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With kind regards.

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Electro-Motive Power of Muscle

by

J. Burdon-Sanderson.

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A REPORT ON PROF. L. HERMANN'S RECENT RESEARCHES ON THE ELECTRO-MOTIVE PROPERTIES OF MUSCLE.

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I HAVE to-day received from Prof. Hermann a pamphlet of 37 pages*, in which he has given a short account of his more recent researches in the field of animal electricity. At the moment that the pamphlet came into my hands I was engaged in preparing, and had indeed in great part written, with a view to its publication in the *Journal of Physiology,* a review of the series of elaborate contributions relating to this subject which have appeared during the last twelve months in *Pflüger's Archiv.* My reason for undertaking this task was that I had come to the conclusion that the investigations therein recorded are likely to exercise a very decided and permanent influence on the progress of this department of our science, and that I should therefore be doing some service to those English students of physiology who either for want of time or for other reasons might be unable to make themselves masters of the original papers. What I proposed to do for them and for myself Prof. Hermann has in part done for us. All that remains is to add to the author's own summary of his work, which I shall endeavour to present to the reader in an English dress, such information as to the methods of investigation employed, and as to the experimental results arrived at, as may conduce to the better understanding of the grounds upon which the author founds his conclusions.

I propose to include in the present paper those parts only which relate to the electro-motive phenomena of muscle, reserving the sections on nerve for a future occasion.

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* *Die Ergebnisse neuerer Untersuchungen auf dem Gebiete der thierischen Electricität* von L. Hermann. 1878. The titles of the papers of which this lecture is a summary, all of which have been published in *Pflüger's Archiv*, are as follows:—

(1) *Untersuchungen über die Entwicklung des Muskelstroms.* Vol. xv. p. 191.

(2) *Versuche mit dem Fall-Rheotom über die Erregungsschwankung des Muskels.* Vol. xv. p. 233.

(3) *Untersuchungen über die Actionsströme des Muskels.* Vol. xvi. p. 191.

(4) *Ueber den Actionsstrom der Muskeln im lebenden Menschen.* Vol. xvi. p. 410.

I. INTRODUCTION.

The author commences with a summary of the fundamental facts which at the time when he entered upon his investigations were regarded as established. These facts were the following :—

Muscle and nerve-fibres exhibit when they are cut across, an electro-motive force which is directed from the cross section to the longitudinal surface, and may amount to a twelfth of that of a Daniell's element. The negativity of the cross section is in much less degree a property of the natural end-surface (*natürlicher Querschnitt* of du Bois) than of the artificial surface. The natural end-surface may indeed be positive. This departure from the norma is called by du Bois "Parelectronomia": it is favoured by cold. A muscle (or nerve) which possesses an artificial cross section exhibits during excitation a diminution of its current (negative variation): in uninjured muscle, the current which exists during excitation represents the sum of the previously existing current (whatever its direction or amount) and of the negative variation.

On these facts du Bois had based the following theory. (1) A muscle (or nerve) fibre contains electro-motive particles suspended in an indifferent (inactive) material, of which the negative surfaces look towards the end-surface of the fibre, the positive surfaces towards its lateral surface. (2) At the natural end-surfaces of muscle, particles of a peculiar kind exist in greater or less degree of development, of which the surfaces directed to the end of the fibre are positive. The "development" of these particles is favoured by cold. They constitute the parelectronomic layer. (3) In consequence of excitation the electro-motive forces of the particles (called by du Bois "molecules") either diminish or they assume a different arrangement, by virtue of which their external action is impaired. The molecules of the parelectronomic layer take no part in this excitatory change.

The distinguished author of this theory (commonly known as the molecular theory) was particularly careful not to found speculations on it relating to the essential nature of the processes of excitation and conduction in nerve or in muscle, or to apply it to the explanation of muscular contraction. It was however generally considered that the electro-motive forces of these molecules were maintained in resting muscle by virtue of its chemical process, and that "state of excitation consisted primarily in motions of the molecules, with which motions increased assumption of oxygen and increased oxidation were in some way or other associated."

I omit the succeeding paragraphs, in which an account is given of the steps which led the author to the discovery of the independence of the two processes by which muscle takes in oxygen on the one hand and gives out CO_2 on the other; and in which he discusses the analogies which exist between contraction and rigor mortis, his views on this subject being well known. I proceed at once to the next section.

II. The Currents of Resting Muscles.

Uninjured resting muscle exhibits no currents, *i.e.* its surface is iso-electric. The surfaces of muscles that are removed from the body present numerous unnoticeable injuries either chemical or mechanical. In du Bois' earliest experiments the muscles used were as a rule moistened with concentrated solutions of salt, and were thereby so acted upon that he was led to attribute to their natural end-surfaces a negativity similar to that observed in cut surfaces. Notwithstanding that the error thus made was corrected by du Bois himself, he continued to attach importance to certain actions manifested at the end-surfaces of muscles, although it was recognised that they were of a different order from those before observed, and that their direction was uncertain and irregular. It was to meet this difficulty that the doctrine of the parelectronomic layer was devised.

For the purpose of showing that any such explanation was unnecessary, Hermann set to work, some ten or twelve years ago, to investigate the condition of uninjured muscle, and found that it is possible to prepare the gastrocnemius (almost the only muscle which admits of being so prepared) in a state of such integrity that the electrical inequalities of the surface are so slight and so irregular, that no physiological meaning can be attached to them.

The conclusion drawn by Hermann from this observation was that the inequalities ("currents") which present themselves in other muscles are the results of injury. The contrary doctrine is that they are in all these cases "pre-existent," in relation to any injury supposed to be inflicted in the process of preparation; hence, the "theory of the muscle-current" came to be designated by its adversaries the "Pre-existence Theory."

Two facts have become known during the last few years which have rendered it extremely difficult to believe that currents exist in inactive muscles otherwise than as the products of the inevitable surface-changes which are incident to their separation from the living body. One of these is the complete absence of such currents in fish when curarized, the other their absence in the resting heart of the frog, the surface of which is now known to be iso-electrical*, so long as it is absolutely uninjured and remains inactive.

Development of the muscle-current. In a paper "On the development of the muscle-current," published only last summer, Hermann has approached the Pre-existence Theory from a new point of view. We have seen that the uninjured terminal surface of a muscle is wanting in that "negativity" which it acquires from the moment that it is "developed" either by mechanical or chemical destruction of the ends of its fibres. If this absence of negativity is due to nothing more than that its active molecules are protected by the parelectronomic layer, then obviously from the instant that this layer is removed, the electro-motive forces of those molecules will be in action. If it can be shown that a measurable delay intervenes between the injury and its effect, *i.e.*, that a certain time is required for these forces to develop, this would afford evidence that the forces in question were not pre-existing forces, which required only unmasking, but that they were called into existence in consequence of changes in the muscular substance produced at the moment of injury. With this consideration in view Hermann has devised a special apparatus—the "Fall-rheotom"—by which a galvanometric circuit comprising the muscle is closed at the same moment that the muscle itself is injured, and opened a very short time afterwards. The result of the experiment is that, however short may be the time during which the muscle acts on the galvanometer, a certain deflection is observed. But, the extent of the deflection is always inferior to that which is observed when a second experiment is made on the now injured muscle, as soon as possible after the first. The difference between the two results admits only of one explanation. In the first observation, the deflection is less than in the second because the electro-motive forces which come into operation at the injured surface have not yet had time to develop. This being so, it is certain that they are not pre-existent.

The fall-rheotome is an instrument contrived for the purpose of measuring the time required for the development of the difference of potential which presents itself between an injured surface and the same surface immediately

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* This fact was discovered by Engelmann in 1873. Engelmann, *Onderzoekingen gedaan in het Physiologisch Laboratorium der Utrechtsche Hoogeschool.* III. 1874, p. 101.

before the injury, or, to use the terms employed by Hermann, the development of the demarcation current. Its construction will be best understood by reference to the diagram, Fig. 1. A weight, let fall from a height of about

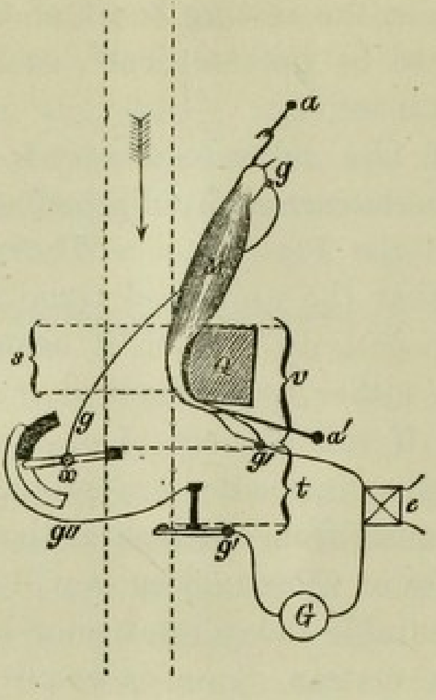

Fig. 1.

The vertical dotted lines indicate the course of the falling block of the rheotome in its descent. *M* is the gastrocnemius muscle, of which the posterior surface looks to the left. *Q* is an ebonite support around which the muscle is stretched by the attachment of the tendons *a* and *a'*. At *g* and *g'* it is connected with the galvanometer circuit, which is closed by the key *x* and opened by the lever *g'*. *G* is the galvanometer. The brackets *s*, *v* and *t* indicate respectively the parts of the descent of the block which are accomplished in the "Streifzeit," the "Vorschlusszeit" and the "Schlusszeit." *e* is a reversing key from which wires, represented by lines above and below *e*, lead to the compensator.

four feet (of which the course is indicated by the two vertical broken lines), comes into contact in its descent, first with the muscle to be investigated, secondly with a lever *x*, which closes the galvanoscopic current $g' g''$, and thirdly, with the lever g', by which that current is opened. The support by which the muscle is held, and that which carries the axis of the lever *x*, are moveable up and down, and can be adjusted and fixed at any required height, so that the time at which the injury is inflicted and the time at which the galvanometric current is closed can be varied at will, and the duration of the period of closure, as well as the interval of time between the injury and the closure, can be determined by reference to the law of falling bodies. The breaking lever g' is fixed.

The muscle used is the gastrocnemius, which is led off by its opposite tendons to the galvanometer at $g\, g''$. The galvanometer circuit includes a compensator (not shown in the diagram), by means of which whatever current exists between the two tendons before and after the injury may be balanced, and its electro-motive force measured. The muscle rests against the support *Q* in such a position that the falling weight, which is shod with shagreen for the purpose, strips off the aponeurotic expansion of the Tendo Achillis. Whatever electrical change is produced by the injury is indicated by the galvanometer. The lever *x* is so constructed that the end opposite to that by which it is caught by the descending weight presses against the circle c (the lower half of which is of ivory, the upper of metal); hence, as the weight passes contact is made between the wires g and g''.

The question to be determined in each experiment is—What is the electrical condition of the injured surface immediately after the injury? To answer it the galvanometer current must be closed at the moment that the injury is completed, and opened a very short time afterwards (in Hermann's experiments, 0″·0034). Under these conditions a certain result is obtained, which however has no value, excepting by comparison with that of a second observation made immediately after, in which the circuit is closed for the same period. If then the two deflections are called A and B, the electromotive force already developed during the $\frac{1}{300}''$ immediately after the injury is to the force eventually developed as A is to B. In all Prof. Hermann's experiments A was found to be less than B.

The first experiment in the series given may be taken as an illustrative example.

Before injury the electrical difference between g and g'' was 0·0018 Daniell. After "injury" it was 0·049. The instrument was so adjusted that the time occupied in stripping off the tendon was 0″·0027. This Prof. Hermann called the "Streifzeit" $= s$. The galvanometer current was closed 0″·0023 after the commencement of the injury; this period of time is designated the "Vorschlusszeit" $= v$. The time during which the circuit remained closed was, in this as in other experiments, 0″·0034.

The falling of the weight produced a deflection of the galvanometer of $3·75 = A$. On withdrawing the muscle out of reach of the shagreen, re-arranging the instrument and allowing the weight to fall again, the deflection was $5·0 = B$. Consequently, although the first occurrence showed that the injured surface had already begun to become negative before the circuit was closed, the difference observed was only three-fourths of that which afterwards existed. If in this experiment the moment at which the injury was inflicted be taken as half-way between the beginning and ending of the "Streifzeit," we have $v - \frac{s}{2}$ as the interval of time between the injury, and the closing of the galvanometer circuit. As the electrical change evidently takes place gradually, so that we cannot fix upon the moment of its occurrence by direct observation, the most accurate method of determining it is to take as representing it, any time at which its sudden occurrence would have accounted for the difference between A and B actually observed. Now in the present instance, in which A was less than B by a quarter of B, the result would have been accounted for if the electrical change had occurred instantaneously a quarter of the "Schlusszeit" after the moment at which the circuit was closed. Stating this generally, the time of the occurrence of the electrical change, reckoned from the opening of the lever g', is $\frac{A}{B}t$, and the time of the injury, reckoned from the opening of the lever g', is $t + v - \frac{s}{2}$. Hence the total interval of time between the injury and the effect is $t - \frac{A}{B}t + v - \frac{s}{2}$, or $\frac{B-A}{B}t + v - \frac{s}{2}$. This period is designated by Hermann the "Entwicklungszeit" $= E$. In the experiment of which the particulars have been given it was 0·0018 sec. From the results of 300 observations the mean value of E for the gastrocnemius was estimated at $\frac{1}{400}$ of a second; but it is to be carefully borne in mind that the period is not sharply limited at either end, both the injury and the electrical effect being gradual processes. It is proved that the latter is not immediate, and, consequently, that the electro-motive forces of which it is the manifestation are not in operation at the moment that the cross surfaces of the muscular fibres are exposed. It was found that by cooling a muscle by exposure to ice, E could be increased to $\frac{1}{250}$ second.

It has probably already suggested itself to the reader that the difference between A and B might be due in whole or in part, not to the delay of "development," but to the "negative variation" produced by the mechanical excitation of the injured surface. The question has been exhaustively discussed in the paper. The most conclusive proof that it is not so is obtained when the experiment is made with a muscle of which the aponeurotic expansion of the Tendo Achillis has been immediately before "developed" by the application to it of the irritating skin-secretion of the frog. By this means an electrical difference is produced between the irritated surface and the rest of the muscle, which is nearly as great as that produced by stripping off the aponeurosis. The result is, if $v = s$, and $t = \frac{1}{300}$ second, that A and B are equal, showing that during the period investigated the excitation due to the mechanical injury has no perceptible influence.

A further series of experiments was made in which "regular" muscles, such as the sartorius, or the semi-membranosus, were substituted for the gastrocnemius, the apparatus being so modified that the weight, in falling, instantaneously crushed one end of the muscle. The results were in so far of greater value that the "Streifzeit," from the nature of the method employed, was indefinitely shortened. Consequently, as the galvanometer circuit was opened in some instances not more than 0″·0024, in others not more than 0″·0014 after the injury, any influence of the excitatory variation was out of the question. There was still a marked difference between A and B.

Conditions which affect the permanence of the electromotive activity of an injured surface. In ordinary muscles it is well known that the negativity of the cut surface once developed is tolerably persistent, but in the case of the heart and of nerves Engelmann has shown that the electrical difference between injured and sound surface rapidly diminishes immediately after the injury. The reason why this is not the case in voluntary muscles is, according to Engelmann, that the histological elements are of much greater length. If, as there seems reason to believe, those elements only which are actually within the range of the destructive action are affected by it, we can readily understand how it is that in a nerve of which the elements are not much more than a millimeter in length, the subsidence of the electrical effect of section takes place much more rapidly than in muscle of which the elements may have a length of several centimeters. These considerations Hermann expresses by saying that "the negativity of a cross-cut surface can only last so long as the cells which are cut still contain remainders of living protoplasm."

The only process by which, in the case of voluntary muscles, complete restoration of the normal electrical state of an injured surface can take place is that of healing. Engelmann has shown that when a muscle is injured subcutaneously, the injured surface is negative to other parts, but that the electrical inequality rapidly disappears, *pari passu*, with the restitution of the other structural and physiological properties.

Influence of temperature. The only condition, according to Hermann, which can be recognised as a cause of electrical inequality (*i.e.*, of current) in resting muscle is inequality of temperature. Some years ago he discovered that in muscles, " warmed parts," provided that the increase of temperature is not sufficient to produce heat rigor, are positive to cooler parts*. Hence if one of two surfaces by which a muscle is led off is warmed, a current is produced which tends in the muscle from the cooler to the warmer surface. By increasing the warming this current is reversed.

Currents of entire muscles. Notwithstanding what has been said as to the absence of currents in wholly uninjured muscles, it is well known that the muscles of frogs, even when prepared with the utmost care, always exhibit slight electrical differences. According to Hermann these differences are due exclusively to injured fibres, all others acting the part merely of indifferent conductors. If this is so, we should expect that the relatively feeble currents which the galvanometer indicates when muscles in this state are led off by various contacts, would, so long as the integrity of the surface is maintained, be purely accidental in their character, and have no relation to the form and structure of the muscle. By experience we know that it is not so, that on the contrary in all muscles we can foretell, by reference to the structural plan of the muscle, what will be found to be the distribution of the electrical inequalities on the surface. The explanation which Hermann gives of this is as follows:—If the surface of a muscle is affected promiscuously by injuries, it is always the case that an electro-motive force directed from the end towards the longitudinal surface manifests itself; for if the surface has been subjected to a slight injury, the resulting loss of vitality of the longitudinal surface is arrested in its progress

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* The results of my own observations as to the remarkable influence of changes of temperature on the surface of the heart, have been recently communicated to the Royal Society in a preliminary note, and will shortly be published *in extenso* in this Journal.

at the junction of the superficial layer of fibres with the layer below; whereas the death of the end-surface gives rise to a persistent alteration*, the result of which manifests itself in a permanent "demarcation current" analogous to that between a cut surface and a natural longitudinal one. The inequality once established is of course increased by the oblique direction in which, in most muscles, the muscular fibres are inserted into the tendinous expansions.

III. Action Currents.

The wave-like propagation of the negative variation. The fact that the electrical effect of excitation is propagated in muscle with a definite velocity was discovered by Bernstein in 1869. By means of investigations made with the aid of the "differential rheotome" he discovered that when a muscle is subjected to direct excitation, the excited part becomes negative to other parts, and that the area or tract of negativity travels along the fibre with a velocity which agrees with that of the wave of contraction. The phenomenon admitted of a ready enough explanation in accordance with the molecular theory, and was so explained by Bernstein. Hermann regards the excitatory negativity not as a diminution of any pre-existing current, but as the manifestation of electro-motive forces which come into operation at the moment and at the seat of excitation. He accordingly calls the currents by which these forces manifest themselves "action currents." Action currents are characterized by Hermann as either phasic or tetanic. By the word phasic he denotes the fact that when a wave of excitation passes along a muscular fibre which is connected with a galvanometer at two points, each led off point is seen to become negative to the other at the moment the wave passes it. The result is that the magnet is acted on, first, by a current of which the direction coincides (in the muscle) with that of the progress of the wave (first phase), and secondly by a current in the opposite direction†. When a muscle is tetanized, and the condition investigated in the same way, no indications present themselves of propagation, for, as in every fibre, wave follows wave in continuous and rapid succession, the two led

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* "Hat eine geringe Schädlichkeit die Oberfläche des Muskels getroffen, so macht das Absterben des Längschnitts an der nächsten Fasergrenze Halt, während das Absterben vom Querschnitt her einen dauernden Strom verursacht."

† The phenomenon is the same as du Bois' *Doppelschwankung*, observed first by G. S. Mayer in the gastrocnemius.

off points are always in the same condition, and would, according to Hermann, remain iso-electrical so long as the tetanic state lasted, if it were not that the effect *i.e.* the negativity of the progressing tract of excitation diminishes as it travels.

Tetanic action currents. What we have hitherto called the "negative variation" of the current which tends from the cut surface to the natural surface of a muscle, Hermann proposes for the future to designate the "ausgleichender Actionsstrom;" because, as he explains it, it consists in this, that "the living part of the muscle undergoes a change in the same direction as that which the dying part (*i.e.* the injured part at the cut surface) has already undergone."

The relatively feeble "negative variation" of the uninjured muscle in tetanus, which du Bois explains by attributing it to the slight participation of the terminal layer of parelectronomic molecules in the excitatory change, Hermann proposes to call the "decremential current." He denies that the change is localized at the terminal surface of the muscle, and regards it as resulting from the fact that "each excitation wave as it travels along the fibre diminishes in intensity." Hence if any spot of the surface of a muscle is, during the tetanic state, compared galvanoscopically with any other spot situated at a greater distance from the origin of the excitation waves, *i.e.* from the excited point, it is found to be negative to it.

Totally tetanized muscles are iso-electrical. The general principle by which we can best explain the preceding facts is this, that in muscle all parts are equally excitable and equally excited when acted on by equal stimuli.

If this principle is true it must follow that if a means exists by which the whole substance of a muscle can be excited in equal degree at the same moment, then, inasmuch as all parts are in the same phase of electrical disturbance at the same moment, there will be no variation; the muscle will remain iso-electrical throughout.

That this is so as regards the muscles of frogs Hermann seems to have proved, for he has found that when an uninjured curarized muscle is "totally" tetanized by induction currents passing through it from end to end, its surface exhibits no electrical differences. Another consequence follows from it of which the empirical proof is more difficult. We have already seen that, according to Hermann, the differences which present themselves in entire muscles after removal from the body during tetanus (*i.e.* the fact that during tetanus the physiological middle zone of a muscle becomes negative to every other zone, and that of any two zones that is most negative which is nearest to the middle zone) are dependent on the circumstance that each of the successive waves of excitation which emanate from the "nervous equator" diminish as they proceed towards the ends of the muscle, and that this diminution is due to exhaustion. If this is so, there ought to be no such effect in muscles in which the circulation is still maintained; and consequently no action currents—no electrical inequalities of any kind arising from muscular action—should exist in the living body. What then becomes of the experiment by which we are in the habit year after year of demonstrating, that when we exert the muscles of one forearm, the resting arm becomes negative to the exerting arm? The reader will perhaps not be surprised to learn that this phenomenon admits of being explained independently of muscular action. Hermann states that he has found by experiments, not yet published, that it is due to a "cutaneous current."

The experimental results on which Hermann's conclusions relating to "tetanic action currents" are founded, are recorded in the 4th, 6th and 7th sections of his paper. At the head of the 4th section stands the following proposition. "The seat of the electro-motive force of the tetanic action current is not at the ends of the fibres, but the electro-motive force is distributed equally throughout the whole of the course along which the excitation is propagated." This proposition had to be proved, first in the case of curarized muscle excited directly, and, secondly, in muscles excited through their nerves. For both purposes the most important observations related to the adductor magnus, with reference to the mode of preparing which the reader must refer to the paper. It will be sufficient to explain that the preparation used consisted of the two adductors, which were connected together at their upper ends by the symphysis, and remained attached to the two femora. The muscles were extended by hooks fixed in each knee-joint, so that their arrangement may be represented by the following diagram, in which the horizontal line represents the two muscles and *S* the symphysis.

The numbers above the line express the distances in millims. between the points *e*, *e′*, *a*, *b*, &c. in the first experiment of the series, of which the following are the particulars. The muscle was excited by the electrodes *e*, *e′*, distant 5 millims. from each other, and connected with the secondary coil, of which the distance from the primary was 5 centims. At each of the zones *a*, *b* and *c* the muscle was surrounded by a loop of twine steeped in salt solution, with which the non-polarizable electrodes of the galvanometric circuit were connected, so that the electric difference could be measured at will between any two zones (*c* standing for *S* so long as the right-hand muscle was not excited). The point to be determined was whether the electrical difference found to exist during tetanus between *S* and any two zones (as *e.g.* the zones *a* and *b*) was proportional to their distance from *S*. The results were not so consistent as could have been wished. Thus in the first experiment the distance a, b was to the distance b, S as 54 to 100, while the electrical difference between a and b was to that between a and S as 63 to 100. This was sufficiently near, but in the next observation on the same muscle, excited with stronger induction currents, we have, between the same points, the ratios between the electro-motive forces and the distances differing in the proportion of 22 to 63. It was to be noted, however, that this, which happens to be the first example given, is quite exceptional; the remainder (see pp. 224, 225) are sufficiently consistent to justify the conclusion of the author as regards the upper half of the adductor magnus, that when it is tetanized by excitation of its lower end its upper end becomes positive to all other parts in proportion to their distance.

By the application of a similar method it was shown that when the adductor was tetanised through its nerve, the electrical condition of the muscle during tetanus is in so far similar that the upper end is positive to any zone of the upper half, the difference being proportional to the distance. The mode of experimentation differed from the former only in respect of the modes in which the muscles were led off and the arrangements for exciting the nerves. The interesting fact was arrived at that in each muscle there was an excitatory negative zone, *i.e.* a zone of greatest negativity during tetanus, the distance of which from the upper end of the muscle was found to be a little greater than the distance of the fibres of the nerve (see p. 232). From this fact, the conclusion is arrived at that, when a muscle is tetanized from the nerve, the effect consists in the propagation along each muscular fibre of continuous successions of travelling discoid tracts of negativity, all of which start from the negative zone (Hermann's *nervöser Æquator*), and make their way to the opposite ends of the muscle.

We now come to the last empirical result relating to tetanic action currents, viz. to the proof that when a muscle is tetanized "totally" no electrical difference manifests itself between different parts of its surface.

Several difficulties stand in the way of the investigation of the electro-motive phenomena of a "totally" tetanized muscle. One is, that the time for observation is limited to the intervals between the successive excitations—periods of perhaps a 50th of a second; and another, that during these periods the condition of the muscle is interfered with by polarization, *i.e.* by the electro-motive force which is brought into operation in the interior of the muscle by the induction currents used to excite it. The influence of this "internal polarization" lasts for a sufficient time after each excitation to affect the galvanometer sensibly.

Professor Hermann employed for the investigation a rheotome so constructed that the excitation circuit (that of the secondary coil of the induction apparatus) and the galvanometer circuit were closed alternately twenty times in a second; as the period of closure of each circuit was $\frac{1}{60}''$, there was an interval between the opening of the galvanometric circuit and each preceding and following period of excitation of $\frac{1}{120}''$, so that the order was as follows, the continuous lines denoting the periods of closure of the galvanometer circuit, and the dotted lines those of the excitation circuit:

The exciting electrodes were non-polarizable, and placed at the ends of the muscle. The interrupter of the primary coil was in constant action, so that at each closure of the secondary coil a succession of induction shocks was sent through the muscle. The muscle was led off by a loop of twine moistened in salt solution, which surrounded its middle, and by a second electrode near one end. A reverser was introduced into the exciting circuit. In all the experiments any existing current was first compensated. The muscle was then tetanized, first with the secondary coil at 10 centims., then at shorter distances. In most of the experiments it was found that so long as the induction currents were not very strong, the galvanometer was unaffected, whatever was their direction. In some instances it was otherwise; but in these the deflections were for the most part inconsiderable, and not to be compared with those which the same muscles immediately afterwards yielded when "developed" by the action of heat or acid on their surfaces—the general conclusion being that in uninjured muscles, whose surfaces are iso-electric, no "action current" is brought into existence by total excitation (p. 216).

Phasic action currents. Bernstein's investigations as to phasic currents, *i.e.* as to the electrical changes which manifest themselves in a muscular fibre during the propagation of a wave of excitation along it, were limited to curarized muscles. Sigmund Mayer, however, used Bernstein's instrument for the purpose of analysing the similar phenomena which present themselves in non-curarized muscles (the gastrocnemius) when they are excited by single induction shocks directed through their nerves. In this case the resulting single excitation wave originates not from the electrodes, but from the end-plate of each nerve-fibre. The observations of S. Mayer have been repeated and very fully discussed by du Bois Reymond in his recent papers on the negative variation*. The phenomenon observed in the gastrocnemius is this, viz. that when this muscle is led off by its opposite tendons the negative variation, of which the total duration is less than $\frac{1}{200}$ of a second, consists of two phases, in the first of which the lower end of the muscle becomes more positive, in the second the upper end, the result as regards the galvanometer being the production of what du Bois calls a "Doppelschwankung." The explanation given by du Bois is that the first phase has its seat at the tendinous expansion, the negative variation being due to the excitatory electro-motive changes which go on at the tendon ends of each muscle-fibre, and that the excitatory change begins somewhat more suddenly, and is accomplished in a shorter time at the Tendo Achillis (the *Achillesspiegel* of du Bois) than at the upper end (the *Kniespiegel*), in consequence of which the effect which proceeds from below has the advantage as regards time. Hermann

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* *Ueber die negative Schwankung des Muskelstromes, &c. Gesammelte Abhandlungen,* Bd. II. p. 521.

rejects this theory on the ground, that in every regularly constructed muscle which consists of parallel fibres which run from end to end, and receives its motor-nerve in the middle, it can be shown that whenever a single excitation is communicated to the muscle by its nerve, two waves start from the nerve (*i.e.* from the nerve-endings) and travel endwards in both directions. The proof of this lies in the observation that if the galvanometer is connected with the middle of the muscle and either end, the deflection observed is found, when analysed by the rheotome, to have the phasic character, the first phase being (as Hermann calls it) atterminal, and indicating that the end of the muscle becomes positive to the middle, the second abterminal. Without the rheotome the deflection is simply atterminal, for the first phase is incomparably stronger than the second.

The result of all this is that in nerved muscles the electrical phenomena which attend the propagation of the excitation wave correspond completely with those observed by Bernstein in nerveless muscles. In Bernstein's fundamental experiment*, a curarized sartorius is led off at two points of its surface, and excited at one end by a single induction shock. The single excitation wave travels from the point of excitation with a velocity of three meters per second, and as it passes each electrode renders it negative, the effect lasting for about $\frac{1}{250}''$. Inasmuch as one of the electrodes is near, the other far from the starting point, the near electrode becomes negative first, then the others: hence the Doppelschwankung.

For the purpose of investigating the excitatory variation consequent on a single induction shock through the nerve the Fall-rheotome is employed. When the instrument is intended to be used for this purpose the only modification required is that the slider by which the muscle is supported is replaced by another, to which a key is fixed, of such construction that the weight in falling opens it (see below). Consequently, as this key is included in the primary circuit of an induction coil of which the secondary contains the exciting electrodes, the time which intervenes between the opening of the primary circuit (*i.e.* the opening induction shock) and the closure of the galvanometer circuit, can be varied at will and measured accurately. As compared with the investigation of the excitatory variation by means of Bernstein's rheotome it has the advantage of greater simplicity and is free from several drawbacks. In the use of Bernstein's instrument the excitations follow each other in such rapid succession that the state of the muscle approaches that of tetanus. Consequently it becomes exhausted during the progress of the observation, and is so far in a different condition at the end of the experiment from that in which it is at the beginning. Observations with the Fall-rheotome are free

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* *Untersuchungen über den Erregungsvorgang*, &c. Heidelberg, 1871, p. 57.

from this objection. The only difficulty is that it is necessary to employ a galvanometer of extreme sensitiveness to weak instantaneous currents.

As in the other case, the method will be best understood by an example. The muscle used was the gastrocnemius, of which the nerve was excited six millims. from its entrance, the distance of the secondary coil being 12·0 centims. It was led off, as in the former experiment, by its tendons, and was compensated by 0·02 Daniell. It responded by a deflection of 41 on the scale to the opening induction current. The interval between excitation and closure of the circuit (the circuit being in all cases closed for 0″·0034) was varied in successive experiments up to 0″·01. If the closure took place sooner than 0″·0021 after the excitation, there was no variation. When the closure occurred between 0″·0021 and 0″·008 the variation was "negative," *i.e.* the lower end became positive to the upper. If the interval exceeded 0″·008 it was "positive" (*i.e.* the lower end of the muscle became negative). If it exceeded 0″·01 there was no effect; so that it was to be concluded, as regards the gastrocnemius, that the variation ends between 0″·01 and 0″·0134*. These results agreed in all essential particulars with those previously obtained by S. Mayer with Bernstein's instrument.

The author next proceeded to apply the same method to the investigation of the electrical effect of total direct excitation. In this investigation the Fall-rheotome presented great advantages. For, in Bernstein's instrument the induction circuit is necessarily closed during the whole period of observation, so that if the induction currents were to enter and leave the muscle by the same contacts as those by which it is led off during the intervals between each excitation and the following one, it is obvious that the secondary circuit would constitute a "side wire" to the galvanometer. The muscles used were the group of the gracilis and semimembranosus, which were attached below to the knee and to a part of the tibia, and above to part of the pelvis, and were extended by hooks fixed in these attachments. The preparation was led off (1) by its lower end, which had been previously immersed in hot water so as to yield a "thermic" injured surface, and (2) by the middles of the muscles. The same electrodes served for the excitation currents as for the connection with the galvanometer. The preparation was excited by a closing induction shock immediately followed by an opening one, the key employed for closing and opening the primary circuit being so constructed that the weight in falling first closed the primary circuit for a period of 0″·0014, and immediately afterwards opened the induction circuit. It was of course necessary to use very strong induction shocks.

In consequence of internal polarization, the extent of the variation differs according to the direction of the primary current, so that in order to get true results the observations must be taken in couples, between each member of which the direction of the primary current was reversed. As the effect of polarization may amount to a considerable proportion of the total effects recorded, this is of course absolutely necessary.

The main result of the investigation can be stated in a few words. The variation of an injured muscle when "totally" excited exhibits no trace of phases. Consequently, whatever be the interval of time between the excitation and the closure of the galvanometer circuit, the direction of the deflection is always such as to indicate that the end of the muscle becomes positive.

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* *Pflüger's Archiv*, Vol. xv. p. 237.

The details are as follows:—The largest deflections were obtained when the closing time was from 0″·0016 to 0″·0069 after the excitation, but exhibited very little diminution so long as it was included within the first hundredth of a second, *e.g.* when the period of closure was from 0″·0055 to 0″·010. After this it diminished.

The most interesting, though not the most important result of Hermann's investigation of "phasic currents" in nerved muscles, is the discovery that the same phenomena as are observed in the entire muscles of frogs, can also be demonstrated in human muscles. In the experiment of du Bois, to which reference has already been made*, a person having immersed the index fingers of his two hands in two basins containing salt solution connected with the opposite terminals of a galvanometer, produces deflections of the needle of which the direction differs according as the one or the other arm is thrown into action. The objection to which this observation is liable, namely that the results may be due to electro-motive forces having their seat elsewhere than in the muscles (see p. 206), does not apply to the case of single contractions. That these are also accompanied by electromotive changes Professor Hermann has now succeeded in demonstrating on the human subject, and employs for the purpose the muscles of the fore-arm. His method consists in surrounding the fore-arm with two zones of twine soaked in salt solution, which are severally in connection with the terminals of the galvanometer. One zone surrounds the arm at the physiological middle (*nervöser Aequator*, an imaginary transverse section of the fore-arm muscles, the distance of which from the elbow is the mean of the distances of the muscular endings of the nerves which are distributed to them), the other at the wrist. The exciting electrodes are applied to the surface of the skin covering the brachial plexus, and the galvanoscopic effect is investigated with the aid of the rheotome. The result is that it is found to consist of two phases, in the first of which the wrist becomes positive, in the second negative. The transition from the positive to the negative takes place about a hundredth of a second after the excitation. Thus the phenomena of the phasic action current as observed in the frog are reproduced in the muscles of the human fore-arm, with this important difference between the two cases, that whereas in the prepared muscle of the frog the "abterminal" phase is even in the first state very inconsiderable as compared with the "atterminal," they are in the living arm sensibly

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* A good description of this experiment will be found in Rosenthal's *Allgem. Physiol. der Muskeln und Nerven*, p. 201.

equal. In this fact Hermann finds a striking confirmation of the truth of his theory, that the diminution which the excitation-wave undergoes in its progress is due to exhaustion.

The author concludes by observing that as regards muscle, all excitatory electro-motive phenomena may be referred to one principle, viz. that the electro-motorial reaction by which all excitable protoplasm responds to destructive as well as to excitatory influences consists in the fact that the substance acted upon becomes negative to the part which is not acted upon. Whatever meaning may be eventually assigned to this proposition, there can be little doubt that, by establishing a more intimate relation than before existed between the electrical and the other essential phenomena of the life of contractile and excitable tissues, the investigations of which I have endeavoured to give an intelligible account have added very considerably to the physiological interest of the subject.