

THE RELATION OF MOTION IN ANIMALS AND PLANTS TO THE ELECTRICAL PHENOMENA ASSOCIATED WITH IT.¹

THE lecturer began by observing that the proper subject of the lecture being "the nature or laws of muscular motion,"² he would discuss the chemical, mechanical and electrical concomitants of this most important function with a view to the elucidation of their mutual causal relations. He would, however, ask the attention of the Society chiefly to the *electrical* phenomena which are associated with muscular action, as being those which he had himself specially studied. Some points relating to the *mechanical* effects of muscular action must be referred to by way of introduction, inasmuch as it is by these that a muscle performs its function as an organ of motion. There were two ways of investigating these effects experimentally. We might observe and record either the change of form which a muscle undergoes in response to a stimulus of very short duration when contracting isotonically, *i.e.* as it does when lifting a weight, or the increase of tension which occurs when it endeavours to overcome a resistance, *i.e.* when it acts isometrically. It was shown that although, as regards an entire muscle, the isometric method was preferable to the isotonic, the time occupied by a single element of muscular structure when directly excited in developing its maximum tension (*i.e.* in the transformation of chemical into mechanical energy) could be best estimated under isotonic conditions. He then proceeded to describe his own method of accomplishing this measurement with the aid of photography. It consists in observing the change of form of the surface of a living muscle when a single break induction current is led through it in such a way that the observed surface is at the cathode. A magnified image of the cathodic electrode, which moves freely with the muscle, is projected on a slit behind which a sensitive plate passes, and in this way a curve is obtained from which the time-relations of the movement can be deduced. It is thus learned that at the cathodic spot, *i.e.* at the spot immediately excited, the process attains its greatest activity before the end of the first hundredth of a second. The importance of this datum consists in its bearing on the question whether or not the electrical change by which the change of form thus observed is accompanied is coincident with it, follows or precedes it. The answer to this question could not, of course, be given until the time-relations of the electrical change had been considered. These were discussed as follows:—

The essential point in investigating the *electrical* changes which occur in muscle is to connect two parts of its surface through a galvanoscope. The general result of such an exploration is (1) that similar parts in a similar physiological state are equipotential; (2) that between similar parts which are not in the same state there is always a difference of potential, measurable by the method of compensation, the less capable of function, *i.e.* the less living, being negative to the more living; and (3) that transitory differences of potential arise between two parts of the living surface when the one is excited to discharge of function, the other remaining at rest. Thus the state of rest or fitness for function of a part is denoted by relative "positivity," discharge of function by relative "negativity."³

¹ Abstract of the Croonian Lecture, delivered before the Royal Society, by J. Burdon-Sanderson, M.A., M.D., F.R.S., on March 16.

² See "The Record" of the Royal Society, 1897, p. 126.

³ The use of these words in the sense above stated has been strongly objected to. It is difficult to see to what obscurity of meaning it can give rise. "Negativity" of a surface means nothing more than it is negative relatively to another surface.

First Fundamental Experiment.—The effect of an excitation which is instantaneous and so localised as to affect in the first instance only one of the two surfaces of contact is the sudden manifestation of a difference of potential between them, this effect being momentary (case 1) or continuous (case 2) according to the duration of the excitation. In either case it is designated "excitatory variation" if the muscle is referred to, or "action current" if the galvanoscope is referred to.¹ If the capillary electrometer is used as galvanoscope, and its excursions are recorded photographically, the curves so obtained truly and faithfully express to us the character and time-relations of the *variation*, provided only that we know according to what rule they are to be interpreted. This rule can be deduced from the well-known properties of the instrument, as has been fully set forth elsewhere.² We may, however, interpret the photographic curves we obtain in the exploration of living muscle by *comparing* them with counterparts photographed under previously determined and known physical conditions. Thus by arranging our physical experiment so as to reproduce the hypothetical conditions of our physiological one, we may prove the truth of our hypothesis by the coincidence of the two results. And inasmuch as the two cases, *i.e.* the two forms of "variation," above referred to, are the only ones that present themselves, provided that we adopt a mode of procedure to be presently explained, there is no difficulty in applying this purely empirical procedure.

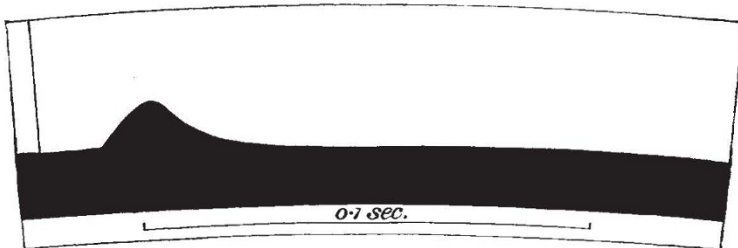


FIG. 1.—Photographic curve of diphasic variation of sartorius muscle. Rate of movement of plate indicated by distance accomplished in $\frac{1}{10}$ sec.; moment of excitation by vertical (radial) line.

The first fundamental experiment is one in which a curarised muscle of simple structure (*i.e.* one which consists of a band of parallel fibres) is subjected to the action of an instantaneous stimulus applied to it near one end, as shown below. The result is that a wave of excitation,



of which the progress is marked by mechanical and electrical changes, passes along each fibre (represented by the black line), starting from the seat of excitation r , and affecting first the nearest contact p , and after an interval the more distant contact d . The photograph (Fig. 1) is the curve obtained under these conditions. But if, as above suggested, we proceed in such a way as to limit the observation to what happens at one contact only, and for this purpose *cancel* the effect at the further contact d , and repeat our photographic observation just as before, we find that the curve has assumed an entirely different form shown in the photograph (Fig. 2). [As in both photographs, the movement of the sensitive plate is circular, the ordinates are polar, and must be measured accordingly.] Before the effect at d was cancelled, the curve had the form shown in Fig. 1. We therefore conjecture that the

¹ Here again our language has been objected to. "Excitatory variation" means the coming into existence of a difference of potential between two surfaces in consequence of stimulation of one or both of them. It is a translation of the German word "Reizschwankung."

² *Journal of Physiology*, xxiii. p. 325.

difference of contour between Figs. 1 and 2 represents the effect of the arrival of the wave of excitation at the distal electrode d . The proof that this is so is as follows (see diagram, Fig. 3):—From the measurement of the polar ordinates of Fig. 1 we obtain by calculation the curve P' , which represents the change which occurs in the

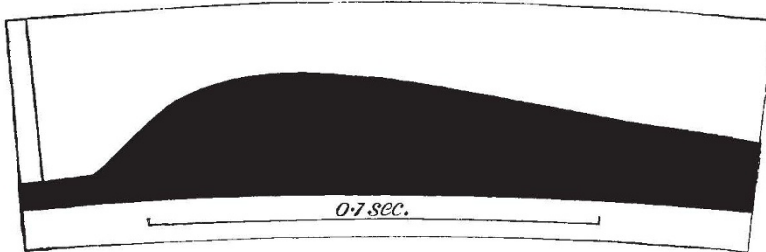


FIG. 2.—The same as Fig. 1 after cancelling the excitatory change at d . (See diagram on p. 343.)

difference of potential between the surface of contact ϕ and the rest of the surface of the muscle during the period of excitation.¹ We assume an identical curve D' in the same relation to the contact d , differing from P' only in the opposite sign of its ordinates, and relating to a period a little (in the case represented $15/1000$ sec.) later than of P' ; and by summing the synchronous ordinates of the two curves P' and D' algebraically, we obtain the curve S' , which expresses what must be the successive differences of potential between ϕ and d when the effect of the change at d is not cancelled. If we deduce this curve by calculation from Fig. 2, the two curves, *i.e.* the deduced curve and the summation curve, ought to coincide. Their actual coincidence shows that the relation between the curves P' , D' and S' has been correctly understood; it affords satisfactory proof that from P' we can deduce S' , and consequently good reason for making the determination of P' , *i.e.* the *monophasic variation*, the aim of our experimental method.

With reference to this method there are two points still to be adverted to. One is that it gives us the means of measuring with great exactitude the rate of propagation of the "excitatory wave," the progress of which from the seat of excitation has been already mentioned, and of proving that, although it varies according to the temperature and the vitality of the muscle, it is, under unchanging conditions, fairly constant. The other point relates to the mode of cancelling the effect of the wave of excitation at the distal electrode. The most effectual and simplest way of doing this is to apply a tight ligature across the path of propagation, the effect of which is to arrest the progress of the wave in its course from ϕ to d . Another method is to devitalise the part of the muscle to which the distal electrode is applied by heat. The result in the two cases is the same as regards the electrical response to excitation. Fig. 1 is converted into Fig. 2. But as regards the electrical state of the muscle when at rest it is different—*i.e.* when the ligature is applied half-way between ϕ and d the contacts remain equipotential, or nearly so; whereas in the other case the unexcited and unexcitable dead surface is found to be strongly negative to the other.

We are now in a position to sum up what is to be learned from the first fundamental experiment. The most important result is that, both as regards the muscle when "at rest" and the change of state which is evoked by excitation, the observed instrumental effect depends exclusively on the state of the surfaces of contact, and consequently, when the distal contact is cancelled, on that of the proximal contact only.

Second Fundamental Experiment.—We have so far

¹ The way in which the curve P' is deduced is fully given in the paper quoted above in the *Journal of Physiology*, vol. xxiii.

only considered experimentally the effects of a single instantaneous excitation on muscle, causing it to give the mechanical effect known as a twitch. We have now to inquire what are the electrical concomitants of *continuous contraction*. This part of the subject has greater interest than the one we have been considering,

inasmuch as it involves the question of the nature of ordinary voluntary muscular action, with reference to which there are reasons for holding that its continuity is apparent only. One of the chief of such reasons is to be found in the supposed resemblance of the sound of a muscle contracting normally to the musical sound of a muscle subjected to a rapid series of instantaneous stimuli. It is ordinarily stated that inasmuch as we can produce continuous contraction by discontinuous stimulation (artificial tetanus), all continuous contraction is so pro-

duced. Putting aside the question of muscle-sound, which does not here concern us, and confining ourselves to the electrical concomitants of continuous action, it can be shown that under certain conditions a continuous effect can be evoked by a single uninterrupted stimulus, and that in the nearest approach we can get to natural contraction, the reflex spasm, there is no evidence of discontinuity *in the sense in which this is usually understood*. Let us first see what are the electrical concomitants of artificial tetanus. If the muscle is completely tetanised, *i.e.* subjected to a succession of stimuli at the rate of over 50 per second, the electrometer gives us a curve, of which the general form is shown in Fig. 4. The muscle passes at once from the state of *capacity for action* into the state of *action*. This is indicated by the sudden manifestation of a difference of potential, which persists as long as its cause.

When the rate of excitation is less frequent, the electrometer curve gives evidence that the tetanus, whether still mechanically complete, or already incomplete, is composed of a series of twitches, *i.e.* of single monophasic effects. [Photographs were shown of the response in a sartorius, devitalised under the distal electrode, and excited by a series of instantaneous stimuli following each other with a frequency of 60 per sec. in one case, 20 per sec. in the other.]

If, however, while still retaining the higher frequency, we subject the muscle to a series of short tetanising excitations, each lasting say for a tenth of a second or more, and succeeded by a rest of similar duration, we obtain a curve of alternate polarisation and depolarisation such as would represent short, but persisting, differences of potential, alternating with periods of indifference (Fig. 5).

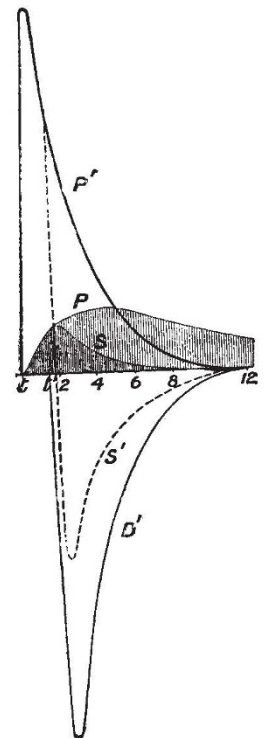


FIG. 3.—Diagram showing the relation between the photographic curves and the curves of difference of potential which they indicate and between the monophasic curves P' and D' and the diphasic S' . The numbers below the horizontal line denote hundredths of a second.

The Reflex Spasm.—We may now pass to *reflex action*, in which, since the motor apparatus of the cord has to be first excited through a sensory nerve, the time which elapses before a response is evoked is necessarily longer than in the cases we have been so far considering. The

by the alkaloid *veratrine*. So long as this is used in sufficiently small quantity ($\frac{1}{10000}$ mgr. to a sartorius), its effect consists chiefly in the annulling of the unknown inhibitory mechanism, by virtue of which a muscle, after having responded to an instantaneous stimulus, at once returns to its previous state. Under the influence of veratrine, when once started to work it is compelled to go on. [It was shown by graphic records that a muscle so treated can do as much work in response to a single instantaneous stimulus, whether in lifting heavy loads or in producing tension, as a normal muscle subjected to a series of instantaneous stimuli.]

The electrical phenomena evoked by a single stimulus in a veratrinised muscle likewise show that the effect is absolutely continuous; there is no trace of unevenness or undulation in the photographic curve (Fig. 7), the contour of which resembles the general contour of artificial tetanus, *i.e.* a

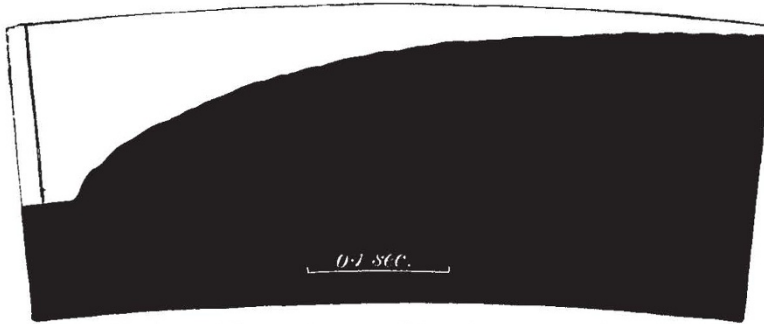


FIG. 4.—The photographic curve of tetanus. The radial indicates the beginning of the period of excitation.

response, if the motor cells of the cord have been rendered extra sensitive by a minute dose of strychnine, is a prolonged contraction [tracing of mechanical effect shown] the graphic of which is often indistinguishable from that of complete tetanus. When the electrical concomitants of such a spasm are recorded photographically (Fig. 6), it is seen that the curve resembles rather that of complete tetanus interrupted at regular intervals, than that of a series of responses to single instantaneous stimuli following each other at intervals of a tenth of a second or more. And by analysing the curve we learn that the difference which in the first instance comes into existence between the contacts, disappears and reappears rhythmically, and finally ceases. A single stimulus to the motor cells of the cord has therefore produced a series of short prolonged responses in the muscle, of which the rhythm is *central*, not muscular. The motor cell pours its influence on the muscle at regular intervals, but its effect each time is that of a continuous action.

sudden difference of potential comes into existence at the moment of excitation, but, notwithstanding that it is evoked by an instantaneous stimulus, it persists as if it were the response to a continuous one.

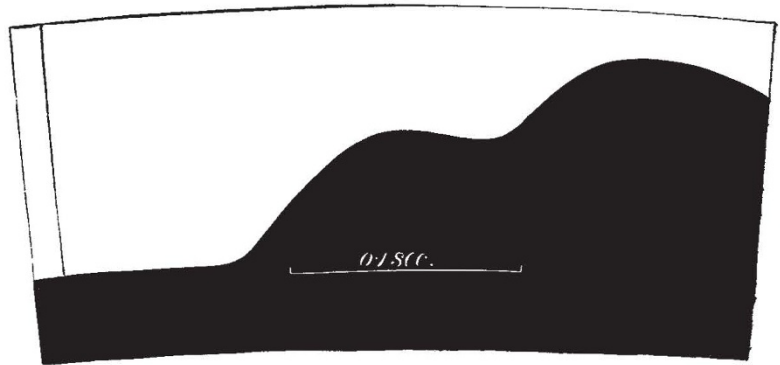


FIG. 6.—Reflex response of sartorius to instantaneous excitation in strychninised preparation.

The property which a muscle has of, under ordinary experimental conditions, relaxing as soon as the exciting

To complete the subject, it is necessary to describe the electrical phenomena which accompany the action of the heart. In all that has preceded, a parallel-fibred muscle has been employed in which the excitatory wave is

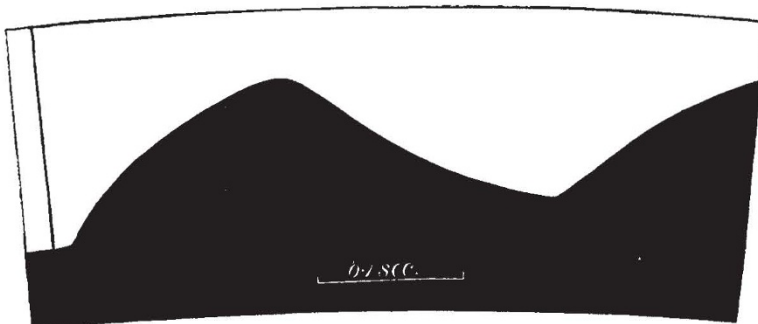


FIG. 5.—Tetanus of short duration, followed by another after an interval during which the muscle was not excited.

cause ceases, appears at first to indicate discontinuity of voluntary action. We have, however, a means of removing this property without materially impairing the functional capacity of the muscle. This means is furnished

propagated along the fibres in two opposite directions only. In the heart the fibres are short, and run in all directions. The wave of excitation may originate anywhere, and may spread in any direction. We employ the ventricle of the heart of the frog, having first arrested its rhythmical beat by a ligature between sinus and auricle. We can then evoke a contraction by an instantaneous excitation at any part of its surface, and thus imitate the first fundamental experiment in muscle. At the excited point the surface becomes instantly negative to all other parts, and the state of relative negativity spreads radially just as in muscle it was propagated longitudinally, the electrical effect appearing to precede the mechanical. Moreover, the duration of the process is ten times as long, and the rate of propagation ten times as slow. But in other respects the two processes in cardiac and skeletal muscle

are so analogous, that if the distance of the contacts, the duration of the change at the seat of excitation (monophasic variation), and the rate of propagation are known, it is easy to forecast the curve of the diphasic variation.

By a similar method to that employed in the study of muscle, the effect at the distal contact can be partially or

and this change spreads from the excited spot to parts at a distance at a rate which varies with temperature. The interval of time between the culmination of the electrical response and that of the change of form is much more obvious in the leaf than in the heart, because the mechanism by which the latter manifests itself works very slowly, as compared even with cardiac muscular fibres. This contrast, however, affords no ground for doubting that the two processes are, as regards their intimate nature, analogous.



FIG. 7.—Response of veratrinised muscle to instantaneous stimulation.

entirely cancelled. All that is necessary is to destroy by heat the surface under the distal electrode. The result of this operation is that, as in muscle, the devitalised area becomes, while unexcited, negative to all uninjured parts, and that if the surface is excited in the neighbourhood of the uninjured contact, the photographic curve assumes characters which correspond with those of the monophasic curve of muscle, with this noteworthy difference that its duration is that of the ventricular beat.

This can be best understood from the photographic curves reproduced in Fig. 8, with reference to which it is to be noted that the rate of movement of the plate on which the movement of the mercury column is projected is *ten times* as slow as the slowest rate of movement used in observations of muscle. Had the excursion been projected on a plate moving at the same rate, the first half of the curve would have had a contour similar to the veratrine curve. It expresses a sudden coming into existence of a difference of potential between the two contacts which may be maintained (in the heart) for more than two seconds.

In the second curve of Fig. 8 the curve begins as in the first, but the effect on the electrometer of the change which is taking place at the proximal electrode is immediately afterwards counteracted and balanced by the similar change at the distal contact, and is followed by a period of indifference, the end of which is marked by a descent of the column. This (as was explained by the lecturer many years ago) means that the effect at the distal electrode over-lasts that which occurs at the proximal.

The lecture concluded with a comparison of the electromotive properties of the leaf of the fly-trap with those of muscle. If the same method of exploration is applied to the surface of the leaf as to the ventricle of the heart of the frog, it is easy to show that the phenomena observed after excitation in the two structures are essentially analogous. In both an electrical change is the immediate result of a localised instantaneous excitation,

Conic Sections will be required, which will show the practical utility of the study of this elegant subject, as presented in Taylor's "Geometry of Conics."

In the first place we can connect up the notation of Darboux and Routh by taking

$$(28) \frac{a, b, c, h}{m} = \frac{HV, HT, HP, HQ}{OD} = \left(\frac{D}{A}, \frac{D}{B}, \frac{D}{C}, 1 \right) \frac{HQ}{OD},$$

Darboux's a, b, c, h being of the same dimensions as m , an angular velocity estimated in radians/second.

From the fundamental property of the herpolhode as the trace of the points of contact of a quadric surface, rolling about its centre O on a fixed plane GH , namely,

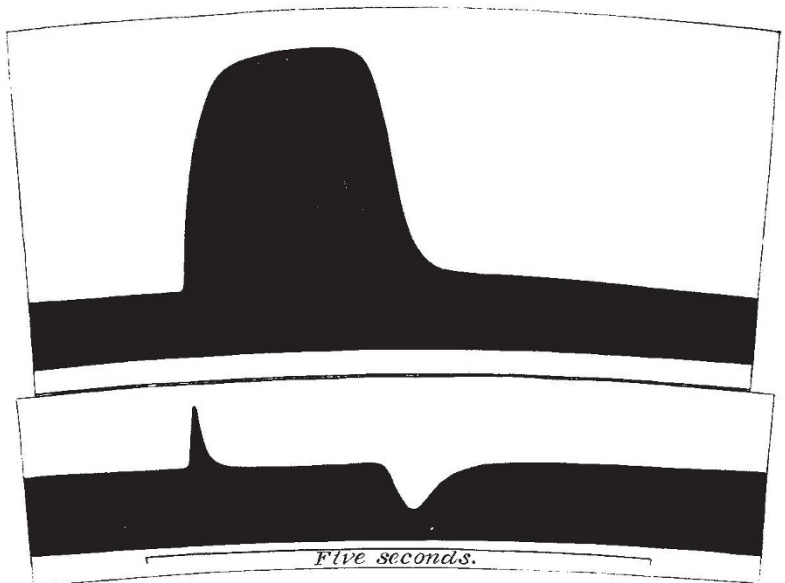


FIG. 8.—Monophasic and diphasic photographic curves of the ventricle of the heart of the frog.

that the radius vector GH and the tangent HK are conjugate on the rolling surface, combined with the properties of conjugate diameters, we can deduce the

¹ "Ueber die Theorie des Kreisels." F. Klein und A. Sommerfeld. Heft 1, ii. Pp. 196 and 197 to 512. (Leipzig: Teubner, 1897-8.) (Continued from p. 322.)