The Influence of Homodromous and Heterodromous Electric Currents on Transmission of Excitation in Plant and Animal.

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I have in a previous paper* described investigations on the conduction of excitation in *Mimosa pudica*. It was there shown that the various characteristics of the propagation of excitation in the conducting tissue of the plant are in every way similar to those in the animal nerve. Hence it appeared probable that any newly found phenomenon in the one case was likely to lead to the discovery of a similar phenomenon in the other.

A problem of great interest which has attracted my attention for several years is the question whether, in a conducting tissue, excitation travels better with or against the direction of an electric current. The experimental difficulties presented in the prosecution of this enquiry are very numerous, the results being complicated by the joint effects of the direction of current on conductivity and of the poles on excitability. As regards the latter, the changes of excitability in the animal nerve under electrotonus have been demonstrated by the well-known experiments of Pflüger. In a nerve-and-

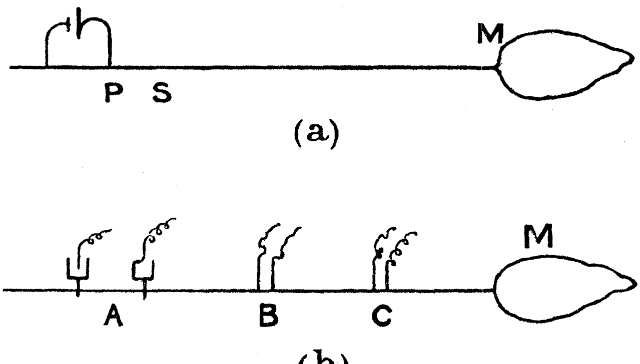

Fig. 1.

muscle preparation, the presence of a pole P is shown to induce a variation of excitability of a neighbouring point S. When P is kathode, the excitability of the point S, near it, is enhanced; stimulation of S, previously ineffective, now becomes effective, and the resulting excitation is transmitted to M,

* Bose, "An Automatic Method for the Investigation of Velocity of Transmission of Excitation in *Mimosa*," 'Phil. Trans.,' B, vol. 204 (1913).

causing response of the muscle. Conversely, the application of anode at P causes a depression of excitability of S. Stimulus previously effective now becomes ineffective. In this manner the transmission of excitation may be indirectly modified by the polar variation of excitability of the stimulated point (fig. 1*a*).

In the above experiment it will be noted that for inducing a variation of excitability, the tract of nerve SM, along which excitation is transmitted, need have no current passing through it. The presence of a given pole is enough to induce a definite variation of excitability in its neighbourhood. For convenience I shall call this the *Inductive action of a pole.*

The characteristic variations of excitability induced by polar action are:—

(1) The enhancement of excitability at or near the kathode;

(2) The depression of excitability near the anode.

The boundary between the two polar extensions is reached at a point between the anode and kathode; this point at which the excitability is unaffected is known as the indifference point.

The question whether the inductive action of electric poles affects the rate of conduction has been investigated by von Bezold* and by Rutherford.† Von Bezold found that both descending and ascending currents at A (fig. 1*b*) increased the propagation-time between B and C above the normal. Rutherford found on the other hand that the descending current diminished it. The results obtained are thus seen to be indefinite as regards the inductive effect of extrapolar current on conduction.

Turning from the inductive effect of neighbouring poles, we have the definite object of enquiry: Does the direction of an electric current, as such, cause any selective variation in the propagation of excitation? In other words, will a homodromous current, *i.e.* one which flows in the direction of propagation, help or retard transmission of excitation? Will a heterodromous current on the other hand give rise to an opposite effect? The object of this particular enquiry is to determine the *pure* effect of direction of current on conduction of excitation in a tissue through which a current is flowing. We shall call this the *Dynamic* effect of a current on conductivity and distinguish it from the *Inductive* effect.

The experimental difficulties in isolating the pure effect of current on the intensity and rate of propagation of excitation are very great. In the experiment where "the whole polar region is interposed between the exciting electrode and the muscle, the conditions are (very) complex. I have been unable to find evidence of any marked alteration in propagation rate, unless

* von Bezold, 'Elektr. Erreg. Nerven u. Muskeln,' Leipzig, 1861.

† Rutherford, 'Journ. Anat. and Physiol.,' London, vol. 2, p. 87 (1868).

the polarising current is intense or of prolonged duration, in which case it is always retarded. The presence of two polar regions, a cathodic accelerating and an anodic retarding, causes the one change to counterbalance the other."* The above would appear to indicate that a current has either no effect or a retarding action on conduction of excitation. These conflicting results are no doubt due to the disturbing influence of the two poles. But this is not the only source of uncertainty in this investigation. Far more serious is the difficulty which arises, as we shall see, from the escape of the induction current employed as the test stimulus. In the course of this paper I shall show how these experimental difficulties have been overcome, and how definite is the characteristic variation of conductivity caused by the directive action of an electric current. The object of my present paper is primarily the demonstration of the selective conductivity induced in the conducting tissue of the plant by the passage of an electric current. After giving the results of this enquiry, I next deal with the question whether the various effects observed in the plant have their parallel in the case of the animal also.

Method of Conductivity Balance.—I have previously carried out an electrical method of investigation dealing with the influence of electric current on conductivity. The method of Conductivity Balance which I devised for this purpose† was found very suitable. Isolated conducting tissues of certain plants were found to exhibit transmitted effect of excitatory electric change of galvanometric negativity, which at the favourable season of the year was of sufficient intensity to be recorded by a sensitive galvanometer. A long strand of the conducting tissue was taken and two electric connections were made with a galvanometer, a few centimetres from the free ends. Thermal stimulus was applied at the middle, when two excitatory waves with their concomitant electric changes were transmitted outwards. By suitably moving the point of application of stimulus nearer or further away from one of the two electric contacts, an exact balance was obtained. This was the case when the resultant galvanometer deflection was reduced to zero. If now an electrical current be sent along the length of the conducting tissue, the two excitatory waves sent outwards from the central stimulated point will encounter the electric current in different ways; one of the excitatory waves will travel with and the other against the direction of the current. If the power of transmitting excitation is modified by the direction of an electric current, then the magnitudes of transmitted excitations will be different in the two cases, with the result of the upsetting of the conductivity balance. From the

* Gotch, "Polar Excitation of Nerve" in 'Text-Book of Physiology,' edited by Schäfer, 1900, p. 502.

† Bose, "Comparative Electro-physiology" (1907), Longmans, Green and Co.

results of experiments carried out by this method on the effect of feeble current on conductivity, the conclusion was arrived at that *excitation is better conducted against the direction of the current than with it.* In other words the influence of an electric current is to confer a preferential or selective direction of conductivity for excitation, the tissue becoming a better conductor in an electric uphill direction compared with a downhill.

The result was so unexpected that I have been long desirous of testing the validity of this conclusion by independent methods of enquiry. In the paper already referred to, I have described an automatic method for recording the velocity of transmission of excitation in *Mimosa* where the excitatory fall of the motile leaf gave a signal for the arrival of the excitation initiated at a distant point. In this method the responding leaf is attached to a light lever, the writer being placed at right angles to it. The record is taken on a smoked glass plate which during its descent makes an instantaneous electric contact, in consequence of which a stimulating electric shock is applied at a given point E of the petiole (fig. 2). A mark in the recording plate indicates the moment of application of stimulus. After a definite interval, the excitation is conducted to the responding pulvinus P, when the excitatory fall of the leaf pulls the writer suddenly to the left. From the curve traced in this manner the time-interval between the application of stimulus and the initiation of response can be found and the normal rate of transmission of excitation through a given length of the conducting tissue deduced. The experiment is then repeated with an electrical current flowing along the petiole with or against the direction of transmission of excitation. The records thus obtained enable us to determine the influence of the direction of the current on the rate of transmission. I shall presently describe the various difficulties which have to be overcome before the method just indicated can be rendered practical.

The scope of the investigation will be best described according to the following plan.

Part I.—Influence of direction of electric current on conduction of excitation in plants.

1. The general method of experiment.
2. The effect of feeble heterodromous and homodromous currents on rate of conduction.
3. Determination of variation of conductivity by the method of minimal stimulus and response.
4. The after-effects of heterodromous and homodromous currents.
5. Phenomenon of reversal under moderate current.

Part II.—Influence of direction of electric current on conduction of excitation in animal nerve.

1. The method of experiment.
2. Variation of velocity of transmission under heterodromous and homodromous currents.
3. Variation in the intensity of transmitted excitation under the action of heterodromous and homodromous currents.
4. After-effects of heterodromous and homodromous currents.
5. Phenomenon of reversal.

Part I.—Influence of Direction of Current on Transmission of Excitation in Plant.

1. *The Method of Experiment.*

I may here say a few words of the manner in which the period of transmission can be found from the record given by my resonant recorder, fully described in my previous paper. The writer attached to the recording lever of this instrument is maintained by electromagnetic means in a state of vibration to and fro. The record thus consists of a series of dots made by the tapping writer, which is tuned to vibrate at a definite rate, say 10 times per second. This method of intermittent contact not only removes the error due to friction, but also enables time-relations to be deduced from the record. In a particular case whose record is given in Curve 1 (fig. 3) indirect stimulus of electric shock was applied at a distance of 15 mm. from the responding pulvinus. There are 15 intervening dots between the moment of application of stimulus and the beginning of response; the time-interval is therefore 1·5 seconds. The latent period of the motile pulvinus is obtained from a record of direct stimulation; the average value of this in summer is 0·1 second. Hence the true period of transmission is 1·4 seconds for a distance of 15 mm. The velocity determined in this particular case is therefore 10·7 mm. per second.

Disturbance caused by the Leakage of Current.—Employing this method of record, an attempt was made to determine the changes of velocity under the action of heterodromous and homodromous currents. But a serious difficulty encountered at the beginning of the investigation arose from the leakage of the induction current used as the testing stimulus. This will be understood from a concrete example. The record in fig. 3, for example, shows 15 intervening dots between the moment of indirect application of stimulus (at a distance of 15 mm.) and the beginning of response. The recorded time-interval for transmission was thus 1·5 seconds. The latent period of the pulvinus

obtained on direct stimulation was, as stated before, 0·1 second. Repetition of the experiment always gave a time-interval of 1·5 seconds for indirect and 0·1 second for direct stimulation. Now, on completing the circuit of the constant current, which for convenience I shall indicate as the polarising circuit, the time-interval for indirect stimulation was at once reduced to 0·1 second, which is the value of the latent period for direct stimulation. This happened on the mere completion of the polarising circuit, with current reduced even to zero. It is evident that this untoward result was due to the escape of the alternating induction current, which went not merely across the short path from E to E′, but also round by the circuitous path of the polarising circuit. It was the escaping current which caused the direct excitation of the pulvinus. This particular difficulty I was finally able to overcome by interposing the electromagnetic device of a choking coil, which effectively prevented the passage of the alternating induction current into the polarising circuit (fig. 2).

Precaution has to be taken against another source of disturbance, namely, the excitation caused by the sudden commencement or the cessation of the constant current. I have shown elsewhere* that the sudden initiation or cessation of the current induces an excitatory reaction in the plant-tissue similar to that in the animal tissue. This difficulty is removed by the introduction of a sliding potentiometer, which allows the applied electromotive force to be gradually increased from zero to the maximum or decreased from the maximum to zero.

The experimental arrangement is diagrammatically shown in fig. 2. After attaching the petiole to the recording lever, indirect stimulus is applied, generally speaking, at a distance of 15 mm. from the responding pulvinus. Stimulus of electric shock is applied in the usual manner, by means of a sliding induction coil. The intensity of the induction shock is adjusted by gradually changing the distance between the secondary and the primary, till a minimally effective stimulus is found. In the study of the effect of direction of constant current on conductivity, non-polarisable electrodes make suitable electric connections, one with the stem and the other with the tip of a sub-petiole, at a distance from each other of about 95 mm. The point of stimulation and the responding pulvinus are thus situated at a considerable distance from the anode or the kathode, in the indifferent region in which there is no polar variation of excitability. By means of a Pohl's commutator or reverser, the constant current can be maintained either "with" or "against" the direction of transmission of excitation. The

* Bose, 'Plant Response' (1906); 'Irritability of Plants' (1913), Longmans, Green and Co., London.

former, as stated before, will be designated as the homodromous, and the latter as the heterodromous current. Electrical connections are so arranged that when the commutator is tilted to the right, the current is homodromous when tilted to the left, heterodromous.

For the purpose of convenience I shall call the constant current the

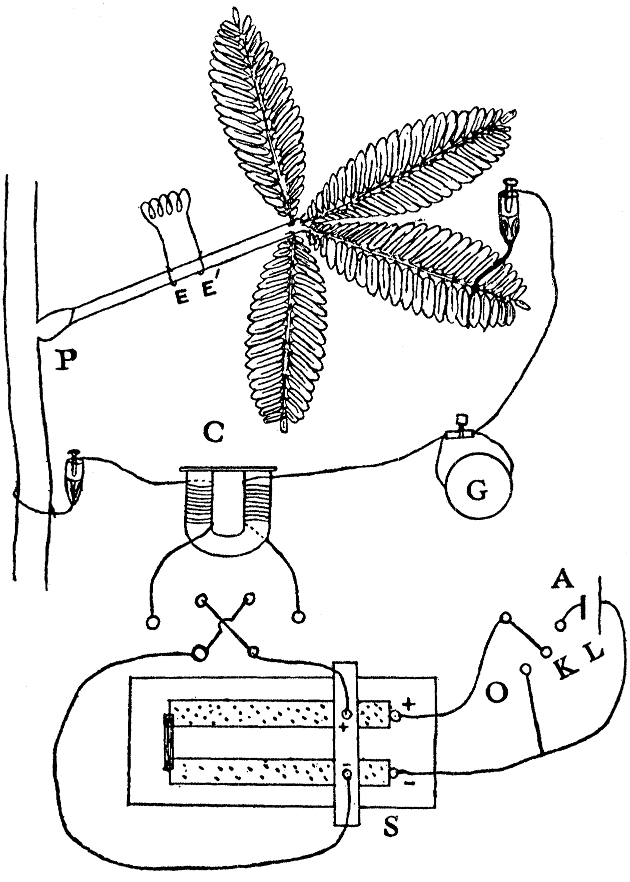

Fig. 2.—Complete apparatus for investigation of the variation of conducting power in *Mimosa*. A, storage cell; S, potentiometer slide, which, by alternate movement to right or left, continuously increases or decreases the applied E.M.F.; K, switch key for putting current "on" and "off" without variation of resistance; E, E′, electrodes of induction coil for stimulation; C, choking coil; G, microammeter.

polarising current, as it will be shown that its effect on conductivity is discriminative or polar, depending on the direction of the current. It should, however, be distinctly understood that under the particular experimental arrangement the possibility of polar variation of excitability at the points of stimulation and region of response is avoided.

The electrical resistance offered by the 95-mm. length of stem and petiole will be from two to three million ohms. The intensity of the constant current flowing through the plant can be read by unplugging the key which short-circuits the microammeter G. The choking coil C prevents the alternating induction current from flowing into the polarising circuit and causing direct stimulation of the pulvinus.

Before describing the experimental results, it is as well to enter briefly into the question of the external indication by which the conducting power may be gauged. Change of conductivity may be expected to give rise to a variation in the rate of propagation or to a variation in the magnitude of the excitatory impulse that is transmitted. Thus we have several methods at our disposal for determining the induced variation of conductivity. In the first place, the variation of conductivity may be measured by the induced change in the velocity of transmission of excitation. In the second place, the transmitted effect of a sub-maximal stimulus will give rise to enhanced or diminished amplitude of mechanical response, depending on the increase or decrease of conductivity brought about by the directive action of the current. And, finally, the enhancement or depression of conductivity may be demonstrated by the ineffectively transmitted stimulus becoming effective, or the effectively transmitted stimulus becoming ineffective.

Exclusion of the Factor of Excitability.—The object of the enquiry being the pure effect of variation of conductivity, we have to assure ourselves that under the particular conditions of the experiment the complicating factor of polar variation of excitability is eliminated. It is to be remembered that excitatory transmission in *Mimosa* takes place by means of a certain conducting strand of tissue which runs through the stem and the petiole. If a point on the petiole of a given leaf be subjected to strong stimulation, an excitatory impulse will not merely be transmitted across its own pulvinus, but will travel farther along the stem, inducing the fall of other leaves. Conversely, a strong stimulus applied on the stem gives rise to an impulse which passes through the pulvinus to the petiole and thence to the sub-petiole, as evidenced by the successive closure of its leaflets. The main pulvinus may thus be regarded as a contractile indicator of excitation, interposed in the path of the conducting strand which connects the stem with the petiole. In the experiment to be described, the polarising current enters by the tip of the petiole and leaves by the stem, or *vice versâ*, the length of the intrapolar region being 95 mm. The point of application of stimulus on the petiole is 40 mm. from the electrode at the tip of the leaf. The responding pulvinus is also at the same distance from the electrode on the stem. The point of stimulation and region of response are thus at the relatively great distance

of 40 mm. from either the anode or the kathode, and may therefore be regarded as situated in the indifferent region. This is found to be verified in actual experiments.

2. *Effects of Direction of Current on Velocity of Transmission.*

A very convincing method of demonstrating the influence of electric current on conductivity consists in the determination of changes induced in the velocity of transmission by the directive action of the current. For this purpose we have to find out the true time required by the excitation to travel through a given length of the conducting tissue (1) in the absence of the current, (2) against and (3) with the direction of the current. The true time is obtained by subtracting the latent period of the pulvinus from the observed interval between the stimulus and response. Now the latent period may not remain constant, but undergo change under the action of the polarising current. It has been shown that the excitability of the pulvinus does not undergo any change when it is situated in the middle or indifferent region. The following results show that under parallel conditions the latent period also remains unaffected:—

Table I.—Showing the Effect of Polarising Current on the Latent Period.

Specimens ……………	I.	II.
	sec.	sec.
Latent period under normal condition……………	0·10	0·09
,, ,, heterodromous current ……	0·11	0·10
,, ,, homodromous current ……	0·09	0·09

The results of experiments with two different specimens given above show that a current applied under the given conditions has practically no effect on the latent period, the slight variation being of the order of one-hundredth part of a second. This is quite negligible when the total period observed for transmission is, as in the following cases, equal to nearly 2 seconds.

Induced Changes in the Velocity of Transmission.—Having found that the average value of the latent period in summer is 0·1 second, we next proceed to determine the influence of the direction of current on velocity.

Experiment 1.—As a rule, stimulus of induction shock was applied in this and in the following experiments on the petiole at a distance of 15 mm. from the responding pulvinus. The recording writer was tuned to 10 vibrations per second; the space between two succeeding dots, therefore, represents a time-interval of 0·1 second. The middle record, N in fig. 3, is the normal. There are 17 spaces between the application of stimulus and the beginning

of response. The total time is therefore 1·7 seconds, and by subtracting from it the latent period of 0·1 second we obtain the true time, 1·6 seconds. The normal velocity is found by dividing the distance 15 mm. by the true interval 1·6 seconds. Thus $V = 15/1{\cdot}6 = 9{\cdot}4$ mm. per second. We shall next consider the effect of current in modifying the normal velocity. The uppermost record (1) in fig. 3 was taken under the action of a heterodromous

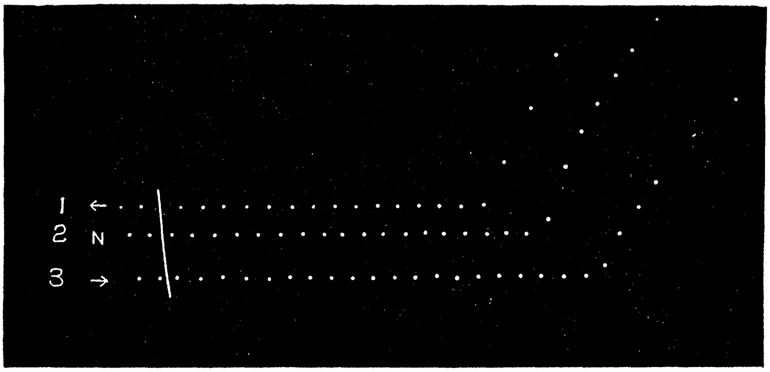

Fig. 3.—Record showing enhancement of velocity of transmission induced by heterodromous (uppermost curve) and retardation of velocity induced by homodromous (lowest curve) currents. N, normal record in the absence of current. ← indicates heterodromous, and → homodromous current.

current of the intensity of 1·4 microampères. It will be seen that the time-interval is reduced from 1·7 seconds to 1·4 seconds; making allowance for the latent period, the velocity of transmission under heterodromous current $V_1 = 15/1{\cdot}3 = 11{\cdot}5$ mm. per second. In the lowest record (3) we note the effect of homodromous current, the time-interval between stimulus and response being prolonged to 1·95 seconds and the velocity reduced to 8·1 mm. per second. The conclusion arrived at from this mechanical mode of investigation is thus identical with that derived from the electric method of conductivity balance referred to previously.

That is to say, the passage of a feeble current modifies conductivity for excitation in a selective manner. Conductivity is enhanced *against,* and diminished *with* the direction of the current.

The minimum current which induces a perceptible change of conductivity varies somewhat in different specimens. The average value of this minimal current in autumn is 1·4 microampères. The effect of even a feebler current may be detected by employing a test stimulus which is barely effective.

Table II.—Showing Effects of Heterodromous and Homodromous Currents of Feeble Intensity on Period of Transmission through 15 mm.

Number.	Intensity of current in microampères.	Period of hetero-dromous transmission.	Period of homo-dromous transmission.
1	1·4	14 tenths of a second	16 tenths of a second
2	1·4	13 ,, ,,	15 ,, ,,
3	1·6	19 ,, ,,	Arrest.
4	1·7	12 ,, ,,	14 tenths of a second.

Having demonstrated the effect of direction of current on the velocity of transmission, I shall next describe other methods by which induced variations of conductivity may be exhibited.

3. *Determination of Variation of Conductivity by Method of Minimal Stimulus and Response.*

In this method we employ a minimal stimulus, the transmitted effect of which under normal conditions gives rise to a feeble response. If the passage of a current in a given direction enhances conductivity, then the intensity of transmitted excitation will also be enhanced; the minimal response will tend to become maximal. Or excitation which had hitherto been ineffectively transmitted will now become effectively transmitted. Conversely, depression of conductivity will result in a diminution or abolition of response. We may use a single break-shock of sufficient intensity as the test stimulus. It is, however, better to employ the additive effect of a definite number of feeble make-and-break shocks.

We may again employ additive effect of a definite number of induction shocks, the alternating elements of which are exactly equal and opposite. This is secured by causing rapid reversals of the primary current by means of a rotating commutator. The successive induction shocks in the secondary coil can thus be rendered exactly equal and opposite.

Experiment 2.—Working in this way, it is found that the transmitted excitation becomes effective or enhanced under heterodromous current. The homodromous current, on the other hand, diminishes the intensity o. :itation or blocks it altogether.

4. *After-Effects of Homodromous and Heterodromous Curre.*

The passage of a current through a conducting tissue in a give: rection causes, as we have seen, an enhanced conductivity in an opposite :ection. We may suppose this to be brought about by a particular molecular arrangement induced by the current, which assisted the propagation of the

excitatory disturbance in a selected direction. On the cessation of this inducing force, there may be a rebound and a temporary reversal of previous molecular arrangement, with concomitant reversal of the conductivity variation. The immediate after-effect of a current flowing in a particular direction on conductivity is likely to be a transient change, the sign of which would be opposite to that of the direct effect. The after-effect of a heterodromous current may thus be a temporary depression, that of a homodromous current a temporary enhancement, of conductivity.

Experiment 3.—This inference will be found fully justified in the following experiment:—The first two responses are normal, after which the heterodromous current gave rise to an enhanced response. The depressing after-effect of a heterodromous current rendered the next response ineffective. The following record taken during the passage of the homodromous current exhibited an abolition of response due to induced depression of conductivity. Finally, the after-effect of the homodromous current is seen to be a response larger than the normal (fig. 4). These experiments show

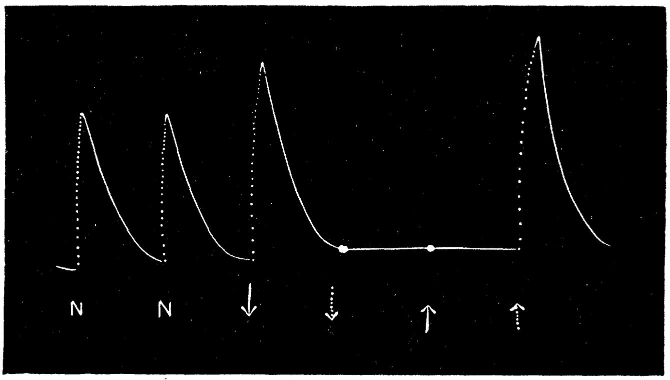

FIG. 4.—Direct and after effect of heterodromous and homodromous currents. First two records, N, N, normal. ↓, enhanced transmission under heterodromous current; ⇣ arrest of conduction as an after-effect of heterodromous current. Next record ↑ shows arrest under homodromous current. Last record ⇡ shows enhancement of conduction greater than normal, as an after-effect of homodromous current. (Dotted arrow indicates the after-effect on cessation of a given current. ↑ homodromous and ↓ heterodromous current.)

that the after-effect of cessation of a current in a given direction is a transient conductivity variation, of which the sign is opposite to that induced by the continuation of the current.

5. *Phenomenon of Reversal under Moderate Intensity of Current.*

In studying the effect of increasing intensity of polarising current, the concomitant variations of conductivity appeared at first sight to be very puzzling. The results obtained at different stages were, however, very definite. In the first stage with very feeble current there was no perceptible change of conductivity. At the second stage with increasing current the conductivity variation increased at a rapid rate, and soon attained a maximum. After this, at the third stage, the conductivity change underwent a decline, and then abolition. The effect outwardly resembled that induced at the first stage. There was, however, a difference, for a critical point had now been reached beyond which there was a complete reversal of normal conductivity variation. These different effects will be clearly understood from the following tabular statement:—

Table III.—Conductivity Variations at Different Stages.

	Heterodromous current.	Homodromous current.
I stage	No perceptible change	No perceptible change.
II ,, ...	Enhanced conductivity	Depression of conductivity culminating in a block.
III ,, ...	Conductivity change reduced to zero at critical point	Conductivity change reduced to zero at critical point.
IV ,, ...	Reversal: diminution of conduction culminating in a block	Enhancement of conduction.

I shall now describe a typical experiment which will clearly demonstrate the phenomenon of reversal.

Experiment 4.—In this I was desirous of obtaining with an identical specimen alternate records showing (1) normal effect under feeble current, (2) reversed effect under moderate current, and (3) normal effect once more under the original feeble current. It took two hours to obtain these six records (fig. 5) at intervals of 20 minutes. The specimen was vigorous, and therefore was little affected by fatigue. The normal enhancement of conductivity under heterodromous current was observed at as low a current-intensity as 1 microampère. In the first of the pair of records (1) we find the interval between stimulus and response under heterodromous current to be 18 tenths of a second; this was prolonged to 21 tenths under homodromous current; the current was next raised to 3 microampères, and we observe in the pair of records (2) the reversal of normal effect by a block of conduction under heterodromous, and transmission under homodromous current; the time-interval in the latter case is 20 tenths of a

second. The pair of records (3) was taken once more under the original feeble current of 1 microampère (fig. 5). The plant had by this time become

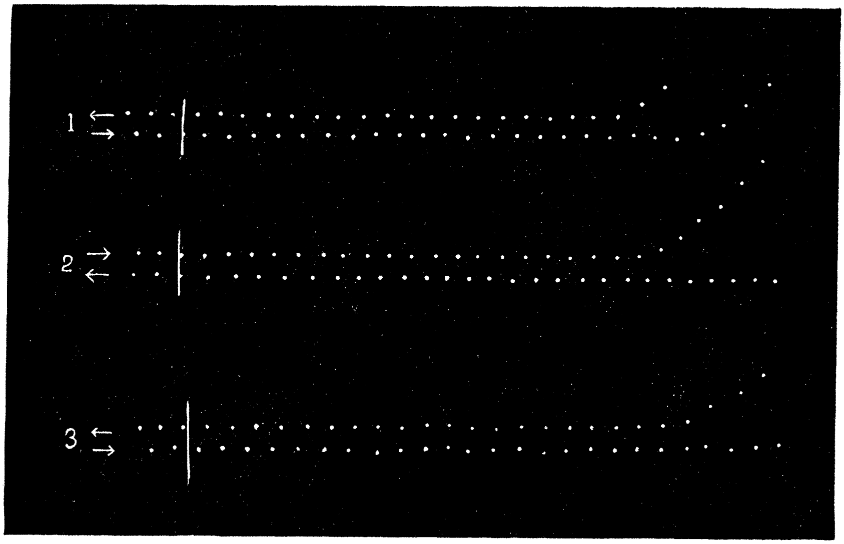

Fig. 5.—Records obtained with an identical specimen showing (1) normal action under feeble current; (2) reversed action under strong current; (3) normal effect once more under feeble current. ⟶ represents homodromous and ⟵ heterodromous current.

slightly fatigued; the results, however, are similar to those of the first series. We have transmission once more under heterodromous current (the time-interval being 20 tenths instead of 18 tenths of a second), and retardation culminating in block under homodromous current. I give below a tabular statement of results of typical experiments on reversal under moderate current.

Table IV.—Reversal under Moderate Intensity of Current.

Number.	Intensity of current.	Transmission period under heterodromous current.	Transmission period under homodromous current.
	microampères		
1	3	Block of transmission	19 tenths of a second.
2	3·5	,, ,,	12 ,, ,,
3	4	,, ,,	16 ,, ,,
4	4	,, ,,	22 ,, ,,
5	4·5	,, ,,	18 ,, ,,

The action of a strong current induces a block of conduction under both heterodromous and homodromous currents.

Part II.—Influence of Direction of Electric Current on Conduction of Excitation in Animal Nerve.

I shall now take up the question whether an electrical current induced any selective variation of conductivity in the animal nerve, similar to that induced in the conducting tissue of the plant.

1. *The Method oj Experiment.*

In the experiments which I am about to describe, arrangements were specially made so that (1) the excitation had not to traverse the polar region, and (2) the point of stimulation was at a relatively great distance from either pole. The fulfilment of the latter condition ensured the point of stimulation being placed at the neutral region.

In the choice of experimental specimens I was fortunate enough to secure frogs of unusually large size, locally known as "golden frogs" (*Rana tigrina*). A preparation was made of the spine, the attached nerve, the muscle and the tendon. The polarising electrodes were applied at the extreme ends, on the spine and on the tendon (fig. 6). The following are the measurements, in a typical case, of the different parts of the preparation.

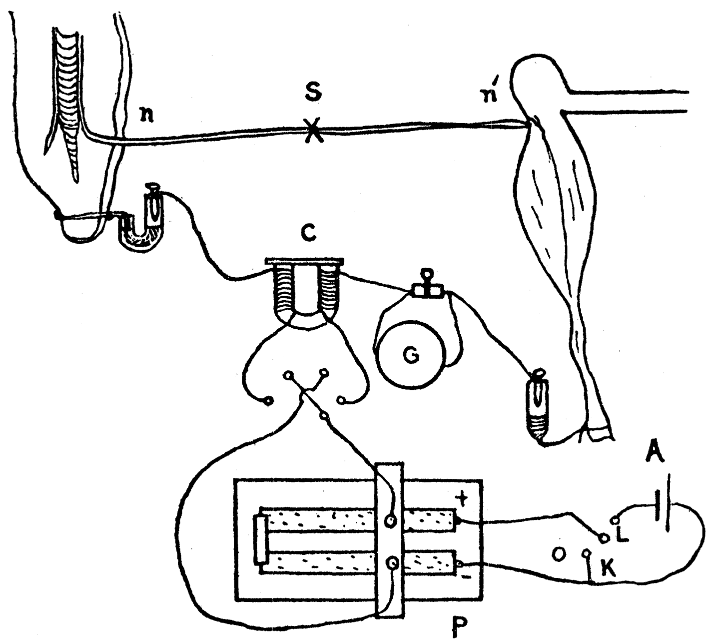

Fig. 6.—Experimental arrangement for study of variation of conductivity of nerve by the directive action of an electric current. n n', nerve ; S, point of application of stimulus in the middle or indifferent region.

Length of spine between the electrode and the nerve = 40 mm.; length of nerve = 90 mm.; length of muscle = 50 mm.; length of tendon = 30 mm. Stimulus is applied in all cases on the nerve, midway between the two electrodes, this point being at a minimum distance of 100 mm. from either electrode. The point of stimulation is, therefore, situated at an indifferent region.

Great precautions have to be taken to guard against the leakage of current. The general arrangement for the experiment on animal nerve is similar to that employed for the corresponding investigations on the plant. The choking coil is used to prevent the stimulating induction current from getting round the polarising circuit. The specimen is held on an ebonite support, and every part of the apparatus insulated with the utmost care.

2. *Variation of Velocity of Transmission.*

In the case of the conducting tissue of the plant a very striking proof of the influence of the direction of current on conductivity was afforded by the induced variation of velocity of transmission. Equally striking is the result which I have obtained with the nerve of the frog.

Experiment 5.—The experiments described below were carried out during the cold weather. The following records (fig. 7), obtained by means of the pendulum myograph, exhibit the effect of the direction of current on the

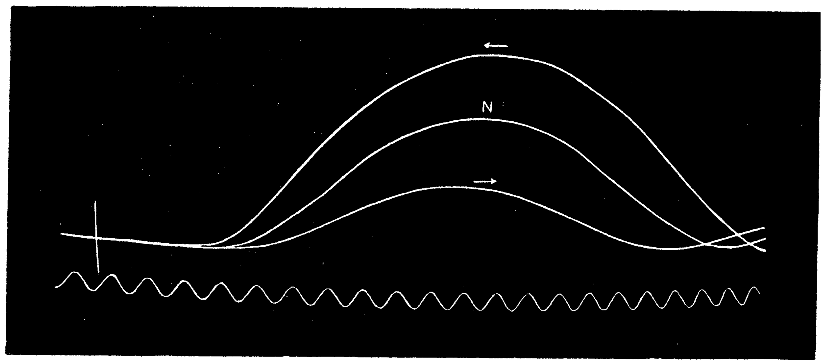

Fig. 7.—Effect of heterodromous and homodromous current in inducing variation in velocity of transmission through nerve. N, normal record; upper record shows enhancement and lower record retardation of velocity of transmission under heterodromous and homodromous currents respectively.

period of transmission through a given length of nerve. The latent period of muscle being constant, the variations in the records exhibit changed rates of conduction. The middle record is the normal, in the absence of any current

The upper record, denoted by the left-handed arrow, shows the action of a heterodromous current in shortening the period of transmission and thus enhancing the velocity above the normal rate. The lower record, denoted by the right-handed arrow, exhibits the effect of a homodromous current in retarding the velocity below the normal rate. I find that a very feeble heterodromous current is enough to induce a considerable increase of velocity, which soon reaches a limit. For inducing retardation of velocity, a relatively strong homodromous current is necessary. I give below a table showing the results of several experiments.

Table V.—Effect of Heterodromous and Homodromous Currents of Feeble Intensity on Velocity of Transmission.

Specimen.	Intensity of heterodromous current.	Acceleration above normal.	Intensity of homodromous current.	Retardation below normal.
	microampère.	per cent.	microampères.	per cent.
1	0·35	16	1	20
2	0·7	13	1·5	19
3	0·8	18	2·0	14
4	0·8	11	2·0	13
5	1·0	18	2·5	12
6	1·5	15	3·0	40

3. *Variation of Intensity of Transmitted Excitation under Heterodromous and Homodromous Currents.*

In the next method of investigation, the induced variation of intensity of transmitted excitation is inferred from the varying amplitude of response of the terminal muscle. Testing stimulus of sub-maximal intensity is applied at the middle of the nerve, where the polarising current induces no variation of excitability. Stimulation is effected either by a single break-shock or by the summated effects of a definite number of equi-alternating shocks, or by chemical stimulation.

Experiment 6.—Under the action of feeble heterodromous current the transmitted excitation was always enhanced, whatever be the form of stimulation. Homodromous current on the other hand inhibited or blocked excitation (figs. 8, 9).

Complication due to Variation of Excitability of Muscle.—In experiments with the plant, there was the unusual advantage in having both the point of stimulation and the responding motile organ in the middle or indifferent region. Unfortunately this ideally perfect condition cannot be secured in experiments with the nerve-and-muscle preparation of the frog. It is true

that the point of stimulation in this case is chosen to lie on the nerve at the middle or indifferent region. But the responding muscle is at one end, not very distant from the electrode applied on the tendon. It is, therefore,

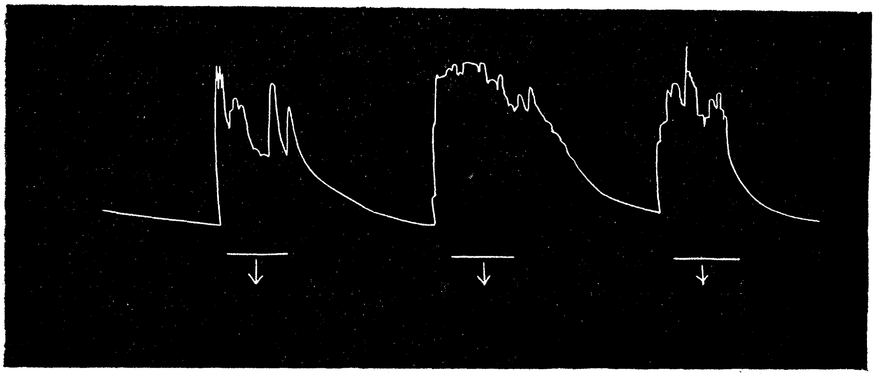

FIG. 8.—Ineffectively transmitted salt-tetanus becoming effective under heterodromous current.

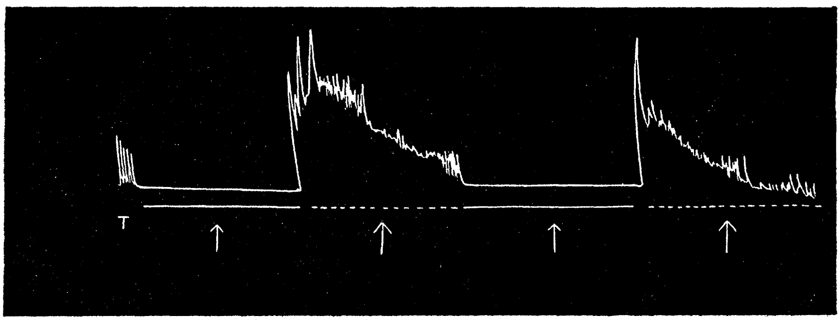

FIG. 9.—Direct and after-effect of homodromous current. Transmitted excitation (salt-tetanus) arrested under homodromous current; on cessation of current there is a transient enhancement above the normal.

necessary to find out by separate experiments any variation of excitability that might be induced in the muscle by the proximity of either the anode or the kathode, and make allowance for such variation in interpreting the results obtained from investigations on variation of conductivity.

In the experimental arrangement employed, the heterodromous current is obtained by making the electrode on the spine kathode and that on the tendon anode. The depressing influence of the anode in this case may be expected to lower, to a certain extent, the normal excitability of the responding muscle. Conversely, with homodromous current, the tendon is made the kathode and under its influence the muscle might have its excitability raised above

the normal. These anticipations are fully supported by results of experiments. Sub-maximal stimulus of equi-alternating induction shock was directly applied to the muscle and records taken of (1) response under normal condition without any current, (2) response under heterodromous current, the tendon being the anode, and (3) response under homodromous current, the tendon being now made the kathode. It was thus found that under heterodromous current the excitability of the muscle was depressed, and under homodromous current the excitability was enhanced.

The effect of current on response to direct stimulation is thus opposite to that on response to transmitted excitation, as will be seen in the following Table.

Table VI.—Influence of Direction of Current on Direct and Transmitted Effects of Stimulation.

Direction of current.	Transmitted excitation.	Direct stimulation.
Heterodromous current	Enhanced response	Depressed response.
Homodromous current	Depressed response	Enhanced response.

The passage of a current, therefore, induces opposing effects on the conductivity of the nerve and the excitability of the muscle, the resulting response being due to their differential actions. Under heterodromous current a more intense excitation is transmitted along the nerve, on account of induced enhancement of conductivity. But this intense excitation finds the responding muscle in a state of depressed excitability. In spite of this the resulting response is enhanced (fig. 8). The enhancement of conduction under heterodromous current is, in reality, much greater than is indicated in the record. Similarly under homodromous current the depression of conduction in the nerve may be so great as to cause even an abolition of response (fig. 9), in spite of the enhanced excitability of the muscle. The actual effects of current on conductivity are, thus, far in excess of what are indicated in the records.

The two factors, namely, the induced variation of the conductivity of the nerve and the excitability of the muscle, being antagonistic, certain effects may be predicted when the relative values of the two are changed in definite ways. Let us first consider the effect of diminishing the factor of conductivity of nerve to zero, by bringing the stimulator near the muscle, this being tantamount to direct stimulation. The result is seen in the third column of the Table given above. We may next increase the value of the conductivity factor

by increasing the length of the conducting path, *i.e.* by taking greater length of nerve for transmission of excitation. The result is seen in the second column of Table VII. It will now be understood how, by shortening the length of nerve, the normal effect may undergo a reversal. I shall in the following Table denote the change of conductivity of nerve by C_n that of the excitability of muscle, by E_m.

Table VII.—Reversal of Normal Effect by Shortening the Length of Nerve.

Length of nerve.	Direction of Current.	Conductivity of nerve *versus* excitability of muscle.	Resulting response.
1. Long	Heterodromous	Enhanced C_n > Depressed E_m	Enhanced response.
	Homodromous.........	Depressed C_n > Enhanced E_m	Depressed response.
2. Short	Heterodromous	Enhanced C_n < Depressed E_m	Depressed response.
	Homodromous.........	Depressed C_n < Enhanced E_m	Enhanced response.

I shall now give experimental verification of the truth of the inferences that have been outlined above.

Experiment 7.—We have seen that, when the nerve is stimulated in the middle or indifferent region, the transmitted effect is normal. From the above we see that this normal effect will persist, as long as the nerve-tract is of sufficient length; and that the effect will undergo an apparent reversal when it is very much shortened. This is fully borne out by results of numerous experiments. For example, the length of nerve in a preparation was 90 mm. When stimulus was applied near the spine (length of transmission = 90 mm.), the transmitted effect was found to be normal, *i.e.* enhanced response under heterodromous, and depressed response under homodromous current. The transmitted effect remained normal as the stimulator was gradually moved towards the muscle, thus reducing the length of transmission. A critical length was now found below which the effects underwent a reversal. This was the case when the length of the nerve was reduced to 15 mm., the reversed effects being an enhanced response under homodromous, and a depressed response under heterodromous current. These are due, as explained before, to the induced variation of excitability of muscle, which now became the predominant factor. The very great influence exerted by the direction of current on conductivity of nerve is forcibly brought to our mind by the fact that under normal conditions it completely overpowers the opposing effect of change of excitability in the muscle.

4. *After-Effects of Heterodromous and Homodromous Currents.*

On the cessation of a current there is induced in the plant-tissue a transient conductivity change of opposite sign to that induced by the direct current (*cf.* Experiment 3). The same I find to be the case as regards the after-effect of current on conductivity change in animal nerve. Of this I only give a typical experiment of the direct and after-effect of homodromous current on salt-tetanus.

Experiment 8.—In this experiment sufficient length of time was allowed to elapse after the application of the salt on the nerve, so that the muscle, in response to the transmitted excitation, exhibited an incomplete tetanus. The homodromous current was next applied, with the result of inducing a complete block of conduction, with the concomitant disappearance of tetanus (fig. 10).

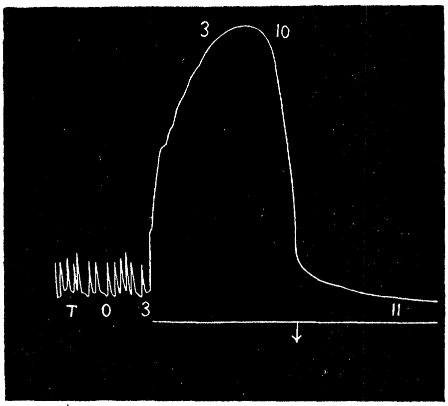

Fig. 10.—Normal transmitted salt-tetanus without current at 0. Enhancement under heterodromous current of 3 microampères. Reversal at 10 microampères.

The homodromous current was gradually reduced to zero by the appropriate movement of the potentiometer slide. The after-effect of homodromous current is now seen in the transient enhancement of transmitted excitation, which lasted for nearly 40 seconds. After this the normal conductivity was restored. Repetition of the experiment gave similar results.

5. *Phenomenon of Reversal.*

In experiments with *Mimosa* it was shown that an increase of polarising current above the critical value gave rise to a reversal of the normal conductivity variation (*cf.* Experiment 4). Even in this matter of reversal I find a very remarkable parallelism between the reactions of the conducting tissue of the plant and the nerve of the animal. The reversal was obtained

both with heterodromous and homodromous currents, the testing stimulus being either electrical or chemical.

Reversal under Increased Heterodromous Current.

Experiment 9.—In this the transmitted excitation due to the application of salt, gave rise to an incomplete tetanus of moderate intensity. After securing this condition, heterodromous current was applied and continuously increased. It will be seen (fig. 10) that a great enhancement of conduction took place when the current attained a value of 3 microampères. A reversal was, however, induced as soon as the current reached a value of 10 microampères, and we observe a complete cessation of normal incomplete tetanus. From this we see that under reversal the conductivity is depressed below the normal.

Table VIII.—Showing Normal and Reversed Effects under Heterodromous Current.

No.	Intensity of current for normal enhancement of conductivity.	Intensity of current for reversed effect of depression of conductivity.
	microampères.	microampères.
1	1·5	6
2	1·5	8
3	2	10
4	2	10
5	3	10
6	3	10·5
7	3	11
8	3	12

Reversal under Increased Homodromous Current.

Experiment 10.—On the appearance of incomplete tetanus T brought on by the application of salt at the middle of the nerve, homodromous current was continuously increased from zero to 10 microampères and then gradually brought back to zero. This was accomplished, as stated before, simply by the forward and backward movement of the potentiometer slide. The resulting record taken on the revolving drum shows the cycle of effects. It is seen that the conduction in this case is arrested as soon as the polarising current attains a value of 2 microampères; at 10 microampères there is induced a reversal with an enhanced conductivity above the normal. Under a continuous diminution of current there is an arrest of conduction once more at 2 microampères, and restoration of normal conduction at zero intensity of current. A continuous increase of current gives

rise once more to an arrest of conduction at 2 microampères and a reversal at 10 microampères. It is a curious fact that the reversal under heterodromous and homodromous currents takes place, generally speaking, at the same intensity, namely, 10 microampères.

Before passing under review the characteristic results obtained under varying conditions of the experiment, I shall discuss briefly the question whether it is possible to explain the observed results merely by considering the induced variation of excitability as the sole cause. We shall take, then, the simple case of arrest of conduction by homodromous current; I find that the arrest takes place just the same, whether the anodic electrode is placed on the spine or on an adjacent point *n*, on the nerve itself (see fig. 6). Discarding from our consideration the possibility of an induced variation of conductivity, we may assume that the arrest was due to the depression of excitability of the stimulated point of nerve on account of the proximity of the anode. But the point of stimulation was, in general, placed not near the anode, but in the middle or indifferent region. In fact the diminution or arrest of transmitted excitation was observed even in the case where the stimulus was applied at the far end of the nerve, at a distance of about 70 mm. from the anode at one end of the nerve, and only 20 mm. from the muscle at the other end. Against this it might be urged that under the action of strong currents the anodic depression might extend to a considerable distance.

It has, however, been shown that for causing a depression or arrest of transmitted excitation a strong current was not at all necessary, such a depression sometimes taking place under an intensity of current as feeble as 0·3 microampère, the applied E.M.F. being less than one third of a volt. The difficulty of explaining the observed results by an assumption of induced variation of excitability would thus appear to be insurmountable. This difficulty is greatly intensified—indeed borders on the impossible—when we follow the same reasoning as regards the action of increasing intensity of homodromous current beyond the critical point. With stronger current, not only will the indifferent point be pushed towards the kathode, but the depression induced by the anode will be so great as to render the stimulated point of the nerve inexcitable. There being no excitation to be transmitted, the response should then undergo an extinction. Instead of this we find that the response shows an actual enhancement, on account of the reversal of the induced variation of conductivity which has already been described. This shows conclusively that the phenomenon we have studied is due not to a variation of excitability, but to that of conductivity.

We have seen further that a perfect parallelism exists in the conductivity variation induced in the plant and in the animal by the directive action of the current. No explanation could be regarded as satisfactory which is not applicable to both cases. Now with the plant we are able to arrange the experimental conditions in such a way that the factor of variation of excitability is completely eliminated. The various effects described about the plant-tissue are, therefore, due entirely to variation of conductivity. The parallel phenomena observed in the case of transmission of excitation in the animal nerve must, therefore, be due to the induced change of conductivity.

I may now briefly recapitulate some of the principal facts established in this paper.

The variation of conductivity induced by the directive action of current has been investigated by two different methods :—

(1) The method in which the normal speed and its induced variation are automatically recorded;

(2) That in which the variation in the intensity of transmitted excitations is gauged by the varying amplitudes of resulting responses.

The great difficulty arising from leakage of the exciting induction current into the polarising circuit was successfully overcome by the interposition of a choking coil.

The following summarises the effects of direction and intensity of an electric current, on transmission of excitation through the conducting tissue of the plant :—

The velocity of transmission is found to be enhanced against the direction of a feeble current, and retarded in the direction of the current.

Feeble heterodromous current enhances conductivity, homodromous current, on the other hand, depresses it.

Ineffectively transmitted excitation becomes effectively transmitted under heterodromous current. Effectively transmitted excitation, on the other hand, becomes ineffectively transmitted under the action of homodromous current.

The after-effect of a current is a transient conductivity change, the sign of which is opposite to that induced during the passage of current. The after-effect of a heterodromous current is, thus, a transient depression, that of homodromous current a transient enhancement of conductivity.

When the intensity of current is gradually increased, the characteristic conductivity variation is also increased, at first slowly, then rapidly. There is a critical intensity of current above which the conductivity variation undergoes a decline, culminating in an actual reversal. The effect of heterodromous

current is then a diminution, and that of a homodromous current an enhancement of conductivity.

The characteristic variations of conductivity induced in animal nerve by the direction and intensity of current are in every way similar to those induced in the conducting tissue of the plant.

These various effects are demonstrated by the employment of not one but various kinds of testing stimulus. Excitation may thus be caused (1) by a single break-induction shock, or (2) a series of equi-alternating tetanising shocks, or (3) by chemical stimulation,

The results that have been given are only typical of a very large number, which invariably supported the characteristic phenomena that have been described. The records given in this paper are photographic reproductions of the original.

Conclusion.

The action of an electrical current in inducing variation of conductivity may be enunciated under the following laws, which are equally applicable to the conducting tissue of the plant and the nerve of the animal.

1. The passage of a current induces a variation of conductivity, the effect depending on the direction and intensity of current.

2. Under feeble intensity, heterodromous current enhances and homodromous current depresses the conduction of excitation.

3. The after-effect of a feeble current is a transient conductivity variation, the sign of which is opposite to that induced during the continuation of current.

4. The normal conductivity variation undergoes a reversal under a strength of current above the critical value. The heterodromous current then induces a depression, while the homodromous current induces an enhancement of conductivity.

In my 'Researches on Irritability of Plants' I have shown how intimately connected are the various physiological reactions in the plant and in the animal. And I ventured to predict that the recognition of this unity of response in plant and animal will lead to further discoveries in physiology in general. This surmise has been justified, for it was by the study of effect of current on the conducting tissue of the plant that I was led to the discovery of the characteristic effects of the direction of an electric current on the conductivity of the animal nerve.

My research assistants, Messrs. Guruprasanna Das, L.M.S., and Surendra Chandra Das, M.A., rendered me very valuable help in this long investigation.