Further Observations on the Electromotive Properties of the Electrical Organ of Torpedo marmorata

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XII. *Further Observations on the Electromotive Properties of the Electrical Organ of* Torpedo marmorata.

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[PLATES 51, 52.]

INTRODUCTORY.

IN my previous paper in the 'Philosophical Transactions,'* I have detailed the results of an investigation of the electromotive properties of the electrical organ of *Torpedo marmorata*, and I stated that I hoped to follow up the lines of inquiry indicated at various points in the account of that research.

My previous work had been done in the winter (January, 1887), and I was anxious to re-open the investigation at a time of year when Torpedoes could be readily procured, were in the most favourable state, and could be kept alive without any difficulty. This I was enabled to do in October, 1887, through the kindness of the Société Scientifique d'Arcachon, who placed at my disposal the rooms I had occupied in the previous winter, and to whom and the Society's Director, M. Durégne, I beg to offer my thanks for their aid.

Dr. BURDON SANDERSON lent me the apparatus with which he and I had worked at Oxford and elsewhere, and with which I was well acquainted. The plan of work was to a great extent thought out before starting, and all the appropriate instruments taken to Arcachon from England. I had determined to attack especially one problem, in the hope that its solution would lead to a more extended view of the excitatory phenomena of the electrical organ. This problem was that opened up by DU BOIS-REYMOND's remarkable discovery of what he terms the "irreciprocal conduction" manifested by the columns of the electrical organ.†

This subject has been already alluded to in my paper in the 'Philosophical Transactions,' and to that paper the reader must be referred for particulars as to the

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* GOTCH, "The Electromotive Properties of *Torpedo marmorata*," 'Phil. Trans.,' B, 1887, pp. 487–537.

† DU BOIS-REYMOND, 'Archiv Anat. Physiol. (Physiol. Abtheilung),' 1887, pp. 75; see also 'Biological Memoirs,' edited by J. BURDON SANDERSON, pp. 500–532, Clarendon Press, 1887.

construction of the organ and the nature of DU BOIS-REYMOND'S experiments.* The main features of the phenomenon in question may, however, be briefly described here, even at the risk of recapitulating what I have already published, in order to make the nature of the present investigation intelligible. In experimenting upon the effect of the passage of electrical currents, both voltaic and induced, through the organ, DU BOIS-REYMOND observed that the organ itself exercised a remarkable influence upon the led-through currents. This was of such a character as to make it appear that the organ is a better conductor for a current directed through it in one particular direction than it is for any other led-through current; this favourable direction coincides with that of the current produced by the excitatory change of the organ itself: that is, of the "shock," or, as for the purpose of the present enquiry I prefer to term it, the "response." If, for instance, a strip of organ containing several columns be taken and connected by its ends, each still covered by an adherent patch of dorsal and ventral skin respectively, with a pair of non-polarisable electrodes, and through these and the strip an intense current of short duration be led first in one direction and then in the other, an inequality shows itself in the amount of the led-through current. This inequality is the more marked the shorter the duration and the greater the intensity (within certain limits) of the external led-through current, and is very marked, therefore, when this current is an induced current.

The conditions for performing the experiment with induced currents are extremely simple, and consist merely in connecting the tissue and electrodes to the galvanometer, the circuit passing through the secondary coil of an induction apparatus. The induction shock is now led through the strip and the galvanometer, first in one direction and then in the other. When it is directed through the tissue from the ventral to the dorsal surface, it has the same direction in the tissue as that of the shock or response, and the current is designated by DU BOIS-REYMOND "homodromous." When directed through the tissue in the reverse direction, namely, from the dorsal to the ventral surface of the organ, it is termed "heterodromous.

DU BOIS-REYMOND finds that the galvanometric value of the homodromous current is always much greater than that of the heterodromous. The homodromous current must, therefore, either encounter less resistance in its passage through the tissue than the heterodromous does, or its electromotive force must be suddenly strengthened, and that of the heterodromous current weakened, presumably by the sudden establishment in the tissue of a new source of electromotive energy; DU BOIS-REYMOND assumes that the first is the true explanation.†

In working with Dr. SANDERSON in the summer of this year (1887) upon the properties and structure of the electrical organ in the tail of the Skate, the question of irreciprocity was entered upon. My previous work with the organ of the Torpedo

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* 'Phil. Trans.,' B, 1887, p. 491.

† E. DU BOIS-REYMOND, 'Archiv Anat. Physiol. (Physiol. Abtheilg.),' 1887, pp. 98–104; see also 'Biological Memoirs,' edited by J. BURDON SANDERSON, 1887, pp. 528–535.

had paved the way to the use of an experimental method which seemed to throw great light on the subject, and on finding this I determined to employ the same method in the present research. It is obvious that if the organ itself responds to the passage of an intense current of short duration, then within a few thousandths of a second after such a current is made there is an electromotive change set up in the organ which exactly fulfils the rôle of the hypothetical change the existence of which is required in the second alternative explanation. Being an excitatory phenomenon, it must always have the same sign, whether evoked by a homodromous or a heterodromous current, and must, in the case of the Torpedo organ, reinforce the former and diminish the force of the latter. My experiments on the nerve organ preparations had shown with what rapidity and intensity the electromotive change appeared, so that it was not improbable that du Bois-Reymond's phenomenon might be entirely due to algebraic summation of several electromotive effects.

The experiments to be detailed conclusively prove that the organ of the Torpedo does respond to the passage through it of an induction shock, irrespective of its direction; and, further, that beyond the irreciprocal galvanometric effect due to allowing both the induction shock and the response of the organ to affect the instrument there is no such irreciprocity, the induction shock in both directions when the response is excluded being equal.

The experiments therefore show that the phenomena of "irreciprocal conduction" are in reality excitatory phenomena, the nature of which, from the method of investigation used, has not been recognised.

Part I.—Direct Excitation of the Electrical Organ by Induced Currents.

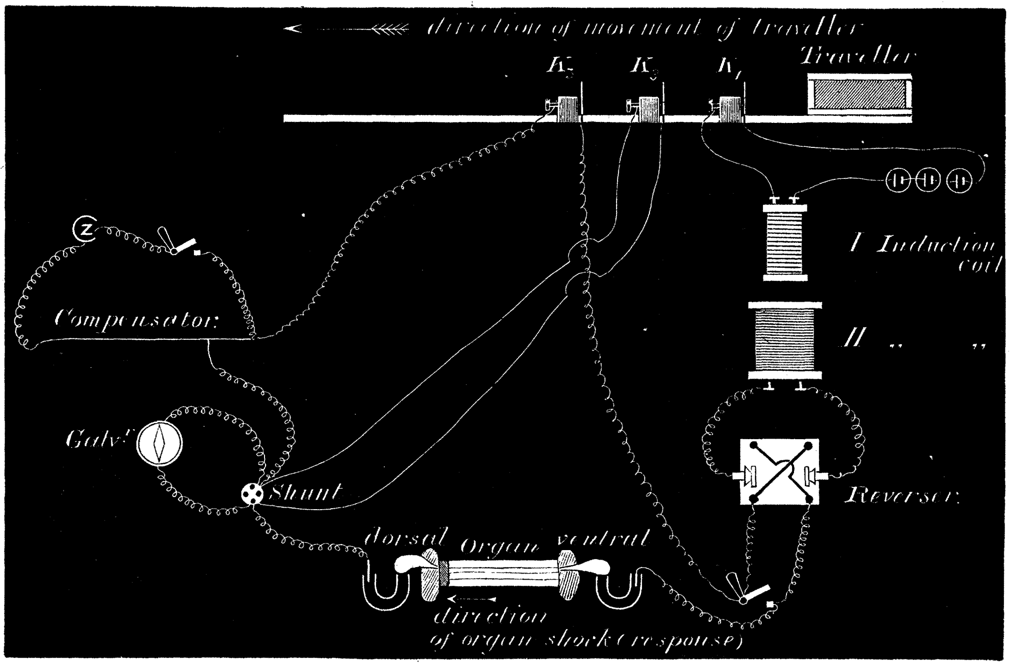
Method of Experiment.

The method employed in these experiments consisted in the use of a rheotome sufficiently accurate in its movement to enable the observer to connect the galvanometer with the tissue under investigation for a period of from two to three thousandths of a second, this period being capable of interpolation at any desired interval between the moment of the passage of the induction shock and five to six hundredths of a second after such passage.

The instrument used was the *Federmyographion* of du Bois-Reymond, this being modified and furnished with three specially-constructed trigger keys.

The galvanometer previously used was now discarded, and a much more delicate instrument was employed. This instrument was a Thomson reflecting galvanometer, made by Elliott, having a resistance at 16° C. of 20,364 ohms. The light astatic system of the instrument has no aluminium vane to reduce the number of oscillations, but is made completely dead-beat by being enclosed between two thin plates of glass one-tenth of an inch apart. The circuit was arranged according to the plan given in fig. 1, in which the keys K_1, K_2, and K_3 are shown: K_1 as the breaking key of the circuit of the primary coil of the induction apparatus, K_2 as a short circuiting key for the galvanometer, and K_3 as a key directly interposed between the tissue and the galvanometer, the opening of which thus opened the experimental circuit.

Fig. 1.



This experimental circuit includes the secondary coil of the induction apparatus, a Pohl's reverser, and the usual compensating arrangement, four Callaud cells being employed as a steady compensating battery.

The induction apparatus was of the usual sliding kind, but with a scale graduated under the kind direction of Professor Kronecker; the numbers given to denote the position of the secondary coil thus bear strict comparison one with another.

Preliminary Experiments.

The first experiments were of a simple character, and were made with the view of ascertaining the existence of the inequality already referred to in the galvanometric readings of the homodromous, as compared with those of the heterodromous, led-through current. For this purpose a large Torpedo, measuring 46 centimetres in length and 32 centimetres in width, was taken, and, the electrical lobe having been destroyed, a mass of organ was removed with its skin surfaces still adherent. From this mass a strip was cut with a razor in the direction of the columns, care being taken to avoid the entry of the large electrical nerves; this strip was then sliced down and reduced to a narrow strip containing four or five uninjured columns, and measuring 40 millimetres in length by 5 millimetres wide and 5 millimetres broad.

It was placed upon a glass plate and led off by pads of kaolin moistened with 0·6 per cent. saline solution, applied to the ends of the strip to which a portion of the ventral and dorsal skin still remained adherent. This is shown on a small scale in fig. 1.

A similar method of preparation was used in all the following experiments. The pads were brought into connection with the U-tubes of the ordinary non-polarisable electrodes, and so with the experimental circuit.

The strip of organ showed a marked electromotive difference between its dorsal and its ventral ends, the "organ-current" previously described by me.* This organ-current was of the usual character, namely, such that the dorsal end of the columns was galvanometrically positive to the ventral; that is to say, the change was of the same sign as that which occurs when the tissue responds to excitation of its nerve. Such an electromotive change will be denoted all through this work by the sign +, which refers to the galvanometric condition of the dorsal electrode. This + effect subsided at first rapidly, then more and more slowly, and in half-an-hour was steady.

The first experiments having reference to the inequality in the led-through currents, the keys K_2 and K_3 were not used, the circuit being made independently of K_3 and kept closed.

The passage of the traveller of the rheotome opened K_1 at a fixed point in its movement, and thus ensured the development of a similar and constant induction shock. The break shock used was that caused by the opening of six GROVE cells placed in the primary circuit of the induction apparatus, the secondary coil standing at 1000. It was led through the electrodes, the tissue, and the galvanometer, first in the homodromous or (+) direction, and then in the heterodromous or (−) direction, and the galvanometric deflection noted.

The deflections were strikingly unequal, that of the (+) induction current being nearly three times as large as the (−).

Direction of induction current.	Galvanometer shunt.	Deflection.
Heterodromous (−)	$\frac{1}{100}$	− 55
Homodromous (+)	,,	+ 148
Heterodromous (−)	,,	− 54
Homodromous (+)	,,	+ 146

Here then was the "irreciprocal conduction" which DU BOIS-REYMOND had observed, and which I had failed to obtain evidence of in my previous experiments.

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* GOTCH, 'Phil. Trans.,' B., 1887, pp. 502, 503.

A preliminary experiment was now made in which the induction shock was made to traverse the tissue, but was not allowed to affect the galvanometer. To effect this the key K_2 was used and was placed at 1/100″ distance from K_1; the galvanometer was thus short-circuited for the first hundredth of a second after the passage of the induction shock. Under these conditions both induction shocks, (+) and (−), were followed by an electromotive effect of the same sign, namely, that of the excitatory response of the organ, and therefore +.

Induction shock direction.	Time of closure of galvanometer.	Shunt.	Deflection.
(+)	·01″ after shock	$\frac{1}{100}$	+ 41
(−)	"	"	+ 19
(+)	"	$\frac{1}{10}$	+ 475
(−)	"	"	+ 228

The signs $\frac{1}{100}$, $\frac{1}{10}$, indicate that by means of an appropriate shunt only one-hundredth or one-tenth of the total effect passed through the galvanometer.

It was now necessary to use the rheotome and determine the time relations of this effect. For this purpose a vigorous female Torpedo was killed the next day, measuring 38 × 25 centims. A strip was prepared, as before, from the median edge of the organ; it measured 60 × 10 × 10 millims. The organ current, considerable at first, was allowed to subside until it became steady. Temperature of organ 15° C. The rheotome was used with all three keys, and the following Table shows the result:—

Galvanometer shunt	Direction of induction current through tissue.	Time of closure of galvanometer circuit.				
		K_2–K_3 0″–·005″	K_2–K_3 ·005″–·015″	K_2–K_3 ·015″–·025″	K_2–K_3 ·025″–·035″	K_2–K_3 ·035″–·045″
$\frac{1}{100}$	(+)	+ 142	+ 45	+ 40	+ 20	+ trace
"	(−)	− 141	+ 245	+ 100	+ 38	+ 4

It is evident that there is no difference in the galvanometric value of the two induction shocks when the galvanometer circuit is so arranged as to exclude any succeeding change in the tissue. With a closure of from 0″ to ·005″, there is no inequality. During the next period of closure from ·005″ to ·015″, however, an electromotive change of considerable intensity occurred in the tissue, which, in this particular instance, was more pronounced after the (−) than after the (+) induction current; the effect was +, and had its maximum somewhere about 1/100″ after the induction shock, whilst it lasted as long as 4/100″. An experiment was now made in order to ascertain more minutely the time relations of this excitatory effect. For this purpose the keys of the rheotome were arranged so as to secure a closing time of the galvanometer circuit of only 25/10,000″; the first 1/100″ was thus subdivided into four periods.

Two Groves in primary; secondary coil, 3000.

Galvanometer shunt.	Direction of induction current.	Time of closure of galvanometer.			
		K_2–K_3 0″–·0025″	K_2–K_3 ·0025″–·005″	K_2–K_3 ·005″–·0075″	K_2–K_3 ·0075″–·01″
$\frac{1}{100}$	(+)	+ 230	+ 15	+ 20	+ 123
,,	(−)	− 230	− trace	+ 55	+ 251

In this case the induction shocks in both directions were equal, as is shown by the readings when the closure of the galvanometer circuit was arranged to include the induction shock only, that is, when the closure was from 0″ to ·0025.″ In the next, the second, period, changes occur indicating the algebraic summation of the commencing tissue change with the remainder of the induction shock. The third period shows the commencement of a marked + change in the tissue, which in the fourth period has attained a very great intensity, being as pronounced a galvanometric effect in one case, even with this short closure, as the induction shock itself. There can be only one source of such a change, and that is the excitatory process of the organ itself; the change resembles that which occurs in the organ when the nerve trunk supplying it is excited, and the strip of tissue apparently responds in a similar manner, whether the trunk or the endings of the nerve are excited.

It is clear now what must happen if the induction shock and the subsequent response are both allowed to affect the galvanometer. Thus in this case the following experiment shows how the two currents will combine to give one galvanometric effect:—

Galvanometer shunt.	Direction of induction current.	Time of closure of galvanometer circuit.		
		K_2–K_3 0″–·005″	K_2–K_3 ·005″–·015″	K_2–K_3 0″–·01″
$\frac{1}{100}$	(+)	+ 231	+ 240	+ 405
,,	(−)	− 231	+ 460	+ 80

The examination of the first hundredth of a second having been thus made, the experiment was continued along broader lines, and a succession of readings obtained which indicated the general characters and duration of the excitatory effect. A long period of closure, 1/100″, was used, and the results are given in the subjoined Table.

Two GROVES in primary; secondary, 3000.

Shunt.	Direction of induction current.	Time of closure of galvanometer circuit.					After-effect.
		K_2–K_3 ·005″–·015″	K_2–K_3 ·015″–·025″	K_2–K_3 ·025″–·035″	K_2–K_3 ·035″–·045″	K_2 K_3 ·045″–·055″	K_2 only. ·055″ onwards.
$\frac{1}{100}$	(+)	+ 297	+ 161	+ 26	+ 10	+ 8	+ 20
,,	(−)	+ 448	+ 162	+ 35	+ 6	+ 5	+ 41

The large electromotive effect is thus seen to subside from its maximum, first rapidly and then slowly, and it is followed by an electromotive change in the tissue of similar sign, the after-effect. A corroborative experiment, selected out of many, all of the same character, may be briefly given. It was made on a strip of organ, prepared as has been previously indicated and led-off as before; the strip was 58 millims. × 6 × 6. The results of the rheotome readings may be divided into three groups, as follows:—

I. MINUTE Analysis of Events of first $\frac{1}{100}$″. Two GROVES in primary; secondary coil, 3000. Temp. 15° C.

Galvanometer shunt.	Direction of induction current.	Time of closure of galvanometer circuit.				
		K_2–K_3 ·0″–·0025″	K_2–K_3 ·0025″–·005″	K_2–K_3 ·005″–·0075″	K_2–K_3 ·0075″–·01″	K_2–K_3 ·01″–·0125″
$\frac{1}{100}$	(+)	+ 220	+ 4	+ 90	+ 145	+ 40
,,	(−)	− 220	− 6	+ 35	+ 206	+ 51

II. GENERAL Analysis of Events of $\frac{5}{100}$″.

Galvanometer shunt.	Direction of induction current.	Time of closure of galvanometer circuit.					After-effect.
		K_2-K_3 ·005″–·015″	K_2–K_3 ·015″–·025″	K_2–K_3 ·025″–·035″	K_2-K_3 ·035″-·045″	K_2–K_3 ·045″–·055″	K_2 only ·055″ on
$\frac{1}{100}$	(+)	+ 302	+ 65	+ 20	+ 5 (G. $\frac{1}{10}$ 46)	G. $\frac{1}{10}$ + 45	G. $\frac{1}{10}$ + 430
,,	(−)	+ 345	+ 95	+ 25	+ 10 (G. $\frac{1}{10}$ 95)	G. $\frac{1}{10}$ + 70	G. $\frac{1}{10}$ + 455

III. The After-effect from 1″ onwards.

Galvanometer shunt.	Direction of induction current.	Time of reading of galvanometer.			
		1″–5″	at 20″	at 35″	at 50″
$\frac{1}{10}$	(+)	+ 320	+ 130	+ 95	+ 40
,,	(−)	+ 210	+ 105	+ 60	+ 31

The prolonged after-effect in Table III. was obtained by closing the circuit 1″ after the passage of the rheotome; the needle swung out and attained its limit of deflection by 5″; its position was then noted as it returned towards zero every 15″, the falling time of the needle itself being 10″.

A comparison of the features of this electromotive change with that obtained in the case of the nerve organ preparation, as given in my previous paper, leaves no doubt that we have here to deal with an excitatory response of similar nature.

In my former experiments I had observed how greatly changes of temperature influence the time relations of the nerve organ response. It was therefore advisable to ascertain if this direct response of the tissue was similarly affected.

Effect of Temperature upon the Response to Direct Excitation.

The method of warming or cooling strips of organ consisted in the use of a metal stage covered with tissue paper soaked in melted paraffin, through which water at different temperatures was allowed to run; but it was subsequently found necessary to adopt a more rapid and effectual plan. This consisted in placing the organ columns upon a previously warmed tile, the temperature of which was kept up by its end being immersed in the water of a small water bath. For cooling, the tile was removed and the strip allowed to rest upon a slab of ice suitably hollowed out to receive it, the surface of which was covered with tissue paper previously soaked in paraffin. The temperature of the organ itself was readily ascertained by placing upon an organ mass the bulb of a thermometer.

Five separate experiments are selected to illustrate the striking effects of temperature, and it will be noticed in all these experiments that there is no inequality between those (+) and (−) galvanometric deflections obtained at the same temperature during the period of closure 0″ to ·0025″; that is to say, that there is no evidence of "irreciprocity" when the induction shock, and that only, is allowed to affect the galvanometer.

EXPERIMENT 1. Large Torpedo, 45 × 32 centims. Strip 50 × 10 × 8 millims. Galvanometer shunt $\frac{1}{100}$. Two GROVES in primary; secondary at 4000.

Temperature of organ.	Direction of induction current.	Time of closure of galvanometer circuit.					
		K_2–K_3 ·0″–·0025″	K_2–K_3 ·0025″–·005″	K_2–K_3 ·005″–·0075″	K_2–K_3 ·0075″–·01″	K_2–K_3 ·01″–·0125″	K_2–K_3 ·0125″–·015″
15° C.	(+)	+ 279	+ 12	+ 45	+ 185	+ 98	
	(−)	− 280	+ 17	+ 22	+ 181	+ 124	
20° C.	(+)	+ 306	+ 98	+ 132	+ 60		
	(−)	− 304	+ 48	+ 136	+ 75		
10° C.	(+)	+ 275	+ 6	+ 23	+ 131	+ 85	+ 18
	(−)	− 275	− 8	+ 18	+ 147	+ 98	+ 17

It is evident that the time relations of the response are considerably affected by temperature; thus we find that with a temperature of 20° C. the response is present from ·0025″ to ·005″ after the passage of the induction shock. Accordingly, we should expect that a closure of from ·0″ to ·005″, including, as it must, both induction current and response, would show the so-called irreciprocity in the warmed, but not in the cooled, tissue. Such is the case, as the following Table shows:—

GALVANOMETER $\frac{1}{100}$ shunt.

Temperature of organ.	Direction of induction current.	Period of closure.	
		K_2–K_3 ·0″–·005″	K_2–K_3 ·0″–·01″
22° C.	(+)	+ 338	+ 475
	(−)	− 290	− 12
8° C.	(+)	+ 270	+ 380
	(−)	− 270	− 174
22° C.	(+)	+ 390	
	(−)	− 267	

It is so obvious that algebraic summation must thus cause "irreciprocity" that further instances of this kind need not be given in the succeeding experiments.

EXPERIMENT 2. Large Torpedo, 45 × 32 centims. Strip 51 × 5 × 5 millims. Galvanometer $\frac{1}{100}$ shunt. Two GROVES in primary; secondary coil at 4000.

Temperature of organ.	Direction of induction current.	Time of closure of galvanometer circuit.						
		K_2–K_3 ·0″–·0025″	K_2–K_3 ·0025″–·005″	K_2–K_3 ·005″–·0075″	K_2–K_3 ·0075″–·01″	K_2–K_3 ·01″–·0125″	K_2–K_3 ·0125″–·015″	K_2–K_3 ·015″–·0175″
15° C.	(+)	+ 290	+ 23	+ 70	+ 235	+ 120	+ 30	
	(−)	− 290	− 18	+ 55	+ 165	+ 75	+ 16	
22° C.	(+)	+ 330	+ 101	+ 110	+ 26			
	(−)	− 322	+ 48	+ 106	+ 18			
6° C.	(+)	+ 298	+ 10	0	+ 88	+ 125	+ 56	+ 5
	(−)	− 298	− 12	0	+ 91	+ 115	+ 52	+ 6

EXPERIMENT 3. Large Torpedo, 48 × 31 centims. Strip 55 × 8 × 10 millims. Galvanometer $\frac{1}{100}$ shunt. Two GROVES in primary; secondary coil at 10000.

Temperature of organ.	Direction of induction current.	Time of closure of galvanometer circuit.									
		K_2–K_3 ·0″ to ·0025″	K_2–K_3 ·0025″ to ·005″	K_2–K_3 ·005″ to ·0075″	K_2–K_3 ·0075″ to ·01″	K_2–K_3 ·01″ to ·0125″	K_2–K_3 ·0125″ to ·015″	K_2–K_3 ·015″ to ·0175″	K_2–K_3 ·0175″ to ·02″	K_2–K_3 ·02″ to ·0225″	K_2–K_3 ·0225″ to ·025″
15° C.	(+)	+ 271	+ 8	+ 65	+ 395	+ 235	+ 76	+ 25	+ 40	+ 25	
	(−)	− 272	− 8	+ 51	+ 428	+ 290	+ 68	+ 60	+ 110	+ 45	
22° C.	(+)	+ 395	+ 90	+ 91	+ 78	+ 64					
	(−)	− 393	+ 85	+ 95	+ 40	+ 20					
3° C.	(+)	+ 217	+ 3	0	0	0	+ 8	+ 54	+ 102	+ 161	+ 136
	(−)	− 216	− 4	0	0	0	+ 22	+ 65	+ 178	+ 203	+ 189

EXPERIMENT 4. Large Torpedo, 62 × 38 centims. Strip 65 × 15 × 10 millims. Galvanometer $\frac{1}{100}$ shunt. Two Groves in primary; secondary coil at 5000.

Temperature of organ.	Direction of current.	Time of closure of galvanometer.			
		K_3–K_2 ·0″–·0025″	K_2–K_3 ·0025″–·005″	K_2–K_3 ·005″–·01″	K_2–K_3 ·01″–·0125″
15° C.	(+)	+ 495	+ 31	+ 18	+ 276
	(−)	− 495	− 32	+ 10	+ 187
23° C.	(+)	+ 585	+ 130	+ 125	
	(−)	− 584	+ 10	+ 82	

EXPERIMENT 5.—Large Torpedo, 52 × 37 centims. Strip 60 × 12 × 8 millims. Galvanometer $\frac{1}{100}$. Three GROVES in primary; secondary coil at 5000.

Temperature of organ.	Direction of induction current.	Time of closure of galvanometer circuit.								
		K_2–K_3 ·0″ to ·0025″	K_2–K_3 ·0025″ to ·005″	K_2–K_3 ·005″ to ·0075″	K_2–K_3 ·0075″ to ·01″	K_2–K_3 ·01″ to ·0125″	K_2–K_3 ·0125″ to ·015″	K_2–K_3 ·015″ to ·0175″	K_2–K_3 ·0175″ to ·02″	K_2–K_3 ·02″ to ·0225″
15° C.	(+)	+ 483	+ 9	+ 178	+ 434	+ 271	+ 69	+ 29	+ 22	
	(−)	− 484	− 7	+ 70	+ 206	+ 171	+ 95	+ 15	+ 11	
2° C.	(+)	+ 382	+ 6	0	0	0	0	+ 7	+ 15	+ 22
	(−)	− 381	− 6	0	0	0	0	+ 5	+ 10	+ 12
10° C.	(+)			0	+ 149	+ 231	+ 81	+ 35	+ 14	

These experiments show that rise of temperature accelerates and fall of temperature delays the commencement of the excitatory change following direct electrical excitation of the organ.* A glance at the curves given in Plate 51 at the end of this treatise shows how completely cold separates the induction shock from the subsequent response, and how warming brings the two galvanometric effects together; the interval of time which elapses between the two is the "period of delay" or "latent period" and is at its shortest, *i.e.*, at 20° C., more than ·0025″. However favourable the conditions, with transmission time excluded by the method of experiment, it would therefore appear that there is an interval of time between excitation and response. This interval may be regarded as the sum of the time necessary for the establishment of the excitatory process in the nerves *plus* that necessary for the development of those chemical changes in the protoplasm of the organ which may lie at the bottom of the obvious electromotive effect. It has been previously pointed out that in the case of the nerve organ preparation the fact that changes in the temperature of the organ affect the length of this period would seem to require the existence of this second factor, for, under the most favourable circumstances and after deducting the time occupied in nerve transmission, there remained an interval of 4/1000″ between excitation of the nerve trunk and the response of the organ. In the present experiments the earliest effect was observed with a closure of from ·0025″ to ·005″; and, as the conditions of these experiments excluded loss of time due to nerve transmission, the existence of a period of delay must be regarded as certain.

Although the passage of an induced current through the columns of the electrical organ evokes an excitatory response of the tissue, it is, however, doubtful if the expression "direct" excitation is a strictly correct one as applied to this phenomenon. In the case of muscle there exists a method (curarisation) by which the nervous channels may probably be eliminated; this is, however, not applicable to the electrical

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* The experiments also show that the resistance of the preparation and the electrodes diminishes as the temperature rises, as is evidenced by the value of the readings given in the first column.

organ. It was shown by MOREAU[*] that in a curarised and immobile fish the organ was still capable of responding by a vigorous reflex discharge to external stimulation of the skin. I have made numerous experiments which have confirmed this fact; indeed, the smartest shock I ever received was from a medium-sized curarised Torpedo, which I grasped when quite immobile between my hands. On dissecting out the nerves I found that electrical stimulation of the spinal cord and motor nerves produced no muscular contractions, whilst vigorous electrical responses of the organ followed excitation of the electrical nerves. The fish were readily curarised in from two to three hours by the injection of 0·5 cub. centim. of a 1 per cent. solution under the dorsal skin near the tail. This being the case, it was certain that the strip of curarised organ would respond, like the uncurarised, to the passage of an induction shock, as was found to be the case. It is, therefore, not improbable that the stimulation of the column by an induction current is not analogous to the direct electrical excitation of curarised muscle, but to that of nerve, it being an excitation of the innumerable nerve branches which pervade the transverse protoplasmic septa of the column rather than the protoplasm of the septa. The singular curare failure would seem to me to point to the conclusion that an electrical organ is pre-eminently a structure in which an immense number of nerve endings are grouped together into a system, and that the excitatory electromotive change may be nothing more than the fact that when an excitatory process travels down a nerve its trunk becomes negative to its terminal cross-section. Although such an effect is relatively feeble in each ultimate fibril, the enormous quantity of fibrils may augment its intensity, even to the height attained by the electromotive change of an electrical column. If an electromotive change in the protoplasmic plates, as distinct from that in the nerves, is to be looked for, then I venture to think that it may be found in that remarkable prolonged "after-effect," details of which have been given in my previous communication.[†]

Effect of Strength and Direction of Exciting Current.

The discovery of the response of the strip of organ is entirely due to the use of the rheotome method, for without it the induction shock masks the response. It is, therefore, essential to use the rheotome even in such simple experiments as those necessary for ascertaining how far the column responds to induction shocks of different strength. As, however, we are now only concerned with the amount of the response evoked, it is sufficient to take one definite time of closure, which, while excluding the induction current, shall include at ordinary temperatures the maximum of the response. The period of closure selected was from ·005″ to ·015″; the induction shock used was the break of 3 GROVES, its intensity being varied by the position of the secondary coil. With the secondary coil at 3000, the shock gave when led through

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[*] MOREAU, 'Annales des Sciences Naturelles (Zoologie),' vol. 18, 1862, pp. 12–14.

[†] *Loc. cit.*

10,000 ohms and the galvanometer (1/100 shunt) a deflection of 332 scale. If 1/3000 of this strength is taken as unity, then the numbers in the Table give relative strengths.

Galvanometer shunt.	Intensity of induction current.	Direction of induction current.	Closing time K_2-K_3.	Deflection.
$\frac{1}{10}$	Secy. 100	(+)	·005″–·015″	0
,,	100	(−)	,, ,,	0
,,	200	(+)	,, ,,	+ 23
,,	200	(−)	,, ,,	+ 20
,,	300	(+)	,, ,,	+ 65
,,	300	(−)	,, ,,	+ 40
,,	400	(+)	,, ,,	+ 174
,,	400	(−)	,, ,,	+ 155
,,	500	(+)	,, ,,	+ 390
,,	500	(−)	,, ,,	+ 395
$\frac{1}{100}$	600	(+)	,, ,,	+ 45
,,	600	(−)	,, ,,	+ 48
,,	1000	(+)	,, ,,	+ 102
,,	1000	(−)	,, ,,	+ 100
,,	1500	(+)	,, ,,	+ 235
,,	2000	(+)	,, ,,	+ 300
,,	2500	(+)	,, ,,	+ 402
,,	3000	(+)	,, ,,	+ 508
,,	3500	(+)	,, ,,	+ 530

The Table shows that the magnitude of the response increases with increasing strength of induction shock, resembling in this particular the behaviour of the organ to excitation of its nerve.

The relation of the response to the *direction* of the exciting current is by no means so simple, since different results have been obtained under apparently similar conditions. This much, however, is certain, that the most effectual exciting current is one which traverses the entire length of a column, and that it is generally most effectual when (+), *i.e.*, directed through the column from the ventral to the dorsal aspect. An analysis of all the instances noted will make this clear; the instances fall into three groups.

Galvanometer shunt $\frac{1}{100}$.	I. Most favourable direction of induction current (+). 14 cases.	II. Both induction currents (+) and (−) equally effectual. 4 cases.	III. Most favourable direction of induction current (−). 4 cases.
	(+) (−)	(+) (−)	(+) (−)
Closing time ·005–·015	+ 255 ; + 145	+ 429 ; + 411	+ 220 ; + 375
,, ,,	+ 455 ; + 311	+ 398 ; + 375	+ 45 ; + 245
,, ,,	+ 465 ; + 320	+ 390 ; + 395	+ 771 ; + 837
,, ,,	G. $\frac{1}{1000}$ + 92 ; + 74	+ 156 ; + 142	+ 160 ; + 305
,, ,,	+ 780 ; + 565		
,, ,,	G. $\frac{1}{1000}$ + 82 ; + 68		
,, ,,	+ 229 ; + 143		
,, ,,	+ 324 ; + 196		
,, ,,	+ 448 ; + 305		
,, ,,	+ 434 ; + 206		
,, ,,	+ 90 ; + 60		
,, ,,	+ 585 ; + 412		
,, ,,	+ 342 ; + 215		
,, ,,	+ 300 ; + 124		

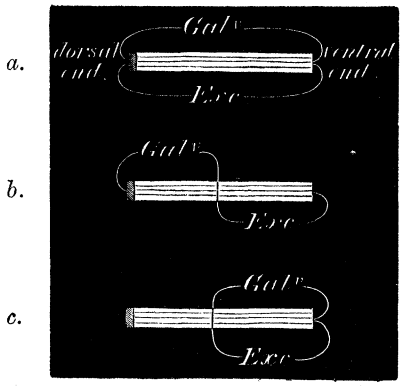
The question of the influence of the direction of the current on the effect is probably in relation with ECKHARD's discovery that the nerve organ preparation responds more fully when the trunk of the nerve is excited by an induction shock, if the induction shock be descending. The (+) induction current through the organ is a descending one as far as the finer nerve fibrils are concerned. It must, however, often happen that a preparation includes a large trunk of nerve which may first run from the dorsal towards the ventral end before dividing into its branches. Although no satisfactory evidence of this being the cause of the greater efficiency of the (—) led-through current observed in certain exceptional instances was obtained, it seems probable that this is the explanation of the anomalous cases.

If the induction current be directed across a strip which is led off by its two skin-covered ends, then a very feeble excitatory + change is seen ; thus, to give an instance, it was in one case (G. 1/10 shunt) + 33 with a rheotome closure of from ·005″ to ·025″ ; whereas the excitation of the whole strip in the usual way gave (G. 1/100) + 585. Occasionally, however, it happened that the cross excitation evoked a much larger response ; on examination, it was found that the strip of organ included between its columns the large trunk of a nerve, and that mechanical injury of the tissue containing this nerve produced the same response. It was thus clear that this was a case of nerve trunk excitation. This leads naturally to the consideration as to how far the response can be localised to the part of the column traversed by the induction shock. The experiments to be now referred to show that the response is absolutely localised to the led through tract. From what has been said, it is of great importance to prepare strips of organ in such a way as to avoid the inclusion in the strip of an obvious nerve trunk. In order to secure this the nerves with their main branches were carefully dissected out, and the part of the organ not cut into by the dissection was used for experimental purposes.

Limitation of Response to Tract of Tissue through which the Current passes.

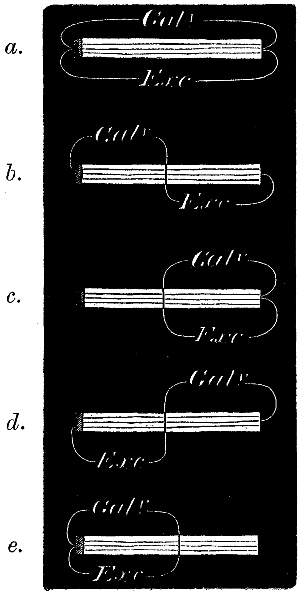
The plan of experiment consisted in the use of two circuits and two pairs of non-polarisable electrodes, one pair *Exc.* being connected with the secondary coil, the other pair *Gal.* being connected with the galvanometer. The galvanometer contacts could thus be placed either within or just outside the led-through tract, this latter being confined in this instance to either the ventral or the dorsal half of the organ columns. The usual kaolin pads were used for leading off, and in addition a loop of thick thread steeped in saline solution was loosely tied round the equator of the strip of organ; the kaolin pads were in contact with the skin covered ends. The results of two such experiments are shown in the following Table :—

Torpedo 52 × 37 centims. Strip 56 × 8 × 10 millims. Period of Galvanometer closure always ·005″ to ·025″.



Induction shock.	Shunt.	Deflection.
a. (+)	$\frac{1}{100}$	+ 90
(−)	"	+ 60
b. (+)	$\frac{1}{10}$	0
(−)	"	0
c. (+)	$\frac{1}{100}$	+ 26
(−)	"	+ 16

Another strip of organ 58 × 7 × 10 millims.



Induction shock.	Shunt.	Deflection.
a. (+)	$\frac{1}{100}$	+ 260
(−)	"	+ 405
b. (+)	$\frac{1}{10}$	− trace
(−)	"	"
c. (+)	$\frac{1}{100}$	+ 105
(−)	"	+ 68
d. (+)	$\frac{1}{10}$	− 15
(−)	"	− 26
e. (+)	$\frac{1}{100}$	+ 168
(−)	"	+ 330

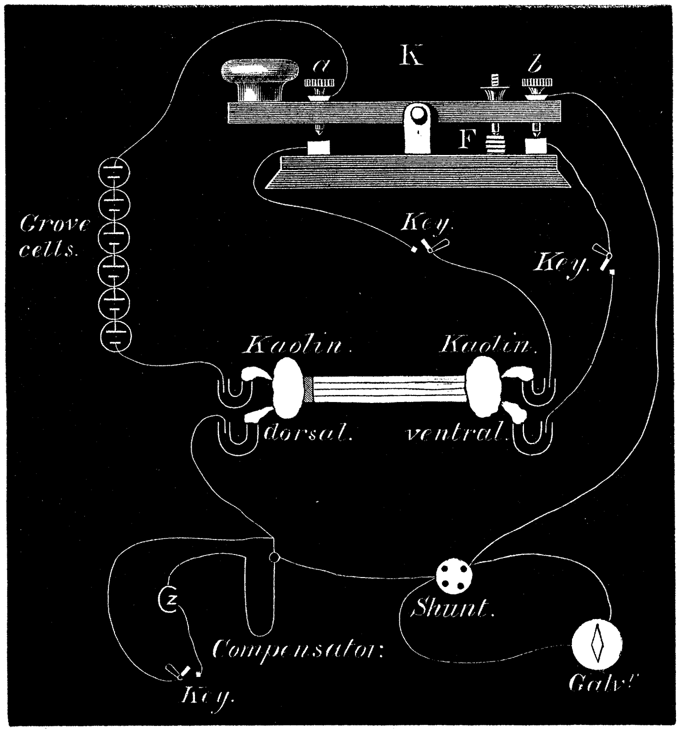
The — effect observed in extrapolar leading-off is undoubtedly due to the spread of the current of the response. The experiment is conclusive as showing that a large response may be evoked which is confined to the led-through tract. *There is thus no propagation of the excitatory state from one plate to another.* This most important fact has its cause in the structure of the organ.

Whatever may be the microscopic characters of the nerve terminations in the plates, and the part which they play in the production of the excitatory electromotive change, there is no evidence of any continuity of protoplasm between one plate and its neighbours. It appears that each plate is physiologically completely severed from all other plates. In order, therefore, to secure the simultaneous response of a whole column, either the nerve trunk supplying the column must be excited or an induction shock must traverse all the septa of the column.

Experiments referring to Excitation by the Voltaic Current.

The use of the rheotome has thus revealed the fact that the passage of an induction current through a strip of organ excites the tissue. In no single instance was such an excitatory phenomenon found to be absent. This being the case, it is evident that unless care is taken to exclude this excitatory effect from influencing the galvanometer, the passage of an induction current in opposite directions must be attended by unequal galvanometric deflections. It is therefore essential to know, with regard to DU BOIS-REYMOND's experiments with induction currents, whether he used a rheotome which would exclude the response. There is no indication in his published works of his having done so; whilst in the case of the voltaic current the duration of his shortest closing time is given as ·03″. This must therefore include both the voltaic current and any response, and the inequality noted may be thus accounted for. It is moreover clear, as regards induction shocks, that, apart from the summation of exciting current and excitatory response, there is no evidence of there being any inequality as dependent upon their direction. I have made twenty-six distinct observations on very vigorous fish, and, with the response excluded by closing the galvanometer circuit from 0″ to ·0025″ only, no irreciprocity in DU BOIS-REYMOND's sense was observed; but, as a large number of DU BOIS-REYMOND's experiments were made with voltaic currents of considerable intensity and short duration, it was desirable to ascertain whether the passage of such currents through the organ did evoke a response. The difficulties of obtaining a satisfactory reply to this inquiry were instrumental, and the experiments are therefore by no means conclusive. I had no instrument of sufficient accuracy to enable me to pass a very short intense voltaic current of known duration through the tissue, since, for this purpose, it was essential that the galvanometer circuit should be completely broken during the passage of the voltaic current. The rheotome was not therefore practicable, and I had to use a very well-made double key with extremely well-insulated junctions. The key was a see-saw key which broke one circuit whilst it closed another. The arrangement adopted will be rendered clear by the diagram in fig. 2; the key (K) is introduced into the circuit so that a tap will cause a short closure of the voltaic current at *a*, whilst the galvanometer circuit is broken at *b*; the strong spring, F, ensures the closure of the galvanometer circuit about 2/100″ after the short closure of the voltaic current. By means of another key worked by hand, the galvanometer circuit was again broken 1″ after the striking of K. The experiments were repeated at intervals of two minutes. The passage of the voltaic current was followed by considerable polarisation, which, in the case of the (−) current would obscure the effect of an excitatory response, since both would have the same sign, +. It was, however, easy to distinguish between the + excitatory response and the − polarisation effect which succeeded the passage of the + voltaic current, especially as the galvanometer circuit only remained closed for 1″. Torpedo 46 × 32 centims.; Strip 51 × 10 × 10 millims.

Fig. 2.



7 GROVES, direction	(+)	Galv. $\frac{1}{100}$	+ 520
,, ,,	(+)	,, ,,	+ 410
,, ,,	(+)	,, ,,	+ 60
,, ,,	(+)	,, $\frac{1}{10}$	+ 460
,, ,,	(+)	,, ,,	+ 150
,, ,,	(+)	,, ,,	+ 170

The (+) current thus produces a + after-effect; and, since a longer duration of (+) current is sufficient to give nothing but − effects, whilst the short tap gives a + effect, it would appear that in this case an excitation had occurred at closure. The reversal of effect is very striking, and shows that with the long closure the + effect had passed off before the galvanometer circuit was connected up again.

Tap closure:	7 Groves,	direction	(+)	Galv.	$\frac{1}{10}$	+ 50
1″	,,	,,	(+)	,,	,,	− 52
Tap	,,	,,	(+)	,,	,,	+ 30
1″	,,	,,	(+)	,,	,,	− 40
Tap	,,	,,	(+)	,,	,,	+ 43
1″	,,	,,	(+)	,,	,,	− 25
Tap	,,	,,	(+)	,,	,,	+ 32

In another preparation, the opening of the current appeared to be followed by excitation and polarisation effects, as the subjoined details show :—

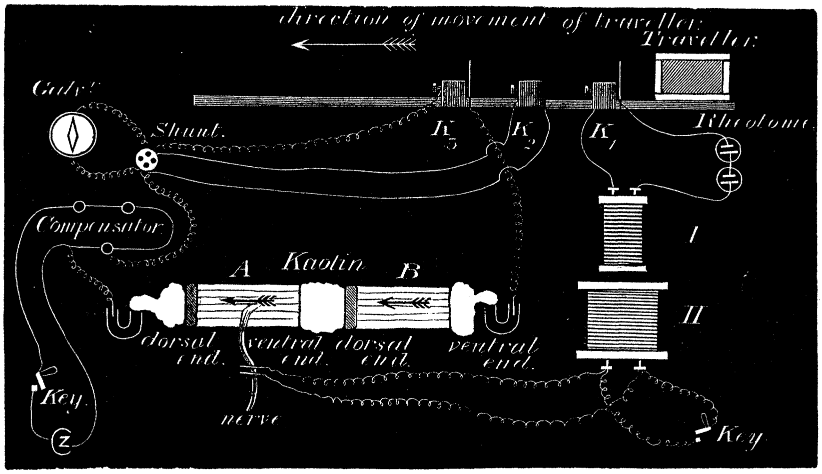
Tap closure:	7 Groves,	direction	(+)	Galv.	$\frac{1}{100}$	+ 150
$\frac{1}{4}$″	,,	,,	(+)	,,	,,	+ 80 − 10
$\frac{1}{2}$″	,,	,,	(+)	,,	,,	+ 50 − 25
1″	,,	,,	(+)	,,	,,	+ 30 − 45
2″	,,	,,	(+)	,,	,,	+ 20 − 60
4″	,,	,,	(+)	,,	,,	+ 15 − 120

It is probable that the voltaic current does excite the strip, just as the induction current does; and, if an excitatory change is evoked by the passage through the tissue of an intense current, then the meaning of du Bois-Reymond's results with the voltaic current would seem to be that he obtained a summation of voltaic current and the current of the excitatory change.

PART II.—EXCITATION OF THE ELECTRICAL ORGAN BY THE CURRENT OF ITS OWN RESPONSE.

Since the organ responds to the passage through its columns of an intense current led through them in the direction of their length, and since such response consists essentially of an electromotive change such that a current traverses each column in the direction of its length, of an intensity almost comparable with that of an induction shock, it follows that the tissue ought to be excited to a further secondary response by the current of its own primary response. If this should be the case, then every response must be of a reverberating character, the initial excitatory change itself producing a secondary feebler one, this a tertiary, still feebler, and so on, the tissue echoing the primary explosion until the individual replies become too faint to be followed. The experiments to be detailed show that this is indeed the true character of the nerve organ response in vigorous summer fish. Before proceeding to set forth these, the following experiments with two separate strips of organ must be referred to. These show that it is possible to evoke a response in a strip of organ by the passage through it of the excitatory electrical current produced by the response of a nerve organ preparation. A nerve organ preparation, A, was made, and the ends of its columns led off by saline kaolin pads. It was excited by electrical stimulation of its nerve at some distance from the tissue, the exciting current being the break induction shock caused by the break of K_1. The current of its response did not proceed directly to the galvanometer circuit, but was led lengthwise through the columns of an interposed separate isolated strip of organ, B, the general arrangement of the circuit being shown in fig. 3. This strip, B, could be placed either so that, if it responded, its response should augment that of A, or so that its response should diminish that of A, as will be seen by a glance at the diagrams accompanying the experimental details. The very first experiment made upon the tissue of a vigorous fish showed that the secondary strip, B, was excited, but the result was not so striking as those afterwards obtained, owing to misjudging the time at which the response of B would show itself.

Fig. 3.



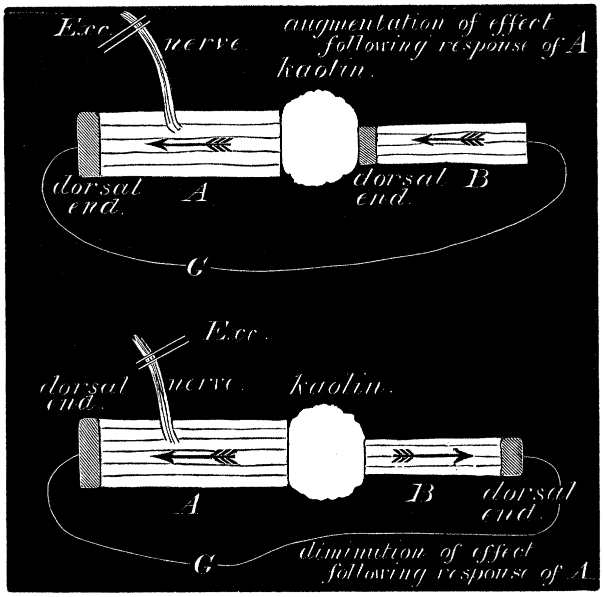
EXPERIMENT 1.—Torpedo 25 × 16 centims. Nerve organ preparation A, 20 × 10 × 15 millims. Strip of organ B, 20 × 5 × 5 millims. Second Nerve excited 15 millims. from entry into A by break of K_1.

Nerve organ response of A only to excitation of its nerve.

	Period of closure of galvanometer circuit.			
*	K_2–K_3 ·01″–·0125″	K_2–K_3 ·0125″–·015″	K_2–K_3 ·015″–·0175	K_2–K_3 ·0175″–·02″
	G. $\frac{1}{10}$ 0	G. $\frac{1}{100}$ + 10	G. $\frac{1}{100}$ + 365	G. $\frac{1}{100}$ + 441

Response of $\underleftarrow{A}$ led through $\underleftarrow{B}$; B favourable.

	Period of closure of galvanometer circuit.			
I.	K_2–K_3 ·0225″–·025″	K_2–K_3 ·025″–·0275″	K_2–K_3 ·0275″–·03″	K_2–K_3 ·03″–·0325″
Augmentation of response of A	G. $\frac{1}{10}$ + 110	G. $\frac{1}{10}$ + 200	G. $\frac{1}{10}$ + 210	G. $\frac{1}{10}$ + 95
II.	Response of $\underleftarrow{A}$ led through $\underrightarrow{B}$; B unfavourable.			
	G. $\frac{1}{10}$ + 180	+ 28	+ 8	+ 30



I.
B favourable.

II.
B unfavourable.

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[*] These rheotome readings indicate the time relations of the development of the nerve organ response of A only.

A second similar strip, B′, was now added on to B, and the response of $\underleftarrow{A}$ led through $\underleftarrow{B}$ and $\underleftarrow{B'}$; both favourable, that is, arranged as in I. (this is indicated by the arrows).

	Period of closure of galvanometer circuit.			
	K_2–K_3 ·0225″–·025″	K_2–K_3 ·025″–·0275″	K_2–K_3 ·0275″–·03″	K_2–K_3 ·03″–·0325″
Galv. $\frac{1}{10}$. Augmentation of A		+ 145	+ 130	
Response of $\underleftarrow{A}$ led through $\underrightarrow{B}$ and $\underrightarrow{B'}$; both unfavourable, that is, arranged as in II.				
Diminution of A. Galv. $\frac{1}{10}$	+ 80	− 2	+ 9	+ 22

EXPERIMENT 2.—Nerve organ preparation, 30 × 10 × 15, A. Three strips, each 20 × 5 × 5, B_1, B_2, B_3.

Response of nerve organ preparation A only to excitation of its nerve.	Period of closure of galvanometer circuit.			
	K_2–K_3 ·01″–·0125″	K_2–K_3 ·0125″–·015″	K_2–K_3 ·015″–·0175″	K_2–K_3 ·0175″–·02″
Galv. $\frac{1}{100}$ . . .	0	+ 305	+ 550	+ 130
Response of $\underleftarrow{A}$ led through $\underleftarrow{B_1}$, $\underleftarrow{B_2}$, $\underleftarrow{B_3}$; all favourable and placed in series.				
I.	·02″–·0225″	·0225″–·025″	·025″–·0275″	·0275″–·03″
Galv. $\frac{1}{10}$. Augmentation of A	+ 130	+ 459	+ 461	+ 310
II. Response of $\underleftarrow{A}$ led through $\underrightarrow{B_1}$, $\underrightarrow{B_2}$, $\underrightarrow{B_3}$; all unfavourable.				
Galv. $\frac{1}{10}$. Diminution of A	+ 48	+ 130	+ 238	+ 252

	·0225″–·025″	
Augmentation $\underleftarrow{A}$; $\underleftarrow{B_1}$, $\underleftarrow{B_2}$, $\underleftarrow{B_3}$ favourable, I.	+ 515	Galv. $\frac{1}{10}$ shunt.
Diminution $\underleftarrow{A}$; $\underrightarrow{B_1}$, $\underrightarrow{B_2}$, $\underrightarrow{B_3}$ unfavourable, II.	+ 134	,,
Augmentation $\underleftarrow{A}$; $\underleftarrow{B_1}$, $\underleftarrow{B_2}$, $\underleftarrow{B_3}$ favourable. I.	+ 680	,,
Diminution $\underleftarrow{A}$; $\underrightarrow{B_1}$, $\underrightarrow{B_2}$, $\underrightarrow{B_3}$ unfavourable, II.	+ 52	,,

EXPERIMENT 3.—Large Torpedo, 45 × 32 centims. Nerve organ preparation, A, 60 × 30 × 20 millims. Nerve excited 30 millims. from point of entry into A. Temperature 12° C. 3 GROVES in primary; secondary coil at 3000.

RESPONSE of A only.

Galvanometer.	Period of closure of galvanometer circuit.			
	K_2–K_3 ·015″–·0175″	K_2-K_3 ·0175″–·02″	K_2-K_3 ·02″–·0225″	K_2-K_3 ·0225″-·025″
$\frac{1}{100}$	0	+ 210	+ 505	+ 232

STRIP of organ prepared 60 × 15 × 12 millims.

Response of $\underleftarrow{\text{A}}$ led through $\underleftarrow{\text{B}}$ Favourable, as in I. Galv. $\frac{1}{10}$ $K_2 - K_3$ ·0275″–·03″		Response of $\underleftarrow{\text{A}}$ led through $\underrightarrow{\text{B}}$ Unfavourable, as in II. Galv. $\frac{1}{10}$ $K_2 - K_3$ ·0275″–·03″	
Augmentation	+ 670	Diminution	+ 51
,,	+ 527	,,	+ 30
,,	+ 501	,,	+ 95
,,	+ 492	,,	+ 145

These experiments show that the electromotive change which is evoked in the nerve organ preparation in response to excitation of its nerve is of sufficient intensity to produce a similar change in another strip through which its current is led. The evidence is in all cases the difference in the readings when this second strip is placed so that its response shall alternately augment and diminish that of the primary nerve organ preparation. It will be noticed that such augmentation and diminution occurs at about 1/100″ after the maximum of the primary nerve organ response has been reached. Now, if the current of the primary response can thus excite an isolated strip of organ, it must much more excite its own tissue, for only a derivation passes through the isolated strip. In this connexion an observation of JOLYET occurred to me, which I state from memory. He noticed in a vigorous fish that his chronograph, which was connected with the end surfaces of the organ columns of a brainless Torpedo, gave, in response to a single excitation of electrical nerves, a wavy fluctuating movement. This he attributed to the fact that, owing to the slow rate of transmission in the electrical nerves of the Torpedo, the excitatory change was probably initiated at different times in different parts of the organ mass. I had myself observed a still more remarkable instance of the same phenomenon.

In making a nerve organ preparation from a vigorous Torpedo, the brain of which had been destroyed, I held a small mass of cut-out organ grasped between the fingers and thumb of my left hand. With the right hand I divided the electrical nerve with a single stroke of a pair of sharp scissors. To my great surprise, I experienced a shock in my left hand which was of a distinctly multiple character. I performed this experiment on three separate occasions, and am now led to think it meant primary, secondary, tertiary, &c., responses. The fact of my not obtaining any evidence of such responses in my previous work would be probably due, first, to the less active condition of the winter fish; secondly, to my not suspecting the existence of, and so not carefully looking for, second and third apices in the electrical curve (a factor of great importance in rheotome work); and, thirdly, to my using a less delicate instrument and too long a period of galvanometer closure. This must explain why I did not then find what I obtained now with great ease, the evidence that the electrical curve of the response of the nerve organ preparation to *single* excitation of its nerve is, in vigorous fish, always multiple in character, the apex of the primary response being followed after an interval of 1/100″ by a second rise, and its apex by a third rise, and so on.

In the following experiments the circuit was arranged as in fig. 1, but the secondary coil was not included in the galvanometer circuit, it being connected with a pair of platinum electrodes upon which the nerve of the nerve organ preparation was placed.

EXPERIMENT 1.—Large Torpedo, 48 × 32 centims. A large mass of organ was cut from median edge of left organ, including entry of second electrical nerve. Mass measured 70 × 60 × 15 millims. Nerve excited 20 millims. from point of entry. 3 GROVES in primary; secondary coil at 5000. Mass led off by saline kaolin pads on skin surfaces.

Galvanometer.	Period of closure of galvanometer circuit.									
	K_2–K_3 ·01″ to ·0125″	K_2–K_3 ·0125″ to ·015″	K_2–K_3 ·015″ to ·0175″	K_2–K_3 ·0175″ to ·02″	K_2–K_3 ·02″ to ·0225″	K_2–K_3 ·0225″ to ·025″	K_2–K_3 ·025″ to ·0275″	K_2–K_3 ·0275″ to ·03″	K_2–K_3 ·03″ to ·0325″	K_2–K_3 ·0325″ to ·035″
$\frac{1}{100}$	0	+ 448	+ ∞ + 95 G. $\frac{1}{1000}$	+ 318	+ 280 + 254	+ 510 + 560	+ 265 + 234	+ 76	+ 70	+ 38

1st apex. — Primary response.

2nd apex. — Secondary response.

Experiment 2.—Large Torpedo, 62 × 38 centims. The brain was destroyed, and the whole organ used. The fish was therefore placed on a glass plate, with the ventral skin over the whole organ resting upon a cloth pad moistened with sea-water. A large pad of filter paper moistened with sea-water was applied over the dorsal skin; the non-polarisable electrodes were connected with the two pads. Nerves exposed and excited by Pt wire electrodes 30 millims. from organ. 2 Groves in primary; secondary coil at 7000. Temperature 10° C.

Galvanometer.	Period of closure of galvanometer circuit.						
	K_2–K_3 ·01″–·015″	K_2–K_3 ·015″–·02″	K_2–K_3 ·02″–·025″	K_2–K_3 ·025″–·03″	K_2–K_3 ·03″–·035″	K_2–K_3 ·035″–·04″	K_2–K_3 ·04″–·045″
$\frac{1}{100}$	0	+ 95	+ 45	+ 30	+ 75	+ 36	+ 10
Repeated	0	+ 61	+ 17	+ 12	+ 70	+ 30	+ 10
,,	0	+ 50	+ 17	+ 8	+ 34	+ 25	+ 10

1st apex. Primary response. (·015″–·02″)

2nd apex. Secondary response. (·03″–·035″)

Galvanometer.	K_2–K_3 ·0125″ to ·015″	K_2–K_3 ·015″ to ·0175″	K_2–K_3 ·0175″ to ·02″	K_2–K_3 ·02″ to ·0225″	K_2–K_3 ·0225″ to ·025″	K_2–K_3 ·03″ to ·0325″	K_2–K_3 ·0325″ to ·035″	K_2–K_3 ·035″ to ·0375″	K_2–K_3 ·0375″ to ·04″
$\frac{1}{10}$	0	+ 85	+ 170	+ 73	+ 34	+ 60	+ 115	+ 65	+ 21
						+ 55	+ 120		

1st apex. (·0175″ to ·02″)

2nd apex. (·0325″ to ·035″)

EXPERIMENT 3.—A mass of organ, including entry and distribution of second electrical nerve. Led off by saline kaolin pads. Nerve excited 30 millims. from point of entry into organ. 2 GROVES in primary; secondary coil at 7000.

Galvanometer.	K_2–K_3 ·01″ to ·015″	K_2–K_3 ·015″ to ·02″	K_2–K_3 ·02″ to ·025″	K_2–K_3 ·025″ to ·03″	K_2–K_3 ·03″ to ·035′	K_2–K_3 ·035″ to ·04″	K_2–K_3 ·04″ to ·045″	K_2–K_3 ·045″ to ·05″	K_2–K_3 ·05″ to ·055″
$\frac{1}{100}$	+ 36	+ ∞ G. $\frac{1}{1000}$ + 80	+ 255	+ 405	+ 190	+ 265	+ 66	+ 35	+ 18
		1st apex. Primary response.		2nd apex. Secondary response.		3rd apex. Tertiary response.			

Galvanometer.	K_2–K_3 ·01″ to ·0125″	K_2–K_3 ·0125″ to ·015″	K_2–K_3 ·015″ to ·0175″	K_2–K_3 ·0175″ to ·02″	K_2–K_3 ·02″ to ·0225″	K_2–K_3 ·0225″ to ·025″	K_2–K_3 ·025″ to ·0275″	K_2–K_3 ·0275″ to ·03″	K_2–K_3 ·03″ to ·0325″	K_2–K_3 ·0325″ to ·035″	K_2–K_3 ·035″ to ·0375″	K_2–K_3 ·0375″ to ·04″	K_2–K_3 ·04″ to ·0425″	K_2–K_3 ·0425″ to ·045′
$\frac{1}{100}$	0	+ 48	+ 367	+ 316	+ 75	+ 120	+ 225	+ 212	+ 89	+ 64	+ 98	+ 130	+ 30	+ 24
			Primary response.				Secondary response.				Tertiary response.			

EXPERIMENT 4.—Slice of organ including 8 to 10 columns, with second electrical nerve supplying it. Strip measured 65 × 15 × 10 millims. Nerve excited 30 millims. from point of entry. Induction apparatus as in 3.

Galvanometer.	K_2–K_3 0·1″–·015″	K_2–K_3 ·015″–·02″	K_2–K_3 ·02″–·025″	K_2–K_3 ·025″–·03″	K_2–K_3 ·03″–·035″	K_2–K_3 ·035″–·04″	K_2–K_3 ·04″–·045″
$\frac{1}{100}$	0	+ ∞ G. $\frac{1}{1000}$ + 75	+ 565	+ 345	+ 330	+ 160	+ 35

This shows no second apex with this galvanometer closure, and is instructive as showing how a long closure, by riding as it were over two wave apices, misses the second rise; a more minute analysis revealed it.

Galvano-meter.	K_2–K_3 ·01″ to ·0125″	K_2–K_3 ·0125″ to ·015″	K_2–K_3 ·015″ to ·0175″	K_2–K_3 ·0175″ to ·02″	K_2–K_3 ·02″ to ·0225″	K_2–K_3 ·0225″ to ·025″	K_2–K_3 ·025″ to ·0275″	K_2–K_3 ·0275″ to ·03″	K_2''–K_3 ·03″ to ·0325″.	K_2–K_3 ·0325″ to ·035″
$\frac{1}{100}$	0	+ 25	+ 460	+ ∞ G. $\frac{1}{1000}$ + 65	+ 518	+ 80	+ 88	+ 150	+ 90	
,,	0	+ 15	+ 580	+ ∞	+ 135	+ 84	+ 90	+ 125	+ 95	+ 28

1st apex. — Primary response.

2nd apex. — Secondary response.

Experiment 5.—Torpedo 25 × 16 centims. Nerve organ preparation including 4 or 5 columns only, with second nerve attached. Nerve excited 15 millims. from organ. 3 Groves in primary; secondary coil at 5000.

K_2–K_3 ·01″ to ·0125″	K_2–K_3 ·0125″ to ·015″	K_2–K_3 ·015″ to ·0175″	K_2–K_3 ·0175″ to ·02″	K_2–K_3 ·0225″ to ·025″	K_2–K_3 ·025″ to ·0275″	K_2–K_3 ·0275″ to ·03″	K_2–K_3 ·03″ to ·0325″	K_2–K_3 ·0325″ to ·035″	K_2–K_3 ·035″ to ·0375″	K_2–K_3 ·0375″ to ·04″	K_2–K_3 ·04″ to ·0425″
0	+ 305	+ 550	+ 130	+ 34	+ 80	+ 98	+ 115	+ 125	+ 79	+ 28	+ 14

1st apex. — Primary response.

Secondary response.

Experiment 6.—Torpedo 40 × 29 centims. Nerve organ preparation including 5 or 6 columns, supplied by second nerve. Preparation 35 × 10 × 8 millims. Temperature 15° C. Nerve excited 25 millims. from organ. 3 Groves in primary; secondary 4000.

Galvano-meter.	K_2–K_3 ·01″ to ·0125″	K_2–K_3 ·0125″ to ·015″	K_2–K_3 ·015″ to ·0175″	K_2–K_3 ·0175″ to ·02″	K_2–K_3 ·02″ to ·0225″	K_2–K_3 ·0225″ to ·025″	K_2–K_3 ·025″ to ·0275″	K_2–K_3 ·0275″ to ·03″	K_2–K_3 ·03″ to ·0325″	K_2–K_3 ·0325″ to ·035″
$\frac{1}{100}$	0	+ 190	+ 118	+ 48	+ 106	+ 124	+ 66	+ 24	+ 6	+ trace

Primary.

Secondary.

Experiment 7.—Torpedo 45 × 32 centims. Nerve organ preparation 50 × 10 × 12 millims., containing 5 or 6 columns, supplied by second nerve. Nerve excited 15 millims. from point of entry. 3 Groves in primary; secondary coil at 5000.

Galvanometer.	K_2-K_3 ·01″ to ·0125″	K_2-K_3 ·0125″ to ·015″	K_2-K_3 ·015″ to ·0175″	K_2-K_3 ·0175″ to ·02″	K_2-K_3 ·02″ to ·0225″	K_2-K_3 ·0225″ to ·025″	K_2-K_3 ·025″ to ·0275″	K_2-K_3 ·0275″ to ·03″	K_2-K_3 ·03″ to ·0325″	K_2-K_3 ·0325″ to ·035″	K_2-K_3 ·035″ to ·0375″
$\frac{1}{100}$	0	+ 175	+ 450	+ 208	+ 60	+ 52	+ 44	+ 45	+ 118	+ 66	+ 16
			Primary.						Secondary.		

These experiments show that not only in the entire fish and in a large mass of organ, but also in a strip containing a few columns, the response to excitation of the nerve is multiple in character. It will be seen that there are some discrepancies in the time interval between the primary and secondary response; it varies from ·01″ to ·015″. This variation is probably connected with the activity of the fish used for experiment. It is not apparently due to temperature. With a rise of temperature the apex of each response moves up towards the zero; that is, they all occur earlier, but at the same interval after one another. To ascertain this, experiments were made with a nerve organ preparation at different temperatures, and the results are shown in the following Tables :—

EXPERIMENT 8.—Torpedo 45 × 32 centims. Nerve organ preparation 60 × 20 × 10 millims. Second nerve excited 30 millims. from point of entry. 2 GROVES in primary; secondary at 3000.

Galvanometer $\frac{1}{100}$.	K_2-K_3 ·075" to ·01"	K_2-K_3 ·01" to ·0125"	K_2-K_3 ·0125" to ·015"	K_2-K_3 ·015" to ·0175"	K_2-K_3 ·0175" to ·02"	K_2-K_3 ·02" to ·0225"	K_2-K_3 ·0225" to ·025"	K_2-K_3 ·025" to ·0275"	K_2-K_3 ·0275" to ·03"	K_2-K_3 ·03" to ·0325"	K_2-K_3 ·0325" to ·035"	K_2-K_3 ·035" to ·0375"	K_2-K_3 ·0375" to ·04"	K_2-K_3 ·04" to ·0425"	K_2-K_3 ·0425" to ·045"	K_2-K_3 ·045" to ·0475"	K_2-K_3 ·0475" to ·05"	K_2-K_3 ·05" to ·0525"	K_2-K_3 ·0525" to ·055"	K_2-K_3 ·055" to ·0575"	K_2-K_3 ·0575" to ·06"
Temperature 10° C.	0	0	0	0	+ 210	+ 505 | 1st apex	+ 232	+ 70	+ 138	+ 175 | 2nd apex	+ 132	+ 85	+ 202 | 3rd apex	+ 105	+ 20	+ 18	+ 31	+ 84 | 4th apex	+ 45	+ 12	
Temperature 18° C.		0	+ 51	+ 523 | 1st apex	+ 421	+ 100	+ 95	+ 138 | 2nd apex	+ 68	+ 87	+ 164 | 3rd apex	+ 89	+ 18	+ 11	+ 9	+ 8	+ 120 | 4th apex	+ 75	+ 20	+ 7	

EXPERIMENT 9.—Torpedo 52 × 37 centims. Nerve organ preparation 60 × 45 × 22 millims. Second nerve excited 30 millims. from point of entry. 3 GROVES in primary; secondary at 5000.

Galvanometer $\frac{1}{100}$.	K_2-K_3 ·075" to ·01"	K_2-K_3 ·01" to ·0125"	K_2-K_3 ·0125" to ·015"	K_2-K_3 ·015" to ·0175"	K_2-K_3 ·0175" to ·02"	K_2-K_3 ·02" to ·0225"	K_2-K_3 ·0225" to ·025"	K_2-K_3 ·025" to ·0275"	K_2-K_3 ·0275" to ·03"	K_2-K_3 ·03" to ·0325"	K_2-K_3 ·0325" to ·035"	K_2-K_3 ·035" to ·0375"	K_2-K_3 ·0375" to ·04"	K_2-K_3 ·04" to ·0425"	K_2-K_3 ·0425" to ·045"	K_2-K_3 ·045" to ·0475"	K_2-K_3 ·0475" to ·05"	K_2-K_3 ·05" to ·0525"	K_2-K_3 ·0525" to ·055"	K_2-K_3 ·055" to ·0575"	K_2-K_3 ·0575" to ·06"
Temperature 11° C.	0	0	0	0	+ 300	+ 750 | 1st apex	+ 586	+ 215	+ 251	+ 302 | 2nd apex	+ 236	+ 254	+ 255 | 3rd apex	+ 112	+ 40	+ 61 | 4th apex	+ 60	+ 25	+ 10	+ 4	+ 2
Temperature 15° C.	0	+ 85	+ 472 | 1st apex	+ 324	+ 146	+ 70	+ 112 | 2nd apex	+ 79	+ 28	+ 4	+ trace										
Temperature 18° C.	+ 80	+ 546 | 1st apex	+ 412	+ 123	+ 45 + 397 G. $\frac{1}{10}$	+ 630 G. $\frac{1}{10}$ | 2nd apex	+ 615 G. $\frac{1}{10}$	+ 244 G. $\frac{1}{10}$	+ 136 G. $\frac{1}{10}$												

The preparations used in these temperature experiments were made from very vigorous Torpedoes, and, as will be noticed, they give four separate responses to one excitation. The activity of the fish has great influence on the result. Occasionally I obtained from sluggish fish a nerve organ response with a very slight, barely perceptible, secondary effect, only revealed by close rheotome analysis. This was not due to the fact that the primary response was of less intensity, but was evidently dependent upon the diminished excitability of the tissue ; since in excitable tissue obtained from vigorous fish a well-marked secondary response occurred following minimal excitation of the nerve. The following experiment shows a maximal and a minimal effect : the maximal effect has four apices :—

EXPERIMENT 10.—Torpedo 46 × 31 centims. Nerve organ preparation 48 × 10 × 20 millims. Nerve excited 40 millims. from point of entry. 3 GROVES in primary.

K_2–K_3 ·0125″ to ·015″	K_2–K_3 ·015″ to ·0175″	K_2–K_3 ·0175″ to ·02″	K_2–K_3 ·02″ to ·0225″	K_2–K_3 ·0225″ to ·025″	K_2–K_3 ·025″ to ·0275″	K_2–K_3 ·0275″ to ·03″	K_2–K_3 ·03″ to ·0325″	K_2–K_3 ·0325″ to ·035″	K_2–K_3 ·035″ to ·0375″	K_2–K_3 ·0375″ to ·04″	K_2–K_3 ·04″ to ·0425″	K_2–K_3 ·0425″ to ·045″	K_2–K_3 ·045″ to ·0475″
Maximal effect. Galv. $\frac{1}{100}$. Secondary coil 7000.													
+ 290	+ 494	+ 198	+ 54	+ 85	+ 70	+ 125	+ 131	+ 52	+ 71	+ 151	+ 75	+ 18	+ 10
Minimal effect. Galv. $\frac{1}{10}$. Secondary coil 30.													
0	+ 900	+ 645	+ 120	+ 80	+ 135	+ 140	+ 75	+ 18					
repeated 0	+ 850	+ 600	+ 65	+ 80	+ 124	+ 61	+ 10						
Maximal effect. Galv. $\frac{1}{100}$. Secondary coil 7000.													
+ 208	+ 435 1st apex	+ 205	+ 69	+ 84 2nd apex	+ 48	+ 125	+ 131 3rd apex	+ 36	+ 84	+ 111 4th apex	+ 62	+ 12	+ 8

The secondary response can be obtained not only in nerve organ preparations when the primary response is evoked by stimulation of the nerve trunk, but also in the strip of organ when the primary response is evoked, as described in Part I., by the passages of an induction shock through the strip. It is, however, more difficult to obtain it in this latter case. It is always obtained with ease when the strip is so prepared as to include the trunk of a nerve supplying it. Since, in this case, the strip becomes in reality an ordinary nerve organ preparation with a very short nerve, it is probable that the difficulty of obtaining it in carefully selected strips containing no obvious nerve trunk is connected with the risk of injury attending the preparation of such strips. Since, however, every such preparation becomes in reality a nerve organ preparation, it is clear that if the preparation is a good one it must occur. The following is an instance of its occurrence in a strip of organ containing no obvious nerve bundles :—

Experiment 11.—Torpedo 52 × 37 centims. Strip of organ 60 × 8 × 8. 3 Groves in primary ; secondary coil 5000. Strip excited by passage through its length of an induction shock, as in Part I. Circuit arranged as in fig. 1.

Galv. $\frac{1}{100}$.						Galv. $\frac{1}{10}$.					
K_2-K_3 ·0″ to ·0025″	K_2-K_3 ·0025″ to ·005″	K_2-K_3 ·005″ to ·0075″	K_2-K_3 ·0075″ to ·01″	K_2-K_3 ·01″ to ·0125″	K_2-K_3 ·0125″ to ·015″	K_2-K_3 ·015″ to ·0175″	K_2-K_3 ·0175″ to ·02″	K_2-K_3 ·02″ to ·0225″	K_2 K_3 ·0225″ to ·025″	K_2-K_3 ·025″ to ·0275″	K_2-K_3 ·0275″ to ·03″
Direction of Induction Shock (+).											
+ 446 Induction shock	+ 12	+ 50	+ 342 Primary response	+ 218	+ 70	+ 243	+ 305 Secondary response	+ 154	+ 54		
Direction of Induction Shock (—).											
— 449 Induction shock	— 6	+ 24	+ 215 Primary response	+ 132	+ 55	+ 271 + 231	+ 375 + 409 Secondary response	+ 257 + 274	+ 88 + 109	+ 62 + 69	+ 41

The experiment shows that the secondary response attains its maximum 1/100″ after that of the primary, and that it is independent of the direction of the exciting induction shock.

In all the preceding experiments the second apex occurs at about 1/100″ after that of the primary response. This fact, together with the fact that the current of the primary response itself excites a strip when led through it, justifies the conclusion that the second rise is a true secondary response excited by the rise of the primary ; but, as the tissue when excited by an induction shock has been shown in Part I. to attain the maximum of its response in rather less than 1/100″, it seemed advisable to devise an experiment which would clearly demonstrate that this second rise noticed in all the preceding experiments is unquestionably an excitation evoked by the current of the primary response. This is proved by the following experiment, in which all the information previously gained was made use of in order to obtain *both* the secondary response in a nerve organ preparation *and* the independent response of an isolated strip to the passage through it of the current of the primary response. There can be no question that the difference in the galvanometric readings obtained by leading the current of the nerve organ preparation through an interposed strip (as in the first experiments of Part II.), when this is placed so that its own response may first coincide with and then oppose that of the nerve organ preparation, is due to the fact that the second interposed strip is excited by the led-through current of the nerve organ response. If, then, the character of this response, apart from the interposed strip, be such that it shows a secondary rise, and the time relations of this rise agree with those of the augmentation and diminution found when the strip is interposed, then we have conclusive evidence that this secondary rise, even though it may begin later after the primary than might be expected, is a true secondary response in the sense that it is caused by the excitation of the nerve organ tissue by the passage through its substance of the current of its own primary response.

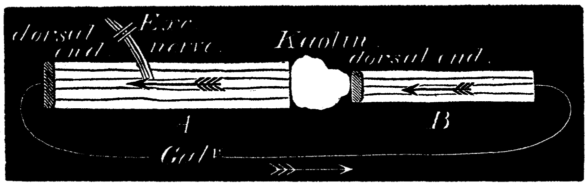
The following experiment will make this clear :—

Experiment 12.—(Selected out of three sets of experiments.) Large Torpedo, 52×37 centims. Mass of organ A, measuring $60 \times 45 \times 22$, including entry of second nerve. Nerve excited 30 millims. from entry into organ. Three Groves in primary; secondary coil at 5000.

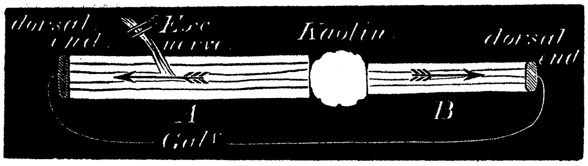
<table>
<tr><td colspan="12">Time relations of excitatory response of $\underleftarrow{\text{A}}$ only; Galv. $\frac{1}{100}$.</td></tr>
<tr><td>K₂-K₃
·015″
to
·0175″</td><td>K₂-K₃
·0175″
to
·02″</td><td>K₂-K₃
·02″
to
·0225″</td><td>K₂-K₃
·0225″
to
·025″</td><td>K₂-K₃
·025″
to
·0275″</td><td>K₂ K₃
·0275″
to
·03″</td><td>K₂-K₃
·03″
to
·0325″</td><td>K₂-K₃
·0325″
to
·035″</td><td>K₂-K₃
·035″
to
·0375″</td><td>K₂ K₃
·0375″
to
·04″</td><td>K₂-K₃
·04″
to
·0425″</td><td>K₂-K₃
·0425″
to
·045″</td></tr>
<tr><td>0</td><td>+ 380</td><td>+ 750
1st apex</td><td>+ 586</td><td>+ 215</td><td>+ 251</td><td>+ 302
2nd apex</td><td>+ 236</td><td>+ 254</td><td>+ 255
3rd apex</td><td>+ 112</td><td>+ 40</td></tr>
<tr><td colspan="12">Strip of organ B prepared 60 × 8 × 10 millims., and interposed between A and galvanometer.
I. Time relations of response of $\underleftarrow{\text{A}}$ with $\underleftarrow{\text{B}}$ interposed favourable; Galv. $\frac{1}{100}$.</td></tr>
<tr><td>0</td><td>+ 105</td><td>+ 295</td><td>+ 275</td><td>+ 86</td><td>+ 160
Au</td><td>+ 166
gmentati</td><td>+ 162
on</td><td>+ 133</td><td>+ 170</td><td>+ 102</td><td>+ 26</td></tr>
<tr><td colspan="12">II. Time relations of response of $\underleftarrow{\text{A}}$ with $\underrightarrow{\text{B}}$ interposed unfavourable; Galv. $\frac{1}{100}$.</td></tr>
<tr><td></td><td></td><td></td><td></td><td>+ 90</td><td>+ 106
D</td><td>+ 94
iminutio</td><td>+ 75
n</td><td>+ 92</td><td>+ 161</td><td>+ 91</td><td></td></tr>
<tr><td colspan="12">I. repeated. Response of $\underleftarrow{\text{A}}$ with $\underleftarrow{\text{B}}$ favourable; Galv. $\frac{1}{100}$.</td></tr>
<tr><td></td><td></td><td></td><td></td><td>+ 84</td><td>+ 141
Au</td><td>+ 172
gmentati</td><td>+ 160
on</td><td>+ 158</td><td>+ 160</td><td>+ 98</td><td>+ 76</td></tr>
<tr><td colspan="12">II. repeated. Response of $\underleftarrow{\text{A}}$ with $\underrightarrow{\text{B}}$ unfavourable; Galv. $\frac{1}{100}$.</td></tr>
<tr><td></td><td></td><td></td><td></td><td>+ 71</td><td>+ 83
D</td><td>+ 76
iminutio</td><td>+ 68
n</td><td>+ 85</td><td>+ 135</td><td>+ 42</td><td></td></tr>
</table>

The comparison is made between the effect when the nerve organ preparation A alone was led off by its skin ends; and that produced when the leading off occurred at one end through B arranged as shown in I. and II. :—

I.



II.



The experiment shows that the response of the strip B, as indicated by the augmentation and diminution due to algebraic summation of electrical effects, begins at about ·03″ and attains its maximum during the period of closure, ·03″–·0325″, which is also the period when the secondary rise of the nerve organ preparation only attains its maximum. I therefore conclude that the secondary rise in the electrical excitatory curve (see Plate 52) is due to a second state of excitation evoked in the nerve organ tissue by the current of the primary response; and, if there is a tertiary, that this is similarly caused by the secondary, and so on.

General Conclusions.

(1.) It has been shown by the experiments of which details have been given in Part 1 that an isolated strip of electrical organ containing a few columns with no large nerve trunk entering them may be excited by the passage through the columns of an electrical current of considerable intensity (such as an induction shock). The response of such a strip of organ resembles in all particulars that of a nerve organ preparation evoked by stimulation of the trunk of the nerve supplying it.

(2.) From this it follows that the phenomena of "irreciprocal conduction," to which attention has been drawn by du Bois-Reymond, are observed only when the galvanometric effect of the exciting induction shock and that of the response are blended.

(3.) Beyond this apparent irreciprocal conduction, which has been shown to be, in these experiments at least, nothing but algebraic summation of two electromotive effects, there is no evidence of any irreciprocity; the induction shocks, when care is taken to exclude all succeeding electromotive changes from the galvanometer, present no inequality dependent on their being "homodromous" or "heterodromous" in direction.

(4.) It has been further shown that a strip of organ can be excited by the passage through its columns of the current due to the response of a nerve organ preparation to stimulation of its nerve.

(5.) Finally, it is shown that the excitatory process in the organ of vigorous fish, whether evoked by stimulation of a nerve trunk or by the passage of an induced current through the organ itself, will itself evoke a second excitatory change; this a third, and so on. The second change is found to be in all probability a secondary response due to excitation of the nerves of the responding tissue by the current involved in the primary state of excitation. The tissue thus reverberates, and the curve indicating the nature and time relations of an excitatory response must be modified, as shown in Plate 52.

In conclusion, it may be well to refer to some remarks of DU BOIS-REYMOND on the teleological significance of the phenomena of "irreciprocal conduction." He considers that these phenomena to some extent solve the puzzle as to how the organ is insulated. It is not insulated, he says, but irreciprocal conduction performs a function similar to insulation. Thus, "the arrangement which does really exist is superior even to the insulating property of the cover of the individual columns, for such a property would indeed oblige the currents, between points of the lateral surfaces of all the columns, to take their route along the column, but it would present no obstacle to the return of the currents from the dorsal to the ventral surface by the shortest route, through the neighbouring columns." And further on:—"However that may be, the instance of internal adaptation to which we have been now led far surpasses all earlier ones in ingenuity. It would certainly have demanded the profoundest reflection of a clever brain to hit upon the idea of making each column as good a conductor for its own shock as any other animal tissue can be, but comparatively a non-conductor for the current of all other columns. In connexion with the extremely transitory nature of the shock, it is not a little remarkable that it is only currents of extremely short duration that the organ conducts irreciprocally. Of what service would it have been to the fish if it had become a perfect non-conductor for continuous heterodromous currents also?" *

As a matter of fact, however, each column conducts with equal facility its own homodromous shock and the returning heterodromous current of the shock of its neighbours, but in the latter case it is excited, as indeed it is by the current of its own response. The teleological significance, then, of the phenomena is not what DU BOIS-REYMOND imagines; if anything, it means that a single response has a reverberating character, due probably to the current of the response acting as a stimulus to the nerves in the columns, and thus each column reinforces by its echoes the effect of the primary explosion.

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* DU BOIS-REYMOND, 'Archiv Anat. Physiol. (Physiol. Abtheilg.),' 1887, pp. 102, 104; see also, 'Biological Memoirs,' edited by J. BURDON SANDERSON, 1887, pp. 533, 534.

Description of Plates.

Plate 51. Electromotive change in an isolated strip of electrical organ following the passage lengthwise through its columns of an induction current. The ordinates represent scale readings of the galvanometer deflection; the abscissæ denote the time after the passage of the induction shock which occurs at zero.

The first electromotive effect is that due to the induction current itself, and is shaded black; the black line is prolonged upwards rather indefinitely, since its apex cannot strictly be compared with the height of the subsequent excitatory change, as owing to its rapidity it fails to give a proportionate galvanometric effect.

Fig. 1 represents the change following a (+) homodromous induction shock in a strip of organ at temperature 15° C.

Fig. 2 represents the same at temperature 3° C., showing the separation of the response from the induction current.

Fig. 3 represents the same change with a (−) heterodromous induction shock at 15° C.

Fig. 4, the same at 3° C.

Plate 52. Electromotive change following a single excitation of nerve trunk of a nerve organ preparation in vigorous summer Torpedoes.

Fig. 1 shows the change in two distinct preparations at 15° C. The smaller one shows a primary (i.), followed by a secondary response (ii.); the larger shows also a tertiary.

Fig. 2 shows the change in two vigorous fish at low temperatures, 10° C.; both show four responses, I., II., III., IV., following the single excitation of the nerve.

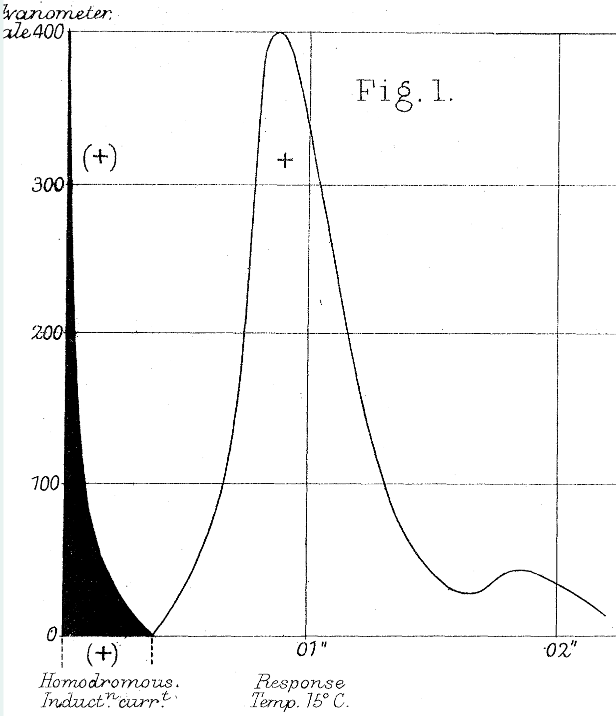
Fig. 1.

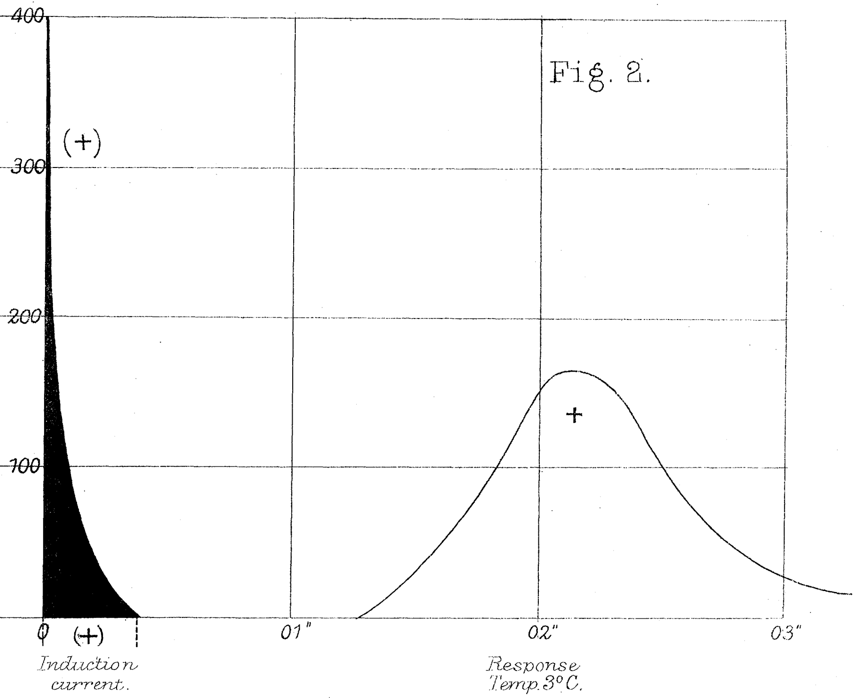
Fig. 2.

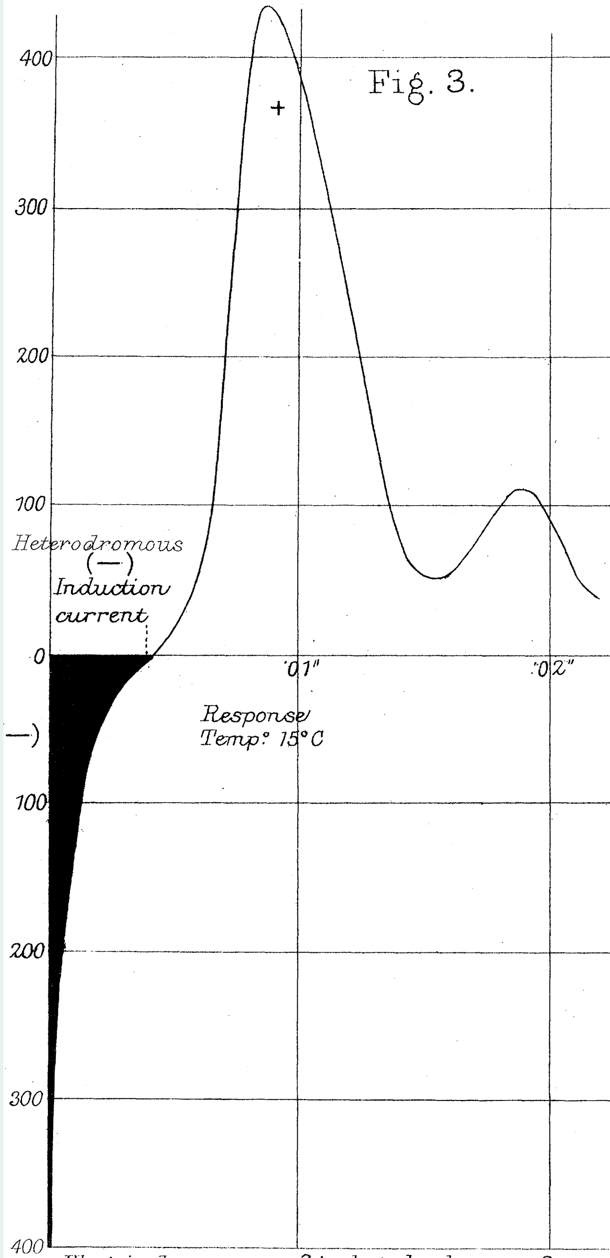
Fig. 3.

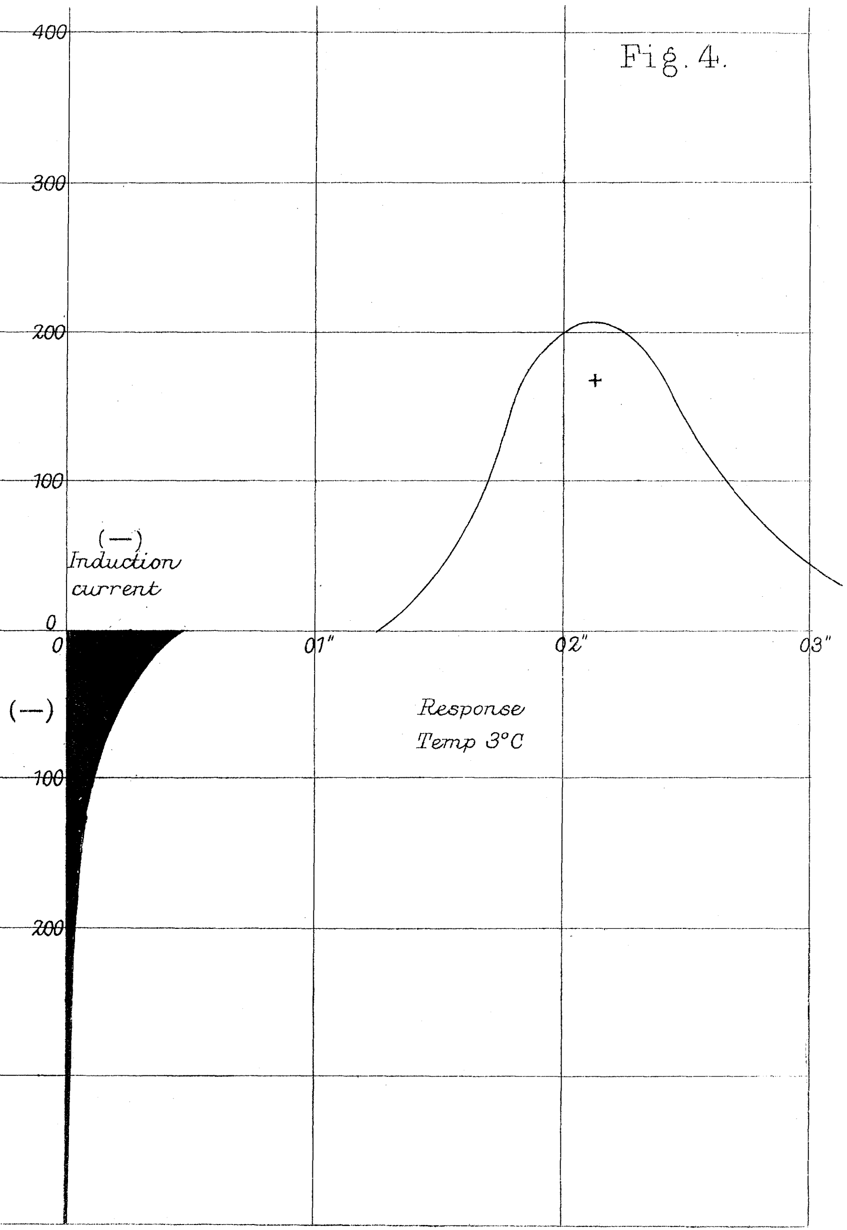
Fig. 4.

Electrical response of isolated columns of organ to the passage through the columns of an Induction current.

West, Newman & C.o lith.

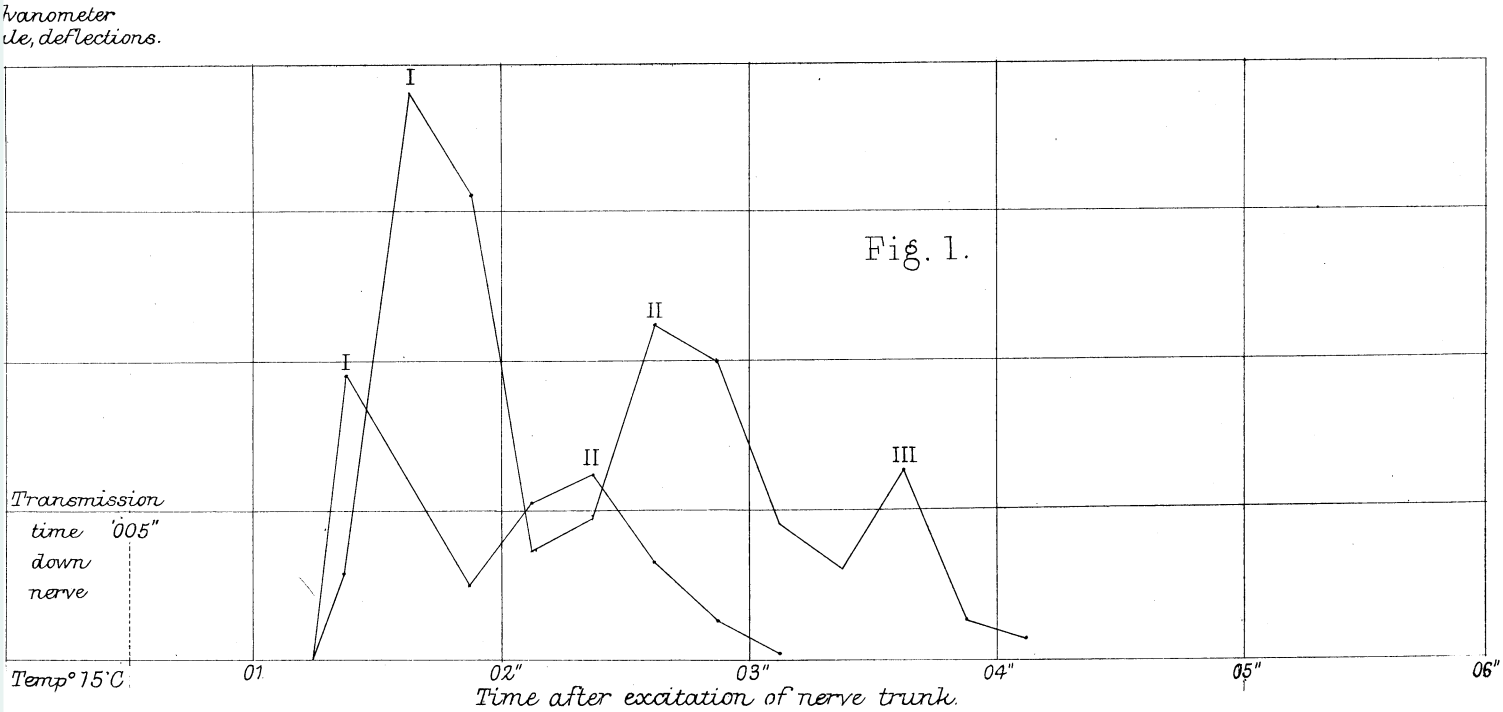

Fig. 1.

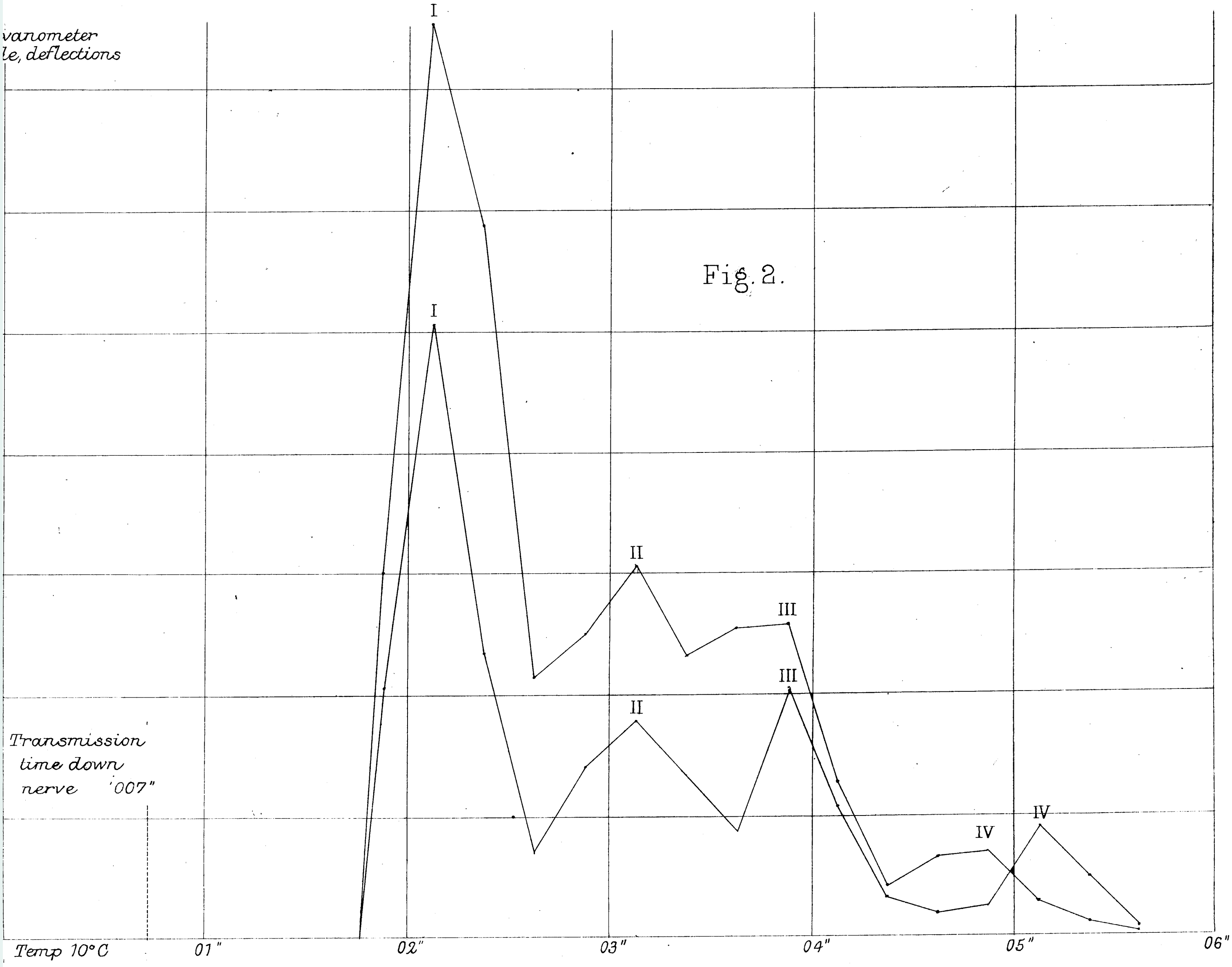

Fig. 2.

Electrical response of nerve organ preparations to single excitation of nerve showing primary, secondary, tertiary &c. responses.

West, Newman & Co. lith.