines as the acute angle is approached. The reverse of this holds true for the position of the points of greatest negative potential upon the transverse surface. Instead of being situated at the centre of the surface, it is now found near the acute angle, from which the tension declines as the obtuse angle is approached. There is, in consequence, a marked displacement in the position of the resulting currents. The equator, in such a rhomb, would be directed obliquely across the muscle, between the two obtuse angles, dividing it into two equal halves. The currents derived from obliquely-directed surfaces du Bois-Reymond has termed "inclination currents," the strength of which increases with the angle of inclination of the transverse surface. Inclination currents are observed in the gastrocnemius muscle, in which the natural transverse surface passes into the tendon in an oblique direction.

The Natural Muscle.—Electrical currents similar to those exhibited by the muscle-prism may be obtained from the natural muscle, which yet retains its tendinous or aponeurotic extremity. The natural ends of the muscular fibre inclosed by sarcolemma and tendon are spoken of as the natural transverse section. In his earlier experiments, du Bois-Reymond recognized no difference in the electrical properties of the natural and artificial cross-sections; but, subsequently, he observed that if certain precautions were taken not to injure the tendon, either chemically or physically, the negativity of the natural cross-section was inconstant. If examined immediately after removal from the body of the animal, after observing the above precautions, the electrical opposition between the longitudinal and natural cross-sections may be entirely absent, or, as is frequently the case, the latter surface may be positive in character. This is particularly true of animals which have been subjected to a temperature of 0° C. The negativity is at once developed if the tendinous expansion is chemically changed, as was the case by the saturated salt solution in the electrodes employed by du Bois-Reymond in his earlier experiments. The layer of muscle-substance in the immediate neighborhood of the tendon which is so often neutral or even positive in its electrical relations he has termed the parelectronomic (from *para nomos*, contrary to law). All muscles possess this paralectronomic layer, and it is only necessary to remove it to make a caustic artificial cross-section, to permit the negativity of the living muscle to manifest itself.

The muscle-currents such as those above described have been shown to be present in the muscles of various representatives of mammals, birds, and reptiles, in the muscles of crustacea, and in the earthworms. The tibialis anticus, from the amputated leg of man, examined hardly a quarter of an hour after the operation, exhibited such a marked electrical difference between the longitudinal and transverse that the needle was thrown violently against the guards. (Du Bois-Reymond, " Untersuchungen über thierische Electricität," Bd. i, S. 524.) Du Bois-Reymond, to whom we are indebted for a knowledge of all the preceding facts, considers the currents to be intimately connected with the living condition of the muscle, and essential to the performance of its functions.

The Electro-motive Force of the Muscle-Current.—The muscle-current developed by connecting the longitudinal and transverse surfaces possesses an electro-motive force the amount of which can be estimated by the method of compensation devised by Poggendorff and modified by du Bois-Reymond. The idea involved in this method is to send first through the galvanometer the maximum strength of the muscle-current, and then, by means of the rheocord, to send a fractional part of the Daniell current in an opposite direction, just sufficient to neutralize the effect of the muscle-current upon the needle. When the two currents are equal and opposite in amount, the needle remains stationary at the zero-point. The fraction of the Daniell thus becomes a measure of the muscle-current, and if the rheocord wire has been previously graduated in millimetres, each of which represents a fraction of the electro-motive force of the Daniell current, it becomes a simple matter to determine the electro-motive force of the muscle in terms of the Daniell from the position of the slides on the rheocord wire. The electro-motive force of the frog-current was found by du Bois-Reymond (*Archiv für Anat. und Phys.*, 1867) to vary from 0.037 to 0.075 D.

Conditions Influencing the Development of the Muscle-Current.—As the existence of the muscle-currents is connected with those chemical changes underlying all nutritive processes, they do not disappear at once upon the death of the animal, but continue for a variable length of time, though with gradually-diminishing power. All those influences, therefore, which hasten or retard destructive chemical changes will influence the time of disappearance of the currents. Though the current diminishes in strength from the first observation, there is not infrequently observed for a short period an increase in the electro-motive force, which has been attributed to an additional current passing from the cross-section to the longitudinal surface, developed by the contact of the fluids of the electrodes with the muscle-tissues. With the separation of the muscle from its blood-supply, it begins to experience a series of retrogressive changes which finally eventuate in rigor mortis. As this condition is approached the muscle exhibits simultaneously a diminution of its currents and a loss of its physiological properties. The dependence of the muscle-current for its existence upon the normal metabolism of the tissue is shown by the fact that, after the disappearance of the current and the beginning of rigor mortis, it will re-appear if the latter condition be removed by the introduction of a stream of fresh defibrinated blood.

Among the influences which affect in a significant manner the muscle-current must be mentioned temperature. It was originally shown by du Bois-Reymond that if a muscle be placed in distilled water at a temperature of 50° C. it contracts to a shapeless mass, loses its irritability, and becomes devoid of electrical properties. This is to be explained by the coagulation of the albuminous constituents, upon the normal composition of which the physiological and electrical properties of the muscle depend. A similar destructive influence upon the muscle-current has that degree of cold which impairs the vitality of the muscle. After thawing of the muscle no current is obtainable. Within the limits of 35° C. and 40° C., as is well known, all vital processes proceed most actively; the electro-motive force will, therefore, be increased with slight elevation, and decreased with a lowering of the temperature. According to Hermann, the variations between the above-mentioned limits will amount to as much as 22 per cent. The same observer (*Archiv für die gesammte Physiologie*, Band iv, 1871) has also shown that heating different points of the longitudinal surface renders them strongly positive toward the cooler portions, though this does not hold true for the transverse surface. Between warmer and colder portions of muscle-substance a difference of potential always exists, the condition of the parts lying between being unimportant.

The dimensions of the muscle-cylinder have also a slight influence upon the current-strength. By employing the method of compensation du Bois-Reymond has made the observation that within certain though not well-defined limits the electro-motive force increases with both the length and thickness of the muscle. By the intercalation of two corresponding pieces of muscle of unequal length in the galvanometer circuit, and by placing the electrodes in such a position that the currents conducted off pass into the galvanometer in an opposite direction, it was observed that the current from the larger muscle exerted a more powerful influence upon the needle than the current from the shorter muscle. In the same way it was shown that if two muscles the same length but of unequal thickness are opposed to each other, the thicker muscle always yields a stronger current than the thinner one.

INFLUENCE OF THE CONTRACTION ON THE MUSCLE-CURRENT.

Negative Variation.—The first accurate observations of the influence of the contraction upon the muscle-current were made by du Bois-Reymond. It was shown by this observer that as soon as the muscle enters the state of activity there is a diminution in the electro-motive force between the longitudinal and transverse surfaces, with a resulting diminution in the intensity of the muscle-current. This change in current-strength has been termed *negative variation.* In order to observe this negative variation of the muscle-current, it is only necessary to insert between the terminals of the galvanometer circuit the longitudinal and transverse surfaces of the gastrocnemius muscle. The powerful current thus obtained causes a marked deflection of the needle, which, after a few oscillations, comes to rest. If now the nerve in connection with the muscle be tetanized with the interrupted or induced current, the muscle passes into the condition of tetanus; at once the needle is observed to return toward the zero-point and remain in this neighborhood as long as the tetanic contraction continues. With the cessation of the stimulation the needle is again deflected outward by the re-establishment of the muscle-current, without, however, attaining its former position. There thus appears to be a decrease in the strength of the muscle-current during muscular contraction, the extent of which is proportional to the intensity and duration of the contraction. From the inertia of the galvanometer needle and the short duration and force of the negative variation du Bois-Reymond was unable to show this change in a single muscle pulsation. It was for this reason that tetanic stimulation was employed.

There can be no doubt that this diminution in the strength of the current is intimately connected with muscle activity, and not the result of an escape of the electrical current from the electrodes, inasmuch as the same variation follows chemical, thermal, or mechanical stimulation. Nor can it be due to any change in the position of the electrodes, for if the muscle be clamped so as to prevent displacement during the contraction the activities arising within the muscle will, nevertheless, produce a diminution of the current.

The question as to whether this negative variation during tetanus is the result of a steady, continuous decrease of the electro-motive force, or of a series of rapid and successive variations in the intensity of the muscle-current, cannot readily be shown by the galvanometer from the inertia of the needle. The physiological rheoscope, however, affords a ready means of elucidating this question. It was discovered by Matteucci that, if the nerve attached to the gastrocnemius muscle be laid upon the thigh of another animal in such a manner that the nerve forms an arch uniting negative and positive surfaces, with every contraction of the latter the gastrocnemius is thrown into pulsation. The explanation of this secondary contraction was furnished by du Bois-Reymond. The current from the primary muscle undergoing a negativity produces a negative variation of the portion of the current which passed into the applied arch of nerve; and, as every change in the intensity of a current excites a nerve-impulse, a secondary contraction follows. Moreover, if the primary nerve be repeatedly stimulated, the thigh passes into the tetanic state, and simultaneously the neighboring muscle—the gastrocnemius—passes into the condition of secondary tetanus. As only the second muscle can be tetanized by a series of discontinuous impulses descending the nerve,—the result of rapid variations in the strength of its current,—it is evident that the primary muscle is experiencing similar variation in its electrical conditions. Confirmatory proofs of alternating variations in the strength of the muscle-current during the tetanic state are furnished by the oscillations of the mercury in the capillary electrometer and by the sonorous vibrations of the telephone when these instruments are employed instead of the physiological rheoscope.

While the above means of investigation reveal an intermittent variation in the intensity of the muscle-current, no evidence is adduced which would indicate whether it undergoes merely a partial diminution, or whether it is entirely obliterated, or whether it experiences a reversal, passing beyond the zero-point to a greater or less extent in a positive direction.

The answer to this, as well as other questions relating to the characteristics of the negative variation, was first given by J. Bernstein ("Untersuchungen über den Erregungsvorgang im Nerven und Muskelsysteme," 1871), who, by means of the differential rheotome, was enabled to study it in all its phases. The principle of this instrument consists in the rotation of a wheel at a given rate, which closes a circuit stimulating a nerve or an end of a muscle, as well as a circuit diverting the muscle-current through the galvanometer; by arranging the apparatus so that the stimulating current is closed at varying intervals before and after the diverting current, it becomes possible to determine the rate of propagation, form, extent, and time durations of this negative change. By these investigations it was shown that, after stimulation of one extremity of a muscle by an induction-shock, a definite and measurable interval of time elapses before the molecular changes thus initiated reach the electrode upon the longitudinal surface of the muscle, and which reveal themselves through the deflection of the galvanometer-needle in a direction indicating a negativity of the original muscle-current. This interval of time increases or decreases with the distance of the stimulating electrodes from diverting electrodes. Inasmuch as the time occupied by the molecular disturbance in arriving at the electrode and the length of muscle are proportional to each other, it is easy to determine the rate of propagation by dividing the latter by the former. This Bernstein calculated to be about three metres per second. It was also shown that this modification of the muscle, after its first appearance, rapidly reaches a maximum and then more slowly declines; in other words, it propagates itself in the form of a wave. The length of time required for an entire wave to pass any given point of the muscle was estimated at 0.0033 second, from which value and from that of the rate of propagation it is easy to see that the wave-length approximates ten millimetres. With reference to the extent of negativity which the muscle-current undergoes during the contraction, Bernstein (*op. cit.*, p. 68) observed that, at the highest point of the negative wave, the muscle-current was entirely obliterated, though there was no evidence of a reversal in the opposite direction. Moreover, a further observation of interest was the apparent fact that the negative variation passes over the muscle entirely during the latent period [1] and actually precedes the movement of the contraction wave.

Burdon-Sanderson ("Proceedings of the Royal Society," May 1, 1890; *Centralblatt für Physiologie*, 1890, Band iv, S. 185), however, has brought forward incontrovertible evidence that the two processes,—the negative variation and the contraction wave,—instead of being separated in time, occur simultaneously. In these careful experiments the moment of stimulation, the electrical response as revealed by the capillary electrometer, and the change of form were recorded at the same instant by photographic methods. An analysis of the results shows that the electrical wave, instead of preceding the contraction wave, actually accompanies it. The latent period also, the time elapsing between the stimulation and the simultaneous appearance of the two processes, was shown to be very much shorter than that given by Yeo, and amounting to not more than the 0.0035 second. Sanderson concludes, from his experiments, that "all those theories, therefore, of the excitatory process in muscle which rest on the supposed fact that electrical disturbance is a concomitant of the period of latent stimulation, fall to the ground."

Electrotonus—The passage of a constant galvanic current through a limited portion of a muscle produces a change in its electrical condition to which the term electrotonus has been given. It has long been supposed that the electrotonic condition was limited to that portion of the muscle included between the two electrodes. The change of condition produced by the constant current relates to the natural muscle-current, and depends upon an inner polarization of the muscle. The constant current develops within the muscle an opposing current which may strengthen or diminish the pre-existing current according to the direction. If the constant current has the same direction as the muscle-current, the opposing current will, by adding itself to the latter, strengthen it; if,

---

[1] It was shown by Helmholtz (Archiv für Anat. und Phys., 1850, S. 276), in his classical researches upon the time relations of the different phases of a single muscular contraction, that a short but measurable interval of time elapsed between the application of a momentary stimulus and the beginning of the contraction, which he termed the "latent period," the duration of which he stated to be 0.01 second. Tigerstedt and Yeo have, by improved methods, reduced it to the 0.005 second.

however, the constant current is opposite in direction to the muscle-current, the opposing current will diminish the strength of the muscle-current. The electrotonic condition endures for some time, though with gradually-diminishing intensity, after the withdrawal of the constant current. Hermann ("Handbuch der Physiologie," Band ii, S. 168) states that he has been able to demonstrate the existence of the electrotonic condition also in the extra-polar region. Currents flowing in the same direction as the polarizing were obtained from the portion of the muscle in connection with the galvanometer, the strength of which increased with the latter. These currents are better developed on the side of the anode than on the side of the cathode.

Electrical Properties of Uninjured Muscle.

Currents of Rest.—The laws formulated by du Bois-Reymond as to the existence of electrical currents in uninjured as well as injured muscle, and the negative variation which they undergo during contraction, have been opposed by Professor Hermann, who, from a long series of accurate experiments, denies the existence of currents in passive and absolutely uninjured muscle, and attributes the currents which are obtained to injuries of the surface of the muscle-substance due to the methods of preparation. However carefully a muscle may be removed from the body, various points on its surface become altered chemically or physically, whereby differences of potential are established, the injured part becoming negative to the uninjured. The currents which are observed during muscular activity Hermann regards as the result of the action of electromotive forces which come into operation at the seat of excitation, and not as the result of a negative variation of pre-existent currents. To such currents the term "action currents" has been applied.

The negativity of the natural cross-section which led du Bois-Reymond to regard these currents as pre-existing in all living muscles was shown by himself to be due to the corrosive action of the salt solutions of the electrodes upon the muscle, thus causing an artificial cross-section. When this source of error was eliminated, it was noticed that the natural muscle-end exhibited electrical actions which were quite irregular in relation to the longitudinal surface, being sometimes neutral, at other times negative or even positive. This difference in the behavior of the natural and artificial cross-sections du Bois-Reymond attributed to a peculiar property of the natural end of the fibres, termed by him parelectronomia. The experiments which were subsequently made by du Bois-Reymond to obtain currents from muscles without removal of the skin were vitiated by the existence of powerful skin-currents, which were directed from without inward. These currents he was enabled to set aside, however, by destroying, at different points, the integrity of the skin by cauterization with a saturated solution of salt, after which the muscle-currents could be obtained. It was concluded, from these experiments, that in animals not deprived of skin natural muscle-currents are pre-existing.

Professor Hermann did not regard this experiment as conclusive evidence for the pre-existence of the currents, and raised the objection that by the time the skin-currents were set aside by the caustic the underlying muscle-substance was also more or less injured, as, indeed, was shown to be the case when nitrate of silver was employed as the caustic agent. This he regarded as a sufficient explanation for the appearance of the current, especially as it increased in strength with the extent of cauterization. In subsequent investigations (*Archiv für die Gesammte Physiologie*, Band iii, 1870) Hermann demonstrated that, by immersing a curarized frog in a solution of corrosive sublimate for ten seconds, the skin-currents could be entirely abolished without producing any discoverable lesion of the muscular surface. After washing and drying the animal, it was only possible to obtain irregular currents of indefinite direction, and to which no physiological significance could be attached. He also succeeded in demonstrating that the gastrocnemius muscle might be so prepared by the avoidance of all pressure, change of temperature, and, above all, the contact of the irritating secretion of the skin; that it would exhibit the same want of constancy and regularity in the distribution of electrical inequalities. In fish, where from the absence of skin-glands there are no skin-currents, and where neither cauterization nor mechanical preparation is necessary, it was impossible to obtain currents from the muscles if the animal was curarized and kept at room temperatures (*Archiv für die Gesammte Physiologie*, Band iv, 1871). One of the most favorable muscles for isolation without injury is the heart, and Englemann showed, in 1874, that when examined in a state of rest no currents whatever could be detected. The same observer has also found (*Archiv für die Gesammte Physiologie*, Band xv, S. 328) that an ordinary muscle which has been divided subcutaneously, and therefore presents an artificial cross-section which is negative to the longitudinal surface, will soon again become streamless under the influence of the circulation and innervation.

From experiments such as these Hermann concludes that, in absolutely uninjured passive muscle, no current is demonstrable, and that the so-called muscle-current is intimately connected with injuries of its surface, and more especially with the artificial cross-section. All the electrical phenomena of a resting muscle depend upon the difference of potential between the living longitudinal surface and the dying transverse surface, which becomes electrically negative to the former.

Action Currents.—The currents which are obtained from a muscle during contraction Hermann regards as the result of electro-motive forces which develop during the propagation of the excitation wave, and not related in any way with a negativity of any pre-existent current. As these currents are connected entirely with the active state, he has termed them "action currents," which, moreover, may be either phasic or tetanic as they relate to a single or a series of successive contractions. The term "phasic" is applied to the two currents which are observed when a wave of excitation passes along the muscular fibre. The first flows in the muscle, in the direction of progress of the excitation wave,—first phase; the second in the reverse direction,—second phase. These currents are due to the fact that each led-off point becomes negative with reference to the other as the excitation wave passes beneath it. The term tetanic, or decremential, is applied to the single current which is observed in a tetanized muscle, the direction of which in the muscle coincides with that of the excitation wave. In the tetanic state, in which the excitation waves follow each other in rapid succession, there should be no difference of potential, the negative tracts following each other so closely that all portions of the muscle remain in the same electrical condition. This would be the case if it were not that the wave of negativity diminishes as it travels. Hence, if any point of a tetanized muscle near the seat of excitation be compared, by means of the galvanometer, with any point situated at a greater distance from it, the former will be found negative to it. The views entertained by Hermann as to the origin and character of the action currents are based upon observations and experiments made by himself and other physiologists.

Du Bois-Reymond, in 1859, observed that when he tetanized an apparently uninjured gastrocnemius muscle, which, owing to the presence of the parelectronomic layer, exhibited no current, a descending current in the muscle always manifested itself. This descending current, or the first phase of the action current, according to Hermann, was comparable in its direction to the negative variation of the resting muscle-current. The passage of this descending current in uninjured muscle, during a single contraction, will develop a secondary contraction, and during tetanus will develop secondary tetanus; from these facts it must be inferred that to each single contraction and to the successive contractions in tetanus there corresponds a momentary descending current. This current is less marked, its development slower, and its after-effect more considerable than the negative variation of the current from an artificial cross-section.

According to the observations of du Bois-Reymond, also, when two symmetrical points on the longitudinal surface are united, no current is obtainable from the muscle, either in the resting or active condition, when stimulated through the nerve. Bernstein showed (*Monatsberichte der Berliner Acad.*, 1867, p. 444), however, when two such points are connected and the stimulation applied directly to the one end of the fibre, that with the progress of the excitation wave each led-off point became negative toward the other as the wave passed over it; in consequence, the needle indicated first a "negative," then a "positive," variation, or a diphasic action current.

The first accurate experiments undertaken with a view of analyzing the negative variation current (action current of Hermann) of an uninjured muscle during a single contraction were made by S. Mayer with Bernstein's rheotome (*Archiv für Anatomie und Physiologie*, 1868, S. 655). He employed for this purpose the gastrocnemius muscle of a non-curarized frog, connecting both tendinous ends with the galvanometer and exciting contraction by single induction shocks directed through the sciatic nerve. The excitation wave proceeded, in this instance, not from the end of the muscle-fibre, but from the end-plate of the nerve. It was observed in these experiments, from the movement of the needle, that the negative variation consists of two phases, in the first of which the lower end of the muscle becomes positive, and in the second the upper end, indicating, according to Hermann, the passage of, first, a descending, and, secondly, of an ascending action current. Holmgren, who had previously observed the same phenomena in the gastrocnemius, believed that the first phase of the negative variation took place entirely in the latent period, and the second in the stage of beginning contraction.

Hermann (*Archiv für die gesammte Physiologie*, 1877) repeated these experiments with a special apparatus,—the Fall rheotome,—by means of which the galvanometer circuit was closed by a falling body, for a brief moment, at a definite period of time after stimulation. In this way he found, contrary to former observations, that the transition of the descending into the ascending current did not coincide with the beginning of the contraction, but took place entirely in the latent period, as both phases appeared even when the rheotome was so arranged that the circuit was closed only up to the moment of contraction. Du Bois-Reymond attributed this double variation to an interference of the effects at the two ends of the muscle, for when he united the middle and tendinous end of a regularly-constructed muscle he observed only the ordinary negative variation or a single action current passing in the direction of the tendon. If both ends are led off, the currents passing in opposite directions from the point of excitation (the end-plate of the nerve), being of equal strength and requiring the same period of time for their propagation, would neutralize each other, and no deflection of the needle would result. Du Bois-Reymond supposes the negative variation here to be due to excitatory changes at the tendinous ends, which appear more suddenly and are accomplished in a shorter time at the lower end than at the upper, in consequence of which the effect from below upward has the advantage, as regards time. Hermann rejects this explanation, and asserts that when the middle and tendinous end of a regularly-constructed muscle are connected with the galvanometer and a single contraction excited through the nerve the deflections of the needle indicate a current of a diphasic character,—the first phase being atterminal, indicating a current directed toward the end of the muscle; the second phase being abterminal, indicating a current in the reverse direction. The second phase was always found to be the weaker, and was always wanting when the end of the muscle had an artificial transverse section.

The explanation of this diphasic variation Hermann finds in the wave-like propagation of the excitation tract. As this tract appears first at the point of entrance of the nerve, and travels thence to both ends of the muscle, there must arise, as a result of the progressing negativity, first, the atterminal action current, indicating that the end of the muscle has become positive to the middle; secondly, the abterminal, indicating the reverse condition. The feebleness of the latter current, as compared with the former, arises from the decrease of the excitation wave during its propagation; and as the decrement increases with a diminution in the functional activity of the muscle, either by fatigue or gradual death, the abterminal phase gradually disappears. As the artificial cross-section cannot develop an electro-motive force, the abterminal is entirely absent.

With regard to the location of the electro-motive force giving rise to the action current, du Bois-Reymond assigns it to the parelectronomic end of the muscle. If, however, this force has its origin in the decrement, as Hermann terms it, then it ought to be distributed almost equally over the entire length of the fibre. This supposition Hermann proved true when he showed that the strength of the action current is proportional to difference in the distances of the conducting electrodes from the nervous equator, meaning by this term that cross-section of a muscle which represents the mean position of the point of entrance of the nerve.

Currents in a Living Man.—The existence of electrical currents in the uninjured muscles of a living man, though assumed by du Bois-Reymond, was rendered difficult of proof by the resistance offered by the skin, by inequalities of temperature, by glandular secretions, etc. Nevertheless, he was able to demonstrate apparently that the voluntary contraction of the muscles of an arm or leg was attended by an electrical change similar to that observed in a muscle after removal from the body, and which he regarded as a negative variation of an hypothetical resting current. The experiment made to show this was as follows: The index fingers were dipped into diverting vessels containing a salt solution, each of which was connected with the galvanometer. As the arrangement of muscles on both sides of the body is symmetrical, the currents conducted off from both fingers were equal in strength and the needle remained quite stationary. When the muscles of one arm were contracted voluntarily, a deflection of the needle took place, which indicated that the contracting arm became negative, and that a current was passing from the passive arm through the galvanometer. When the opposite arm was contracted, the deflection occurred in the reverse direction. The objections to the conclusions drawn from this experiment are numerous. Hermann denies that the current observed is the result of changes in the muscle, but is a skin-current directed from without inward. In curarized cats it was shown that, when both feet were connected with the galvanometer, stimulation of the sciatic nerve was followed by a simultaneous secretion of perspiration and the development of a powerful current, which passed into the irritated limb. In atropinized cats, on the contrary, stimulation of the nerve was followed neither by sweating nor the development of a current, even though the muscles were contracting vigorously. From this experiment Hermann asserts that a curarized man would show the du Bois-Reymond current, even in the absence of the muscular contraction; while in an atropinized man it would be absent, in spite of the contraction.

Hermann subsequently (*Archiv für die gesammte Physiologie*, 1877, Bd. xvi) demonstrated, however, the presence of action currents during a single contraction of the muscles of the human forearm, similar to those observed by him in the uninjured muscles of the frog. The arrangement of the experiment was, briefly, as follows: The forearm was surrounded by two twine electrodes saturated with zinc solution, one being placed at the physiological middle,—the nervous equator,—the other at the wrist. Both electrodes were then connected with the galvanometer. When the brachial plexus was stimulated in the axillary space, the deflections of the galvanometer needle, when analyzed with the repeating rheotome, indicated phasic currents with each single contraction. In the first phase—atterminal—the wrist became positive, and in the second—abterminal—it became negative. The action currents which are observed in the frog's muscle were thus shown to be present in the living human muscle, with this difference, however: that the second phase,—abterminal,—instead of being weaker in man, is equally strong with the atterminal. This experiment also revealed the fact that the rapidity of propagation of the excitation wave was much greater in man, amounting to about twelve metres per second.

THEORIES OF THE ELECTRICAL PHENOMENA OF MUSCLE.

The Molecular Hypothesis.—Starting from the view that the electric currents of muscles have their origin in the peculiar structure of living muscle, du Bois-Reymond assumed, in explanation of such currents, the existence in the muscle of electro-motive molecules imbedded in some indifferent medium. He supposes that the muscle consists of peripolar-electric molecules, positive at the equator and negative at either end, each of which is composed of two smaller dipolar-electric molecules with their positive ends turned toward each other. In addition to this structural arrangement, it is also assumed that every pair of dipolar molecules is inseparably united, so that injury to one is immediately followed by death of the other. It can thus be explained why every artificial surface of the muscle is negative. If the section be made between two adjacent pairs of dipolar molecules, then only negative surfaces present themselves at the surface, and if the section be made through the positive plane of a dipolar pair, the non-injured twin molecule at once dies, thus enabling the negative surface of an adjoining molecule to present itself. To explain the parelectronomic phenomena, du Bois-Reymond assumes that at the natural end of the fibres there is a layer of bipolar "parelectronomic molecules" which do not turn the negative, but the positive, surface to the tendon.

The negative variation is explained by a decrease of electro-motive force of the molecules, or a new arrangement of them by which their electro-motive effect is weakened. The negative variation of parelectronomic muscles is explained by the hypothesis that the parelectronomic molecules, which compensate to a greater or less extent the current of the resting muscle, do not partake of the negative variation to the same degree as the normal molecules, and, in consequence, their own variation is unable to compensate that of the remaining normal part of the muscle. It is for this reason that a streamless parelectronomic muscle shows the same variation as if it had an artificial cross-section. The negativity of the excitation wave is explained by the further assumption that the portion of the muscle being stimulated represents a relatively indifferent conductor, because its former positivity is now momentarily abolished from the negative variation of its molecular forces. The negative electricity, therefore, which is always present at the negative cross-sections of the resting part, is simply conducted to the stimulated part, which becomes momentarily negative.

The Alteration Hypothesis.—In 1867, Professor Hermann proposed a new theory as to the origin of the electro-motive forces which, so far, has apparently explained all the phenomena. He terms this the alteration theory, because it reduces all electro-motive phenomena of muscle to a two-fold alteration of its substance. In the first place, he starts from the fact that a section of a muscle is followed, in a short time, by death of the contents of its fibre. Assuming that the dying substance reacts negatively toward the living, he is enabled to explain readily and satisfactorily all the phenomena of the resting muscle. As the electro-motive force, according to this view, has its seat at the surface of separation between the dying and living substance, he terms the current the demarkation current. The phenomena observed during activity are further explained by the simple and plausible assumption that not only beginning death, but even stimulation, makes the affected substance negative to the remainder of the muscle. All the forms of action currents can thus be explained without any further auxiliary hypothesis.

Hermann regards the following four propositions sufficient to explain the origin of all the galvanic phenomena of living tissues: 1. Localized death in continuity of protoplasm, whether caused by injury or by metamorphosis (mucous, horny), renders the dead part negatively electrical to the unaltered part. 2. Localized excitation in continuity of protoplasm renders the excited part negatively electrical to the unaltered part. 3. Localized warming in continuity of protoplasm renders the warm part positive; localized cooling, the cold part negative to the unaltered part. 4. Protoplasm is strongly polarizable on its limiting surfaces (first shown as regards the protoplasm inclosed in tubes of muscles and nerves); the polarization constant decreases on excitation and on dying. ("Translations of Foreign Biological Memoirs," 1887, p. 328, edited by Burdon-Sanderson.)

ELECTRICAL PROPERTIES OF INJURED NERVES.

After the discovery of the existence of electrical currents in muscles, numerous attempts were made to determine the existence of similar currents in nerves and to identify, if possible, the nerve-principle with electricity. It was reserved for du Bois-Reymond, however, to first definitely detect the presence of electrical currents in nerves, which he was enabled to do by means of the improved methods of investigation alluded to in the previous section. This observer discovered that the electrical properties of nerves have a striking similarity to those of muscles, and that the laws governing the latter are equally applicable to the former.

Nerve-Cylinder.—The nerve-cylinder, obtained by making two transverse sections of any given nerve at right angles to its long axis, is best adapted for the application of the nerve-current. Such a cylinder presents, as in the case of the muscle, a natural longitudinal surface and two artificial transverse surfaces; a line drawn around the nerve-cylinder, at a point lying midway between the two end-surfaces, constitutes the equator. An artificial longitudinal surface is difficult to obtain, from the small size of the nerve-bundles. The electrical phenomena of the nerve-cylinder, when examined with the galvanometer, are found to obey the same laws as those governing the muscle. Strong currents are obtained when the natural longitudinal and the transverse surfaces are placed in contact with the diverting cushions of the electrodes. The direction of the current, of which the deflection of the needle is an indication, is constantly from the longitudinal surface through the galvanometer to the transverse surface. The strength of the current obtained by uniting these two surfaces will diminish or increase, according as the electrode on the longitudinal surface is removed or brought near to the equator. Weaker currents are obtained when two asymmetrical points on the longitudinal surface are connected, in which case the point lying nearer the equator becomes positive, to that more distant, which is negative. When two symmetrical points on the longitudinal surface, equidistant from the equator, are united, no current is obtainable. From these facts it is evident that all points on the longitudinal surface of the nerve-cylinder are electrically positive to the transverse surface, and that the point of greatest positive tension is situated at the equator, from which it gradnally decreases toward the transverse section. As to whether this latter surface exhibits differences of potential between its centre and circumference it is difficult to determine, as the small area of the surface excludes it from accurate investigation, though it is quite probable, from the analogous electro-motive properties of muscle, that similar differences of potential are present. Mendelssohn (*Archiv für Anat. und Physiologie*, 1885) has recently shown that when the two transverse sections of a nerve-cylinder are united, a current—the axial current—is obtained which flows in the nerve in a direction opposite to that of the direction of the nerve-impulse. In motor or efferent nerves it flows from the periphery toward the centre, and in sensory or afferent nerves in the contrary direction. The small size of the nerve-trunks renders an investigation of oblique surfaces for evidences of inclination currents impossible.

The Electro-motive Force.—The electro-motive force of the nerve current, obtained by uniting the longitudinal and transverse surfaces, varies in strength with the length and thickness of the nerve, a long section of a nerve showing, under similar conditions, a more powerful current than a short section, while a nerve with a large transverse section will exhibit a stronger current than a nerve with a small transverse section. From the experiments of du Bois-Reymond, the electro-motive force of the strongest nerve-current in the frog is equal to the 0.002 of a Daniell, and in the rabbit to 0.026 D.

Conditions Influencing the Development and Duration of the Nerve-Current.—The current present in any given nerve-fibre does not disappear at once upon the death of the body, but disappears gradually until, sooner or later, it entirely ceases to manifest itself. After the transverse section of a nerve-cylinder has ceased to exhibit negativity in relation to the longitudinal surface, independent of either mechanical or chemical injuries, the production of a new section will be followed by a return of the current in its original intensity. Inasmuch as the development of the current is intimately related to the living condition of the nerve, all those influences which hasten the molecular disintegration will cause a disappearance of the current. Excessive heat or cold, mechanical injuries, acids, alkalies, repeated induction shocks, all tend, through the production of changes in the contents of the nerve-fibre, to diminish the current. The duration of the current varies considerably in different parts of the nervous system and in different classes of animals, there being no physiological change comparable to that producing rigor mortis in muscles, which determines definitely the cessation of the current. Indeed, there does not appear to be any absolute connection between the existence of excitability and the development of the current, as the observations of Schiff ("Lehrbuch der Muskel und Nervenphysiologie," 1858, S. 69) have shown that after separation from the central nervous system the nerves will exhibit a current for from eight to fourteen days after they have lost their excitability through degenerative changes. The electro-motive forces disappear first in the nerve-fibres of the brain, then of the spinal cord, and lastly in the nerves themselves, and in a direction from their origin toward their termination. In warm-blooded animals, both mammals and birds, the electro-motive properties disappear more rapidly than in cold-blooded animals, most probably in consequence of the more rapid decline of all those chemical changes underlying the general nutritive process. Not unfrequently in warm-blooded animals, less frequently in frogs, a reversal of the current is observed, more especially if the nerve be rapidly dried or subjected to heat, although the same phenomenon is observed under normal conditions. In the latter case, it has been attributed to an accumulation of electrolytic products at the limiting surface, which have given origin to a polarization current flowing in a direction opposite to that of the natural current.

THE INFLUENCE OF STIMULATION UPON THE NERVE-CURRENT.

Negative Variation.—It was shown by du Bois-Reymond, shortly after the discovery of the nerve-current, that the activity of the nerve, as well as the activity of the muscle, is accompanied by a change in its electro-motive condition or a diminution of potential between the longitudinal and transverse surfaces, and in consequence a negative variation of the natural pre-existing current. This change in the electro-motive forces can be readily demonstrated by means of the galvanometer during tetanic stimulation, or by the capillary electrometer during a momentary stimulation by a single induction shock. When the transverse and longitudinal surfaces are connected with the terminals of the galvanometer wires, and the current permitted to deflect the needle, stimulation of the nerve is at once followed by a return of the needle toward the zero-point, indicating a diminution in the strength of the natural current; with the cessation of the stimulation, the needle is again deflected outward to its previous position, indicating a re-establishment of the electro-motive forces. This negative variation of the current is observed equally well whether the current is conducted from the central end and the periphery stimulated, or whether the current is conducted from the peripheral end and the central stimulated. Indeed, if both ends are connected with galvanometers and the nerve stimulated in the middle, the negative variation is observed simultaneously at both ends. The excitation propagates itself, therefore, equally well in both directions.

Du Bois-Reymond, in his investigations, found that the negative variation was intimately connected with changes in the molecular condition of the nerve, and not to an escape of the current into the galvanometer circuit, nor to the establishment of an electrotonic condition, nor to an increase in the resistance of the nerve. In these respects the phenomenon is comparable to that observed in the muscle. As a further proof that the negative variation is not the result of any extraneous electrical influence, it is only necessary to employ chemical, mechanical, or thermal agents for purposes of stimulation. Whatever the character of the exciting agent may be, provided it is sufficiently powerful, a negativity of the current is always observed. Du Bois-Reymond was also enabled to obtain a negative variation of the current in the nerves of a living frog which were yet in connection with the spinal cord. In this experiment the sciatic nerve was divided at the knee and freed from its connections up to the spinal column; the transverse and longitudinal surfaces were then placed in connection with the electrodes of the galvanometer wires and the current permitted to influence the needle. The animal was then poisoned with strychnine. Upon the appearance of the muscular spasms the needle was observed to swing backward toward the zero-point to the extent of from 1 to 4 degrees, and, upon the cessation of the spasms, to return to its previous position. In an experiment of this nature it is obvious that the negative variation was the result of a physiological stimulation of the nerve arising within the spinal cord.

The question also here arises as to whether the negative variation is due to a steady, continuous decrease of the natural current, or whether it is due to successive and rapidly-following variations in its intensity, similar to that observed in muscles. Though this cannot be demonstrated with the physiological rheoscope, as was the case with the muscle, there can be no doubt, both from experimentation and analogy, that the latter supposition is the correct one. Wedenskii (*Centralblatt für die Med. Wissenschaft*, 1883–1884) has shown that when non-polarizable electrodes connected with Siemen's telephone are placed in connection with the longitudinal and transverse sections of a nerve, low, sonorous vibrations are perceived during tetanic stimulation,—a proof that the active state of the nerve is connected with the production of discontinuous electrical currents. The oscillations of the mercurial column of the capillary electrometer also reveal similar electrical changes.

It was also shown by Bernstein ("Untersuchungen u. d. Erregungsvorgang im Nerven- und Muskelsysteme," 1871), with the repeating rheotome, that the negative variation is composed of a large number of single variations, which succeed each other in rapid succession, and summarize themselves in their effect upon the needle; that the change in the nerve which follows the stimulation propagates itself in the form of a wave, whose length has been estimated at eighteen millimetres, and whose time duration is about 0.0007 of a second. The rapidity with which the negative variation travels through the nerve of a frog is about twenty-eight metres per second.

ELECTRICAL PROPERTIES OF THE UNINJURED NERVE.

Currents of the Resting Nerve.—The pre-existence of electrical currents in living and wholly-uninjured nerves has also been denied by Professor Hermann, who regards all portions of the nerve as iso-electrical, any difference of potential being the result of some mechanical or chemical injury to its surface. As to whether the natural transverse section would exhibit a negativity with reference to the longitudinal surface, it is almost impossible to determine by direct experimentation, as the terminations of the nerves, both central and peripheral, are deeply imbedded in tissues, which themselves are the seat of electro-motive forces, and which cannot be distinguished, by present means of investigation, from those of the nerves. The existence of a parelectronomic layer at the periphery of the nerve which would, under certain circumstances, exhibit a positive electrical tension is, for this reason, impossible to state. The only currents thus far observed are those obtained by uniting the longitudinal and artificial transverse sections.

Action Currents.—For reasons to be stated below, it is very difficult to determine the presence of diphasic action currents during the passage of an excitatory impulse through the nerve-fibre. The so-called negative variation of the resting-nerve current,—the demarkation current,—which passes from the transverse to the longitudinal surface, and which is occasioned by tetanic stimulation, Hermann regards as the expression of an action current which flows in the nerve in an opposite direction to the natural current. The origin of this action current is to be sought for in the continuous negativity of that portion of the longitudinal surface of the nerve in contact with the diverting electrode, while the dying substance of the transverse surface takes no part in the excitation. This tetanic action current, or negative variation, was discovered by du Bois-Reymond. Bernstein also succeeded in obtaining this action current with the differential rheotome during the passage of a single excitation wave. When any two points in the longitudinal surface which exhibit no current are connected with the galvanometer and a single wave of excitation passes beneath the electrodes, it might be expected that, as in the case of the muscle, a diphasic action current would be observed, from the fact that the portions of the nerve beneath the electrodes became alternately negative with reference to all the rest of the nerve. This, however, is not the case, the absence of the two opposing phases of the action current being explained on the supposition that the negativity of the two led-off points is of equal amount, and that, owing to the great rapidity with which the excitation wave travels, the two phases fall together too closely in time to alternately influence the galvanometer needle. During stimulation of the nerve, when two currentless points are connected, there is also an absence of the action current, as was observed first by du Bois-Reymond, and which is to be explained on similar grounds. It is true that an apparent action current is sometimes seen when the stimulating current is very powerful or the seat of stimulation too near the diverting electrodes. This, however, must be attributed to an electrotonic state of the nerve.

Influence of a Constant Galvanic Current on Nerves.

In investigating the electric phenomena of nerves, du Bois-Reymond ("Untersuchungen über thierische Electricität," Bd. ii, S. 289) discovered, in 1843, that the passage of a constant galvanic current through a portion of a nerve produced a change in the electro-motive forces existing between the longitudinal and transverse surfaces, whereby the resulting nerve-current was either increased or diminished, according to the direction of the constant current. To this condition du Bois-Reymond applied the term electrotonus. It was subsequently shown by Pflüger (" Untersuchungen über die Physiologie des Electrotonus," 1859) that a definite change in the irritability of the nerve is also caused by the passage of the galvanic current, and, as it is intimately related to the change in the electro-motive forces, he applied to this alteration of excitability also the term electrotonus. This word has thus been employed to express two distinct series of effects exhibited by a nerve through a portion of which a constant galvanic current is passing. It appears desirable, for the sake of clearness, to limit the term electrotonus to the electrical or electrotonic currents which can be led off from either extremity of the nerve, and to apply to the modifications of irritability which accompany electrotonus the expression electrotonic alteration of excitability. The electrotonic currents and the associated changes in the nerve-excitability, while intimately related to each other, are, nevertheless, two distinct effects of the constant current, and can be studied independently of each other.

Electrotonus.—If a nerve be so arranged that its longitudinal and artificial transverse surfaces are connected with the terminals of the galvanometer, the deflections of the needle will indicate the usual nerve-current. The passage of the constant current through the portion of the nerve beyond the diverting electrodes will then produce a change in the strength of the nerve-current which will vary according to the direction of the experimental or " polarizing " current. If this current be transmitted through the nerve in a direction corresponding to the nerve-current, the latter will be strengthened or increased, thus constituting the positive phase of electrotonus. If the polarizing current be transmitted in the reverse direction, the natural nerve-current is weakened or decreased, thus constituting the negative phase of electrotonus. The same positive and negative phases, however, are observed when any two points on the longitudinal surface are connected with the galvanometer and the polarizing current applied to the projecting end of the nerve; the deflections of the needle indicate the existence of electrotonic currents having the same direction as the polarizing current. The natural nerve-currents have, therefore, no connection with the electrotonic currents, except in a purely accidental way, as the latter are present even when the former are entirely absent. These fundamental experiments indicate that when a constant galvanic current is flowing through a limited portion of a nerve, all other portions exhibit the presence of electrical or electrotonic currents, which are in some way dependent upon or related to the galvanic current. The electrotonic current in the neighborhood of the positive pole, or anode, is called the anelectrotonic current, and has, in the nerve, a direction toward the polarized region. The current in the neighborhood of the negative pole, or cathode, is called the catelectrotonic current, and has, in the nerve, a direction away from the polarized region.

The electrotonic currents vary considerably in strength and extent, according to the intensity of the polarizing current, increasing steadily with the intensity of the latter without attaining a maximum so long as it is not destructive in its action upon the integrity of the nerve. The electro-motive force of these currents surpasses that of the natural currents, as shown by the method of compensation, and may amount to 0.5 Daniell. The electrotonic current is strongest in the immediate neighborhood of the electrodes, but gradually diminishes in strength as the distance between the polarized and led-off portions is increased. The distance to which the electrotonic currents extend along the nerve will depend very largely upon the strength of the polarizing current, though it is conditioned by the physical state of the nerve; for if it be ligated or injured beyond the polarized portion the current is abolished.

Other conditions being equal, the strength of the anelectrotonic current is greater than the catelectrotonic. When means are taken to increase the electro-motive force of the polarizing current, *pari passu* with the increasing resistance of the nerve both currents are increased in intensity in proportion as the polarized region is increased in extent. The electrotonic condition is established at the instant the polarizing current is closed, and disappears rapidly after it is opened, even when it is of short duration. Momentary currents, such as single induction shocks, are sufficient to develop electrotonus. The anelectrotonic current, after its origination, increases slowly, attains its maximum, and then gradually declines; the catelectrotonic current, on the contrary, attains its maximum much more quickly, and declines also more rapidly.

From the preceding statements, it is evident that the electrotonic current differs in many respects from the resting-nerve current, as well as from the action current, and is not the outcome of an excitatory state of the nerve, but that it is rather of artificial origin, connected in some way with the polarizing current. That it is not merely due, however, to an escape of the latter into the galvanometer circuit is evident from the fact that other structures, such as dead or degenerated nerves, wet threads, etc., which offer favorable conditions for the current escape, do not exhibit electrotonic currents. These facts would indicate that the phenomena of electrotonus are dependent upon the living condition of the nerve, or at least upon its anatomical integrity.

Polarizing After-Currents.—The passage of a constant galvanic current through a nerve produces an internal polarization which gives rise, upon its withdrawal, to after-currents, whose extent and direction can be determined by galvanometric observations. If the intra-polar region be connected with the galvanometer, the deflection of the needle will indicate immediately, upon the opening of the galvanic current, an after- or internal polarization current, the direction of which will depend upon the strength and time of closure of the former. When the galvanic current is strong and of short duration, the after-current is always *positive*,—that is, has the same direction as the polarizing current itself; on the contrary, the after-current is always *negative*,—that is, has a direction the reverse of the polarizing when the latter is feeble and long-continued in its action. The positive after-current is especially well developed when the direction of the galvanic current is the same as that of the propagation of the normal nerve-impulses. The presence of after-currents can also be shown in the extra-polar regions. Immediately upon the opening of the galvanic current, the deflection of the galvanometer needle indicates that the after-current in the anodic region is at first in the same but subsequently in the opposite direction to that of the anelectrotonic current, while the current in the cathodic area is always in the direction of the catelectrotonic current.

Secondary Contraction from a Nerve.—It was shown by du Bois-Reymond that when an excised nerve was laid on the sciatic nerve of a nerve-muscle preparation, stimulation of the former was always followed by contraction or even tetanus of the muscle, according as the stimulation was momentary or continuous. At first glance it might be supposed, from the analogy of secondary contraction from a muscle, that in this instance also the contraction might be due to a variation of the natural nerve-current or to an active current which would excite an impulse in the second nerve. That this is not the explanation of the contraction, however, is evident from the fact that stimulation of the nerve by any other than electrical means fails to excite a contraction. It was for this reason that du Bois-Reymond attributed the generation of the nerve-impulse in the second nerve to the development of the electrotonic condition. When the primary nerve is traversed by the electrical current, whether induced or galvanic, and passes into the electrotonic state, the secondary nerve also develops a secondary electrotonus, which persists as long as the nerve is traversed by the current. Upon the opening of the latter the secondary electrotonus also at once disappears. It is this alternate appearance and disappearance of the secondary electrotonic condition to which the excitement of the nerve giving rise to the contraction must be attributed.

A striking illustration of the production and stimulating effects of secondary electrotonus is offered by the so-called "paradoxical contraction," first observed by du Bois-Reymond ("Untersuchungen über thierische Electricität," Bd. ii, S. 545). The sciatic nerve of the frog divides at the lower third of the thigh into two branches,—the tibial and the peroneal,—the former of which supplies principally the gastrocnemius and the tibialis posticus muscles. If the sciatic nerve be divided above and the peroneal nerve below the point of separation, and the latter stimulated by alternately opening and closing the constant current, the gastrocnemius at once contracts and, if the stimulation be sufficiently rapid, passes into the tetanic condition. The explanation of this contraction rests, as above mentioned, in the establishment of a secondary electrotonus.

Electrotonic Alterations of Nerve Excitability.—In addition to the electrotonic state into which the nerve passes upon the passage of a constant galvanic current through a portion of its extent, there is also produced a marked alteration in both its excitability and conductivity, whereby the results of nerve stimulation, muscular contraction, and sensation are increased or decreased, according to the strength and direction of the current.

The first accurate observations upon the alterations of the excitability were made by Valentine (" Lehrbuch der Physiologie des Menschen," 2 Auflage ii, S. 655), who discovered that the excitement aroused in a nerve experienced great difficulty in passing through the portion of the nerve traversed by the constant current, and that, if the latter were ascending, an irritant applied between it and the muscle was much less efficient in exciting muscular contractions. Eckhard (*Zeitschrift für rationale Medizin*, 2, iii, S. 198) continued and extended these observations with improved methods of research, and discovered the fact that the excitability of the nerve was always increased below the portion through which a descending current was passing He also surmised that the excitability above this portion was decreased, and, in consequence, formulated the law that the excitability is increased on the side of the cathode and decreased on the side of the anode. Pflüger finally (" Untersuchungen über die Physiologie des Electrotonus," 1859), with the aid of improved and accurate methods of investigation, enlarged our knowledge of the changes in excitability caused by the action of the galvanic current, and arranged and co-ordinated them under one general law, as follows: If any portion of a nerve be traversed by a descending or an ascending constant current, the excitability of the intra-polar as well as the extra-polar regions undergoes a change which, upon investigation, is found to be decreased in the neighborhood of the anode, or positive pole, and increased in the neighborhood of the cathode, or negative pole. The zone of diminished excitability, and to which Pflüger gave the name of anelectrotonus, extends for some distance on both sides of the anode; the zone of increased excitability, or catelectrotonus, extends in a similar manner on both sides of the cathode. These alterations of the normal excitability are most marked in the immediate vicinity of the electrodes, but extend for some distance into both the intra- and extra- polar regions, though with gradually-diminishing intensity, until they finally disappear. Between the electrodes there is a point where the anelectrotonic and catelectrotonic states merge into each other, and at which the normal excitability of the nerve is preserved. This is known as the neutral or indifferent point. The degree to which the excitability is increased at the negative and decreased at the positive pole, and the extent to which these alterations spread themselves into both the intra- and extra- polar regions, will depend largely upon the strength of the constant current and the normal excitability of the nerve. If, while the nerve is traversed by currents of varying degrees of intensity, it be tested at all points with reference to the change in its excitability, a series of results will be obtained which can be represented graphically somewhat according to the accompanying illustration. Let the abscissa line *N N* represent the nerve, the decrease in the excitability of which is indicated by an ordinate directed downward, and the increase in excitability by an ordinate directed upward. The electrodes conveying the current to the nerve are represented by *A*, the positive, and *B*, the negative pole. The relative extent of the alterations of the excitability, as revealed by the energy of the muscular contraction following the application of a uniform stimulus, is shown by the three curves, the size and extent of which represent the changes produced by a weak, medium, and strong current. The curve also shows that with a weak current (*a*, *b*, *c*) the excitability in the anodal zone is decreased and in the cathodal zone increased, and that the neutral point, *b*, lies close to the side of the positive pole.

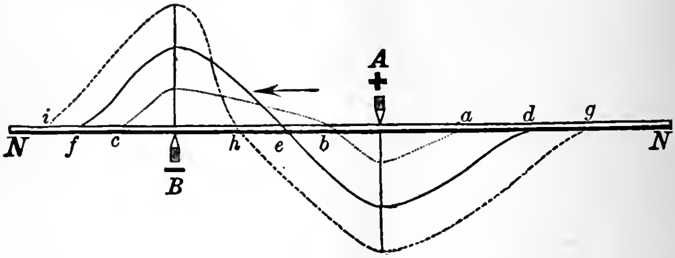

FIG. 9.

From this point the changes in the excitability gradually increase, and reach their maximum in the neighborhood of the electrodes, from which both phases gradually decline. The position of the neutral point also indicates that by far the larger portion of the intra-polar region is in the condition of increased excitability, or catelectrotonus. The curve *d*, *e*, *f*, similar in its general form to the preceding, represents the alterations in the excitability produced by a current of medium strength; *pari passu* with the increase in current-strength, there is an increase in the amount of both anelectrotonus and catelectrotonus and the distance to which they spread themselves into the extra-polar regions. The indifferent point has advanced toward the centre of the intra-polar region, indicating that this portion of the nerve is almost equally occupied with the opposed states of excitability. The curve *g*, *h*, *i* represents still further the same changes following the employment of a strong current. The neutral point has now been shifted toward the cathode, and the intra-polar portion is in the condition of anelectrotonus.

The demonstration of corresponding changes in the excitability of the nerve in the intra-polar region presents many difficulties, owing to the close proximity of the electrodes conveying the polarizing and the stimulating currents and their consequent interference with each other. Pflüger overcame this difficulty by employing as the testing agent a concentrated solution of salt, and succeeded in demonstrating the above-mentioned intra-polar changes. From this fact it is clear that the changes in the excitability are not dependent upon or related to the special nature of the electrical stimulus, as they exhibit themselves upon the application of all forms of stimuli, whether chemical, mechanical, or thermal.

In order that the opposed electrotonic conditions of the nerve may correspond with the direction of the electrotonic currents, the region *A g* (Fig. 9) is designated as that of extra-polar descending anelectrotonus, and the region *B i* as that of extra-polar ascending catelectrotonus, when *g* represents the central and *i* the peripheral end of a motor nerve. When the conditions are reversed, however,—that is, when *i* is the central and *g* the peripheral end,—then the region *A g* is termed that of the extra-polar ascending anelectrotonus, and the region *B i* as that of descending catelectrotonus. The conditions of ascending catelectrotonus and anelectrotonus cannot, without much difficulty, be directly proved, owing to the fact that the excitement following an irritation applied to the ascending regions must traverse the portion of the nerve through which the constant current is passing, as well as through the portion which is already in the opposite electrical condition. The conductivity of the nerve appears to be impaired in the neighborhood of the anode,—a condition which increases with the decrease in the normal excitability. On the contrary, the excitation originating in the descending catelectrotonic and anelectrotonic regions passes directly, without interference, into the muscle. Hence it is that only in these regions can the law of the electrotonic changes in the excitability be successfully demonstrated.

The excitability of the nerve which has been altered in the manner related above, during the passage of the constant current, undergoes yet further modifications immediately upon the opening of the current. The normal condition is not at once re-established, this being regained only after the lapse of some minutes, especially if the current has been strong and of long duration. These after-results of the action of the constant current have been carefully investigated by Pflüger, who has termed the increase of excitability the positive modification, the decrease of excitability the negative modification. If, for example, the nerve be examined with reference to these changes, it will be found that the excitability in the region of the anode will undergo a positive modification which lasts for a few seconds only, after which it returns to the normal condition. In the region of the cathode the excitability passes in a similar manner for a few seconds into a negative phase, after which it again undergoes a continuous positive modification which may last for a variable length of time. Its duration appears to be a function of the current-strength, for, with feeble currents, it lasts from one to two minutes, with strong currents from ten to fifteen minutes. The opening of the constant current very frequently produces in the nerve such a change in its excitability that a series of pulsations or an apparent tetanus follows, which has long been spoken of as the opening tetanus of Ritter.

The Law of Contraction.—The general law of electrical stimulation was first accurately formulated by du Bois-Reymond in 1845, in the following words: "It is not the absolute value of the current density at any moment to which the motor nerve reacts, as shown by the contraction of its related muscle, but the change of this value from one moment to another; the stimulus to the contraction which follows these changes is the more considerable the more rapidly they follow each other, or the greater they are in any unit of time." From this law it follows that the mere passage of a constant current through a nerve does not, in general, excite it to activity, this being accomplished only by a change in the current-strength. These variations, however, must occur with a certain rapidity, otherwise even the strongest currents have no appreciable effect when they are very gradually increased or diminished. The sudden variation of a weak current is often very effective in the stimulation of a nerve. The exact law, however, of the dependence of stimulation upon variations in current-strength has not yet been definitely stated, but it is probable that within certain limits the sought-for function consists in a simple proportionality.

There are certain facts which appear, however, to contradict the general law just mentioned. With regard to the centripetal nerves, it is well known that, independent of the sensations which occur upon the opening and closing of the circuit, the constant flow of the current also gives rise to persistent sensations, which may become unbearable. But, as Professor Hermann remarks, an exact analysis of these phenomena shows that the sensory end organs, as well as the sensory central organs, are not sufficiently excluded to justify a change in the general law, as the end organs are so constituted that they are stimulated not only by variations, but also by constant conditions. With regard to centrifugal nerves, it was observed by du Bois-Reymond that tetanizing effects occasionally follow the passage of very strong currents; and, as they continue after the cessation of the current, he attributed them to an electrolytic change in the nerve. It was subsequently shown by Pflüger, however, that weak constant currents also had a tetanizing effect, even when all polarization of the electrodes was carefully excluded. He assumes, therefore, that the nerve is stimulated by the steady flow of the current, as well as by variations in its strength, and that probably the stimuli proceed from the cathode. If the constant current is capable of developing stimuli, it must be assumed either that they are very weak, as compared with those produced by a sudden variation in the strength, or that their character is such that not every organ is capable of responding to them.

The law of contraction, which expresses the effects in a motor nerve which follow the closure and opening of the constant current, has been established by the observations of many physiologists. Pfaff made the discovery, in 1793, that for the occurrence of a closing or an opening contraction it was not a matter of indifference whether the current in the nerve was ascending or descending in its direction. Ritter, in 1798–1805, made an elaborate series of experiments, the chief merit of which was the discovery of the influence which the excitability of the never has upon the law of contraction. In 1829 Nobili stated clearly, for the first time, the law of contraction free from Ritter's theory of a contrast between flexors and extensors. This was confirmed by du Bois-Reymond in his classic investigations, and later by Heidenhain, who, in addition, first determined the influence of the intensity of the current upon the results obtained. Corresponding, in many respects, to the law of contraction as stated by previous observers, is that of Pflüger's, as follows:—

CURRENT INTENSITY.	ASCENDING CURRENT.		DESCENDING CURRENT.	
	Closing.	Opening.	Closing.	Opening.
Weak	Contraction.	Rest.	Contraction.	Rest.
Medium	Contraction.	Contraction.	Contraction.	Contraction.
Strong	Rest.	Contraction.	Contraction.	Rest or weak contraction.

Pflüger attempted to explain all the phenomena of the above law of contraction on the assumption that the current stimulates the nerve only at the one electrode, at the cathode in closing, and at the anode in opening, or, in other words, by the appearance of catelectrotonus or by the disappearance of anelectrotonus,—not, however, by the opposite changes. He further assumes that the appearance of catelectrotonus is more effective in exciting the nerve than the disappearance of anelectrotonus. The law of contraction can, then, be explained as follows: Very feeble currents, either ascending or descending, produce contraction only upon the closure of the circuit, the sudden increase of the excitability in the catelectrotonic area being alone sufficient to generate an impulse. The contraction which follows the closing of the ascending current depends upon the fact that the decrease of excitability at the anode is insufficient to interefere with the conduction of the cathodal stimulus. Medium currents, either ascending or descending, produce contraction both in closing and opening the circuit. The appearance of catelectrotonus and the disappearance of anelectrotonus are both sufficiently powerful to generate an impulse without, however, impairing the conductivity of the nerve.

Very strong currents produce contraction only upon the opening of the ascending and closure of the descending currents, or upon the passage of the excitability in the former from the marked anelectrotonic decrease to the normal condition, and in the latter from the normal to that of catelectrotonic increase, the absence of contraction upon the closure of the ascending current being dependent upon the blocking of the cathodal stimulus by the decrease of the excitability at the anode. With the opening of the descending current the disappearance of anelectrotonus should also be followed by contraction, which would indeed be the case if the stimulus so generated was not blocked by the sudden decrease of the conductivity at the cathode.

Nothing analogous to the law of contraction has as yet been observed in secretory nerves, but Donders confirmed it in his experiments upon the inhibitory fibres of the vagus.

Experiments on Man.—The preceding statements as to changes in the excitability produced by a constant current, as well as to the law of contraction, are based entirely upon experiments made on the isolated nerve of the frog, and under what may be regarded as abnormal conditions. It is not to be expected, therefore, that the results which have been obtained by the application in the same manner of a constant current over the course of a human nerve, surrounded by tissues possessed of different degrees of resistance, would strictly correspond to those obtained by purely physiological methods. Nevertheless, when rightly applied, the physiological effects of the constant current on the normal human nerves, though differing somewhat in detail, are the same in principle, and confirm Pflüger's laws.

Eulenburg (*Deutsches Archiv für klinische Medicin*, Bd. iii, S. 117, 1867), in his investigations of the electrotonic effects of the constant current applied percutaneously in man, found Pflüger's law confirmed, and stated his results in the following words: "There can be no doubt that, by the percutaneous application of stable galvanic currents of moderate intensity, we can succeed in producing phenomena in superficially-lying motor nerves which agree very well with those of the descending extra-polar anelectrotonus and descending extra-polar catelectrotonus,—*i.e.*, in producing in the first case a negative and in the second a positive increment of the excitability of that part of the nerve lying behind the current. He admitted, however, that differences sometimes occurred, and attributed them to the influence of the undisturbed nutrition of the nerve, and to central innervation modifying the electrotonic excitability. Erb (*Deutsches Archiv für klin. Med.*, Band iii, S. 238, 513, 1867), however, found, as a constant result of many experiments, performed according to the usual physiological methods, that there occurs a diminution of the excitability in the extra-polar catelectrotonic region and an increase in the extra-polar anelectrotonic region, as shown by stimulation with the induced current.

Helmholtz subsequently suggested that the cause of the deviation from Pflüger's law might be the position of the nerve in the uninjured body. As the nerve is in relation with a relatively large amount of well-conducting tissue, the current density must quickly decrease with the distance from the electrodes; whilst, of course, under the polarizing electrode, the current density in the nerve is the greatest; this density, on account of the moist conductors surrounding the nerve, so rapidly decreases that it becomes almost *nil* for the nerve at even a small distance from the electrodes. At a short distance, therefore, from the positive pole the density is so slight that it may be assumed without error that the current now leaves the nerve, or, in other words, that the cathode is to be found at this point. It is to be expected, therefore, that the effects of the opposite pole would be observed only at a short distance from the applied pole. As Erb did not apply the exciting electrode near enough to the polarizing electrode, he obtained, not far from the anode, the phenomena of normal catelectrotonus, and from the cathode those of normal anelectrotonus. Acting on the suggestion of Helmholtz, Erb so arranged the electrodes that the polarizing and exciting currents could be applied either simultaneously or consecutively to the same tract of nerve. By this method of investigation he obtained results which harmonized in the most complete manner with those of physiological experiment, viz., increase of excitability in the catelectrotonic and decrease of excitability in the anelectrotonic regions.

The changes in the excitability of a nerve of a living man and the contractions which follow the closing and opening of the constant current have been thoroughly studied by Waller and de Watteville ("Physiological Transactions of the Royal Society, 1882"). These observers employed a method similar to that of Erb, conjoining in one circuit the testing and polarizing currents. By the graphic method they recorded first the contraction produced by an induction shock alone; and, secondly, the contraction produced by the same stimulus under the influence of the polarizing current. As a result of many experiments, they also demonstrated an increase of the excitability in the polar region when it is cathodic, and a decrease when it is anodic. Following the suggestion of Helmholtz, that the current density quickly decreases with the distance from the electrodes, they recognize, at the point of entrance and exit of the current from the nerve, two regions,—a polar, having the same sign as the electrode, and a peripolar, having the opposite sign. (See Figs. 10 and 11.) The peripolar regions also experience similar alterations of excitability, though less in degree, according ast hey are cathodic or anodic.

As it is impossible to confine the current to the trunk of the nerve when surrounded by living tissues, as is easily the case when experimenting with the frog's nerves, it is incorrect to speak of either ascending or descending currents. Waller ("Human Physiology," p. 363, 1891), who has thoroughly studied the electrotonic effects of the galvanic current from this point of view, sums up his conclusions in the following words: "We must apply one electrode only to the nerve and attend to its effects alone, completing the circuit through a second electrode, which is applied according to convenience to some other part of the body.

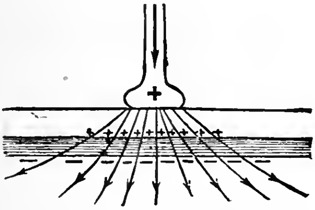

FIG. 10.—ANODE OF BATTERY.

Polar region of nerve is anodic. Peripolar region of nerve is cathodic.

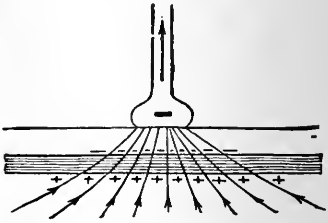

FIG. 11.—CATHODE OF BATTERY.

Polar region of nerve is cathodic. Peripolar region of nerve is anodic.

"Confining our attention to the first electrode, let us see what will happen according as it is *anode* or *cathode* of a galvanic current, Figs. 10 and 11. If this electrode be the anode of a current, the latter enters the nerve by a series of points and leaves it by a second series of points; the former, or proximal series of points, collectively constitutes the *polar* zone or region; the latter, or distal series of points, collectively constitutes the *peripolar* zone or region. In such case the polar region is the seat of entrance of current into the nerve,—*i.e.*, is *anodic;* the peripolar region is the seat of exit of current from the nerve,—*i.e.*, is *cathodic.* If, on the contrary, the electrode under observation be the cathode of a current, the latter enters the nerve by a series of points which collectively constitute a 'peripolar' region, and it leaves the nerve by a series of points which collectively constitute a 'polar' region. The current, at its entrance into the body, diffuses widely, and at its exit it concentrates; its 'density' is greatest close to the electrode, and, the greater the distance of any point from the electrode, the less the current density at that point; hence it is obvious that the current density is greater in the polar than in the peripolar region. These conditions having been recognized, we may apply to them the principles learned by study of frogs' nerves under simpler conditions. Seeing that, with either pole of the battery, whether anode or cathode, the nerve has in each case points of entrance (constituting a collective anode) and points of exit to the current (constituting a collective cathode), and admitting as proved that make excitation is cathodic, break excitation anodic, we may, with a sufficiently-strong current, expect to obtain a contraction at make and at break with either anode or cathode applied to the nerve, and we do so in fact. When the cathode is applied, and the current is made and broken, we obtain a *cathodic make contraction* and a *cathodic break contraction;* when the anode is applied, and the current is made and broken, we obtain an *anodic make contraction* and an *anodic break contraction.* These four contractions are, however, of very different strengths; the cathodic make contraction is by far the strongest; the cathodic break contraction is by far the weakest; the cathodic make contraction is stronger than the anodic make contraction; the anodic break contraction is stronger than the cathodic break contraction. Or, otherwise regarded, if, instead of comparing the contractions obtained with a sufficiently-strong current, we observe the order of their appearance with currents gradually increased from weak to strong, we shall find that the cathodic make contraction appears first, that the cathodic break contraction appears last, and the formula of contraction for man reads as follows :—

"Weak current .... K. C. C.
Medium current...... K. C. C. .... A. C. C. .... A. O. C.
Strong current........ K. C. C. .... A. C. C. .... A. O. C. .... K. O. C.

"That such should be the normal order of appearance is fully accounted for by the following considerations :—

In the	The Nature of Stimulus is	The Situation of Stimulus is	
K. C. C.	Cathodic	Polar	= Best stimulus in best region ;
A. C. C.	Cathodic	Peripolar	= Best stimulus in worst region ;
A. O. C.	Anodic	Polar	= Worst stimulus in best region ;
K. O. C.	Anodic	Peripolar	= Worst stimulus in worst region ;

which also account for an apparent anomaly, viz., that sometimes the anodic closure contraction precedes the anodic opening contraction, while sometimes this order is reversed. This difference depends upon relative current densities in the two regions, which are determined by the nature of the tissues by which the nerve is surrounded."

THEORIES OF THE ELECTRICAL PHENOMENA OF NERVES.

The Molecular Theory.—In explanation of the origin of the currents in nerves obtained by uniting the longitudinal and artificial transverse surfaces, du Bois-Reymond assumed, as in the case of muscle, the existence of electro-motive molecules, arranged one behind the other and imbedded in an indifferent conducting medium. These molecules are supposed to have their positive poles directed toward the longitudinal, their negative poles toward the transverse surfaces. This scheme accounts for the existence of strong but not for weak currents, unless the further assumption be made that the electro-motive force of the molecules diminishes with varying rapidity from the equator. The negative variation of the nerve-current is accounted for on the assumption that the electro-motive force, during the state of excitation, is diminished, or that the molecules themselves become differently arranged, whereby their electro-motive forces become less evident.

The electrotonic currents are explained on the assumption that the molecules have the peripolar arrangement, but are capable of being separated and rotated by the polarizing current. When the current is applied to the nerve, the peripolar molecules become dipolar, and their position becomes such that their negative surfaces are turned toward the positive pole and their positive surfaces toward the negative pole. The molecules thus more or less reversed, according to the strength of the polarizing current, discharge their individual currents in the same direction as the polarizing current, and thus give rise to the electrotonic current. The gradual diminution in the strength of the electrotonic currents in the extra-polar regions is explained on the assumption that the normal tendency of the molecules to maintain their peripolar arrangement gradually asserts itself and resists, in proportion to their distances from the electrodes, the reversing action of the polarizing current.

The Alteration Theory.—According to Hermann, the currents obtained from nerves are not natural, but artificial. When uninjured and in a condition of rest, the nerve is devoid of electrical properties. In order to obtain a current, it is necessary to make a transverse section of the nerve, whereby the cut surface undergoes disorganization and becomes negative to the living substance. The electro-motive forces which then make their appearance at the line of separation between the dead and living tissue—the so-called demarkation surface—give rise to the current which has been termed the demarkation current. The so-called negative variation of the nerve-current Hermann regards as an action current, the result of an electrical opposition between the excited (negative) and the resting (positive) portion of the nerve. Hermann's conclusions as to the origin of the electrical currents in living protoplasm are stated on page 26.

An explanation of the electrotonic currents is based upon an experiment of Matteucci's, who discovered that, if a wire be surrounded with a moist conductor and brought into connection with the electrodes conveying a constant current, additional currents are developed, which are similar to the electrotonic currents of nerves, and which are due to polarization. Hermann subjected these phenomena to a further investigation, and found a yet more striking analogy, which he explained as follows: The current conducted to the sheath tends to equalize itself in the well-conducting metallic core; but as polarization takes place between the sheath and core, a counter-resistance is established which, adding itself to the ordinary transition resistance, causes the current to escape in longitudinal loops, the extent of which is proportional to the degree of polarization. Electrodes applied to the extra-polar regions will send off parts of these currents, which will have, as shown by the galvanometer, the same direction as the polarizing or constant current. The anatomical structure of the nerve bears some resemblance to the metallic core and its sheath. While there may not be the same difference in conductivity between the nerve-sheath and its axis-cylinder as in the former instance, the fact that the transverse resistance of a living nerve to the passage of a galvanic current is about five times as great as the longitudinal resistance would support the view that the electrotonic condition of the nerve also is developed in consequence of an internal polarization. The internal polarization, moreover, is a property of living nerve-fibre only, as it is entirely absent in the dead fibre. The electrotonic currents are, therefore, due to an escape of the polarizing current.

"This *International System* is copiously illustrated, and the full chapters are all well written both as to conciseness and careful selection of correct language to convey the proper meaning. We have not space to call attention to any special points of discussion as to what electricity can or cannot do; but the purchaser may feel assured that the latest advances are herein well described. In short, any one having electro-therapeutic appliances and wishing to perfect himself by books in the absence of experience, cannot do well without this system, either for reference or text-book."—*Virginia Medical Monthly*, April, 1894.

International System of Electro-Therapeutics.

For Students, General Practitioners, and Specialists.

Chief Editor HORATIO R. BIGELOW, M.D., Phila.

Fellow of the American Electro-Therapeutic Association; Member of the Société d'Electro-Thérapie; Author of "Gynæcological Electro-Therapeutics," etc. Assisted by thirty-eight Eminent Specialists in Europe and America as Associate Editors.

The character and scope of this work are such that, though it has been issued but a few short months, it already stands unrivalled as the *vade mecum* of the profession, and has taken the foremost place as the standard text-book in the colleges upon this increasingly important branch of medical science.

It is handsomely and clearly printed, thoroughly illustrated with engravings, drawings, and plates where these elucidate the text, and at the end of the volume there is a full reference index. It is the most satisfactory and complete work on medical and surgical electricity yet issued. IN ONE ROYAL OCTAVO VOLUME OF 1160 PAGES.

Price in United States, Extra Cloth, $6.00 net; Sheep, $7.00 net; Half-Russia, $7.50 net. In Canada (duty paid), Cloth, $6.50 net; Sheep, $7.75 net; Half-Russia, $8.25 net. In Great Britain, Cloth, 33s.; Sheep, 38s.; Half-Russia, 41s. In France, 38 fr. 40; Sheep, 44 fr. 45; Half-Russia, 48 fr. 20.

CIRCULAR GIVING FULL LIST OF SUBJECTS AND CONTRIBUTORS SENT ON POSTAL-CARD REQUEST.

THE F. A. DAVIS CO., Publishers, 1914-16 Cherry St., Philadelphia.

BRANCH OFFICES:
117 West Forty-Second Street, New York City, U. S. A.
9 Lakeside Building, 214-220 So. Clark St., Chicago, Ill., U. S. A.
F. J. REBMAN, 11 Adam Street, Strand, London, W. C., England.

FOR SALE BY ALL BOOKSELLERS.