PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Electromotive Properties of the Electrical Organ of Torpedo marmorata

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Phil. Trans. R. Soc. Lond. B 1887 **178**, 487-537
doi: 10.1098/rstb.1887.0017

XVII. *The Electromotive Properties of the Electrical Organ of* Torpedo Marmorata.

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Received May 5,—Read June 16, 1887.

The electrical organ of the Torpedo is so remarkable a structure that it would be surprising if it had not engaged the attention of anatomists and physiologists. A brief account, which may embody the principal results of their labours, is a necessary prelude to that of the present investigation.

Historical.—The discovery of the electrical nature of the shock of the Torpedo by Walsh (1)* was followed by the remarkable experiments of Cavendish (2).

Cavendish constructed an artificial Torpedo by placing charged Leyden jars in a leather case, which in size and shape resembled the actual fish, and made experiments upon this schema, in order to ascertain the influence of its surroundings—whether sea-water, wet sand, or air—upon the distribution of the electrical discharge. The results obtained were in close accord with those phenomena which prevailed during the activity of the fish, and the experiments thus confirmed in a most conclusive manner the views propounded by Walsh as to the electrical nature of this activity.

Anatomy of organ.—Redi (3) and Lorenzini (4) had described, previous to Walsh's discovery, and termed "musculi falcati," the peculiar organs which are present in the Torpedo. They rightly conjectured that these were connected with the special powers which the fish possessed, though they were quite in the dark as to the real nature of these powers. After the discovery just referred to, the structure of the fish was more fully investigated, among others by John Hunter (5), Cuvier and Jobert de Lamballe (6). In 1844 Savi (7) published a monograph on the anatomy of the nervous system and the electrical organs of the Torpedo which gives an accurate picture of the relations of the organ to its nervous supply, and the mode of origin of its four large electrical nerves from a special central mass, the electrical lobe, situated behind the medulla oblongata, and immediately below the cerebellum.

In his splendid monograph on the more minute structure of the brain of Fish, Fritsch (8) has described the relations of this lobe. It may be considered as a ganglionic mass forming a protuberant swelling on each side of the calamus scriptorius. The

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* The numerals in parenthesis refer to the list of works at end.

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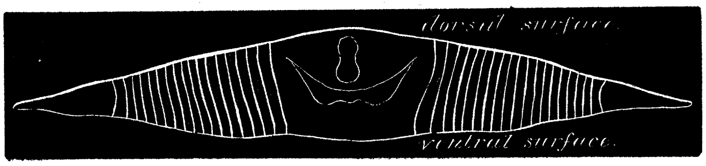
second, third, and fourth electrical nerves are homologous to the branches of the eighth pair (vagus) in the Skate, whilst the first nerve is said to be homologous to the fifth.

Minute structure of organ.—The organ consists of hexagonal columns extending from the ventral to the dorsal surface of the animal. Each column is a connective-tissue framework enclosing a number of septa so arranged as to resemble a pile of plates in close apposition one to another. The relation of the columns to each other is shown in fig. 1, which represents a transverse section through the two organs and the body of the animal, the figure being very diagrammatic.

Fig. 1.



Transverse section of fish, with organ cut through on each side; about one-fifth natural size.

The more minute structure of the columns and septa has been investigated by Pacini, R. Wagner, Ranvier, and others, for the details of which the work of Ranvier (9) gives ample references, and a special investigation of the termination of the electrical nerves has been made by Ewald (10). Leaving debatable matter on one side, it may be asserted that the column contains a large number of transversely disposed protoplasmic septa, in which are numerous conspicuous nuclei. The nerves enter the column in such a way that the branches lie between the septa. From these branches a very large number of finer branches proceed to the ventral surface of the septa. The physiological change, which follows the arrival of the excitatory nervous impulse, is produced almost coincidently in all the septa, and is of such a character that the ventral surface of each septum becomes negative to the dorsal surface. It must, however, be borne in mind that when examined in the fresh state no distinct surfaces are seen on the septa; the fluid, which in fresh preparations appears to intervene between the septa, being in reality the semi-fluid protoplasm of which these consist, in which Brownian movement of granules can be seen even in close proximity to the nuclei.

Physiology of organ.—If we now direct our attention to the physiological side of the subject, we find that among the numerous investigations which have been made upon the electromotive activity of the Torpedo, those associated with the names of Colladon, Matteucci, Marey, and du Bois-Reymond stand out as the most important, and the results arrived at by these observers will indicate with sufficient accuracy the present position of our knowledge.

Previous investigations.—The work of Colladon (11), published in 1836, was passed by almost unnoticed until du Bois-Reymond, in his treatise entitled "Lebende

Zitterrochen in Berlin," drew attention to it and confirmed the main statements contained in it. COLLADON determined galvanometrically the distribution of electricity on the surface of the Torpedo when the animal discharged its shock, a distribution which CAVENDISH sixty years before may be said to have forecast. The results are summed up by DU BOIS-REYMOND as follows (12) :—

"(1.) All points on the back are positive to any point on the belly. The strength of the current diminishes in proportion to the distance of these points from the organ, and almost entirely disappears at the tail.

"(2.) Any two unsymmetrical points of the back, or any two of the belly, almost always yield a current in the galvanometer. The one nearest to the organ is positive in the back, negative in the belly.

"(3.) When contact is made with two symmetrical points either of the back or belly, there is no deflection in the galvanometer.

"As COLLADON was the first to determine the electrical condition of the dorsal and ventral surfaces of the Torpedo, I have given the name of COLLADON's currents to the currents between points on either of these surfaces."

As DU BOIS-REYMOND has shown, the distribution is further modified by the unequal length of the columns, every point of the dorsal surface of the organ being positive to a point of the same surface which is situated further away from the median edge of the organ. The reverse must naturally be the case with reference to two points on the ventral surface of the organ.

MATTEUCCI.—In 1837 MATTEUCCI (13) published his researches on the electro-physiological phenomena of animals, and devoted a large portion of his work to the electromotive phenomena manifested by the Torpedo. The earlier observations had been made upon the discharge produced in the organ on irritation of the uninjured fish. This discharge was therefore a reflex effect, the efferent path of which was clearly indicated by the electrical lobes and the large electrical nerves which proceeded from these to the organs. MATTEUCCI commenced along the same lines, and ascertained that cold abolished and moderate warmth restored this reflex discharge, that after a prolonged series of shocks the reflex was so weak as to be inappreciable, but that after an interval of rest the discharge returned with all its former intensity.

He found that a strychnised Torpedo gave a very prolonged discharge which, whilst very intense at first, grew feebler and feebler, until, as might be expected, no further effect could be detected.

Division of the electrical nerves or destruction of the electrical lobes completely abolished the discharge. He employed both the galvanometer and a much more sensitive instrument, the rheoscopic frog, for determining the presence of electromotive differences. With the nerve of a nerve-muscle preparation in contact with the surfaces of the organ, he found that a rapid electromotive change occurred in the organ on division of the electrical nerve, as evidenced by the twitch of the muscle, and that this effect occurred whenever the peripheral end of the divided nerve was excited, whether mechanically or by the passage through it of a voltaic current. A descending direction of current was found to be more favourable than an ascending for the production of such an organ response.

The response of the organ to electrical excitation of its cut nerve thus afforded an opportunity for investigating the activity of the organ by using "nerve-organ" preparations, just as the phenomena of muscular activity had been investigated by observations made upon nerve-muscle preparations. It was, however, some years before the subject was approached along these lines.

ECKHARD.—In 1858 ECKHARD (14) showed that the observation as to the more complete response of the organ to electrical excitation of its cut nerve, when the exciting current used was a descending one, held good not only in the case of voltaic currents, but also when induction currents were used. He endeavoured with the imperfect means at his command to ascertain the character of the organ response, and came to the conclusion that its duration was longer than that of an induction shock of much the same intensity.

MAREY.—In 1871 a series of experiments was begun by MAREY (15) at Naples, which were continued at Paris (16); the full results were published in 1877, and the conclusions which he arrived at are as follows:—

(1.) Each excitation of the peripheral end of a cut electrical nerve gives rise in the organ to a single shock (flux), just as the similar single excitation of a motor nerve gives rise to a single contraction of the muscle which it supplies.

(2.) The time relations of the "flux," as ascertained by the frog signal, show a period of inactivity (*temps perdu*) amounting to about $\cdot 01''$ between the excitation and the response, and a duration of the response equal to six hundredths of a second.

(3.) The reflex discharge (*décharge*) of the fish consists of a series of such single shocks. These may follow one another with great rapidity, at a rate of one to two hundred per second, and under such circumstances must blend just as successive muscular contractions fuse when the excitations which produce them occur at intervals of time which are less than the duration of the individual contractions.

(4.) The frequency and strength of the successive shocks which form the powerful reflex discharge are affected by variations in temperature, by fatigue, &c.

The experiments upon the nature of the reflex discharge were particularly ingenious; attention may be drawn to such methods, for instance, as that of leading the Torpedo discharge through the primary circuit of an induction apparatus and ascertaining by a telephone the state of the secondary coil, and as that of leading the discharge through a modified DESPREZ electro-magnetic signal and recording its movements.

JOLYET.—With regard to the time relations of the single response, it was shown in 1883 by JOLYET (17) that a different interpretation must be given to the interval which was found to elapse between the excitation of the nerve and the response of the organ. JOLYET found that a large part of the lost time was in reality consumed in the passage of the nervous impulse down the nerve to the organ; the nerve conducting more slowly than MAREY had supposed—according to JOLYET, at a rate of 7 metres in a second.

DU BOIS-REYMOND.—The extensive work of DU BOIS-REYMOND (18) remains to be referred to. This deals not so much with the response of the organ to excitation of its electrical nerve as with the peculiar behaviour of the organ itself in respect to the passage through it of electrical currents. The main facts which are thus brought out may be broadly stated as of two kinds. First, those relating to the electromotive properties of the organ after the passage through it of an electrical current; and, secondly, those relating to the influence exerted by the organ upon the traversing current itself—in other words, phenomena of polarisation or after-effect, and of conduction.

In both these respects the behaviour of the tissue varied with the direction of the electrical experimental current. It was thus necessary to definitely label the experimental current with regard to its direction through the organ, and with this view a current passing through the tissue from the ventral to the dorsal surface was termed "homodromous," since its direction was similar to that of the response, and a current passing in the opposite direction was termed "heterodromous." A strong galvanic current of short duration, whether "homodromous," or "heterodromous," is followed by an electromotive change which shows itself galvanometrically as a current passing through the organ in the direction of the shock. With weaker galvanic currents or currents of long duration after-effects are produced which are opposed in direction to the experimental current.

The influence of the organ upon the experimental current itself is very surprising, for it would appear that the organ is a better conductor for "homodromous" than it is for "heterodromous" currents. This remarkable fact is not, according to DU BOIS-REYMOND, due to the development of an excitatory change which adds to the amount of one current whilst it diminishes that of the one oppositely directed; it can therefore only be called, for want of intelligible physical explanation, a case of "irreciprocal conduction."

He states further that both facts are of great teleological importance, since they show that the shock of the organ, instead of being weakened by polarisation in the tissue, will be strengthened by the production of an after-effect in the same direction as itself, and that the organ is of such a character as to distinctly disfavour any short-circuiting of the current present in one column by its neighbour. To quote his own words, "the organ is not insulated, but the irreciprocal conduction which we have recognised performs, as has been already stated, a function similar to complete insulation. Each column conducts its own homodromous current comparatively well, but bars the passage to the heterodromous current threads of all the other columns; and, as this is the same for all the columns, the heterodromous current threads are forced to take the circuitous route round the edges of the organ, just as if the organ consisted of a non-conducting substance" (19).

Besides these two important facts the work of DU BOIS-REYMOND brings into notice the presence of an organ-current in the quiescent tissue (20). This organ-current is a feeble counterpart, as far as its direction and distribution are concerned, of the electromotive changes which are present during the state of activity. The existence of this current is a matter of very great interest in relation to the well-known diversity of opinion as to the so-called "demarcation" currents and "currents of rest" present in muscle and nerve.

There are thus three distinct aspects under which the electrical organ of the Torpedo has been and may be studied.

I. As an inactive organ with reference to the effect produced upon it by the operation of such agents as galvanic currents, mechanical injury, temperature, &c.

II. As an active organ, the activity of which has been evoked by excitation of the peripheral end of its divided electrical nerve, with reference to the influence of varying conditions on the time relations of this activity.

III. As an active organ, the index of a central nervous discharge.

The experiments which form the subject of this communication are concerned with the first and second aspects of the organ, the reflex discharge being reserved for further investigation at a period when the conditions should be more favourable than they were at the particular time of year (December, 1886, and January, 1887) in which the present observations were made.

Object of present research.—If we now consider to what extent our knowledge of the electromotive phenomena of the Torpedo still remains obscure, we shall be better able to appreciate the direction of the present research.

The nerve-organ response.—It has been shown that MAREY has investigated the time relations of the response of the organ to excitation of its nerve. The subsequent correction by JOLYET, previously referred to, shows that the first investigation omitted to take into consideration one most important detail. The investigations are defective in omitting other details, which, as far as the phenomena of muscle and nerve are concerned, are of great importance, such as temperature, strength of stimulus, &c. Moreover, the methods employed hitherto cannot be regarded as furnishing thoroughly reliable data. The frog-signal may be described as a touch-and-go instrument, a delicate galvanoscope which does not appreciate differences in the amount of the currents which excite it. It gives approximately accurate information as regards the commencement of a sudden electromotive change in the tissue with which it is connected, and when used, as MAREY used it, with a pendulum rheotome, may indicate the duration of that change, although it is uncertain to what extent it would respond to any slight electromotive change which may attend the subsidence of the main effect. As it gives no data from which to construct the curve which may represent the development and decline of an electromotive change, MAREY used the DESPREZ signal for this purpose. The signal was modified by substituting for the usual spring an elastic cushion between the magnet and the armature. From the curve traced by this signal when the organ response is led through it he deduces the character of the curve, developing rapidly and subsiding more slowly.

A more accurate curve might be obtained by photographing the movement of a quick capillary electrometer, but even this could not be considered satisfactory unless a series of galvanometric readings corresponding to known time intervals had been also made. The great improvement in the construction of galvanometers renders this last method still more satisfactory.

A series of galvanometric readings may not, owing to the short closures necessitated by the rheotome, give a complete account of an electromotive change, but as far as it goes it is perfectly trustworthy. It was, therefore, with the object of making such series of galvanometric readings that the electromotive phenomena of the response were re-investigated in the present research.

The organ-current.—The uncertain and meagre character of our knowledge with respect to the organ-current is much more pronounced. We are able to predict with certainty that, if in muscular or nervous tissue a violent local molecular change is effected by mechanical injury or by the application of heat or chemical reagents, a change such that there is on the one side complete death of tissue, and on the other side tissue of which the vitality is unimpaired—the former state shading into the latter—then this will manifest itself by an electromotive effect in the neighbourhood of the injury. This electromotive change is always of such a character that the impaired tissue becomes strongly negative to the unimpaired tissue.

But with regard to the possibility of producing such electromotive phenomena in the electrical organ we know nothing. The great importance of experiments upon this subject is sufficiently obvious, and the first part of the present research is, therefore, devoted to the results of such experiments. The remarkable character of the discoveries of DU BOIS-REYMOND, already referred to, warranted re-investigation, and a large number of experiments have been made with reference to these.

The results embodied in the present preliminary account may, therefore, be grouped under three heads :—

I. Experiments relating to the organ-current.
II. Experiments relating to the time relations of the excitatory change produced in the organ by excitation of its nerve.
III. Experiments connected with the passage of electrical currents through the organ.

All the experiments were carried out in the months of December, 1886, and January, 1887. Through the kindness of the Société Scientifique d'Arcachon, several rooms in the Zoological Station at Arcachon were placed at the disposal of Dr. BURDON SANDERSON and myself. The methods and lines of work had to be decided upon in England, as it was necessary to take out all the essential apparatus from the Oxford Physiological Laboratory.

It thus necessarily happened that in some instances work had to be given up whilst still incomplete, as some essential piece of apparatus was wanting.

In the summer the shallow water of the Bassin d'Arcachon contains many Torpedoes; but in the winter the fish leave the basin for the deeper water outside. There was, however, no difficulty in procuring them, provided the weather was sufficiently favourable to allow the steam trawlers to work. The Torpedoes were found in sufficient numbers on the sandy bottom of the sea, at some little distance from the shore. They were caught in the trawl, and were, undoubtedly, exhausted by the process. Here, however, the cold acted favourably, for, the fish being caught at night and kept in tubs on the deck, the temperature was sufficiently low to abolish the organ reflex. When brought to the laboratory, the fish rarely showed any movement except the winking of the spiracles. Placed in water at 10° C., they recovered, and buried themselves in the sand at the bottom of the tanks. They were easily sorted by size into small, medium-sized, and large full-grown fish. The small fish were newly-born, and measured 13 centimetres in length and 8 centimetres in breadth. Nine of these were taken from the uterus: five from one Torpedo, and four from another; the four last-named lived for one or two weeks, and were very vigorous little fish. Of Torpedoes of this class, eight were used for experiment.

The medium-sized fish were probably the last year's young. They measured from 22 to 25 centimetres in length, and from 14 to 17 centimetres in breadth. Four such fish were used for experiments.

The large fish measured from 40 to 52 centimetres in length, and from 25 to 32 centimetres in breadth; of these, seven were used for experiment.

Although only 19 fish were experimented upon, it must be borne in mind that one Torpedo furnishes a mass of material for work, since the organ preserves its excitability for many hours when kept in the cold.

I. *Experiments relating to the Organ-Current.*

The organ-current is essentially what in other tissues has been termed a "current of rest." It has been ascertained by du Bois-Reymond to be present both in the entire organ and in cut-out strips of organ as a persistent effect. The current in the unexcited tissue has the same direction in the organ as that produced by the response of the organ to excitation (the shock); that is to say, it is directed through the columns from their ventral to their dorsal surfaces. Its amount, though always inconsiderable as compared with that of the response, is, like the latter, dependent upon the length of the organ columns; and, consequently, the current has the same general distribution over the surface of the organ as the excitatory effect. This is thus expressed by du Bois-Reymond: "If we put out of account the smallness of the differences of potential, the electromotive surface of the quiescent fish differs from that of the same animal when giving a shock only in the induction which accompanies the shock" (21). Its presence in small strips of tissue enabled du Bois-Reymond to calculate the electromotive force of a single plate of a column in the unexcited state, which he finds may equal ·0000117 of a DANIELL. No comparison is given between the current found to be present in the entire organ and that existing in the cut strip of tissue, from which it would seem that the different condition of the tissue in the two cases was considered as standing in no relation to the production of the current. My experiments show that, so far from this being the case with the tissues which I examined, there is a very marked difference between the organ-current shown by an entire organ and that shown by a cut strip. The galvanometer used in these experiments was a THOMSON of high resistance, made by ELLIOTT, which was brought to such a degree of sensibility that ·0001 RAOULT gave, with a resistance of 10,000 ohms in the circuit besides that of the instrument (5332 ohms), a deflection of 230 scale. By means of the compensator (described by BURDON SANDERSON (22)) the organ-current could be "balanced," and the electromotive condition of the tissue thus measured. The balancing circuit was arranged in the manner described by the same writer, but a CALLAUD cell was used as the constant balancing battery, and the measurements were made in terms of this. The CALLAUD cell is a gravity battery used in telegraphy, and is a modification of THOMSON'S gravity battery. As the copper is immersed in sulphate of copper, and the zinc in sulphate of zinc, its electromotive force is that of a RAOULT. The requisite determinations for the purpose having been made, the differences of potential are here given in terms of a RAOULT.

The amount and direction of the organ-current in the entire organ were ascertained in ten instances; the fish were killed by destruction of the brain, but were otherwise uninjured. The whole fish was therefore used for experiment, and was fixed with its ventral surface against a vertical board; this was perforated so as to allow the ventral surface of the organ to be reached by a leading-off electrode. The dorsal and ventral surfaces of the organ were now led off by kaolin cushions moistened with ·6 per cent. saline, and connected with U-shaped non-polarisable electrodes. The points selected for leading off were opposite one another on the respective surface, and were situated in the middle of the organ. It is surprising, in the light of DU BOIS-REYMOND'S statements, what contradictory results were thus obtained, as the following Table shows. The difference of potential existing between the dorsal and ventral electrodes is indicated in terms of the dorsal electrode. The sign +, therefore, signifies that the dorsal surface led off is galvanometrically positive to the ventral surface, and that a current passes through the organ columns from their ventral to their dorsal ends.

SMALL Torpedoes.—Six animals investigated.
(Dorsal surface as compared with ventral surface.)

+ ·002 R; + ·001 R; + ·0006 R.
− ·0009 R; + ·0005 R; + ·0015 R.

MEDIUM-SIZED Torpedoes.—Four animals investigated.

+ ·0017 R; − ·0011 R; − ·0008 R; − ·0012 R.

The difference between the two contacts is thus seen to be very small, and in four cases out of ten was opposite in character. It was evident that nothing could be made out with certainty as to the state of matters in the entire animal. On the other hand, the blocks of tissue which were cut from these and other animals for rheotome experiments never showed any such discrepancy. In these the difference was always such that the dorsal end of the block was positive to the ventral end. It is needless to give examples of this now, for the experiments which will be given will afford convincing proof of the truth of this statement; but it may be stated that in 45 instances in which the organ-current of a cut strip or block of tissue was observed and noted there is no instance of the current being otherwise than +, and that in all cases the strength of the current far exceeded that which was observed in the case of the entire animal.

The difference observed very early in the work between the organ-current in the cut-out block of tissue, and that in the organ when *in situ*, suggested the view that the increased current found to be present in the former tissue was dependent upon the nature of the preparation—upon the fact that the piece of organ used was bounded by incisions. It was, therefore, determined to ascertain how far such incisions did affect the result. For this purpose the following experiment was carried out:—A medium-sized Torpedo, 18 centims. long by 12 wide, and 15 millims. thick at the median border of the organ, was fixed on a perforated vertical board; the brain had been previously destroyed, but the other parts of the fish remained intact. The skin covering the dorsal and ventral surfaces of the right organ was now led off by kaolin plugs, the leading-off points being situated in the middle of the length of the organ, and 5 millims. outside its median border; and care was taken that the one electrode should be exactly opposite the other. The dorsal surface was found to be negative to the ventral; the difference of potential was, however, quite inconsiderable, and amounted to — ·001 RAOULT.

The organ, with its skin coverings, was now cut through a few millimetres in front of the leading-off electrodes. The direction of the cut was from without inwards and slightly backwards, and did not extend beyond the median border of the organ. On examining the tissue two or three minutes after the incision, the difference of potential was found to be the reverse of what it had been; the dorsal contact being now positive to the ventral, the difference amounted to + ·0005 R.

A second cut was now made at right angles to the first cut, and thus nearly parallel with the long axis of the fish. It was external to the leading-off contacts, and extended through the length of the organ. The tissue now led off was, therefore, a long block bounded internally by the median border of the organ, anteriorly by the first cut, externally by the second cut, and posteriorly by the posterior boundary of the organ. The difference of potential was found to be still further increased after this incision, and amounted to + ·0015 R.

The left organ of the same fish was now taken, and a large wedge-shaped block cut from it. This was effected by two vertical incisions through the organ in the direction of its columns, extending from the median to the external border of the organ. The cuts were parallel, and were 12 millims. apart. The block of tissue was separated from the gills which lie close to the median border of the organ. It was thus a slice of organ the dorsal and ventral surfaces of which remained covered by skin. This preparation was placed upon a glass plate, resting with one of its cut surfaces in contact with the glass; the dorsal and ventral skin surfaces were now led off by kaolin cushions, and the difference found to be + ·0002 R. The slice was now reduced in thickness by cutting it into two thinner slices, the cut being parallel to the previous ones. One of these long slices, which resembled the previous one in all respects except that it was only 6 millims. in thickness, was now examined, and the difference found to be + ·0007 R. This slice was still further reduced by another cut, and now measured only 3 millims. in thickness. The skin still remained covering the ends of the columns, and when led off a marked difference of potential was observed. This difference declined slowly; it was compensated at intervals of one minute.

	R.
2 minutes after the cut difference	= + ·0047
3 ,, ,, ,, ,,	= + ·0043
4 ,, ,, ,, ,,	= + ·0037
5 ,, ,, ,, ,,	= + ·0032
6 ,, ,, ,, ,,	= + ·0030
7 ,, ,, ,, ,,	= + ·0027
8 ,, ,, ,, ,,	= + ·0025
15 ,, ,, ,, ,,	= + ·002

It declined now very slowly, and another incision was therefore made. This was across the slice at right angles to the previous cuts. The experimental portion was therefore reduced to a small block of tissue, of the same thickness as before (3 millims.), but with a cut edge running parallel to its median border. The difference of the skin contacts was + ·002 R. before the cut, and after the cut it was found to have largely increased.

	R.
1 minute after the cut difference	= + ·0051
2 minutes ,, ,, ,,	= + ·0039
3 ,, ,, ,, ,,	= + ·0031
4 ,, ,, ,, ,,	= + ·0028
5 ,, ,, ,, ,,	= + ·0025
6 ,, ,, ,, ,,	= + ·0023

This block was now divided in the direction of the columns, a small prism of organ being thus made 12 mm. in length in the direction of the columns, 5 mm. in breadth, and 3 mm. thick. Three minutes after its preparation it was examined, and the difference of the ends of the columns found to be + ·0039 R.

From the preceding experiments we are led to conclude that after cutting the organ an electromotive change occurs in the columns bordering on the cut, of such a character that the dorsal ends of the columns are positive to the ventral ends. The change is evidently that observed by DU BOIS-REYMOND in strips of tissue, and called by him the organ-current. It subsides rapidly at first, and then more and more slowly, and is in this respect analogous to the demarcation-current produced by injury in muscle and nerve.

In the latter tissues a prolonged electromotive change is produced when a portion of the tissue is injured by mechanical, thermal, or chemical means; this effect slowly subsides; it is increased when the tissue in the neighbourhood of the injury is warmed, diminished when that part is cooled. In both muscle and nerve the demarcation-current is the sum of changes produced by the injury in a number of electromotive elements, and its amount is therefore dependent upon the number of muscle fibres or nerves which are involved in this injury. The effective injury for its production in these tissues is thus a section which shall cut at right angles to their length as many fibres as possible.

Now, in the organ of the Torpedo the electromotive elements, plates, and nerves are disposed at right angles to the length of the framework which encloses them, and which constitutes a column.

A proceeding analogous to that of making a transverse section of the nerve fibres of a nerve trunk is thus carried out upon the organ columns when an incision is made through the organ parallel to the columns. Such an incision must cut at right angles to their length a large number of plates and nerves; this should be followed by an electromotive change which expresses the sum of the local changes occurring in the immediate neighbourhood of the cut.

This is what I conceive to be the meaning of the organ-current. Like all "demarcation" currents, it is the expression of a protracted state of excitation of the still living tissue in the neighbourhood of the injury. The corresponding electromotive change must manifest itself as all the excitatory phenomena of the Torpedo manifest themselves, namely, as a current passing through the column from the ventral to the dorsal surface.

In support of this assertion we will now pass to experiments as to the effect of local warming of an incised surface.

From a small Torpedo 13 centims. long by 9 centims. wide a slice of organ was cut, which was then divided up into three blocks. Each block comprised the whole length of the columns which remained covered by skin at their dorsal and ventral ends. Each was 2 mms. wide and 3 mms. thick, and thus consisted of several unimpaired columns surrounded by columns which had been cut through parallel to their length. These cylinders of tissue were now examined, the skin ends being led off by kaolin cushions. The first cylinder, examined five minutes after its preparation, showed a difference of potential = + ·0045 R., subsiding rapidly to + ·0034 R., and then more slowly.

A hot iron wire was now brought within a few millimetres of one of the cut sides of the preparation; the difference immediately began to rise, as was shown on the galvanometer by a slow deflection amounting to more than 200 scale. On withdrawing the wire, the difference subsided; on approaching it, it rose again. The second cylindrical block was examined in the same way half-an-hour after its preparation. The difference was found to be + ·0017 R. One of the cut sides was now warmed as before, and the difference rose; when it had attained its maximum of rise it was compensated and found to be + ·002 R. On withdrawing the hot iron wire it fell again, but on again bringing the hot wire near the cut surface it rose to + ·0022 R.

Similar results were obtained with the third cylinder, and could always be brought about in such preparations. In this respect, then, the organ-current resembles the demarcation-current of muscle and nerve.

One of the most efficient methods for the production of a demarcation-current in the last-named tissues is that of making what is termed a "thermal section." This method has the advantage of injuring the tissue locally without altering its dimensions to any considerable extent. It should be possible to produce similar thermal sections in the case of the Torpedo. From what has been said as to the structure of the electrical organ it is evident that the appropriate thermal section would be obtained if a block of tissue could be prepared which should consist of a few unimpaired columns surrounded by other columns partially in a state analogous to heat rigor. This was effected by the following simple plan:—A cubical block of tissue, consisting of several columns with their ends covered by skin, was held by its dorsal skin in the forceps, and then plunged in hot water so as to be wholly immersed for two seconds. On examining the block, the sides were seen to be opaque-looking. They were undoubtedly destroyed, but in the interior the substance of the columns appeared to be unimpaired. In such a block a thermal section has therefore been made on every plate and nerve branch within a millimetre or so of the surface. The resulting difference should therefore be very large, and investigation showed that this was the case.

Three strips were cut from the organ of a large Torpedo. The first was cut from the median edge of the organ. The length of its columns was 55 mms., and the strip was 3 mms. in thickness and in width. It was immersed in hot water for two seconds, and then examined by leading off the skin covering the ends of the columns. The difference was found to be very large, amounting to as much as + ·052 R.

The second strip was cut from the organ midway between its median and outer borders. Its length (23 mms.) was less than the previous one, owing to the columns being shorter at this point, but in other respects it resembled the first strip. On examining the difference two minutes after immersion it was found to be + ·0336 R.

A third strip was cut from the outer border of the organ, where the columns measured only 12 mms. in length. It was otherwise of the same dimensions as the preceding ones. It was immersed in hot water for two seconds, and the difference two minutes afterwards was found to be + ·0192 R.

This experiment left no doubt as to the possibility of producing effects comparable with those of thermal section by an analogous mode of injury, and it is to be remarked that the electromotive change produced is the greater, the longer the columnar strip. This is due to the fact that the number of electromotive elements operated upon is proportional to the length of the strip.

Another experiment was made upon a strip cut from a medium-sized Torpedo, and measuring 25 mms. in length and 3 mms. in thickness and breadth. This strip was kept in the cold for one hour and then examined; the difference was found to be + ·0021 R. It was now immersed for a few seconds in hot water and re-examined, when the difference had increased to as much as + ·0226 R.

Since the effect is produced by injury of the plates, which injury causes an electromotive change in the plates such that the ventral aspect of the plate is negative to the dorsal, it must follow that, whether the injury extends along a whole column or only along a small portion, the effect is always of similar direction and character.

The electromotive plates respond to the local excitation of injury as they do to nerve excitation, but the response in the former case is comparatively feeble, and is very prolonged. Wherever the injury may be, the effect must, therefore, be that the dorsal surface of the column is positive to the ventral surface. If, for instance, the dorsal half of a column be immersed in hot water, the effect must be of similar character to that produced by total immersion, and the same must be the case if the ventral half be immersed. The difference between partial and complete immersion is merely a difference in the amount, not in the direction of the effect produced, the amount being proportional to the number of electromotive elements affected.

Three strips were cut from the organ of a large Torpedo, each measuring 20 mms. in length of column, and 3 mms. in thickness and width. The first strip, when examined half-an-hour after its preparation, showed a difference of + ·0091 R. The dorsal half of the strip was immersed in hot water for two seconds, and the difference rose to + ·0209 R. The second strip showed a difference of + ·0084 R.; the ventral half of this was immersed, and the difference rose to + ·0254 R. The third strip was wholly immersed, and the difference amounted to ·0340 R.

In another experiment upon a strip cut from a medium-sized Torpedo, the columns of which measured 25 mms. in length, the strip was found to show a difference, an hour and a half after its preparation, amounting to + ·0007 R. The dorsal fourth of the strip was immersed for two seconds, and the difference rose to + ·003 R.; as soon as possible the ventral fourth of the same strip was immersed, and the difference rose to + ·0065 R.; the whole strip was now immersed, and the difference rose to + ·0228 R.

These results justify the statements which preceded them, and show that, whatever the part injured, the effect is the same, the organ-current being *always similarly directed through the columns, namely, from the ventral to the dorsal surface.*

There is a possible source of fallacy connected with the nature of the preparation. The skin may have electromotive properties, and electromotive changes may follow its injury. The subject has been investigated by DU BOIS-REYMOND, but without any decisive results (23). It would appear, however, that if the skin is electromotive it is only feebly so, and any change from the skin must, in blocks of organ, be swamped by the larger organ-current. Experiments were, however, made upon the subject at Arcachon which showed that in the injured skin the surface becomes negative to the deeper uninjured parts. We should, therefore, expect that injury of the dorsal skin in the case of an immersed block of tissue would cause an electromotive change opposing that of the organ, whilst similar injury of the ventral skin would cause a change favouring that of the organ. If this be so, then in the case of a strip of organ with skin remaining on its dorsal and ventral surfaces, which has been totally immersed in hot water, the total electromotive change is that of the plate's organ-current *plus* that of the ventral skin *minus* that of the dorsal skin; the skin effects, one opposing and the other favouring the total organ effect, thus balance each other. But, if a strip be cut and the organ-current allowed to subside, injury to the dorsal skin only should be followed by sinking of the difference, injury of the ventral skin only by rise of the difference. The following experiments justify this view. In a strip 25 mms. long and 3 mms. in width and breadth, examined one hour after preparation, the difference between dorsal and ventral surfaces was + ·0021 R. The strip was now held up by its ventral skin, and the dorsal skin allowed to touch a hot surface. On examining the difference, it had diminished to − ·0008 R. The same strip was now held up by its dorsal skin, and the ventral skin was allowed to touch a hot surface: the difference, when examined, had increased to + ·002 R. Finally the whole strip was immersed in hot water for two seconds, when the difference was found to be + ·0226 R.

In another strip, cut from a small Torpedo, and measuring 13 millims. in length, the difference 15 minutes after preparation was found to be + ·002 R. The dorsal skin was now carefully removed, and the contacts were made upon the ventral skin and the dorsal ends of the columns respectively. The difference had diminished to + ·0015 R. The ventral skin was carefully cut off, the contacts now being made upon the uncovered ends of the columns, and the difference found to be + ·0027 R. In the operation of removing the skin it is difficult to avoid injuring the organ columns; such injury would always produce a + effect, which would have to be taken into consideration.

It seems, then, that in the injured skin the surface becomes negative to the uninjured deeper parts. It is, therefore, not improbable that the very small currents observed in entire Torpedoes are, to a large extent, skin currents, these being produced by the injuries which the skin must receive in the process of capture, handling, &c.; but the question is one which demands further investigation. It is obvious that it does not affect the present inquiry.

An "organ-current" may be reproduced in a strip of tissue 24 hours after the preparation of the strip. Thus a block of organ was cut from a medium-sized

Torpedo: the difference amounted to + ·0062 R.; it was left until the next day, being kept in the cold and surrounded with other fragments of organ to keep it moist.

When examined after 24 hours, the difference was found to be very small—indeed hardly perceptible. It was now wholly immersed for two seconds in hot water, and the difference was examined. It amounted to + ·0195 R.; in three minutes it sank to + ·013 R., then to + ·008 R., + ·006 R., + ·005 R., + ·0043 R., + ·0036 R., &c., the difference being compensated every three minutes.

It has been observed that the difference following injury is of such a character that it declines at first rapidly and then more slowly.

Experiments were made to ascertain the rate of this decline. For this purpose the effect was recompensated at regular intervals; the results of three series are now given with strips led off by their dorsal and ventral skin ends:—

Time after preparation.	Cut strip 40 millims. long.	Cut strip 15 millims., immersed for 2 minutes in hot water.	Cut strip 15 millims., immersed for 2 minutes in hot water.
minutes.			
2	diff. +·0275 R.	+·0255 R.	+·0226 R.
3	+·0230	+·0180	+·0175
4	+·0205	+·0135	+·0145
5	+·0180	+·0125	+·0135
6	+·0160	+·0117	+·0112
7	+·0140	+·0110	+·0106
8	+·0126	+·0102	+·0100
9	+·0117	+·0095	..
10	+·0110	+·0090	..
11	+·0100	+·0086	..
12	+·0092	+·0083	..
13	+·0087	+·0081	..
14	+·0082	+·0078	..
15	+·0076	..	..
16	+·0071	..	..
17	+·0068	..	..
18	+·0065	..	..
19	+·0062	..	..
20	+·0059	..	..
21	+·0056	..	..
22	+·0053	..	..
23	+·0050	..	..
24	+·0048	..	..
25	+·0046	..	..
26	+·0045	..	..
27	+·0044	..	..

The effect is seen to decline rapidly at first and then slowly. This is a very characteristic feature of the organ-current, and, apart from its obvious resemblance to the demarcation-current observed in cardiac tissue, is strongly suggestive of the excitatory nature of the whole phenomenon. A point of great interest in this connection is the influence on the rate of the decline of a nerve-organ response. The experiments which were made on this subject were not, however, satisfactory, owing to the lack of suitable methods; they only showed that the decline was more rapid when the organ was excited.

The facts relating to the organ-current may now be summed up as follows:—

The difference between the dorsal and ventral surface of the organ is very small in the uninjured organ when examined *in situ*, and under these circumstances is often of opposite sign in different animals.

When a portion of cut tissue is examined an electromotive difference is always found to be present, and is such that the dorsal surface of the columns is positive to the ventral.

This difference subsides at first rapidly, and then so slowly that it may be observed one or two hours after the preparation has been made.

The difference is produced by incisions which cut through the columns in the direction of their length, thus cutting the electromotive elements at right angles to their length.

The most effective method for its production is the thermal section of the external columns contained in a strip of the tissue.

The amount and not the direction of the effect is affected by partial injury of a column, whether this be dorsal or ventral.

The organ-current is thus analogous to the demarcation-current of muscle and nerve, and is believed to correspond to a prolonged local excitation of the vital electromotive elements in the immediate neighbourhood of the injury.

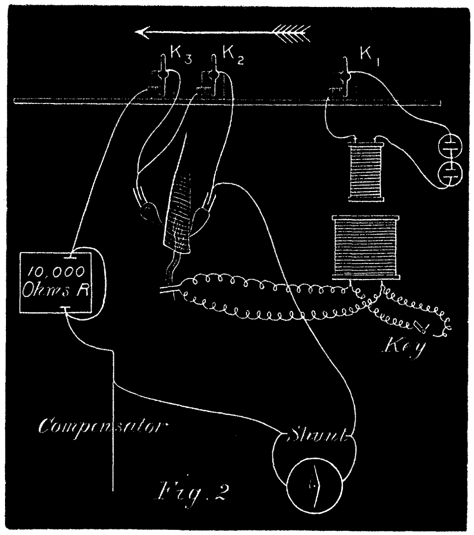
II. *Experiments relating to the Time Relations of the Excitatory Change in the Organ following Excitation of its Nerve.*

The method used in these experiments was that rendered familiar by its employment in experiments of a similar kind upon other tissues, particularly cardiac tissue. This consists in the use of a rheotome which shall connect the galvanometer with the tissue under investigation during a known period after excitation of the tissue. In the experiments of MAREY upon the Torpedo (24) a fast-travelling plate, such as that of the pendulum or spring myograph of DU BOIS-REYMOND, was used. The movement of the plate was arranged to ensure both the passage of an induction shock at a given point in its course and a definite closure (for $\frac{5}{1000}''$) of the circuit which connected the organ of the Torpedo with the "physiological galvanoscope," this being the nerve muscle preparation of the frog—the movements of which were recorded on the travelling plate. This method had been used by myself in ascertaining the time relations of the response of the Malapterurus to excitation of its skin (25). The information which this method gives is, however, of relatively little value, since it is obtained in terms which bear no sort of relation to those applicable to electrical phenomena in general, such as the deflections of a galvanometer needle of known sensibility, &c. To obtain such information as this latter was the object of the following experiments.

For this purpose I had taken with me a spring myograph, constructed on the plan of DU BOIS-REYMOND, but furnished with three special keys to fit it for use as a rheotome.

The passage of the traveller opened these keys in succession; they could be adjusted with great accuracy at any distance one from the other. The three keys may be distinguished as K_1, K_2, K_3. These were arranged so that the break of K_1 opened the primary circuit of an induction apparatus; that of K_2 a circuit which, when closed, short-circuited the galvanometer; and K_3 the galvanometer circuit itself. The galvanometer was the same as in the previous experiments, and was brought to a degree of sensibility that, with a resistance of 10,000 ohms, besides that of the instrument, ·0001 R. gave a deflection of 230 scale. It was often necessary to allow only $\frac{1}{10}$, $\frac{1}{100}$, or $\frac{1}{1000}$ of the total current in the circuit to pass through the instrument. This was effected by the shunt provided with the instrument, and the terms G. $\frac{1}{10}$, G. $\frac{1}{100}$, G. $\frac{1}{1000}$, express this in all the experimental data which follow. Since the use of the shunt diminishes the total resistance in the circuit, a resistance of 10,000 ohms was introduced in order to ensure the complete short-circuiting of the galvanometer by K_2 when the shunt was used. The whole arrangement is given in fig. 2. The traveller of the rheotome moved with sufficient rapidity to allow an accurate adjustment of the keys to within $\frac{1}{1000}''$ of each other; the movement was timed by recording on the plate of the traveller the vibrations of a tuning-fork vibrating 100 times in a second.

Fig. 2.



The induction apparatus used for excitation was constructed and graduated under the kind direction of Professor KRONECKER, of Berne.

The first experiments were made with the view of testing the arrangements, as it was necessary to see how far the organ response could be investigated in this manner. For this purpose a small Torpedo 13 cm. × 9 cm. was selected, and, the brain having been destroyed, the second, third, and fourth electrical nerves were exposed and freed as far as the gills. The organ was left untouched, and the animal fixed on a perforated vertical board. Through the perforation the ventral surface of the organ was led off by one non-polarisable electrode, the other being placed upon a corresponding point on the dorsal skin covering the organ. A pair of fine platinum electrodes were placed under the second nerve.

There was a slight electromotive difference between the dorsal and ventral contacts, amounting to + ·002. The nerve was now excited by the break of the current of two Grove cells placed in the primary circuit of the induction apparatus. It was noticed that a considerable strength of induction current had to be used before an organ response could be obtained. This point has been observed and commented upon by DU BOIS-REYMOND (26). With the secondary coil at 5 cm. the galvanometric effect obtained by excitation was = + 750 scale G. $\frac{1}{10}$; the sign + signifying that a current passed through the galvanometer directed from the dorsal to the ventral leading-off electrode.

A preliminary rheotome experiment was now made, the short-circuiting key K_2 being fixed at ·01″ after the exciting key K_1, whilst K_3 was moved so as to lengthen the duration of the galvanometer closure.

Time of closure of galvanometer, the moment of excitation being zero	·01″–·014″	·01″–·015″	·01″–·016″	·01″–·0165″	·01″–·0225″	·01″–·0275″
Deflections observed in galvanometer. (Where more than one reading is given, it indicates another experiment under same conditions.)	0 0 0	+ 65 + 72 + 65	+ 240 ··	+ 550 ··	+ 500 G. $\frac{1}{10}$	+ 650 G. $\frac{1}{10}$

This showed that in this preparation the electromotive response, as indicated by the galvanometer, commenced at $\frac{15}{1000}$″ after excitation of the nerve, and was fully developed by $\frac{22}{1000}$″ after excitation.

The rapid development of the response is also shown in the next experiment, in which the organ of the other side of the same animal was led off, and all the electrical nerve trunks excited. Here, with a galvanometric closure of from ·01–·014, no effect occurred after excitation; with ·01–·0155, an effect of + 195 scale; with ·01–·0165 a large effect shot the needle off the scale (+ ∞).

On examining this same preparation half-an-hour or so later, the time relations of the effect were found to have changed thus :—

Galvanometer closure . .	·01″–·012″	·01″–·0125″	·01″–·014″	·01″–·015″
Deflections	0 0	+ 55	+ 165	+ ∞

This change was subsequently found to be due to the high temperature of the room (20° C.) affecting that of the preparation. The experiment showed that it was possible to obtain with the instrument very sharp differences, with small differences in time, amounting to only $\frac{1}{1000}''$.

It was now necessary to see if the same would hold good of a cut piece of organ with nerve attached, a nerve-organ preparation. A large fish, 48 cm. × 30 cm., was selected, and the brain destroyed. The largest electrical nerve (the 2nd) was then prepared from its exit from the skull to its entry between the gill clefts. A great sector of organ, comprising the distribution of this nerve, was then made by two clean cuts with a razor through the skin and the organ in the direction of the columns, the cuts reaching from the median to the outer border of the organ. The mass of separated organ measured 40 millims. in thickness at its median edge; this, therefore, represents the length of the columns at this point. It was fixed on a vertical board, and led off by cushions of saline kaolin similarly placed on its dorsal and ventral surfaces. The fish had been caught the night before the experiment, and the temperature of the organ was still very low, only 5° C.

The block of tissue gave the usual "organ-current," $= + \cdot 0052$ R., which subsided slowly during the experiment. The nerve was excited 6 centims. from its point of entry into the organ by the break of two Groves in the primary coil.

No response to the passage of the induction shock was observed until the secondary coil was pushed up to 8 cm., when a response of + 105 G. $\frac{1}{10}$ occurred. On pushing the coil to 5 cm., the response increased to + 350 G. $\frac{1}{10}$.

Closure	·015″–·02″	·02″–·0225″	·0225″–·0275″	·0275″–·0335″
Deflection	0 0	+ 70 G. $\frac{1}{10}$	+ 150 G. $\frac{1}{10}$	+ 260 G. $\frac{1}{10}$

Closure	·0335″–·0385″	·0385″–·0435″	·0435″–·05″
Deflection	+ 220 G. $\frac{1}{10}$	+ 15 G. $\frac{1}{10}$	+ 3 G. $\frac{1}{10}$

The temperature of the room subsequently affected the time relations of the response, as one hour afterwards the response was found to begin earlier.

Galvanometer closure . .	·01″–·015″	·015″–·0165″	·0165″–·018″
Deflection	0	+ 15	+ 150

The interval between nerve excitation and the commencement of the response was much longer than had been anticipated.

In the particular experiment just given, about ·006″ would be occupied by transmission along the nerve trunk, leaving ·01″ still unaccounted for. The influence of temperature seemed to indicate that the delay was connected with the low temperature of the fish. To obviate this, the Torpedoes were now kept in water at 12° C. It was now deemed necessary to repeat JOLYET's experiments on transmission.

Experiments on Transmission in the Electrical Nerves.

Three distinct sets of experiments were made on this subject.

A medium-sized vigorous Torpedo, 26 cm. × 17 cm., which had been kept for some days in water at 12° C., and gave smart shocks to the hand, was killed by punching the brain. The second electrical nerve was now prepared to its point of entry into the organ, and a wedge of this tissue was then cut out corresponding to the distribution of the nerve. The preparation was placed upon a glass plate, and the dorsal and ventral skin led off by cushions of kaolin. The nerve hung free in air, supported on the platinum exciting electrodes. It had been observed in previous experiments that the nerve was much less excitable in that part of its course which was in close proximity to the organ; the electrodes could not, therefore, be shifted with safety any great distance along the nerve.

Organ-current = + ·0042 R.

Induction coil without core in primary coil.

Secondary coil at 0. Two Groves in primary circuit.

EXCITATION 25 millims. from organ.

Closure . . .	·008″–·01″	·008″–·011″	·008″–·012″	·008″–on
Deflection . .	0 0	+ 170	+ ∞	+ 255 G. $\frac{1}{100}$

EXCITATION 12 millims from organ.

Closure . .	·007″–·008″	·008″–·009″	·008′–·01″	·008″–·011″	·008″–on
Deflection .	0	+ 55	+ 660	+ ∞	+ 85 G. $\frac{1}{100}$

EXCITATION 25 millims. from organ.

Closure	·008″–·01″	·008″–·011″	·008″–·012″
Deflection . . .	0	+ 220	+ ∞

EXCITATION 12 millims. from organ.

Closure	·007″–·008″	·008″–·009″	·009″–·01″
Deflection . . .	0	+ 60	+ 650

Another preparation was made from the organ of the opposite side of the same fish, of same character and dimensions. It was examined four hours after the first preparation had been begun, and gave the following results :—

EXCITATION 25 millims. from organ.

Closure	·008″–·01″	·01″–·012″	·01″–·0125″
Deflection . . .	0	0 0	+ 255

EXCITATION 12 millims. from organ.

Closure	·008″–·01″	·008″–·011″
Deflection . . .	+ 20	+ 195

In the fresh preparation the commencement of the electromotive change in the organ occurs $\frac{2}{1000}''$ earlier when the excitation of the nerve is 13 millims. nearer the organ. The excitatory process in the nerve thus travels at a rate of 6·5 metres per second. As the total electromotive change is less when the nerve is excited at the point nearer the organ, the actual commencement of the response may be too small to be observed; if there be any such error, it would imply that the above transmission rate is too rapid.

The second experiment, made four hours later, gives a transmission rate of 5·2 metres per second.

In another experiment on a nerve-organ preparation, made from the organ of a large Torpedo, the organ was kept at 5° C., whilst the nerve was kept at the temperature of room, 12° C.

EXCITATION of nerve 23 millims. from organ.

Closure	·016″–·017″	·017″–·018″	·018″–·019″	·019″–·02″
Deflection . . .	0 0	+ 90	+ 340	+ 480

EXCITATION of nerve 43 millims. from organ.

Closure	·016″–·017″	·017″–·018″	·018″–·019″	·019″–·02″	·02″–·021″	·021″–·022″
Deflection . . .	0	0	0	0	+ 50 + 65	+ 310

This gives $\frac{3}{1000}''$ as the time of transmission along 20 millims. of nerve, a rate of 6·6 metres per second.

A third experiment was made upon a nerve-organ preparation of a large vigorous Torpedo, measuring 52 cm. × 37 cm. The fish had been kept at 12° C., and the preparation differed from the preceding, since it consisted of *one* long uninjured column surrounded by cut columns. This column measured 6 centims. in length, and was 5 millims. in cross-section. The nerve entering it was carefully dissected out, and measured 8 centims. in length. The very large organ-current was allowed to subside, the experiment being deferred for an hour or more. A small patch of skin remained on each end of the column, and was led off in the usual way: O.C. = + ·0031 R. Induction apparatus as in preceding experiment.

EXCITATION of nerve 65 millims. from organ.

Closure	·01″–·012″	·01″–·014″	·014″–·016″	·016″–·018″	·018″–·02″	·02″–·022″
Deflection	0	0	0	+ 70	+ 140	+ ∞

EXCITATION of nerve 25 millims. from organ.

Closure	·01″–·012″	·011″–·013″	·012″–·014″
Deflection . . .	0	+ 120	+ ∞

EXCITATION of nerve 65 millims. from organ.

Closure	·015″–·016″	·016″–·017″	·017″–·018″
Deflection . . .	0	0	+ 70

EXCITATION of nerve 25 millims. from organ.

Closure	·011″–·012	·011″–·013″
Deflection . . .	+ 20	+ 220

The mean of these readings gives ·0055″ as the time occupied by transmission down 40 centims. of nerve—that is to say, the nervous impulse travels down the trunk of the electrical nerve at the rate of 7·3 metres per second.

This is practically the same result as that obtained by JOLYET (27) with vigorous summer fish, and gives substantial confirmation of his statements as to the slow rate of transmission in the electrical nerves of the Torpedo.

Experiments upon the Time of Delay.

When we have made the necessary deduction for transmission time, we find that an interval between excitation of nerve and response of organ still remains. In the particular experiments just given this amounts to ·006″. This is the "temps perdu," or time of delay, and we now pass to experiments having reference to the influence upon the length of this period of varying conditions of the organ itself. The principal conditions which affect the response in this respect—that is to say, which affect its commencement—may be considered under three heads:—(1) The temperature of the organ; (2) the strength of the nerve stimulus which evokes the response; (3) the vigour of the particular organ under investigation, and thus the vigour and size of the fish.

(1.) *Influence of temperature.*—A ready means of altering the temperature of the organ was secured by the use of a long water-box, through which water at different temperatures could be run, and which supported on its surface the organ preparation. To prevent any galvanometric disturbance through the metal of the box, the metal was covered with thin paper soaked in melted paraffin.

A nerve-organ preparation was made from a large Torpedo, 50 cm. × 34 cm., and placed upon the tubes in such a way that, whilst the organ rested upon the warming apparatus, the nerve hung free in air. Rheotome observations were made every five minutes, so as to allow time for shifting the keys, it being necessary to catch the beginning of the response. The organ was at 5° C. at the commencement; it was warmed to 20° C. by allowing water at 45° to flow through the apparatus, and when the quickening-up of the response had ceased it was re-cooled. The result is given in the following Table. In the first experiment the nerve was excited 45 millims. from the organ, so that $\frac{6}{1000}''$ must be deducted from the interval as transmission time. With this deduction the time of delay is only $\frac{5}{1000}''$ with an organ at 20° C., whereas it is $\frac{12}{1000}''$ to $\frac{14}{1000}''$ when the same organ is at 5° C.

In Experiment 2 the time of delay is to be reduced to $\frac{4}{1000}''$ at a temperature of 20° C., from $\frac{14}{1000}''$ at a temperature of 5° C., the transmission time being ·0065″.

Effect of Temperature on Interval of Time between Excitation of Nerve and Response of Organ.

Galvanometer closure :—	·009″ to ·01″	·01″ to ·011″	·011″ to ·012″	·012″ to ·013″	·013″ to ·014″	·014″ to ·015″	·015″ to ·016″	·016″ to ·017″	·017″ to ·018″	·018″ to ·019″	·019″ to ·020″	·020″ to ·021″	·021′ to ·022″
Time of observation.	*Experiment* 1.—Temperature of organ 5° C.												
4.10	..	..	..	..	..	..	0	0	0	+15	+60	+∞	..
	Temperature of organ slowly raised to 25° C.												
4.15	..	..	..	..	..	..	..	..	..	..	+330	..	..
4.20	..	..	..	..	..	..	..	0	..	+550	..	..	..
4.25	..	..	..	..	..	..	..	+410	..	..	..	..	..
4.30	..	..	..	..	..	..	+90	..	..	..	..	..	..
4.35	..	..	..	..	..	..	+∞	..	..	..	..	..	..
4.40	..	..	..	..	..	+680	..	..	..	..	..	..	..
4.45	..	..	..	0	+115	..	..	..	..	..	..	..	..
4.50	..	..	..	+ 50	..	..	..	..	..	..	..	..	..
4.55	..	..	..	+580	..	..	..	..	..	..	..	..	..
5	..	..	+180	..	..	..	..	..	..	..	..	..	..
	Temperature of organ slowly cooled to 5° C.												
5.5	..	..	0	..		..		..		..		..	..
5.10	..	..	..	+∞		..		..		..		..	..
5.15	..	..	..	+45		+∞		..		..		..	..
5.20	..	..	..	..		+30		..		..		..	..
5.25	..	..	..	..		..		+∞		..		..	..
5.30	..	..	..	..		..		+180		..		..	..
5.35	..	..	..	..		..		+130		..		..	..
5.40	..	..	..	..		..		0		..		..	..
5.45	..	..	..	..		..		..		+45		..	..
5.50	..	..	..	..		..		..		..		+420	..
Temperature of organ.	*Experiment* 2.—Fresh nerve-organ preparation.												
5° C.	..	..	..	..	..	..	..	..	..	..	..	..	+80
20° C.	0	+50	+110	..	..	..	..	..	..	..	..	..	..
7° C.	..	..	..	..	..	..	..	0	+70	+230	+340	+500	..

(2.) *Effect of strength of stimulus.*—In all the preceding experiments a stimulus had always been used of such strength as to procure a large response of the organ. The importance of procuring a maximal contraction in the investigation of similar phenomena in muscle is well known, but in endeavouring to obtain a maximal response of the electric organ to stimulation of its nerve we are confronted with a difficulty which is not present in the case of muscle. The range of stimuli which call forth minimal effects in the latter is very limited; in the nerve-organ preparation, on the other hand, it is large. The organ is a better interpreter than the muscle of the change produced in a nerve by the passage of an induction current. A far stronger stimulus is necessary to excite the nerve-organ than the nerve-muscle preparation; but, once this strength has been reached, the nerve-organ preparation responds more and more fully, the stronger the stimulus, until, with a damaging strength of current, the nerve itself is injured. The following experiment is selected from several to illustrate this.

A nerve-organ preparation was made from the organ of a large Torpedo, 42 cm. × 29 cm. The nerve was excited by the break of K_1, and K_2 was so placed as to be broken ·005″ later; the third key, K_3, was not used. The point of excitation was 20 millims. from the organ.

Primary circuit with 2 Groves.	Coil with core.	Effect.
Secondary coil, 20 centims. (150) . . .	G. $\frac{1}{10}$	0
" 17 " (300) . . .	G. $\frac{1}{10}$	+ 30
" 16 " (400) . . .	G. $\frac{1}{10}$	+ 700
" 15 " (700) . . .	G. $\frac{1}{10}$	+ ∞
" 17 " (300) . . .	G. $\frac{1}{10}$	+ 15
" 16·5 " (350) . . .	G. $\frac{1}{10}$	+ 45
" 16 " (400) . . .	G. $\frac{1}{10}$	+ 650
" 15 " (700) . . .	G. $\frac{1}{100}$	+ 110
" 12·5 " (2000) . .	G. $\frac{1}{100}$	+ ∞
" 12·5 " (2000) . .	G. $\frac{1}{1000}$	+ 90

(The numbers in brackets denote the relative strengths of the induction shocks.)

After an interval the strength of stimulus was still further increased.

Primary circuit with 2 Groves.	Coil with core.	Effect.
Secondary coil, 12·5 centims. (2000) . .	G. $\frac{1}{100}$	+ 365
" 10 " (4500) . .	G. $\frac{1}{100}$	+ 670
" 7·5 " (7000) . .	G. $\frac{1}{100}$	+ 620

With the secondary coil varied from 17 to 10 centims.—that is to say, with relative strengths of shock from 300 to 4500—the organ response became fuller, the stronger the stimulus. In the case of a large Torpedo the nerve bundles are of great thickness; the second nerve in the above experiment measured 5 millims. in diameter.

It is possible that the weaker induction current excites only the nerves upon the surface of the trunk; as the strength of the stimulus increases, more nerve fibres are traversed by currents of sufficient intensity to excite them. That this is not, however, all may be inferred from the existence of similar phenomena in the case of small newly-born Torpedoes, when the nerve bundles are small. Thus the minimal response of the organ to the excitation of the second nerve by the induction shock caused by the break of 4 Groves in the primary circuit occurred when the secondary coil stood at 24 centims., and the effect amounted to + 220 scale (Galv. without shunt); whereas the fullest response was only obtained when the secondary coil stood at 10 centims., and amounted to + 170 scale, G. $\frac{1}{100}$.

As in the case of muscle, so here we find that the magnitude of the response affects the period of delay. Thus in a small Torpedo the nerve was excited 10 millims. from the organ. The rheotome was used as in the temperature experiment, the galvanometer "window" (*i.e.*, interval between K_2 and K_3) being moved along so as to catch the commencement of the response.

Galvanometer closure.	·016″–·018″	·018″–·02″	·02″–·022″	·022″–·025″
Position of secondary coil, 20 centims. (150) . .	..	0	0	+ 10
,, ,, 17·5 ,, (320) . .	..	0	+ 110	
,, ,, 12·5 ,, (2000) . .	..	+ 15	+ ∞	
,, ,, 10 ,, (4500) . .	+ 5	+ 200		
,, ,, 5 ,, (9500) . .	+ 5			

The period of delay is here increased by ·004″ when the response is minimal.

(3.) *Influence of vigour and size of animal.*—The influence of the state of the fish is an obvious one: the organ responds more quickly, the more active and vigorous the fish used. It is needless to illustrate this, but a more interesting rider to the above is the influence of the size of the fish. In contrasting the results obtained from different fish, all in an equally good state, but of different size, it was found that the period of delay was always shorter, the larger the fish. Thus in four selected fish, all of which were kept at 12° C. for some days, all active and vigorous, giving sensible shocks to the hand, and in all of which the organ, as is shown below, responded very fully to nerve excitation, the following results were obtained.

a. Nerve-organ preparation from large Torpedo, 42 cm. × 29 cm. Total response to nerve excitation with Galv. $\frac{1}{100} = + 650$. The response commenced ·007″ to ·008″ after excitation of the nerve. The nerve was excited 20 millims. from organ, and, deducting ·003″ for transmission time, the period of delay is ·004″.

b. Nerve-organ preparation of medium-sized Torpedo, 26 cm. × 17 cm. Total response with Galv. $\frac{1}{100} = + 400$. The response commenced ·008″ to ·009″ after excitation of nerve. The nerve was excited 13 millims. from organ, and, deducting ·002″ for transmission time, the period of delay is ·006″.

c. Nerve-organ preparation of Torpedo 19 cm. × 12 cm. Total response, Galv. $\frac{1}{100} = +50$. The response commenced ·009″ after excitation. The transmission time was ·002″, and the period of delay ·007″.

d. Nerve-organ preparation from Torpedo born in laboratory five days before; active, giving distinct shocks to the hand; length 12 centims., breadth 8 centims. Total response, G. $\frac{1}{100} = +80$. The response commenced ·012″ after excitation, and, the transmission time being at most ·002″, the period of delay is ·01″.

The increased time of delay shown by the organ of the smaller Torpedoes might be explained as simply a case of the preceding results, which showed that, the smaller the total response, the later its apparent commencement; but a comparison of Cases *c.* and *d.* shows that such an explanation is insufficient, since the response in *d.* is larger than that in *c.*, yet it begins later.

These experiments upon the "time of delay" show the striking resemblance between the activity of the organ and that of muscle, nerve, &c. Experiments made eighteen months ago at Oxford, not yet published, upon the electromotive phenomena of skeletal Frog's muscle by the repeating rheotome method, showed that there is such a period of delay between the excitation of the nerve and the commencement of the electromotive change in the responding muscle. This period of delay was found to be about ·004″, but could be shortened by warmth and prolonged by cold. In the case of the cardiac tissue of the Frog the delay between direct excitation of the tissue and the appearance of an appreciable electromotive change under the proximal leading-off electrode varied with the distance between the exciting and leading-off electrode. When this distance was made very small the time was shortened to ·03″ (28). A longer interval still is found in the case of the Tortoise heart (29).

In the Dionæa a period of ·05″ intervenes between the excitation and the first appreciable electromotive change (30).

On the other hand, the Malapterurus discharge can be appreciated very soon after excitation of the organ itself; the time of delay here was with appropriate leading-off (31) shortened to ·002″.

The recognition of this delay is equivalent to the admission that existing methods of observation are inadequate, for it implies that with the best known methods of investigation there is an interval of time left unoccupied by any of the known phenomena of functional activity. The existence of a real time of rest in the molecular processes of the excitatory state, when these processes pass from nerve-trunks into nerve-end organs, is not scientifically admissible.

The apparent resting time may, perhaps, be considered as time during which these molecular processes are being transmitted along the excitable tissue very slowly. The blocking of the excitatory process in cardiac tissue by pressure, &c., is a case in point. The Torpedo presents us with a similar phenomenon, and this in spite of the fact that, once developed, the response of the electrical organ is far the largest, and therefore the most easily appreciated, vital electromotive change which has up to this time been examined by the rheotome method. The extraordinary prolongation of the delay by cold, although apparently connected with the condition of the nerve endings, may, however, be at least partially accounted for by the increased time of transmission down the nerve branches contained in the organ itself. It is hoped that an early opportunity will afford means for ascertaining to what extent this is the case.

Experiments upon the Character and Duration of the Response.

For information on these points the experiments had to be of such a character that the results should indicate the extent of the electromotive change as appreciated by the galvanometer at successive periods after excitation, and it was found that the most practicable plan consisted in massing together all the changes which occurred during a period of $\frac{1}{100}''$. The galvanometer circuit was closed for ·01″ at periods of ·01″, ·02″, ·03″, &c., after excitation of the nerve.

The results of such observations show that when the temperature of the organ is not below 10° C. the electromotive change develops with such rapidity that it reaches its maximum in less than one-hundredth of a second from the time at which it first becomes appreciable. If the change is expressed by a curve, the curve must thus be represented as rising very steeply from start to summit. The effect is always declining in the second and third hundredth of a second, and declines more slowly than it rose; but the rate of decline varies in different preparations, and thus the duration of the appreciable effect must vary. There is so marked a difference in this respect that, whereas in some cases no further change could be appreciated in the fourth hundredth of a second, in others a change was still perceived thirty seconds after the commencement of the response. This prolonged decline was, however, of such a character that it could be distinguished from the main decline of the organ response, and may be termed an "after-effect." Temperature, strength of response, and vigour and size of animal influence the above features of the response.

The influence of temperature is shown by the following experiment upon a nerve-organ preparation from a large Torpedo, 42 cm. × 31 cm., the response of which did not show the prolonged "after-effect." It was placed upon the apparatus previously described; the total response to excitation with Galv. $\frac{1}{100}$ was + 7·0 scale.

The quickening of the response as the temperature rose rendered it necessary to shorten the time of closure of the galvanometer circuit, which was thus fixed at ·005″.

Time of galvanometer closure :—	·005″–·001″	·01″–·015″	·015″–·02″	·02″–·025″	·025″–·03″	·03″–·035″	·035″–·04″
Temperature of organ. 5° C.	..	..	..	+ 100 G. $\frac{1}{10}$	+ 165 G. $\frac{1}{10}$	+ 80 G. $\frac{1}{10}$	+ 10 G. $\frac{1}{10}$
20° C.	..	+ 130 G. $\frac{1}{10}$	+ 40 G. $\frac{1}{10}$	..	..	..	..
10° C.	..	..	+ 100	+ 170 G. $\frac{1}{10}$	+ 40 G. $\frac{1}{10}$	+ 5 G. $\frac{1}{10}$	..
Interval of twenty-five minutes.							
8° C.	..	..	+ 240	+ ∞	+ 320	+ 30	+ 5
20° C.	..	+ ∞	+ 300	+ 70	+ trace	..	..

In all cases the maximal intensity of effect is reached in ·01″ from its commencement, but at a high temperature this maximum is reached in the first half of this time, viz., ·005″; at the low temperature it is reached in the second half of this time. The response is thus more suddenly developed at the higher temperature. This shortens the duration of the effect in the two cases, the decline of the effect not being so markedly affected as the rise is.

In the following experiment the minimal is compared with a maximal response of same organ. Small Torpedo, 13 cm. × 9 cm. Organ led off *in situ.* Induction apparatus with 2 Groves in primary coil (coil without core). Right side and left side used. Nerves excited *in situ.*

Galvanometer closure :—	·005″–·015″	·015″–·025″	·025″–·035″	·035″–·045″	·045″–·055″
Galv. $\frac{1}{10}$.					
Secondary coil 0 centims. . .	..	+ 370	+ 120	+ 25	+ trace
,, 7 ,, . .	..	+ 60	+ 20	0	..
Left organ used. 4 Groves in primary circuit of coil.					
Secondary coil 15 centims. .	..	+ 85	+ 6	0	..
,, 0 ,, .	..	+ ∞	+ 200	+ 50	+ trace
,, 15 ,, .	..	+ 100	+ 13	+ trace	..

The minimal differs from the larger response more in its duration than in the rate of its development. Expressed as a curve, it would represent the cut-off summit of the large response. There are sometimes considerable differences in this respect between the duration of the responses of the two organs of the same fish, and the larger response is always the longer one. Thus the left organ of a small Torpedo gave a total response of + 100 G. $\frac{1}{10}$. Its character and duration are expressed by the following readings :—

	Closure.	Deflection.
		Galvanometer without shunt.
Galvanometer closure	·014″–·016″	0
" "	·016–·018	+ 105 ; + 115
" "	·018–·2	+ 308 ; + 310
" "	·02 –·022	+ 360
" "	·022–·024	+ 95
" "	·024–·026	+ 90
" "	·026–·03	+ trace
" "	·03 on	0

The right organ of the animal gave a response of + 50 with G. $\frac{1}{100}$, and the decline of this response is much slower.

	Closure.	Deflection.
		G. $\frac{1}{10}$.
Galvanometer closure	·014″–·016″	0
" "	·016–·018	+ 95
" "	·018–·02	+ 380
" "	·02 –·03	+ 220
" "	·03 –·04	+ 15
" "	·04 –·05	+ 10
" "	·05 –·06	. .

Even a large Torpedo may give a response of short duration, but the response in such cases is always small in amount, and is, in fact, minimal.

Apart from the necessary effect of the vigour of the organ, there is that of the size of the fish, and so of the columns. The larger the fish, other things being equal, the longer the duration of what must be considered as the true response. This is shown by the results embodied in the annexed Table, in which the length of the columns of the organ is given.

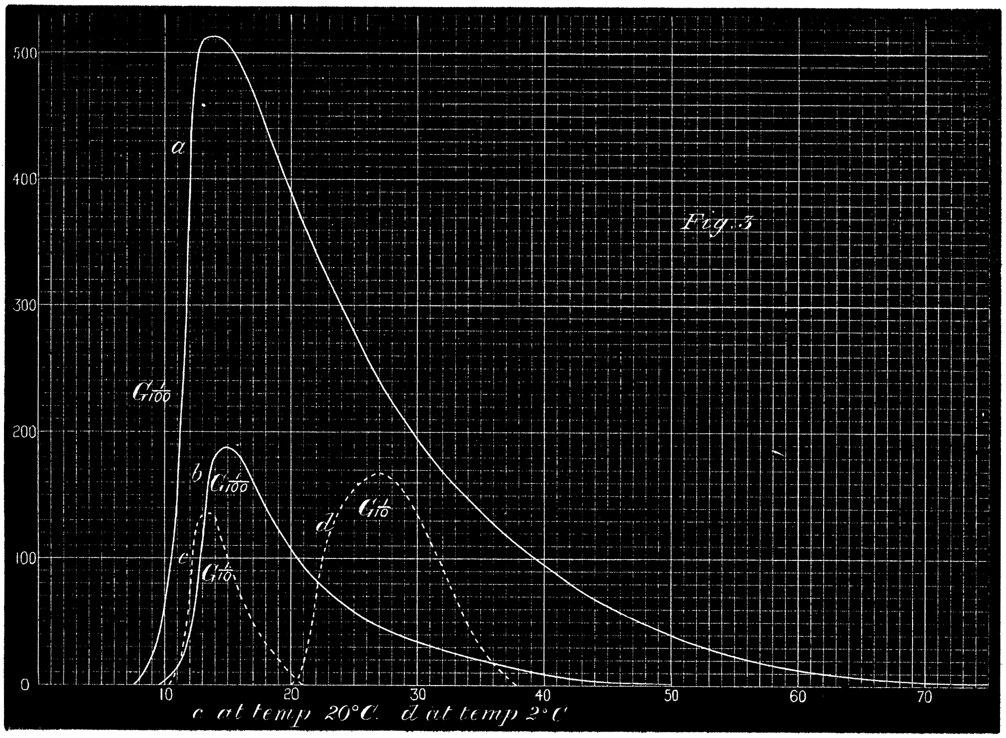
l = length of column. r = total response.

Time of galvanometer closure:	·01″–·015″	·015″–·02″	·02″–·025″	·025″–·03″	·03″–·035″	·035″–·04″	·04″–·045″	·045″–·05″
Small Torpedo, l = 12 mm. G. $\frac{1}{10}$.	+ 12	+ 492	+ 400	+ 45	+ 20	+ 20	+ 4	. .
Ditto. G. $\frac{1}{10}$	0	+ 400	+ 470	+ 60	+ 10	+ trace	. .	. .

Closure :—	·01″–·02″	·02″–·03″	·03″–·04″	·04″–·05″	·05″–·06″	·06″–·07″	
Medium-sized Torpedo, $l = 25$ mm.	+ ∞ G. $\frac{1}{10}$ + 185 G. $\frac{1}{100}$	+ 620 G. $\frac{1}{10}$	+ 190 G. $\frac{1}{10}$	+ 16 G. $\frac{1}{10}$	+ 5 G. $\frac{1}{10}$		
”	+ ∞ G. $\frac{1}{10}$ + 105 G. $\frac{1}{100}$	+ 740 G. $\frac{1}{10}$	+ 155 G. $\frac{1}{10}$	+ 35 G. $\frac{1}{10}$	+ 4		
”	+ ∞ G. $\frac{1}{10}$ + 155 G. $\frac{1}{100}$	+ 465 G. $\frac{1}{10}$	+ 22 G. $\frac{1}{10}$	+ 5 G. $\frac{1}{10}$	+ trace		
Large Torpedo, $l = 53$ mm.	+ 700 G. $\frac{1}{100}$	+ 450 G. $\frac{1}{100}$	+ 120 G. $\frac{1}{100}$	+ 23 G. $\frac{1}{100}$	+ 7 G. $\frac{1}{100}$	+ 13 G. $\frac{1}{10}$ + trace	followed by after-effect
”	+ 510 G. $\frac{1}{100}$	+ 305 G. $\frac{1}{100}$	+ 165 G. $\frac{1}{100}$	+ 60 G. $\frac{1}{100}$	+ 25 G. $\frac{1}{100}$	+ 15 G. $\frac{1}{100}$	”

The characters of the vigorous response are given by the above readings; and by taking the deflections as ordinates, and the times of closure as abscissæ, a curve may be drawn which will indicate the response. Such curves are given in fig. 3, and show the rapid rise and slower decline of the electromotive change. In the figure the curve a is that of a preparation made from a large vigorous Torpedo, b is that

Fig. 3.



The numbers 100, 200, 300, &c., indicate scale of Galvanometer. The numbers 10, 20, 30, 40, &c., correspond to thousandths of seconds; 0 representing the moment of nerve excitation.

The transmission time in a and $b = \frac{3}{1000}$″.

of one from a medium-sized vigorous fish. The curves *c* and *d* are short curves representing the change in the organ of a large Torpedo, *c* being that of the organ at 20° C., and *d* that of the organ at 5° C. In the curve *a* the ordinates represent the readings of the galvanometer with the $\frac{1}{100}$ shunt, and the curve corresponds in duration to the duration of the effect as ascertained by MAREY.

In reality, however, the effect is prolonged far beyond seven hundredths of a second. This prolongation was apparently not capable of affecting MAREY'S "physiological" galvanoscope, viz., the muscle-nerve preparation; its existence is, however, easily ascertained by the galvanometric method when the galvanometer is used without the shunt, and, owing to its slow subsidence, it produces well-marked galvanometric deflections. The large response has a long tail, if the expression may be used. It is termed here the "after-effect" of the response.

The after-effect of the response.—The fast-moving rheotome previously used was not adapted to the examination of the after-effect, since the range of the instrument did not extend beyond ·08″. The rheotome was therefore now used for giving an induction shock of constant intensity and duration for purposes of excitation, and the key K_2 was placed so as to be broken ·06″ after the exciting key K_1. For K_3 there was substituted a key which could be closed quickly by the hand, this closure being effected at various intervals after the release of the traveller of the rheotome. Successive experiments were now made, first with the galvanometer circuit closed, but short-circuited by K_2; the deflection obtained thus indicated the effect which followed the excitation from ·06″ onwards. The galvanometer circuit was then closed 1″ after the release of the rheotome, and the resulting deflection observed. The difference between the two readings was a measure of the amount of the slowly subsiding change during the period ·06″ to 1″. The same plan was adopted with a closure 2″, 3″, 4″, &c., after excitation.

As the after-effect following a response is a new feature of the excitatory change, it will be advisable to describe an experiment with some detail.

A block of organ was cut from a large vigorous Torpedo; the block measured 53 millims. in the direction of the columns, and was 35 millims. in width and 30 millims. in thickness. Its cut surface showed four injured columns, and, consequently, it contained twelve uninjured columns, all supplied by branches of the second electrical nerve. This was excited 20 millims. from its point of entry into the organ by the break of 2 Groves in the primary circuit of the induction apparatus at intervals of three minutes. The organ-current obtained by leading off the skin-covered ends of the columns amounted to + ·0125 R. It subsided rapidly, and then slowly, but sank after each excitation, and was compensated. This fall is given in terms of the galvanometer scale, it having been ascertained that a deflection of 130 scale corresponded to a difference of potential = ·0003 R. The fall is, of course, opposed to the after-effect. The galvanometer was used without its shunt.

Galvanometer closed] $\frac{6}{100}$″ after excitation	+ 650	
Fall of organ-current, which subsided slowly, until in three minutes it sank 150 scale. It was then compensated.		(·06″–1″) 350
Galvanometer closed 1″ after excitation . .	+ 300	
Fall of organ-current as before = 80 scale.		(1″–2″) 90
Galvanometer closed 2″ after excitation . .	+ 210	
Fall of organ-current = 75 scale.		(2″–3″) 45
Galvanometer closed 3″ after excitation . .	+ 165	
Fall of organ-current = 75 scale.		(3″–4″) 45
Galvanometer closed 4″ after excitation . .	+ 120	

Experiment repeated:—

Galvanometer closed $\frac{6}{100}$″ after excitation	+ 640	
Fall of organ-current = 60 scale.		(·06″–1″) 400
Galvanometer closed 1″ after excitation . .	+ 250	
Fall of organ-current = 45 scale.		(1″–2″) 60
Galvanometer closed 2″ after excitation . .	+ 190	
Fall of organ-current = 35 scale.		(2″–3″) 35
Galvanometer closed 3″ after excitation . .	+ 155	
Fall of organ-current = 35 scale.		

It was evidently necessary to extend the observations far beyond the limit of 3″, and this was now done in a similar preparation made from the organ of the other side of the same large Torpedo. In this the organ-current was very steady, the preparation having been made an hour before, and being first used for a rheotome experimen-on the duration of the first part of the response. It amounted to ·01 R., and was observed to sink after each excitation; the decline, being opposed to the after-effect, was only indicated after the return of the needle to zero, which occurred in about half a minute, by a slow movement of the needle in the opposite direction, amounting in three minutes to 75 scale.

Galvanometer	closed	·06″	after	excitation	+ ∞ (+120 G. $\frac{1}{10}$)	
						(·06″–1″) 450
,,	,,	1″	,,	,,	+ 750	
						(1″–2″) 175
,,	,,	2″	,,	,,	+ 575	
						(2″–3′) 125
,,	,,	3″	,,	,,	+ 450	
						(3″–4″) 85
,,	,,	4″	,,	,,	+ 365	
						(4″–5″) 95
,,	,,	5″	,,	,,	+ 270	
						(5″–10″) 65
,,	,,	10″	,,	,,	+ 205	
						(10″–15″) 45
,,	,,	15″	,,	,,	+ 160	
						(15″–20″) 25
,,	,,	20″	,,	,,	+ 135	
						(20″–25″) 35
,,	,,	25″	,,	,,	+ 100	
						(25″–30″) 25
,,	,,	30′	,,	,,	+ 75	

The difference between the successive readings is given in the right-hand column, from which it is seen that the after-effect sinks much more rapidly during the first 5″ than subsequently, and that with regard to this first five seconds its fall is most rapid in the first two seconds.

The great prolongation of the after-effect allowed the employment of another method of reading, which had been used with good results in the investigation of prolonged polarisation after-effects. The "falling time" of the galvanometer needle was known to be fifteen seconds. The galvanometer was, therefore, closed for fifteen seconds, and the closure followed by a break of the circuit for the same time, this by a re-closure, and so on.

The deflections obtained are strictly comparable, each being procured with the galvanometer needle at zero, and any instrumental error thus obviated.

Galvanometer	circuit	closed	1″–15″.	Effect	+ 650
,,	,,	broken	15″–30″	,, ..	+ 130
,,	,,	closed	30″–45″	,,	+ 60
,,	,,	broken	45″–60″	,, ..	+ 5
,,	,,	closed	60″–75″	,,	+ trace, followed by –.

The two gaps 15″–30″ and 45″–60″ were filled up by repeating the experiment, reversing the times of closure and of break.

Another experiment on the same subject was suggested by the applicability of this method—an experiment in which the nerve should be excited mechanically.

Such mechanical excitation had been tried with the aid of Tigerstedt's excitor (32), modified for this special research, but without any good result—the low excitability of the nerve being a bar to the use of this method, as only feeble and uncertain organ responses followed excitation of this character. It had, however, been noticed that section of the nerve always produced a large response of the organ. The investigation of the after-effect following the response evoked by section of the nerve was therefore quite practicable. In order to follow the change in the after-effect, the sensibility of the galvanometer was decreased by raising the control magnet, so that the falling time of the needle should be ten instead of fifteen seconds.

With the galvanometer circuit closed, the nerve of a nerve-organ preparation from a large vigorous Torpedo was divided with sharp scissors 35 millims. from the organ; a very large response followed the section, the deflection amounting to + 750 G. $\frac{1}{100}$.

On comparing this with the fullest response to electrical excitation which could be obtained in the same preparation, it was found to be of about equal amount, the latter giving + 670 G. $\frac{1}{100}$.

The galvanometer circuit was now closed and opened alternately at stated intervals after section of the nerve, and the prolonged after-effect thus observed:—

Circuit	closed	5″	to	15″	after section	+ 440
,,	broken . . .	15″		25″	,, ,,	. .
,,	closed	25″		35″	,, ,,	+ 230
,,	broken . . .	35″		45″	,, ,,	. .
,,	closed	45″		55″	,, ,,	+ 160
,,	broken . . .	55″		65″	,, ,,	. .
,,	closed	65″		75″	,, ,,	+ 110
,,	broken . . .	75″		85″	,, ,,	. .
,,	closed	85″		95″	,, ,,	+ 65
,,	broken . . .	95″		105″	,, ,,	. .
,,	closed	105″		115″	,, ,,	+ 20

The prolongation of the after-effect, or "excitation remainder," is most marked in this experiment. It will be noticed that it is always present when the response is such as to reach a great maximum of intensity, and this suggests the inquiry whether a similar change cannot be brought about by the passage through the tissue of an intense current of short duration. The experiments of DU BOIS-REYMOND previously referred to show that such is the case. To this subject we now proceed.

III. *The Electromotive Changes following the Passage of Electrical Currents through the Organ.*

The term "secondary" electromotive is applied by DU BOIS-REYMOND (33) to the changes produced in excitable tissues by the passage through these of electrical currents. The work of DU BOIS-REYMOND, followed by that of HERMANN (34), HERING (35), and BIEDERMANN (36), has shown that, in addition to the ordinary phenomena of electrolytic polarisation, there are special electromotive changes which are intimately connected with the vitality of the tissues experimented upon. The main fact may be broadly stated thus: the passage of a galvanic current of considerable intensity, and of short duration, through a tract of muscle or nerve, is followed not only by the electromotive changes accompanying ordinary polarisation, but by a prolonged electromotive change which presents the characteristics of being the electrical index of a prolonged excitation. This is not, strictly speaking, the view which DU BOIS-REYMOND took as to the nature of his discovery. According to the upholders of the molecular hypothesis, the passage of a galvanic current is followed by two sorts of polarisation—the ordinary negative polarisation, and a special positive polarisation, this last being an alteration in the condition of the vital electromotive molecules. It is simpler to call the latter effect an excitatory effect, and it will be thus designated here. The earlier work of DU BOIS-REYMOND has been succeeded by the publication of the results of similar experiments carried out upon the electrical organ of the Torpedo (37), which show that here, too, the passage of an intense current of short duration is followed by electromotive changes of two kinds, those due to electrolytic polarisation, and special phenomena, due, probably, to excitation of the tissue. The latter reveal themselves as prolonged changes, in which the dorsal surfaces of the columns are galvanometrically positive to the ventral.

A polarising current directed through the tissue in the direction of that of the organ response is the most effectual for the production of the change in question. Such a polarising current has been termed by du Bois-Reymond "homodromous"; it will be denoted in this work by the sign (+), since the cathode of the polarising circuit is on the dorsal surface of the columns. A current oppositely directed through the organ columns will be denoted by the sign (—).

If the phenomena of electrolytic polarisation, and these only, are present in the led-through tract, then a (+) polarising current will be followed by a (—) after-effect, a (—) polarising current by a (+) after-effect, the signs referring in all cases to the condition of the dorsal electrode.

Such is the case in the following example, which is given to show the polarisable character of the tissue.

A strip of organ, consisting of several entire columns, having been prepared from a small Torpedo, and measuring 13 mm. in length and 2 mm. in thickness, was placed upon a glass plate and led off as usual from the dorsal and ventral ends. Upon the kaolin plugs of the leading-off electrodes were placed the kaolin plugs of another pair of non-polarisable electrodes, which served to lead the polarising current through the tissue. A paraffin switch of the kind used by Hermann was introduced into the galvanometer and polarising circuits. By its movement the galvanometer circuit was broken, and the polarising circuit closed about $\frac{1}{10}''$ afterwards; the return of the switch broke the polarising and then re-closed the galvanometer circuit. The movement of the switch was effected in the one direction by the hand, in the other by an elastic spring. The sensibility of the galvanometer was the same as in the early experiments, and the falling time of the needle was fifteen seconds. The effect was therefore accurately indicated by reading the amount of the deflection every fifteen seconds.

Polarising current.	15″ readings.	15″ readings.	15″ readings.
4 Groves, duration ½″, direction (+), galvanometer $\frac{1}{10}$	− 265 − 170 − 130 − 100 − 70 − 50 − 30	− 230 − 110 − 50 − 30 − 15	− 230 − 110 − 40 − 10
4 Groves, duration 1″, direction (+), galvanometer $\frac{1}{10}$	− 360 − 200 − 110 − 70 − 45 − 30	− 380 − 200 − 100 − 60 − 40 − 20	− 400 − 200 − 110 − 60 − 40 − 20
4 Groves, direction (−), galvanometer $\frac{1}{10}$	duration ½″ + 170 + 70 + 45	duration 2″ + 260 + 120 + 60 + 40	duration 3″ + ∞ + 350 + 190 + 140 + 110 + 100 + 85 + 80

Besides showing the susceptibility of the tissue to polarisation, and the subsidence of the effect, the experiment shows that the (+) polarising current is more effectual than the (−) for the production of the polarisation after-effect. The polarising current was increased to 6 Groves without altering the result as regards the direction of the after-effect. When, however, the current of 6 Groves was led through narrow strips of fresh tissue cut from the organs of vigorous fish, a different result was obtained. The passage of the (+) current was now followed by a (+) after-effect; on repeating the experiment, the effect soon disappeared, and only the (−) polarisation after-effect was observed. Two examples may be given.

Strips of organ, 22 mm. long and 3 mm. thick, were cut from the organ of a medium-sized fish. Organ-current, + ·0062 R.

Polarising current.	Duration.				
	½″	¼″	¼″	¼″	¼″
6 Groves, galvanometer $\frac{1}{10}$ (+)	− 70	+ 190	− 65	− 110	− 190

Polarising current.	Duration ¼″
Galvanometer $\frac{1}{10}$ (−)	+ 135

Another strip, 30 mm. long and 4 mm. in thickness.

Polarising current.	Duration.				
	¼″	½″	¼″	¼″	¼″
6 Groves (+), galvanometer $\frac{1}{10}$	+ 150	− 40	+ 110	+ 30 − 20	− 120

The strip was now pared down in the direction of the columns, so as to reduce it to a long strip only 2 mm. in thickness.

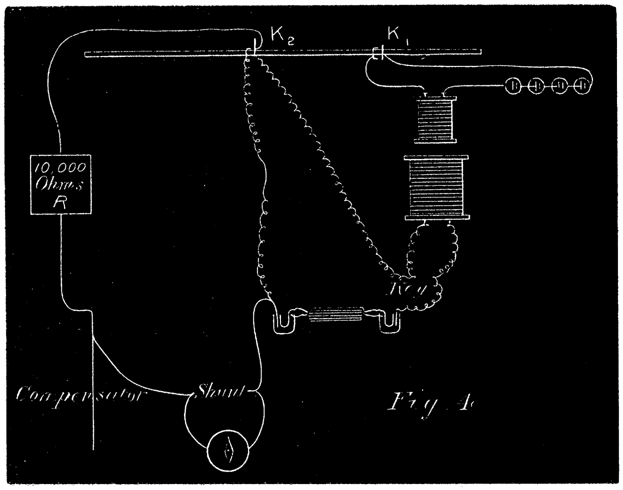
Polarising current.	Duration.			
	¼″	¼″	¼″	¼″
6 Groves (+), galvanometer $\frac{1}{10}$	+ ∞	+ 400	− 100	− 160

Polarising current.	Very short.	Very short.
6 Groves (+), galvanometer $\frac{1}{10}$	+ 220	− 50

In all these cases further experiments with (+) currents gave only (−) after-effects. It is obvious that, whereas the (+) after-effect obtained with (−) currents was only the ordinary change of electrolytic polarisation, the (+) after-effect following (+) currents was something of a different nature, and was the effect noticed by du Bois-Reymond (38). In order to obtain it with more distinctness, it was necessary to use stronger polarising currents, but unfortunately more than 6 Groves were not obtainable. In considering the question of its production, and especially the characteristics of the current which produced it, the essential feature is seen to be the necessity of using polarising currents of short duration and great intensity. The reason is probably that with these the ordinary phenomena of electrolytic polarisation are not developed in an overwhelming degree. If the polarising currents are long, the polarisation after-effects are so marked as to swamp every other electromotive change. This being the case, the use of strong induction currents at once suggested itself. The experiments of du Bois-Reymond with repeated induction currents (39) gave every hope of success, and, as the ordinary electrolytic phenomena would be reduced to a minimum, the confusion between polarisation and other changes would be largely avoided.

The after-effect of the passage of induction shocks.—In order to carry out the experiment, the previous method was modified as follows:—The spring myograph was substituted for the paraffin switch. The key K_1 of the instrument was placed in the primary circuit of the induction apparatus. The galvanometer circuit was arranged as in fig. 4, the secondary coil being directly in the circuit, the induction shock being short-circuited by the key K_2 so as to prevent any disturbance of the instrument; to render this effectual, a resistance of 10,000 ohms was introduced between the key and the galvanometer. It was ascertained that with K_2 placed so as to be opened ·003″ after K_1 no appreciable effect was observed by the passage of a strong induction shock through the electrodes. By this method an induction shock could be led through the tissue, and the galvanometer would respond to all electromotive changes which followed that at an interval of ·003″. The same electrodes must obviously be used both for leading in and leading off. It was ascertained by experiment that any after-effect due to polarisation in these was extremely small.

Fig. 4.



From the organ of a medium-sized fish a strip was cut measuring 16 mm. in length, 7 mm. in width, and 2 mm. in thickness. The induction apparatus was used with 3 Groves in the primary coil; the secondary coil stood at 5 cm., organ-current + ·006 R.

Direction of induction shock through tissue			After-effect.
Direction of induction shock through tissue	(−)	Galv. $\frac{1}{10}$	+ 150
,, ,, ,, ,,	(+)	,,	+ 650
,, ,, ,, ,,	(−)	,,	+ 180
,, ,, ,, ,,	(+)	,,	+ 730

This (+) after-effect thus occurred with both (+) and (−) currents, but the former were far the most effectual for its production. Since the polarisation phenomena are by this method reduced to a minimum, the after-effects here observed are due to the particular change which the tissue shows apart from those. This change was noticed to be prolonged in character, like the after-effect which follows the nerve-organ response. Its duration and rate of subsidence were investigated in the same way as the latter had been, by closing the galvanometer circuit for 15″ after excitation, opening it for 15″, re-closing it for 15″, &c. The readings of the deflections obtained in four experiments were as follows :—

	Closure.	Experiment 1.	Experiment 2.
Direction of induction shock coil 5 cm. (+) Galv. $\frac{1}{10}$	·003″–15″	+ ∞, sinking to + 500	+ ∞, sinking to + 400
	30″–45″	+ 500	+ 110
	60″–75″	+ 98	+ 62
	90″–105″	+ 58	+ 40
		(+) Experiment 3.	(−) Experiment 4.
Direction of induction shock coil 7 cm. Galv. $\frac{1}{10}$	·003″–15″	+ 510, sinking to + 260	+ 225, sinking to + 170
	30″–45″	+ 85	+ 68
	50″–75″	+ 52	+ 40
	90″–105″	+ 33	+ 25

The induction shock is thus followed by a prolonged electromotive change which subsides at first rapidly and then more slowly, thus resembling the after-effect of the response. It differs from this as regards its duration, as it lasts somewhat longer. As it can be produced by induction currents in either direction, (+) or (−), it can only be an excitatory change. It is always of the character which the excitatory changes of the organ follow, the dorsal surface of the organ becoming (+). It is remarkable that it is more effectually produced by (+) than by (−) induction currents. This does not prevent our regarding it as an excitation phenomenon, for the nerve itself is more readily excited by descending than by ascending currents, and a (+) current through the organ may play the part of a descending one for the majority of nerves and nerve endings which lie in its path. If it is an excitation phenomenon, the organ must behave like the nerve with respect to increasing strength of stimulus. That this is so the following experiment shows, the numbers indicating readings of the position of the light on the scale made at intervals of 15″ after the maximum deflection had been reached. Strip of organ, 36 mm. long, 5 mm. wide.

FIVE Groves in Primary Coil.

	Deflections.	
Secondary coil, 12 centims. (+) G. without shunt	0	
" " 11 " " " "	+ 65	15″ readings.
	+ 15	
	0	
" " 10 " " " "	+ 105	15″ readings.
	+ 40	
	0	
" " " " " " "	+ 90	15″ readings.
	+ 35	
	0	
" " 9 " " " "	+ 350	15″ readings.
	+ 180	
	+ 120	
	+ 90	
	+ 85	

The galvanometer circuit was now closed, and opened alternate 15″.

	Closure.	Deflections.
8 cm. (+)	·003″–15″	+ 550
Interval during which the galvanometer circuit was broken	..	..
Galvanometer circuit re-closed	30″–45″	+ 110
" " broken	..	..
" " re-closed	60″–75″	+ 50
" " broken	..	..
" " re-closed	90″–105″	+ 5
7 cm. (+)	1″–15″	+ ∞
	30″–45″	+ 300
	60″–95″	+ 180
	90″–105″	+ 125
	120″–135″	+ 95
5 cm. (+) G. $\frac{1}{10}$	..	+ 270
"	..	+ 160
"	15″ readings	+ 108
"	..	+ 70
"	..	+ 55
"	..	+ 35
0 (+) G. $\frac{1}{10}$	1″–15″	+ ∞
"	30″–45″	+ 240
"	60″–75″	+ 110
"	90″–105″	+ 60
"	120″–135″	+ 40

The effect, when small in amount, lasts only 30″; it increases in amount as the induction shock increases in intensity, and, when very large, lasts over 2′. The same is true of the effects produced by the passage of (−) induction shocks of different intensity, but in this case a stronger induction shock must be used to secure the production of the effect than is necessary when (+) induction shocks are employed.

The following experiment, made upon a strip 45 millims. long and 5 millims. broad, illustrates this point. Organ-current, + ·009 R.

Six Groves in Primary Circuit.

Secondary coil	Centims.		G.	Deflections (15″ readings).	
Secondary coil,	16 centims.	(+)	G. without shunt	0	
,, ,,	15	,,	,, ,,	0	
,, ,,	14	,,	,, ,,	+ 300	15″ readings.
			,, ,,	+ 80	
			,, ,,	+ trace	
,, ,,	,,	(−)	,, ,,	0	
,, ,,	12	(+)	,, ,,	+ ∞	15″ readings.
			,, ,,	+ 285	
			,, ,,	+ 160	
			,, ,,	+ 20	
,, ,,	,,	(−)	,, ,,	+ 150	15″ readings.
			,, ,,	+ 10	
			,, ,,	0	

The effect is thus dependent upon the intensity of the current, which must vary with the dimensions of the preparation, so that an induction current which produces no effect upon a large thick block of tissue will produce an effect upon a long narrow strip cut from this block. Such a thin strip can be procured most readily from the organ of a small Torpedo, and it was with a preparation of this kind that the largest effects were observed. Thus a strip 15 millims. long, and only a little more than a millimetre wide, gave the following result :—

Six Groves in Primary Coil.

	Deflections.	
Secondary coil, 8 cm. (+) G. $\frac{1}{100}$	+ ∞	
,,	+ 240	15″ readings.
,,	+ 100	
,,	+ 20	

As in the case of the nerve-organ response, so here the effect is more pronounced when the strip is cut from a vigorous Torpedo, but it may still be obtained in a strip which has been left for 24 hours. The same strip as that used for the preceding experiment gave the following results when examined at intervals of 15 and 24 hours :—

Six Groves in Primary Coil Circuit.

			Slowly subsiding.
Secondary coil, 8 cm.	(+)	G. $\frac{1}{10}$	+ 600
,, ,, ,,	(−)	,,	+ 250
,, ,, 24 hours later, 8 cm.	(+)		0
,, ,, ,, ,, 5 cm.	(+)	G. all in	+ 545
,, ,, ,, ,, ,,	(−)	,,	+ 160

The effect entirely disappears when the tissue is immersed for 15″ in hot water.

The effect being obviously an excitatory one, it is conceivable that it is nothing more than the response of the organ to the excitation of the nerve branches contained in the tissue. A strip of organ contains a very large number of nerve fibres, which may be traversed by the induction shock, and, if so, may be excited; on the other hand, the result may be due to excitation of the plates themselves. Any such confusion in the case of muscle and nerve is obviated by the use of curare, but this drug does not appear to be applicable to the Torpedo (40). In order, then, to determine whether or no the after-effect is a nerve-organ response, its character must be determined precisely as that of the true nerve-organ response has been determined—namely, by the rheotome method. The presence of the induction shock during the first three hundredths of a second is, however, a serious difficulty in the prosecution of such rheotome experiments. It is, however, quite easy to determine the relative values of the effect as disclosed by closures of from ·03″ to ·05″ and from ·05″ to ·07″; and it appears that the effect is always visible during these periods, but, though quite appreciable, it is not so strong as the nerve-organ response would be at the periods in question, especially when we take into consideration the magnitude of the total effect. Thus the largest nerve-organ response was imperceptible with the galvanometer ($\frac{1}{100}$ shunt) after an interval of one second. In the experiment to be next given the after-effect was so large that after an interval of one minute it was perceptible with the galvanometer $\frac{1}{100}$ shunt. There should, therefore, be a very large effect if the galvanometer circuit be closed for from ·03″–·05″ after the excitation. As a matter of fact, the effect is small under these conditions.

STRIP of Tissue from Small Torpedo. Six Groves in Circuit of Primary Coil.

	Closure.		
Secondary coil, 9·5 cm. (+) G. $\frac{1}{100}$		+ 420	15″ readings.
,, ...		+ 190	
,, ...		+ 70	
,, ...		+ 30	
,, ...		+ 10	
,, ,, 8 cm. (+) G. $\frac{1}{10}$ . .	·03″–·05″	+ 50	
,, ,, ,, (+) ,, . .	·03″–·07″	+ 250	

It had been ascertained that, with a closure of ·03″–·05″, the passage of the induction shock, through the electrodes only, produced no galvanometric effect; the deflections were thus undoubtedly due to the presence of the after-effect. The amount of the after-effect from ·03″–·07″ shows that in this case there was an increase between ·05″ and ·07″. This was, however, by no means a uniform result. In the first of the two experiments to be next referred to the after-effect was equal during the two periods, in the second it was greater during the earlier closure.

STRIP of Tissue from Large Torpedo. Five Groves in Circuit of Primary Coil.

Secondary coil, 0 cm. (+) G. $\frac{1}{10}$	+ 310	15″ readings.
,,	+ 150	
,,	+ 80	
,,	+ 45	
,,	+ 25	
,,	+ 8	

	Closure.	
,, ,, ,, (+) G. without shunt	·03″–·07″	+ 65
,, ,, ,, (+) ,, ,,	·03″–·05″	+ 30
,, ,, ,, (+) ,, ,,	·03″–·07″	+ 45

STRIP of Tissue from large vigorous Torpedo. Five Groves in Circuit of Primary Coil.

	Closure.	Alternate 15″ closure.
Secondary coil, 0 cm. (+) G. $\frac{1}{10}$	·003″–15″	+ ∞
,,	30″–45″	+ 240
,,	60″–75″	+ 112
,,	90″–105″	+ 60
,,	120″–135″	+ 40

	Closure.	
,, ,, ,, (+) G. all in	·03″–·05″	+ 200
,, ,, ,, (+) ,,	·05″–·07″	+ 65
,, ,, ,, (+) ,,	·03″–·05″	+ 190
,, ,, ,, (+) ,,	·05″–·07″	+ 105

If we attempt to get still nearer in time to the excitation, and ascertain if a response is perceptible during such intervals as 0″ to ·01″ and ·01″ to ·02″ after the passage of the induction shock, this induction shock itself becomes perceptible. The only method of getting such information is thus to compare the relative deflections produced by the passage through the experimental circuit of (+) and (—) induction shocks respectively. If the excitation effect is present during the first two hundredths of a second, it must add to the (+) and diminish the (—) deflection. This DU BOIS-REYMOND has done, and he finds that the (+) induction current is considerably greater than the (—) one. This, he says, cannot be explained, and is a case of "irreciprocal conduction." A simpler explanation, and one more in accordance with present knowledge, seems to be indicated by the above considerations, and would be supported here, were it not for the astonishing circumstance that no evidence was furnished by our experiments of there being in the conditions under which we worked any such remarkable difference between the apparent strengths of the (+) and (—) induction currents. It is not stated in DU BOIS-REYMOND'S experiments whether he cut off the after-effect which follows the passage of the induction current by closing the galvanometer circuit only up to ·05″ after the shock. If he did not do so, the full after-effect must obviously be present, and his results are thus explained (41). If he did so, then his results were not observed at Arcachon with winter Torpedoes; but perhaps a future investigation will disclose them.

Thus a strip of Torpedo, 60 mm. long, gave the following results, when the rheotome was arranged so as to break the galvanometer circuit for good at ·05″ after the passage of the induction shock, the after-effect being thus excluded from observation:—

The two readings were always taken in the same direction, the galvanometer wires being reversed so as to admit this in the case of both (+) and (−) shocks.

Five Groves in Primary Coil.

			Deflections.
Secondary coil, 10 centims.	(+)	G. $\frac{1}{100}$	440
„ „	(−)	„	435
„ 0 centim.	(+)	G. $\frac{1}{1000}$	185
„ „	(−)	„	185

In another preparation experiments were carried out upon the whole organ and a cut strip.

Two Groves in Primary Circuit.

		Deflections.
Secondary coil, 5 centims., G. $\frac{1}{100}$	(−)	420
„ „ „	(+)	410
„ „ „	(−)	408
Whole organ	(+)	415
„	(−)	412
„ 0 centim., G. $\frac{1}{100}$	(+)	622
„ „ „	(−)	626
Cut strip, 0 centim., ·0055 R.	(+)	492
„ „ „	(−)	483

An important fact must be taken into consideration in this connection, since it is not inconsistent with so-called "irreciprocal" conduction, namely that the (+) induction current is more efficacious than the (−) one in producing the after-effect. How far this distinction is related to the difference of behaviour of the nerve itself to ascending and descending exciting currents can only be decided by experiments specially contrived to bear upon the subject. It is, however, more satisfactory to approach the whole subject of irreciprocity from the point of view of irreciprocal excitation than from that of irreciprocal conduction. Such experiments will have to deal with the production of states of anelectrotonus and catelectrotonus in the organ. They were not attempted in the present research.

There can, however, be little doubt that the organ is thrown, by the passage of an induction shock through its substance, into a state of prolonged excitation which slowly passes off, and, if this is so, then the rapid development of a large nerve-organ response must, if sufficiently intense, be itself capable of throwing the tissue into a state of prolonged excitation. Now it is only in cases of very vigorous response to nerve excitation that the peculiar prolongation of the response referred to in Part II. is seen. There is thus every reason to suppose that this prolonged change is the same, whether its precursor be an induction shock or the shock of the nerve-organ response itself. The fact that in the one case the tissue is quiescent, whilst in the other it is in a state of functional activity, does not really affect the matter. The experiments on summation to be now referred to show that the tissue is capable of responding to two stimuli occurring within ·01″ of each other, and that an after-effect may be procured even when the tissue is in a state of activity by leading an induction shock through the organ ·02″ after a response has been evoked by excitation of its nerve. To these experiments we now turn.

Summation of effects.—Before proceeding to experiments designed to show the summation of after-effects, it was first necessary to obtain satisfactory proof of the summation of two successive nerve-organ responses produced by two successive excitations of its nerve. It was found that the results were not satisfactory if the second stimulus followed the first at a very short interval, and was applied to the same portion of the nerve. It appeared that for ·03″ to ·04″ after the passage of the exciting induction current the excitability of the nerve at the exciting electrodes was lowered, and the second stimulus, if occurring in this interval only, produced a small inadequate response of the organ. This difficulty was got over by using two pairs of platinum exciting electrodes, and exciting different parts of the same nerve. The exciting electrodes may be indicated as X_1 and X_2. Of these, X_1 was 35 mms. from the organ, X_2 45 mms., the length of the whole nerve being 55 mms. The transmission time along the intervening 1 centim. of nerve is probably not more than ·002″. The spring myograph was used for the production of the induction shocks, K_1 being placed in the primary circuit of the induction apparatus connected with X_1, and K_2 in that connected with X_2. The traveller could be made to break K_1 or K_2 only, or K_1 and K_2 successively. Although the induction shocks were made equal as far as the galvanometric reading of the deflection caused by their passage through it allowed, it will be noticed that excitation at the more centrally situated electrode gave a feebler response than that produced by the one situated nearer the middle of the nerve trunk.

	Deflection.
Excitation at X_1, G. $\frac{1}{100}$	+ 95
,, X_2 ,, ...	+ 60
,, X_1 and X_2, K_1 being at 0 and K_2 at ·03″, G. $\frac{1}{100}$	+ 178
,, ,, ,, ,, ,, ·02″ ,,	+ 160
,, ,, ,, ,, ,, ·01″ ,,	+ 122
,, X_1 only, G. $\frac{1}{100}$	+ 80
,, X_2 ,, ,, ...	+ 54
,, X_1 and X_2, K_1 at 0, K_2 at ·005″, G. $\frac{1}{100}$ . . .	+ 111
,, ,, ,, ,, ,, . . .	+ 106
,, ,, ,, 0 ,, 0 ,, . . .	+ 75

This shows that two nerve-organ responses are summed even when produced ·005″ after one another. It is, therefore, to be expected that the after-effects should also be summed, and experiments were now made as to summation of the after-effect of a nerve-organ response and that produced by the passage of an induction current. In order to obtain this result, it was necessary to lead an induction shock through the organ at a short interval of time after the organ response had been evoked by excitation of its nerve. For this purpose the rheotome was so arranged that K_1 should break the primary circuit of one induction apparatus and thus excite the nerve, whilst after an interval of ·02″ K_2 broke the primary circuit of an induction apparatus arranged so as to allow the break-shock to traverse the organ. Finally, K_3 was arranged so as to short-circuit the galvanometer up to ·05″. The deflections obtained thus showed either the after-effect of the nerve-organ response only, or that following the passage of the induction shock only, or the summation of the two after-effects.

A nerve-organ preparation was made by carefully dissecting out a long piece of the second nerve, and then cutting out a thin strip which should contain columns supplied by it. It was then necessary to ascertain that the preparation gave a large nerve-organ response followed by a prolonged after-effect. With K_1 at 0″, K_2 at ·02″, and K_3 at ·05″, the results were as follows :—

		After-effect.
Break of K_1 and K_3— After-effect following nerve-organ response	15″	+ 220
	30″	+ 100
	45″	+ 50
	60″	+ 35
	75″	+ 18
Break of K_2 and K_3— After-effect following passage of induction current only.	15″	+ 240
	30″	+ 110
	45″	+ 40
	60″	+ 25
	75″	+ 5
Break of K_1, K_2, and K_3— Summation of two effects	15″	+ 500
	30″	+ 250
	45″	+ 100
	60″	+ 50

The experiment shows with the greatest distinctness the striking resemblance between the electromotive change following the nerve-organ response and that following the passage of the induction current. It shows how completely the summation of the two after-effects is effected, and hence is decisive as to the efficacy of the induction current for the production of the after-effect, whether the organ be in a state of quiescence or in that state of activity into which it is thrown by stimulation of its nerve. There is thus no escape from the conclusion that, as the passage of an induction shock through a strip of organ is followed by a prolonged excitatory change, the passage of the current produced by the nerve-organ response itself must, if equal in intensity to the induction shock, be followed by a similar prolonged excitatory change.

Conclusion.

The work done at Arcachon has thus brought out the different excitatory changes which are produced by different methods of excitation in the organ.

The electrical organ of the Torpedo responds to a stimulus by a change in the electromotive character of the elements which make up its hexagonal columns. These elements are plates composed of nucleated protoplasmic masses and nerve-fibres. An extraordinary number of these are present in, and as it were bound together by, the former. In the active state of the organ the ventral surface of each plate with its contained nerves becomes negative to the dorsal surface; the effect in all the plates of a column when summed up is, therefore, such that the dorsal end of the column becomes positive to the ventral end. This effect may be produced in at least three different ways, and in each case it presents features which are those of the excitatory process.

i. The obvious method of production is that of excitation of the trunk of the electrical nerve. The nerve-organ response is characterised by a short period of delay, an extremely rapid development, occupying less than $\frac{1}{100}''$, and a less rapid decline. If the response is very pronounced, the main effect lasts $\frac{6}{100}''$, but is followed by a prolonged after-effect in the same direction.

ii. This after-effect is itself an excitatory change, and may be produced by the passage of a sufficiently intense current of short duration through the organ. This excitatory change is probably developed more or less rapidly, but is especially characterised by its slow subsidence, as it does not entirely disappear until several minutes after its production.

iii. A more prolonged electromotive change of the same character is produced when by mechanical or thermal means a large number of electromotive elements are injured. The adjacent parts are then thrown into a state of prolonged excitation, the effect taking some hours to subside.

Whilst then response i. is an affair of fractions of seconds, ii. is an affair of fractions of minutes, and iii. of fractions of hours. All three effects are characterised by positivity of the dorsal aspect of the column, and thus of the plates; and in all three the decline occurs at first rapidly and then more slowly.

The production of these three conditions not only brings the Torpedo organ into analogy with other electromotive tissues, muscle, nerve, &c., but throws some light upon the phenomena displayed by the latter tissues. It is the special characteristic of the electrical organ that any excitatory change must always, whether local or general, produce electromotive phenomena of the same kind; the dorsal surface of the columns must become positive to the ventral.

In the organ of the Torpedo it is easy to recognise the fact that in the effect of injury which corresponds to the demarcation-current we are dealing with a state of excitation. This is not so easily recognised in such tissues as muscle and nerve, owing to the direction of the excitatory change. The demarcation-current in the Torpedo is a strong support for the view that in nerve and muscle the negativity of an injured as compared with an uninjured part is the electromotive expression of a prolonged local excitatory process occurring in the neighbourhood of the injury.

In future experiments I hope to follow up the lines of inquiry which have been indicated at various points in this research.

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