IV. *The Electromotive Properties of* Malapterurus electricus.

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Contents.

Part I.—Observations with the Nerve Muscle Galvanoscope upon the Living Uninjured Fish.

Section 1.—*Preliminary Observations.*

In the spring of the year 1895, Dr. H. O. Forbes, the Director of the Corporation Museum at Liverpool, obtained several living specimens of *Malapterurus electricus*, which were brought from the mouth of the river Senegal by Mr. A. Ridyard (s.s. "Niger"), and through the liberality of the Museum Committee four of these were placed at our disposal.

The fish remained in excellent health for a period of over six months; they were kept in tanks placed in a warm room at a temperature of 80° Fahrenheit and were fed with small worms or pieces of meat; the specimens were from 5 to 6 inches long and gave powerful shocks to the hand when touched.

A number of experiments were carried out on the living fish in the Liverpool Corporation Museum, and the results thus obtained were controlled and extended by further experiments in the Physiological Laboratories at University College, Liverpool, and at Oxford, these embracing both the examination of the live fish and that of isolated nerve organ preparations of recently killed specimens.

In order to connect the living fish with some form of galvanoscope, the following simple method was used. The fish was caught in a small net and transferred to a bell jar containing water at 20° C. Into this experimental tank a special small boat-shaped net could be dipped and passed under the fish; on raising this the fish lay evenly in the trough of the net. To the net were attached two multiple-strand copper wires, which were enclosed in tubes of india-rubber; small side openings in the tubes allowed the ends of the strands to project; these ends consisted of a brush of fine wire which was woven into the net, and the body of the fish was thus brought in contact with the fine copper strands without any risk of injuring the skin. The distance between the fine wires which thus formed the leads was capable of being adjusted by the simple method of altering the position of their attachment to the net. In most of the experiments, unless otherwise indicated, the distance was 2 centims., and the fish lay with the middle part of the body against the strands.

Some preliminary observations were made, the fish contacts being connected with the nerve of a nerve muscle preparation and with a large-bore capillary electrometer. These showed that whenever the fish was lifted into the net, the organ was discharged, but that when the net was kept steady the fish could be gently raised above the surface of the water and yet remain for several seconds quite passive. If

the fish skin was then lightly tapped with the finger, a single discharge of the organ occurred, which was evidenced by what to the eye appeared to be a single movement of the electrometer and a single twitch in the rheoscopic preparation, whilst a single intense shock was felt in the finger. The electrometer showed that the tail end of the organ was the positive pole of the derivation effect; a current thus flowing through the organ in consequence of its activity from head to tail, as observed first by Du Bois-Reymond. If the organ was gently squeezed by the hand a series of strong shocks were felt thrilling the hand muscles; a series of meniscus movements in the capillary were seen and the frog muscle was more or less tetanized.*

Some observations were now made as to the best means of evoking the apparently single shock produced by a single tap on the organ. It was found that a similar single shock could be obtained by passing through any part of the skin covering the organ a strong induced current, using for this purpose a pair of platinum electrodes with blunt points, 1 millim. apart, lightly pressed on the external surface of the skin. It was more difficult to evoke such a response if a similar exciting induction current was passed through the skin at the extremity of either the head or the tail, these parts being beyond the limits of the electrical organ, which is situated in the skin and wraps round the fish like a mantle, except at these points.

It seemed then from these preliminary experiments that a single mechanical or electrical stimulus of the surface of the skin over the organ could always evoke a response which gave the impression of being one single shock, and that an effect giving the impression of a series of such shocks was evoked by more prolonged skin pressure. Such a series was often observed when the fish happened to struggle on being caught in the net or when such struggles occurred on his being lifted in the net out of the water. Since the multiple series is obviously made up of a number of successive organ responses, the first object of inquiry was that of the time-relations and character of each of these apparently single shocks.

A discrepancy in connection with this apparently single effect was noted at the outset. On recording upon a fast-travelling surface, the contraction of the gastrocnemius of the frog when its nerve was excited by what to the hand appeared a single electrical response in the organ, it was found that the contraction was in many cases both higher and of longer duration than the maximal contraction evoked by any single stimulus, such as the break-induced current, when this was applied directly to the nerve of the muscle. It thus appeared probable that in many instances this apparent single shock of the fish was in reality a short multiple series of shocks occurring at rapid intervals.†

* Du Bois-Reymond, 'Gesammelte Abhandlungen,' vol. 2, p. 601, &c.

† See also Du Bois-Reymond, who notes that the intense shock of the *Malapterurus* is one in which several maxima can be distinguished. 'Gesammelte Abhandlungen,' vol. 2, p. 619.

Section 2.—*The Time-Relations of the Direct Response evoked in the Living Fish.*

The muscle-nerve preparation forms an extremely sensitive galvanoscope for the determination of the time of commencement of the discharge of an electrical organ, but its employment demands the adoption of certain indispensable precautions.

The moment of stimulation of the organ can only be exact if a break-induction current is used for excitation, and since the relative immunity of the fish necessitates the employment of exciting induced currents of considerable intensity, an escape along the wet body of the fish from the exciting circuit into the leading-off contacts is almost unavoidable. To guard the muscle-nerve preparation from such an escape is thus essential. It was accomplished by using a spring traveller as a rheotome and placing in the path traversed by the instrument three breaking keys, K_1, K_2, K_3. The keys were broken in succession at each passage of the traveller, and the distances between them could be altered at will. The first key, K_1, was placed in the primary circuit of a standard induction coil (KRONECKER'S graduated inductorium) with a battery of storage cells in the primary circuit; the second key, K_2, was arranged so as to effectively short circuit the muscle-nerve preparation, while the third key, K_3, was a double one, and its break opened both sides of the muscle-nerve circuit. It was ascertained by control experiments, in which wet saline conductors replaced the fish, that if the exciting electrodes were 3 centims. away from the leading-off contacts, and the short-circuiting key, K_2, so placed as to be broken $\frac{2}{1000}$ second after the break of K_1, no response occurred in the muscle-nerve preparation, even with the secondary coil pushed quite over the primary, thus showing that the short-circuit was effectual and that the subsidiary effect of the very strong induction shock employed did not, with this distance between excitation and leading-off contacts, cause a derivation intense enough to excite the nerve.

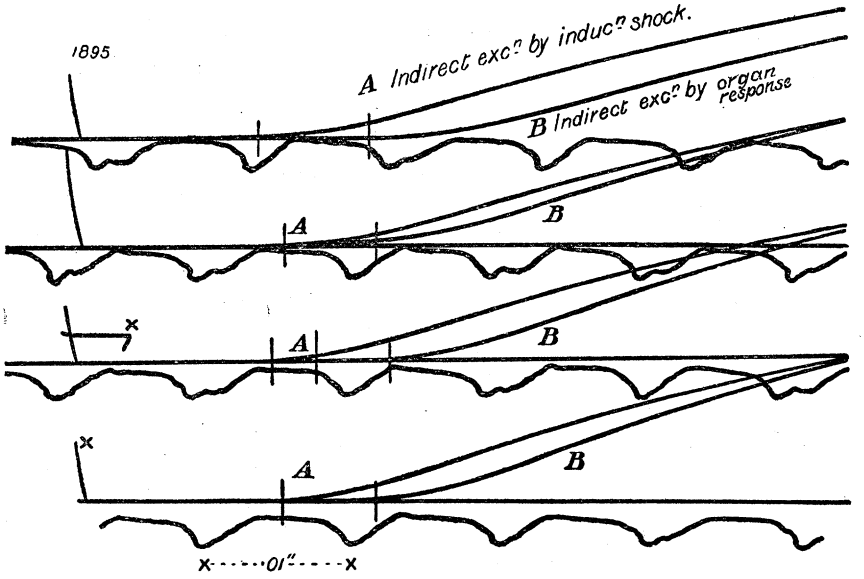
With the keys arranged so that K_2 was broken $\frac{2}{1000}$ second after K_1, and K_3 broken $\frac{32}{1000}$ second after K_2, each passage of the traveller first caused a break induction current to traverse the exciting electrodes, and then connected after an interval of $\frac{2}{1000}$ second the muscle-nerve preparation with the leading-off contacts for $\frac{3}{100}$ second. An adequate exciting current was produced by the break of 5 small portable Lithanode cells (10 volts) in the primary circuit of the Kronecker induction coil, the core being removed, and the secondary placed so as to be at least half-way over the primary; the induction shock was thus an intense one.

The traveller of the rheotome carried a smoked glass plate, on which the muscle of the galvanoscope inscribed its contraction, and the rate of its movement was timed in the usual way by recording the vibrations of a standard tuning-fork making 100 DV. per second.

The fish, which was kept at 20° C., having been caught in the experimental net, was raised out of the water, and the exciting electrodes, with platinum points 1 millim. apart, were placed on the skin over the organ at a point near its caudal

termination, 5 centims. distant from the nearest leading-off contact. It was found that, at each passage of the traveller, the muscle gave a vigorous response, evidently evoked by the shock with which the organ responded to its excitation. After each such experiment, the fish was replaced in the water by lowering the net, and the nerve of the muscle preparation was then excited by allowing a far weaker but adequate induced current, obtained in the same way by the break of K_1, to pass through the leading-off circuit. In this way two muscle curves were obtained—one, A, due to the excitation of the nerve by the induced circuit; the other, B, due to the excitation of the fish, and the subsequent excitation of the nerve by the organ shock; the interval of time between the two is obviously the time lost in the

Fig. 1.



development in the fish of the shock, *i.e.*, the period of delay of the organ response. This interval in five experiments was as follows: ·005 second, ·004 second, ·066 second, ·0055 second, ·005 second. An example of the record is given in fig. 1. This experiment shows that a response to stimulation may occur in the living fish at 20° C. as early as ·004 second after the electrical excitation of the skin over the organ, and it thus appears that the period of delay of the organ effect in the entire living fish, when evoked by an adequate induction current sent through its skin surface, may be excessively short, and the same as that subsequently found to exist when the nerve of an isolated nerve-organ preparation at the same temperature was excited. It is clear, therefore, that this response as regards its initial start was not a reflex one, since the delay was far too short, but that it was evoked by the direct excitation of the organ and its contained nerves. It is well known that the whole organ on each side is innervated by the branches of one axis cylinder, and that the excitation of any one terminal

branch evokes a nerve impulse which is propagated along the axis-cylinder branches to every part of the organ, and thus a localised excitation of the skin can undoubtedly cause a response of the entire organ. Similar periods of delay were observed by one of us (F. G.) in the response to skin excitation over the organ upon a living specimen of *Malapterurus* in 1884. An increased delay on exciting some way off the organ was then noticed, but the present experiments seem to show that the increase then noted was due to excitation beyond the organ limits, and that the response was in that case a reflex.*

The muscle-nerve preparation was now used to determine the duration of the direct response. For this purpose the third key K_3 was brought close to K_2, so that with the speed of traveller used, an interval of $\frac{1}{1000}$ second (closing time) should elapse between the break of K_2 and K_3.

By a special arrangement the two keys, K_2 and K_3, could be shifted so that the nerve-muscle preparation should be placed in communication with the fish at any interval from $\frac{2}{1000}$ second to $\frac{2}{100}$ second after excitation.

A series of observations were then made, the muscle being allowed to inscribe its contraction upon a stationary cylinder, which was moved on by hand between each experiment. The following chart indicates some of the results thus obtained :—

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Galvanometer closing time after excitation.	·002 to ·003 sec.	·003 to ·004 sec.	·004 to ·005 sec.	·005 to ·006 sec.	·006 to ·007 sec.	·007 to ·008 sec.	·008 to ·009 sec.	·009 to ·011 sec.	·011 to ·012 sec.	·012 to ·013 sec.	·013 to ·014 sec.	·014 to ·015 sec.	·015 to ·016 sec.			
Exp. (1)	nil	nil	C	C	C	C	nil	nil	nil	nil	nil	nil	nil	} First fish		
Exp. (2)	nil	nil	C	C	C	nil	nil	nil	nil	nil	nil	nil	nil			
Exp. (3)	nil	nil	nil	C	C	nil	nil	nil	nil	nil	nil	nil	nil			
Exp. (4)	nil	nil	nil	C	nil	nil	nil	nil	nil	nil	nil	nil	nil			
Exp. (5)	nil	nil	C	C	C	C	nil	nil	nil	nil	nil	nil	nil	} Second fish		
Exp. (6)	nil	nil	C	C	C	C	C	nil	nil	nil	nil	nil	nil			
Exp. (7)	nil	nil	C	C	C	nil	C	C	C	C	C	nil	nil	nil	nil	Third large fish
,,	...	...	...	...	C	nil	C	...	...	...	...	...	...	...	...	
,,	...	...	...	...	C	nil	C	...	...	..	...	...	..	...	...	
Exp. (8)	nil	nil	C	C	nil	nil	C	nil	nil	nil	nil	...	...	...	...	
Exp. (9)	nil	nil	C	C	C	nil	nil	nil	nil	nil	nil	...	...	...	..	

The letter C signifies a contraction of the rheoscopic muscle. When it is borne in mind that the method necessitated a large number of excitations, one for each new closing time, and that for each one the fish had to be raised out of the water by means of the net, the results are on the whole surprisingly alike. In experiment (6), which was done at a considerable interval after (5), upon a fish which gave very powerful shocks to the hand, the effect commenced with a closure of from ·004 to ·005 second and lasted until ·008 to ·009 second. In experiment (1),

* See Gotch, 'Proceedings of Journal of Physiology,' vol. 6. Physiological Society, Dec., 1885, vol. 28.

on a fresh vigorous fish, the effect began at ·004 to ·005 second and lasted until ·007 to ·008 second. As the creature became fatigued so the time relations of the response as estimated by this method appeared to alter; thus experiments (3) and (4) were made on an obviously fatigued fish, and in (4) a response was obtained only with the closure ·005 to ·006 second. It was evident that the organ response varied with the condition of the fish and that a vigorous response, commencing about $\frac{5}{1000}$ second after excitation, tailed off in its subsidence, so that some electrical effect remained in the organ for at least $\frac{5}{1000}$ second after its production.

Finally, in experiments (7) and (8), every precaution was taken in order to secure that the fish should be in a very active state, and that the necessary preliminary handling should be as little as possible. The experiments were carried out upon the largest of the fish in the tanks of the Liverpool Corporation Museum, and one which sensibly gave most powerful shocks.

The results are given in the chart under (7) and showed that the rheoscopic muscle responded with closing times of ·001 second, from ·004 up to ·007 second, and not at all with a closing time of ·007 to ·008 second, but that with a closing time of ·008 to ·009 second a muscle response was again obtained, and so on up to ·013 to ·014 second. In order to make certain of the failure of the rheoscopic muscle response at ·007 to ·008 second, this closure, with its immediate predecessor and successor, was repeated three times. A repetition of the whole series from the beginning gave the results shown in experiment (8), in which a similar hiatus in the series presented itself, but this time from ·006 to ·008 second. Finally, the whole repeated yet again, gave a result precisely similar to experiment (2).

The interpretation of these observations seemed to be, on the face of it, the existence of a rhythmical double response of the organ, the initial or primary shock commencing at about ·004 second and tailing off by about ·006 to ·007 second, and the secondary one commencing at ·008 to ·009 second, that is $\frac{5}{1000}$ second after the first and similarly tailing off. Such rhythmical effects in the electrical organ, as the result of a single stimulus, may be due either to multiple reflex discharges of the central nervous system following and enforcing the direct response, or to a peripheral rhythmical state of excitation in the organ itself.

The response of the isolated nerve organ of *Torpedo* was found by one of us * to be in some cases a multiple one, and the observations then made have been since confirmed by SCHOENLEIN.† In the *Malapterurus* convincing evidence will be afforded by the galvanometer and capillary electrometer observations, to be detailed in Parts II. and III., of the tendency of the isolated organ to respond to a single stimulus by a multiple series of excitatory changes, so that the part played by the central nervous system, even in the reflex response of the entire uninjured fish may

* GOTCH. "Further Observations on the Electromotive Properties of *Torpedo Marmorata*." 'Phil. Trans.,' vol. 179, B, p. 347, 1888.

† SCHOENLEIN. 'Zeitschrift f. Biologie,' vol. 31, 1895.

be reduced to the initiation of such a peripheral series by the production of the first initial effect.

In the experiments just described this initial effect is evidently evoked by the induction shock stimulating the organ and its contained nerves. It may, however, be reflexly evoked by the excitation of the afferent nerves in the skin.

Section 3.—*The Reflex Response of the Organ.*

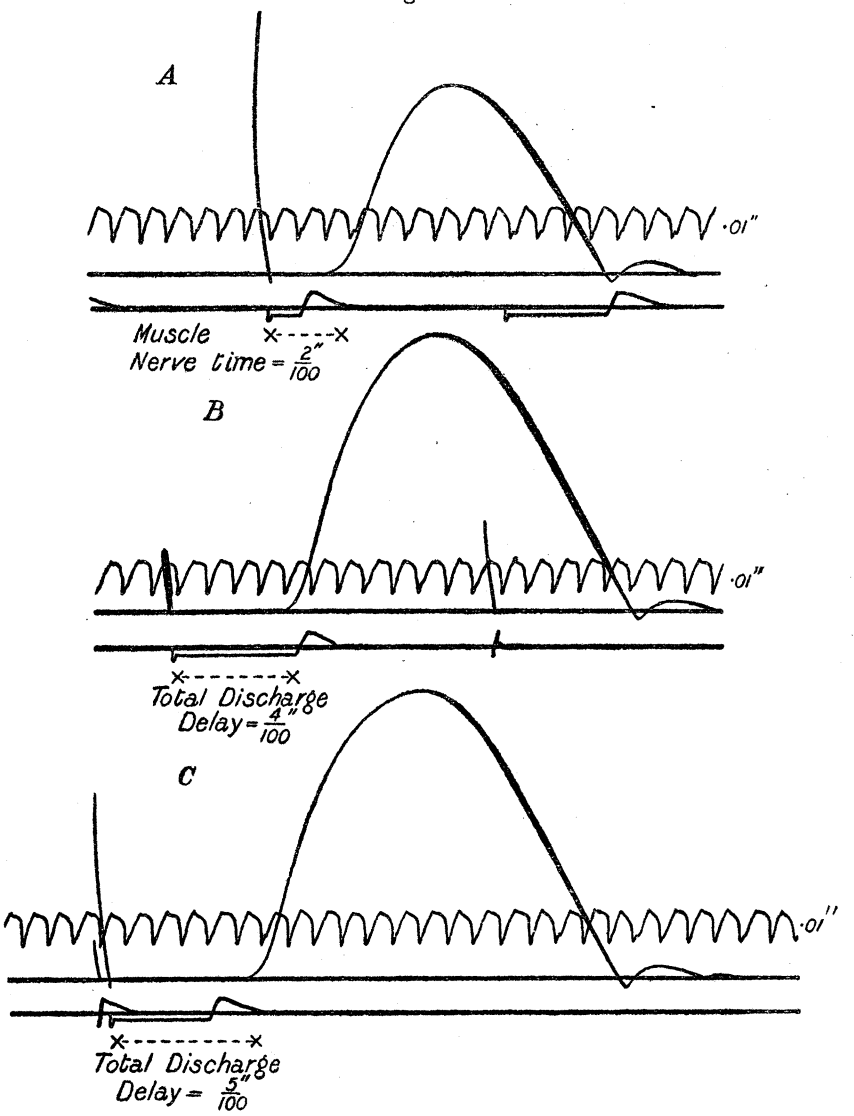
The character of the reflex response of the *Malapterurus* organ is of special interest, owing to the well-known central structural relations of the electrical nerves. Each of the two nerves is the axis-cylinder branch of the single large nerve cell situated in the dorsal grey matter of the spinal cord near its bulbar end.* The reflex response is thus evoked by nerve impulses, which are, in each lateral organ, the central discharge of a single nerve cell, and its investigation is that of a reflex arc reduced to its utmost simplicity. It offers us, in short, a possible means for ascertaining the characters of the nervous discharge of a single efferent nerve cell. Further, since the response of an electrical organ is in our opinion (see Part III., Section 3) a nerve phenomenon, and is not transformed, as in the case of muscle, into the reaction of a second excitable structure, its investigation during reflex activity furnishes more reliable information than can be derived from any other terminal organ as to the efferent discharge of the central nervous system. The special feature which we have endeavoured to examine, and which alone will be referred to here, is that of the time-relations of the reflex response, in so far as these throw light upon the functions of the central mechanism.

The Time-Relations of the Reflex Response.—The experiments were all carried out on the uninjured fish by means of the special net alluded to in the first section of this communication, the fish being kept in water at from 20° to 25° C. The records of the response to be now referred to were those of the rheoscopic nerve-muscle preparation of the frog, which afforded excellent information as to the first essential point, viz., the period of delay. It was found that a response could be obtained from the fish with tolerable certainty when the skin over the extreme end of the tail fin beyond the organ limits was excited by a light tap, or by an electrical stimulus in this region, although this second method often failed. The muscle-nerve preparation was placed in connection with the fine wire leads of the net previously described, and the preparation recorded its contraction upon a fast-travelling drum. In order to signal the moment of the tap, the following device, which experience had shown to be reliable, was employed. A light thin metal bar was cautiously placed across the fin of the fish as it lay in the net when raised out of the water. This bar was connected by flexible wire with one terminal of a strong battery, the other terminal being similarly connected to a metal rod through a delicate electro-magnet signal, which recorded its

* Bilharz. 'Das elekt. Organ des Zitterwelses;' Leipzig, 1857. G. Fritsch. 'Die elektr. Fische,' Leipzig, 1887 and 1890.

movement upon the drum. On tapping the bar with the rod, the signal current was closed and the closure recorded, whilst the fish tail was at the same instant lightly struck by the bar. Control experiments showed that the loss of time with the signal did not amount at the most to ·001 second. The discharge of the fish caused a strong contraction of the muscle of the nerve-muscle preparation, and the time between the

Fig. 2.



blow and the discharge of the fish was easily ascertained by ascertaining in each instance what portion of the total delay was due to the nerve-muscle preparation itself. The results were tolerably uniform, but as in all reflex effects varied between a minimum delay of hundredths of seconds and a maximum of tenths. The minimum total delay in four quite reliable experiments was ·04 second, and in two it was ·05 second, of which time ·02 second was that of the nerve-muscle galvanoscope. In fig. 2, the results of three experiments are shown. A is the muscle curve when the

nerve was excited by a single induction shock, B and C are those of the contraction evoked by the excitation of the nerve through the fish response. We ascertained subsequently that the fish nerve propagation rate, at 20° C., is at least 33 metres in 1 second; and, as the greatest length of both afferent and efferent fish nerves was at the most 300 millims., this gives from $\frac{1}{100}$ to $\frac{2}{100}$ second as the time lost in the peripheral and central electrical organ mechanisms; of this, $\frac{5}{1000}$ second is undoubtedly lost in the peripheral electrical organ, so that the minimal central time lies between ·005 and ·015 second.

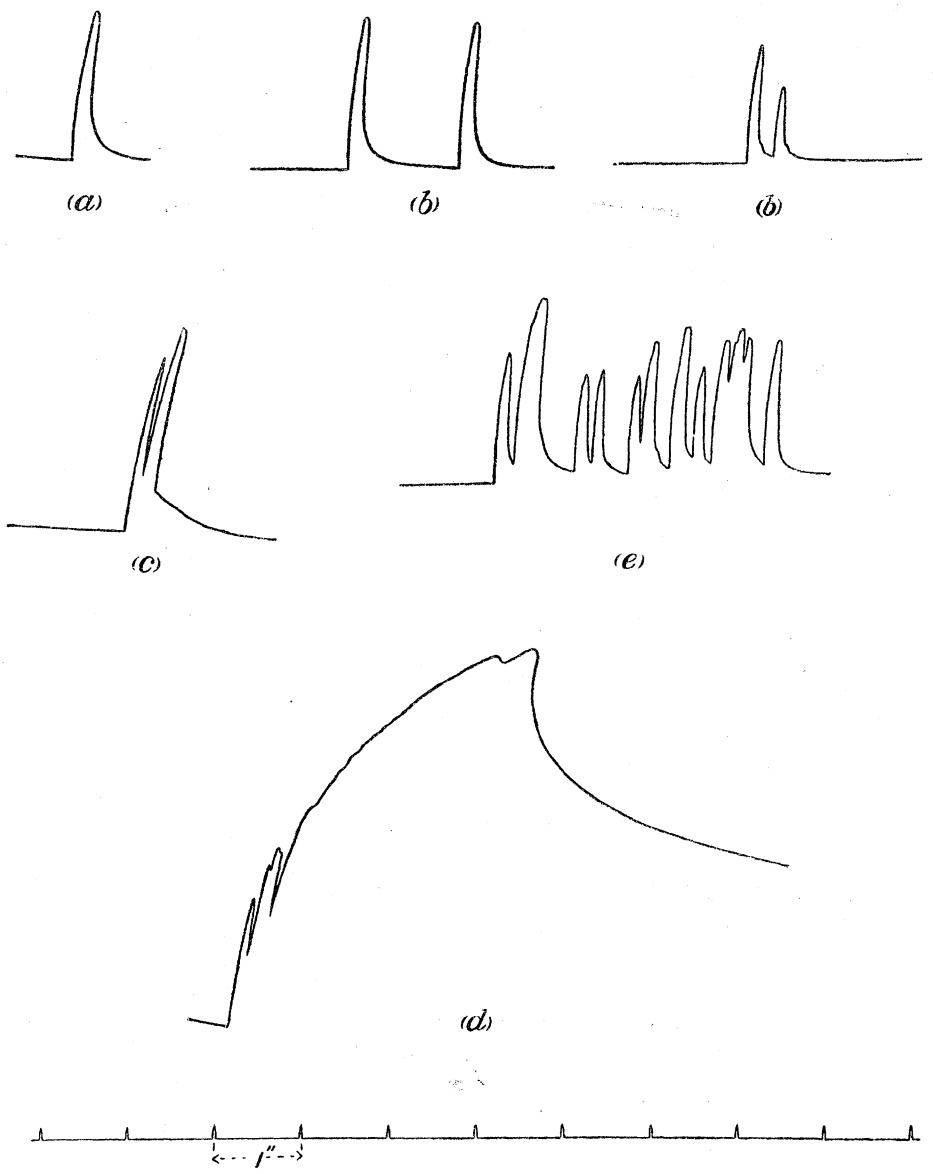
The Rhythm of the Reflex Response.—The second point, viz., the frequency at which such nervous discharges reach the organ, we found a far more troublesome matter to investigate by the frog galvanoscope. In the first place, the reflex response varied enormously with the nature of the awakening sensory stimulus; and, secondly, the existence of a peripheral organ rhythm, which itself will excite the muscle, must obscure a record of the succession of organ responses due to the central nervous discharge. The first difficulty was palliated by adopting the plan of always using such a forcible prolonged stimulus as would arouse the fish to great central activity; the particular form which we found best adapted for the purpose being to grasp the body of the fish with the hand. The fish then struggled and discharged a series of intensely powerful shocks. The second difficulty could not be wholly avoided. It is obvious that the nerve-muscle preparation may respond to any peripheral organ rhythm by a tetanus of variable duration. Each fresh accession in such a rhythm would then be only obscurely indicated by an increase in the continuous contraction; but when, as frequently happened, the muscular contraction had subsided before the next contraction occurred, the time interval between the two groups of muscle tetanic effects furnished some indication of the rate of the successive organ responses evoked by the central discharge. Thus, a series of 62 observations was made on one fish, the net wires being connected through needles to the nerve of the galvanoscope, and at the same time to a large-bore capillary electrometer. The fish was raised out of the water in the net, and squeezed on both flanks about every two or three minutes, the water being kept at 20° C.

A reflex organ response was evoked every time, although the experimental handling of the fish was continued for two hours. The character of the recorded frog-muscle galvanoscope contractions in reply to the organ reflex response varied very greatly, and the whole series may be roughly divided into four classes.

Class 1, of which fig. 3 (a) is an instance, consisted of apparently single contractions; these, with a fast rate of recording surface, were seen to be in many cases larger and longer than a single maximal muscular response and are summated muscular contractions, such as would be caused by two or three stimuli occurring in very rapid succession (100 to 200 per second). There were no less than thirty-three such records. The reflex discharge was, therefore, in all probability a single one, but the organ response showed a brief multiple organ rhythm.

Class 2, of which fig. 3 (*b*) is an example, comprises instances in which the muscular contractions consisted of two or three isolated muscle curves, each similar in character to those of Class 1. There were thirteen such instances, the interval between the contractions varying from a minimum of $\frac{1}{4}$ second to a maximum of 1 second or more.

Fig. 3.



Here, then, we conclude that two or three reflex discharges from the central nervous system have occurred at these intervals of time.

Class 3, of which fig. 3 (*c*) is an example, comprises instances in which a short second muscular tetanic contraction occurred at such a close interval as to be superimposed on the first; there were thirteen such cases, and the minimal time between the two muscular responses was $\frac{1}{12}$ to $\frac{1}{10}$ second, the maximal being $\frac{1}{7}$ second.

Class 4, of which fig. 3 (*d*) is an example, comprises three cases in which the effect comprised a prolonged muscular tetanus, and as it is difficult to judge how far this is due to an intense peripheral organ rhythm mixed up with a succession of responses to central reflex nerve discharge, they throw little light on the present question. In the figure it appears probable that the final tetanus is due to the peripheral rhythm.

The observations thus appear to show that the organ can respond reflexly to both mechanical and electrical stimulation of its skin, and that such a response differs from the direct one, first, in its longer period of delay, and secondly in the fact that it can be renewed at variable intervals, the minimum time between such a renewed outburst and its predecessor being, as far as this method can determine it, $\frac{1}{12}$ second. It appeared, moreover, that this renewal of the organ response is one which the fish is able to bring about with the rapid frequency of twelve per second only a very few times, so that with a repetition or prolongation of the skin stimulus in the vast majority of cases the response is renewed two or three times, at intervals of $\frac{1}{4}$ to $\frac{1}{2}$ second, then fails to be renewed again after about 1 second. In fig. 3 (*e*) is the rheoscopic record of the organ response produced by such a prolonged skin pressure; there are evidently four or five groups of such responses, the last but one consisting of three contractions at intervals of $\frac{1}{10}$ second; the whole comprises members of all the above Classes 2, 3, and 4, and lasts nearly 4 seconds.

Part II.—Galvanometer Experiments on the Organ when Removed from the Fish.

Section 1. The Response of the Isolated Organ to Excitation of its Nerve.
„ 2. Experiments on Irreciprocal Resistance.
„ 3. Excitation of the Isolated Organ and its contained Nerves by the passage of an Induced Current.

One fish was killed, and the organ utilised for galvanometer observations. The results were obtained by one of us (F. G.) in the Physiological Laboratory of University College, Liverpool, with the assistance of J. S. Macdonald (B.A., Cantab.), and they fall naturally into two sections, namely, those in which the response was obtained by excitation of the nerve trunk outside the organ, and those in which the exciting current was led through the organ and its contained nerve endings. In addition, a few experiments were made upon irreciprocal resistance.

Section 1.—*The Response of the Organ to Excitation of its Nerve.*

In order not to injure the nervous system, or any part of the organ, the fish was killed by placing it in water at 3° C. At this temperature the fish rapidly became immobile, and in four or five minutes was apparently either dead or completely anæsthetised. It was ascertained, by keeping the hand close to the fish, that during

this process the organ had not discharged. The fish was then taken out, two median longitudinal incisions were made, one dorsal and one ventral, the organ on one side was then rapidly dissected up from the tail towards the head. During this dissection the operator (F. G.) held the tail portion in a pair of metal forceps, and, having freed it from its subjacent attachments until only the nerve which enters it near the head end remained, he divided the nerve with a pair of scissors. The mechanical stimulus of the nerve division caused a powerful response in the piece of organ, a distinctly multiple shock passing through both* the arms of the operator.

This portion of organ with its nerve was then placed, with its inner surface uppermost, on a glass plate in a moist chamber; it measured 8 centims. in length and about 3 centims. in width, the organ being about half a centimetre thick. It was connected to a pair of non-polarisable electrodes by means of thick cables soaked in 0·6 per cent. NaCl, the cables being plastered with kaolin similarly soaked. The nerve was then lightly stretched, and placed in contact with a pair of fine needle electrodes.

The non-polarisable electrode cables were arranged so as to lie right across the organ at a distance of 6 centims. from each other, and were connected with a circuit comprising a high resistance galvanometer (THOMSON), shunt, compensator, and the spring rheotome with the three keys previously alluded to, as used with the frog galvanoscope.†

Just as in the case of the Torpedo organ preparations, described by one of us (F. G.), an injury organ-current was observed, the direction of which was similar to that of the shock of the response (*i.e.*, the caudal end of the organ was galvanometrically positive to the head end), and, for convenience, effects producing currents in this direction will be denoted thus +; this resting difference of potential was very small, being compensated in the galvanometer by a counter potential difference of ·0075 D. It was not observed in the entire uninjured fish.

The nerve trunk was now adequately excited 1 centim. from its entry to the organ by a comparatively feeble induced current, *i.e.*, the induction shock produced by breaking two Daniell cells in the primary coil of the Kronecker inductorium, the secondary coil being placed halfway over the primary. It was ascertained by a few preliminary experiments that the galvanometer effect due to the organ response was not appreciably increased by any greater intensity of exciting shock.

A series of rheotome observations were now made, the closing time being ·001 second in duration, and being shifted with each experiment to different periods from the moment of nerve-excitation, the temperature of the organ being throughout that of the room, averaging 17° C. The results are shown in the annexed chart.

* A similar effect, but very much less intense, was felt by me on dissecting out the organ of *Torpedo*, and described 'Phil. Trans.,' vol. 179 (1888), B, p. 352. F. G.

† The rheotome arrangement was similar to that employed by GOTCH in the case of the *Torpedo*, and the connections were those figured in 'Phil. Trans.,' vol. 178, B, p. 504.

Closing time after excitation.	·001 to ·002 sec.	·002 to ·003 sec.	·003 to ·004 sec.	·004 to ·005 sec.	·005 to ·006 sec.	·006 to ·007 sec.	·007 to ·008 sec.	·008 to ·009 sec.	·009 to ·010 sec.	·010 to ·011 sec.
Galvanometer total effect .	0	0	+25	+∞ *	+∞					
Galvanometer with $\frac{1}{10}$ shunt	..	..	..	+260	+200	+40	+10	+6	0	0
Galvanometer total effect .	0	0	+15	+∞	+∞					
Galvanometer with $\frac{1}{10}$ shunt	0	0	..	+250	+210	+50	+ 8	+6	0	0

The above experiment showed that the organ response to nerve excitation began about ·004 second after the moment of stimulation, this being its period of delay. The very slight foreshadowing effect observed with a closure of from ·003 to ·004 second indicates that this period was just sufficient to catch a fraction of the suddenly developed electrical change. The results show also that the change is developed very suddenly and then more slowly subsides, the whole effect lasting from ·04 to ·01 second, *i.e.*, about $\frac{6}{1000}$ second.

The rheotome closing time was now shortened to ·008 second to be able to make more exact observations, and a new series of experiments was made, special attention being paid to the subsidence of the effect. The results of these observations are shown in the next chart.

Closing time.	·0016 to ·0024 sec.	·0024 to ·0032 sec.	·0032 to ·0040 sec.	·0040 to ·0048 sec.	·0048 to ·0056 sec.	·0056 to ·0064 sec.	·0064 to ·0072 sec.	·0072 to ·0080 sec.	·0080 to ·0088 sec.	·0088 to ·0096 sec.	·0096 to ·0104 sec.	·0104 to ·0112 sec.	·0112 to ·0120 sec.	·0120 to ·0128 sec.	·0128 to ·0136 sec.
Galvanometer total effect	0	0	+15	+∞	+∞	+340	+45	+30	+12	+4	+55	+35	+20	2	
Same repeated between ·0088 and ·0128 sec.	...	...	...	...	...	...	...	...	...	+6	+25	+10	+2	0	

The second experiments show as before that the period of delay is ·004 second, but they show that a more careful analysis of the subsidence reveals a second effect following the first, the galvanometric reading from ·0096 to ·0104 second, being in excess of its immediate predecessors or successors. It is perhaps scarcely necessary to say that the periods of closure must not be taken as exactly corresponding with the numbers given ; but as far as could be ascertained the duration of closure was always ·008, and the keys were carefully moved along a scale this amount ; the errors of accurate timing which undoubtedly existed, do not however invalidate the conclusion,

* The sign +∞ means that the spot of light shot off the screen, *i.e.*, over 600 scale.

that the response of the nerve organ preparation to a single stimulus of its nerve is one in which the initial effect is succeeded by a second one.

The strip of organ was now carefully divided across the middle of its length, the electrodes being left untouched. This operation left the head end of the strip alone in connection with the stimulated nerve, and thus diminished to about one half the number of elements (electric plates) supplied by the excited nerve. A series of rheotome observations were now made, and as the object was to compare the general magnitude of the response of the shorter with that of the whole strip, the closing time was altered back to ·001 second, and the whole experiment carried out precisely like those given in the first chart with which it is to be compared.

Closing time after nerve excitation.	·001 to ·002 sec.	·002 to ·003 sec.	·003 to ·004 sec.	·004 to ·005 sec.	·005 to ·006 sec.	·006 to ·007 sec.	·007 to ·008 sec.	·008 to ·009 sec.	·009 to ·01 sec.
Galvanometer total effect	..	0	30	∞					
Galvanometer $\frac{1}{10}$ shunt .	..	..	..	104	70	14	6	Trace	0

The above is an illustration of the familiar fact that the intensity of the electrical response varies directly with the number of elements thrown into activity.* If it is compared with those in the first chart, it is evident that the primary initial effect commences in the same way, and subsides in the same way, but that its intensity is decreased to a little less than one half.

Section 2.—*Experiments on Irreciprocal Resistance.*

As in the case of *Torpedo*† and of *Raia batis*,‡ it was found that strips cut from the isolated organ respond to the passage of an electrical current through their substance. For this purpose the exciting current must obviously be a tolerably intense one, and the most convenient to use is the induced current.

A strip of the *Malapterurus* organ was cut, measuring 3 centims. long in the direction from head to tail and 1 centim. wide; the electrodes were connected with its cut ends, and the galvanometer circuit now arranged so as to comprise the secondary coil of an induction apparatus with two Daniell cells in the primary and the secondary placed fully over the primary.

The spring rheotome with keys K_1, K_2, K_3 was used as before, K_1 being the

* "Further Observations on the Electromotive Properties of Torpedo Marmorata," Gotch, 'Phil. Trans.,' 1887, vol. 179, B, p. 344.

† Gotch, 'Phil. Trans.,' vol. 178, B.

‡ Sanderson and Gotch, 'Journal of Physiology,' vol. 9.

breaking-key of the primary circuit, K_2 a key effectively short-circuiting the galvanometer, and K_3 a key directly interposed in the galvanometer circuit. As in previous experiments, the keys were broken successively, the time between the break of K_1 and K_2 (Übertragungszeit) being the interval between the passage of the induced current through the organ and the connection of the organ with the galvanometer, that between K_2 and K_3 (closing time) the period during which the galvanometer current remained closed. The first experiments were directed to ascertain whether there was any alteration in the intensity of the induced current dependent upon its direction through the organ; whether, in short, the electrical resistance of the organ showed any irreciprocity in the sense in which Du Bois-Reymond used the term and which was not confirmed by one of us (F. G.) in experiments upon *Torpedo*.*

To ascertain this it was necessary to arrange so that no part of the electrical response of the organ in addition to the exciting current should flow through the galvanometer, otherwise an apparent irreciprocity must be produced, due to the algebraic sum of the variably-directed exciting current with the constantly-directed organ response.

In order to effect this, K_2 was put ·001 second before K_1, and K_3 ·001 second after K_1, so that the galvanometer closing time embraced the exciting induced current, and that only. The sign (+) indicates in all cases an exciting current which traverses the organ from head to tail, *i.e.*, in the direction of the organ response, termed by Du Bois-Reymond "homodromous;" the sign (−) one in the opposite direction, "heterodromous."

As will be seen by the following readings, there was no appreciable difference in the intensity of these currents, as indicated in the galvanometer; that is no evidence by this method of marked irreciprocal resistance.

Direction of current.	Galvanometer effect.	Induction apparatus.
Direction (+) . . .	Deflection +520 . . .	Two Daniells in primary, secondary coil at 13,000.
,, (−) . . .	,, −515 . . .	
,, (+) . . .	,, +415 . . .	Two Daniells in primary, secondary coil 9000.
,, (−) . . .	,, −415 . . .	
,, (+) . . .	,, +405 . . .	,, ,, ,,
,, (−) . . .	,, −410 . . .	,, ,, ,,
,, (+) . . .	,, +408 . . .	,, ,, ,,
,, (−) . . .	,, −410 . . .	,, ,, ,,
,, (+) . . .	,, +385 . . .	Ditto, but secondary coil 8000.
,, (−) . . .	,, −385 . . .	,, ,, ,,
,, (+) . . .	,, +200 . . .	In this case an additional resistance of 100,000 ohms was introduced.
,, (−) . . .	,, −198 . . .	

* Gotch, 'Phil. Trans.,' vol. 179, B.

Section 3.—*Excitation of the Isolated Organ and its Contained Nerves by the Passage of an Induced Current.*

There is thus no evidence in this organ of irreciprocal resistance, but it is not so clear that the response is not affected by the direction of the exciting current. In the following observation the central or primary response of the organ was investigated by moving the galvanometer keys K_2, K_3 so that the closing time should take place at the intervals given in the annexed chart, and the character of the response to the (+) and (−) induced current examined. It was found that the (−) induced current (*i.e.*, the heterodromous one) was apparently more effectual than the (+) homodromous one, and that the time relations of the response were slightly different. The following is an example (two D. in primary, coil 5) :—

Closing time interval, measured from excitation.	·003 to ·004 sec.	·004 to ·005 sec.	·005 to ·006 sec.	·006 to ·007 sec.
Galvanometer total effect. Excitation current (+)	+ 5	+ 60	+350	+240
Excitation current (−)	+70	+450	+260	+ 40

This experiment was afterwards confirmed by several observations on other fish made with the capillary electrometer, and detailed in Part III., Sections 4 and 6; and, as the organ thus appeared to respond with less certainty to the homodromous induction current, it seemed advisable, in order to obtain an accurate series of time relations of the total response, to employ throughout the heterodromous exciting current. The employment of this (−) current has the further advantage that there is less danger of the tail of the induction current through its being (−) becoming confused with the commencement of the + organ response.

The response of the organ was investigated by moving the closing-time keys K_2, K_3 forward in steps $\frac{1}{1000}$ second at a time from ·002 second after excitation to ·03 second, &c. As will be seen from the following chart, the organ response showed a marked peripheral rhythm. It was impossible to follow it to its complete subsidence, owing to the want of a more extended rheotome; but it will be seen that the primary response begins at ·003 to ·004 second; that this develops rapidly and subsides, to be succeeded at ·008 to ·009 second by a second of the same intensity, which is succeeded by a third at ·014 second, this by a fourth at ·021 second, by a fifth at ·028 second, and in all probability a succession of others, since a general closure from ·033 to about ·045 second gave a very large galvanometric effect.

The response of this strip of *Malapterurus* organ evoked by the (−) single induced current when this traverses its substance is thus a multiple one in which a fresh

electromotive change is developed every ·006 second, *i.e.*, there are at this temperature 18° C. successive changes at a rate of about 170 in 1 second.

MULTIPLE Response of Organ to the Excitation of a Single Induced Current through its substance.

Primary response.						
Closing time.	·002 to ·003 second.	·003 to ·004 second.	·004 to ·005 second.	·005 to ·006 second.	·006 to ·007 second.	·007 to ·008 second.
Galvanometer effect . .	+ trace	+180	+480	+260	+80	+35

Secondary response.						
Closing time.	·008 to ·009 second.	·009 to ·010 second.	·010 to ·011 second.	·011 to ·012 second.	·012 to ·013 second.	·013 to ·014 second.
Galvanometer effect . .	+60	+450 +460	+230	+50	+35	+14

Tertiary response.							
Closing time.	·014 to ·015 second.	·015 to ·016 second.	·016 to ·017 second.	·017 to ·018 second.	·018 to ·019 second.	·019 to ·020 second.	·020 to ·021 second.
Galvanometer effect	+145 +135	+240 +230	+220 +220	+65	+35	+15	+ trace

Fourth response.						
Closing time.	·021 to ·022 second.	·022 to ·023 second.	·023 to ·024 second.	·024 to ·025 second.	·025 to ·026 second.	·026 to ·027 second.
Galvanometer effect . .	+120	+220	+110	+45	+20	+10

	Fifth response.						Remainder.
Closing time.	·027 to ·028 second.	·028 to ·029 second.	·029 to ·030 second.	·030 to ·031 second.	·031 to ·032 second.	·032 to ·033 second.	·033 to ·045 second.
Galvanometer effect . .	+35	+200	+280	+160	+45	+15	$+\infty$

PART III.—OBSERVATIONS WITH THE CAPILLARY ELECTROMETER UPON THE RESPONSE OF THE ELECTRICAL ORGAN WHEN REMOVED FROM THE FISH.

Section 1. Description of the Special Methods of using the Electrometer.
„ 2. The Peripheral Rhythm of the Isolated Organ in response to a single excitation of its Nerve.
„ 3. The Causation of the Peripheral Organ-Rhythm.
„ 4. The Excitation of the Organ by the Heterodromous Induced Current.
„ 5. The Influence of Change of Temperature upon the Response to Stimulation by the Induced Current.
„ 6. The Excitation of the Organ by the Homodromous Induced Current.
„ 7. The Single Initial Shock. Its time-relations and character.
„ 8. Estimation of the E.M.F. and Quantity of the Discharge.

Section 1.—*Description of the Special Methods of using the Electrometer.*

For the experiments to be detailed in this and the succeeding parts of the present work, a capillary electrometer was used, which combined great sensitiveness and rapidity of action. Its movements were photographed by means of the special apparatus in the Oxford Physiological Laboratory invented by BURCH and described both by Professor SANDERSON* and by him.† It will be sufficient here to state that the position of the meniscus is recorded upon a photographic plate travelling past a slit upon which the image of the capillary tube is thrown. The dark-slide is placed in a holder at the upper end of a balanced pendulum started by a weight which, as in Atwood's machine, ceases to act just before the plate reaches the slit, thus imparting to the apparatus a velocity which is sensibly constant during the required interval, and which can be made fast or slow by altering the ratio between the moving masses.

In the experiments to be now described this velocity is measured by a tuning fork making 500 double vibrations per second, fixed close to the slit, and producing the undulating line at the bottom of each photograph. This will be called the "time-line," the "line of reference" being the circular arc recorded by the extreme end of the slit, which is sharply defined, and therefore most suitable to measure from.

* BURDON SANDERSON, 'Journal of Physiology,' vol. 18, p. 125.

† G. J. BURCH, 'Phil. Trans.,' vol. 183 A, p. 91, and 'The Electrician,' July 17, 1896, et seq.

With slower rates an electro-magnetic time-marker, driven by a fork making 8 double vibrations per second, was employed. The different character of the record in these cases is sufficiently marked in the photographs to identify it.

Immediately below the fork (*i.e.*, above it in the figures) was placed an electro-magnetic signal (BURCH'S pattern), arranged so that the release of the armature, and its removal from the magnet poles by a strong spring, constituted in itself the break of a current in the primary coil of the induction apparatus. The induced current thus caused was used in these experiments as the exciting stimulus. In order that the release should be effected by the traveller, and yet in no way impair its constant velocity, the pendulum carried near its axis a light rod projecting horizontally which in its passage upwards opened a mercurial key placed in the circuit of the bobbin wires of the electro-magnetic signal and thus released the armature. Thus the exact instant of the stimulus was recorded automatically upon each plate by the sudden change in position of the shadow of the armature. Electric light was used for the projection, and the records were taken on Wratten and Wainwright's Rapid Plates, Sensitometer No. 24.

The electromotive changes which constitute the response of the organ are sufficiently powerful to cause immediate electrolysis of the acid of a capillary electrometer, and it is therefore necessary to employ some means of shielding the instrument from them. Three methods are possible, namely to introduce a high resistance, to employ a shunt, or to interpose a condenser in the circuit on each side of the electrometer. The first method was not suitable for our purpose, because the introduction of a high resistance causes the meniscus to move more slowly without reducing the extent of the excursions, and therefore renders it less able to follow rapid changes of electromotive force.

The second plan, viz., the employment of a shunt, or short-circuit across the terminals of the electrometer, is free from this objection, as the rapidity of the motion is unaltered, while the extent of an excursion can be brought within any desired limits by suitably adjusting the resistance of the shunt. For alternating currents this method leaves little to be desired, but when the discharges, as in the *Malapterurus* response, are all in the same direction, the return of the meniscus between successive shocks is too slight, if they follow one another very closely, to give a well marked record of the first two or three.

In such cases the third, or condenser arrangement, offers marked advantages.

It may be convenient to point out in this place the characteristic difference between the records obtained with the shunted electrometer and with the condenser.

Shunt Experiments.

The sudden communication to the electrometer of a difference of potential (P.D.) from a source of infinite capacity—*e.g.*, a rheocord connected with a battery—

produces, as has been shown by one of us (G. J. B.),* an excursion of which the record is a logarithmic curve. That is to say, the movement, rapid at first, gradually becomes slower as the meniscus approaches its ultimate position of equilibrium.

If the source of the electromotive force is of small electrostatic capacity, the curve produced is similar in appearance, but smaller, both vertically and horizontally, than it would be for an equal difference of potential from a constant source.

If a second discharge from the same source of limited capacity is communicated to the electrometer, the meniscus again shoots suddenly onwards through a distance smaller than the first, and so on, each excursion becoming smaller and smaller, till the final position corresponding to that due to the same P.D. from an infinite source is ultimately reached.

Manifestly these successive sudden movements would be fused into one curve, unless they occur at sufficient intervals for the velocity of the meniscus to have sensibly diminished before a fresh impulse is given to it. In a good instrument the time required for this is comparatively small, but it is greatly diminished by using a shunt, or short circuit, through which the electrometer can discharge itself. Thus not only does the shunt protect the instrument from currents of undue intensity, but it increases its capability of indicating the rhythm of a series of rapid discharges in the same direction, which was one of the objects we had in view. Between each single shock of a multiple organ-response the charge is able partly to get away, and consequently the rapidity of the motion of the meniscus, which is proportional to the Acting Difference of Potential between the terminals of the electrometer, falls off more rapidly. This is well seen in some of our negatives.

From the nature of the experiments the electrometer is always to a certain extent short-circuited by the preparation itself and the moisture surrounding it, but with a shunt of 1000 ohms, unless the response is very feeble, the changes of velocity corresponding to the successive impulses received by the electrometer are comparatively unnoticeable, whereas with a shunt of 100 ohms they are well marked, and one of 10 ohms produced on a slowly moving plate a succession of sharp spikes, in which the electrometer practically returned to zero in something like ·005 second.

With currents of short duration, such as those of the *Malapterurus* response, the impedance of the circuit becomes an important factor. In order, therefore, to render our records available more easily for a subsequent mathematical investigation, the later ones were taken with a shunt composed of three incandescent lamps, which could be grouped in series or in parallel. In the arrangement found most suitable the filaments offered a resistance of about 80 ohms, practically free from self-induction.

This will be referred to as the "Lamp shunt."

* G. J. Burch, "On the Time-Relations of the Capillary Electrometer," 'Phil. Trans.,' vol. 183, A, pp. 81–105.

Condenser Experiments.

The apparatus used consisted of two air-condensers, each made of a pair of zinc plates 5 millims. thick and 3 millims. apart. They were about 40 centims. square and had each an approximate capacity of 537 C.G.S. units. They were suspended upon stout rubber supports, so as to face each other at a distance of 40 centims. apart.

The wires from the preparation were connected with the two inner plates, and the outer plates were in electrical communication with the terminals of the electrometer.

It must be born in mind that whereas the condenser and the electrometer circuits were insulated as perfectly as possible, there was always necessarily, as has been already pointed out, a leakage in the circuit of the preparation which was, in view of the small electrostatic capacity of the condenser, a considerable one.

The result of this condition of things was that, whereas in the experiments with a shunt of 100 ohms the meniscus was still moving onwards after each shock when the next impulse came, so that the record showed a continually mounting curve with rounded notches each followed by a sharp rise, in the condenser records the falling off of the E.M.F. between the shocks is marked by a sharp return, almost as sudden as the shock itself. The significance and explanation of this will be discussed from a mathematical point of view in another communication.

Meanwhile one other point may be briefly referred to. It has been pointed out by one of us* (G. J. B.) that some electrometers move more freely in one direction than in the other.

This was the case with the instrument employed in this research, which gave larger excursions in response to condenser shocks of the same intensity, when the movement was directed away from the tip of the capillary than when the excursion was in the opposite direction.

This peculiarity is farther complicated by that form of overshooting due to the elasticity of the meniscus itself,† which becomes distinctly noticeable when dealing with large differences of potential by the condenser method. Its general effect is to cause a short swift downward swing after the cessation of an upward movement, and a comparatively slow return through a similar distance, after a downward impulse.

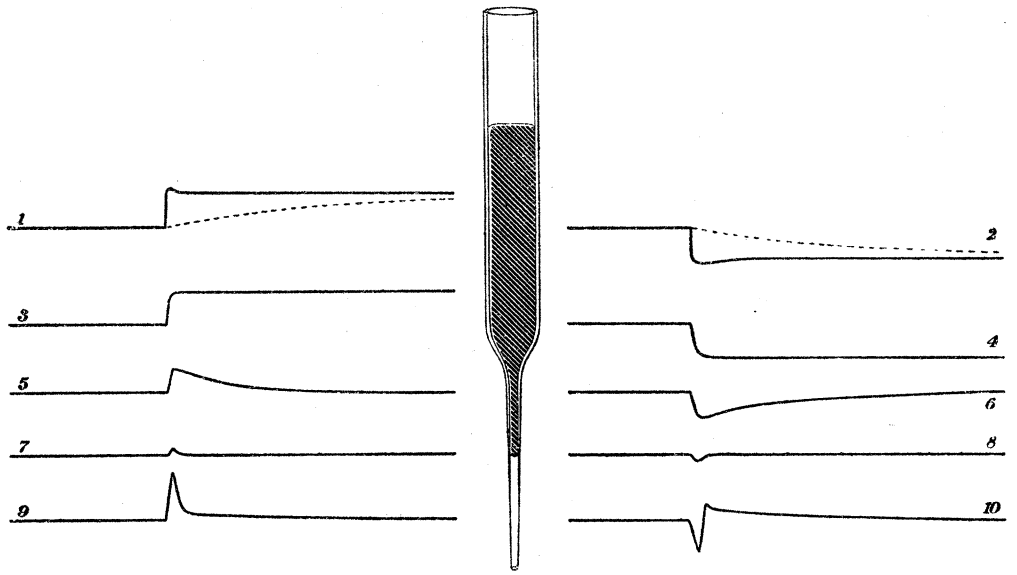
The result is that the photographic record of the response to excitation of the *Malapterurus* electrical organ assumes in some cases a form which might, without this explanation, lead to the erroneous supposition that the change is in reality biphasic like that of muscle. In order to make this matter clearer, and to facilitate the study of the records shown in the plates, we give in fig. 4 a number of curves illustrating diagrammatically the effect of a single unidirectional discharge upon the

* G. J. Burch, "Time-Relations of the Capillary Electrometer," 'Phil. Trans.,' vol. 183 A, p. 90.

† Burch, "On Determining the Value of Rapid Variations of a Difference of Potential," 'Proceedings Roy. Soc.,' vol. 48, p. 93.

electrometer under the various conditions which obtained in our observations of the organ response. These curves represent the results of actual experiments.

Fig. 4.



Discharge upwards. Discharge downwards.

Nos. 1 and 2 show the excursions produced by a condenser-charge of 26 volts and 537 C.G.S. units capacity. The over-shooting of the meniscus, about one-seventh of the whole excursion, is plainly seen.

The dotted lines represent what would be the path of an excursion of the same extent, under the action of a constant P.D. from an infinite source.

Nos. 3 and 4 are the upward and downward excursions respectively caused by a condenser-shock of less intensity (5 volts) and larger quantity (2800 C.G.S. units) than in Nos. 1 and 2. The electrometer is not shunted, and there is no return of the meniscus, nor is there any marked over-shooting as in the previous case.

Nos. 5 and 6 are copied from curves given with a shunt of 100 ohms. In these the elasticity of the meniscus produces a slight rounding of the top of the downward excursion, and the curve of the return to zero is that due to the escape of the charge through the shunt.

For Nos. 7 and 8 a shunt of 10 ohms was employed. The resulting excursion, which is greatly diminished in extent, might be easily mistaken for a biphasic effect.

No. 9 is the characteristic shape of the curve produced by the same discharge with the condenser arrangement. It will be noticed that it closely resembles No. 7, but is much larger. The return movement caused by the escape of the charge is extremely sharp, but does not carry the meniscus to its original level, probably because in this particular instrument it does not move so freely towards the point of the capillary as away from it.

No. 10 is the condenser curve corresponding to No. 9, but with the direction of the discharge reversed. In this case the return movement carries the mercury beyond its original position, and upon its cessation there is the short downward jerk noticeable in No. 1, and due apparently to the elasticity of the meniscus.

Each of these curves is the representation, under different instrumental conditions, of a single unidirectional change of potential difference, and each of them corresponds with the curves obtained in the *Malapterurus* experiments under like conditions. If the *Malapterurus* response were biphasic, it should show signs of a reversal of P.D. when, as occurred once or twice, the response is so feeble that the electrometer can be used without a shunt. But this is not the case. We have not in any of the 250 experiments with the capillary electrometer, found the slightest trace of such a reversal, nor could it be detected in the long series of galvanometer observations made by one of us (F. G.) with the rheotome.

Section 2.—*The Peripheral Organ Rhythm of the Isolated Organ.*

The time relations and rhythmical character of the response of the organ to a single stimulus are far more beautifully displayed by photographs of the movements of the mercurial meniscus of the sensitive capillary electrometer previously alluded to, than by the galvanometer experiments detailed in Part II.

The electrometer was used as indicated either in direct connection with the organ tissue with a resistance of 80 to 100 ohms interposed between its terminals, or in connection with the outer plates of the condenser, the inner ones being in connection with the organ. The arrangement of both methods is shown in fig. 5, in the text.

The fish was killed by cold, and the organ was then dissected out in the manner described in Part II. Section 1. As before, distinct multiple shocks were felt by the operator whenever the organ nerve or any nerve branch was cut. An organ strip measuring 8 centims. in length and 2 in width was placed with its inner surface uppermost upon a glass stage through which water at different temperatures could flow, and the organ was then connected with the non-polarisable electrodes by thick cables plastered with kaolin soaked in 0·6 per cent. NaCl, which were disposed athwart the length of the strip at a variable distance.

A slight organ-current in the direction of the organ shock, was always observed if the shunt was opened. Electrical or mechanical stimulation of the exposed nerve evoked an intense organ response, but, as far as we have seen, no response followed the application to the nerve of such chemical stimuli as NaCl, glycerine or weak acid.* The nerve was excited 1 centim. above its entry into the strip by the single break induction current (10 volts in primary, secondary half way over primary), this

* See also SCHÖNLEIN, 'Zeitschrift für Biologie,' vol. 21, p. 461, who states that KÜHNE had noticed the same insusceptibility to chemical stimuli in *Torpedo* nerves.

being led through the nerve by placing needles one each side of the fine nerve-trunk, their points being fixed below into a small cork block.

Fig. 5A.

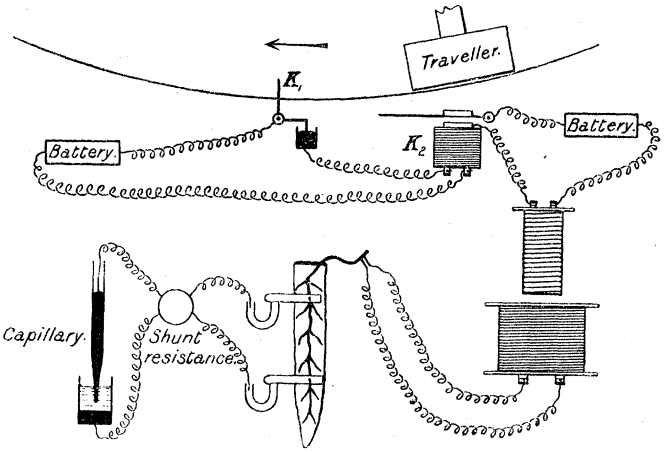
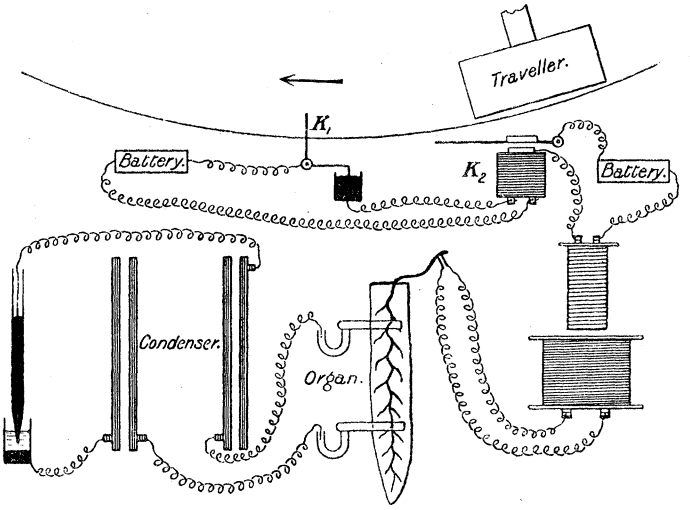


Fig. 5B.



The first photographs on a fast rate of travelling surface plainly showed (1) that the response to a single excitation was a rhythmical series of monophasic electromotive changes; (2) that the number of successive changes in such series was variable; (3) that between the moment of stimulation and the development of the initial change an interval elapsed, viz., the period of delay; (4) that the total amount of each change depended upon the length of the tissue between the electrometer leads, and thus upon the number of the plates.

Examples in illustration of these features are given in Plate 1, figs. 1, 2, the organ being in all these experiments at a temperature of from 12° to 15° C. In fig. 1 the electrometer was connected directly with the organ strip, a resistance of 100 ohms

acting as a shunt for the instrument. The single excitation of the nerve was given at the moment signalled on the plate by the break of the magnetic signal key; after a period of delay of ·0085 second, the electrical response occurred and consisted of sixteen recorded electromotive changes, each change being monophasic in character, and occupying not more than ·004 second in duration. The interval between the commencement of one change and that of its successor averaged ·0076 second, so that the rhythm of the peripheral response was in this case 130 per second.

Fig. 2 shows the record of the response to a similar excitation when the organ was connected to the two outer plates of the condenser and the electrometer to the two inner plates. With this arrangement the commencement and cessation of each monophasic organ-change causes an induced condenser effect (see Part III., Section 1). After a period of delay of ·008 second an initial change occurred occupying not more than ·0035 second in duration. It was succeeded by a second similar change, and this by a third, &c., the average interval being ·0076 second as in the preceding instance, there being fifteen such successive effects recorded on the plate.

It will be observed further, that since each change is rapidly succeeded by another before the mercury can return to its original position, the total result, as shown in all these records, is to cause the meniscus to alter its average level in the direction of the movement produced by the response. This alteration of level is due in the shunt method to the monophasic character of each discharge, there being no opposed electromotive change to bring the meniscus back again. In the condenser method, although the cessation of the monophasic change causes a static inductive effect of opposite sign to the previous one, this is not so intense as that produced by the passage of the organ response, nor does the mercury move as freely towards the reference time-line as away from it. The tail of instrumental subsidence is well shown in Plate 2, fig. 15. Its instrumental origin has been verified by photographing a series of successive monophasic discharges from a condenser; it is, therefore, of no physiological interest, but it furnishes an easy method for seeing at a glance the direction of the response.

Section 3.—*The Causation of the Peripheral Organ Rhythm.*

It is well known that the excitability of nerve is raised by section, and that this augmentation persists for a considerable time; a very beautiful instance of this was furnished in the course of our experiments upon the *Malapterurus* organ. In one piece of this tissue we found that the response of the organ to the excitation of its nerve trunk by a single induction shock, was markedly different to that obtained in the great majority of cases. It consisted of a single electrical response without any succeeding peripheral rhythm.

We were thus able to record the full character of the movement which such a single electrical response produces in the electrometer. This will be referred to in

a later section, and is introduced here merely to show that after thirteen such recorded observations at different temperatures had been made, the single electrical response which alone presented itself in all these instances, was at once converted into the peripheral rhythmical series by dividing the nerve half-way down the organ. Thus, Plate 2, fig. 13, is the response of the whole strip obtained just before such division, whilst Plate 1, fig. 6, is that obtained from a portion of this strip immediately after the nerve division. In both cases the organ strip was similarly connected directly to the electrometer shunted by a resistance of 80 ohms, the temperature was 5° C., and this nerve was excited 1 centim. from its point of entry. A glance at these two facsimile records will show the striking differences just referred to, and demonstrate the fact that the production of the peripheral rhythm is dependent as a first essential factor upon the excitability of the tissue. The influence of temperature upon the rate of the rhythm (see Section 5) affords further evidence of this sufficiently obvious fact.

Although, in accordance with the preceding remarks, the peripheral rhythm is essentially bound up with the excitability of the organ, the causative factor in its production appears to be the excitation of the organ by its own electrical response, thus resembling the similar phenomenon observed by KÜHNE and others in the case of the Sartorius muscle when the upper end is squeezed.* As is well known the Sartorius muscle under these circumstances responds to a single stimulus by a prolonged tetanus, due to self-excitation by the excitatory electrical changes in its own fibres. That this factor is operative in the present instance is strikingly brought out by the following three series of experiments.

Excitation of one Organ Strip by the Response of another.

Exp. 1. An organ strip was completely separated into two parts by a cut at right angles to its length, and the strips placed one touching the other, but so disposed that the excited primary strip A and the secondary strip B touched by their caudal ends only. See fig. 6 in text (first arrangement). The strip B now serves as a conductor for the response of A, and if it is excited by the derivation of the electrical change in A proceeding through its substance, its response will be such that the resulting currents will be directed in the opposite direction to those of A, since these always proceed in the organ from the head to the tail end.

Further, as a definite period of delay occurs between nerve-excitation and organ response and must be present in both A and B, then if B is aroused by the response of A, a longer delay period should be found between the excitation of A and the secondary response of B, than exists in the case of the primary strip only.

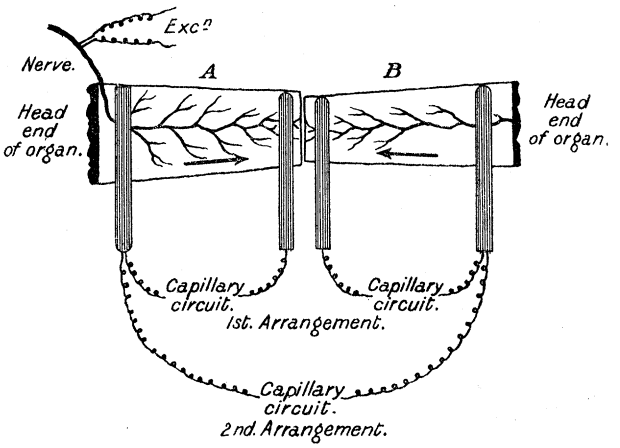
The photograph, Plate 1, fig. 3, shows the response when the electrometer was

* KÜHNE, 'Zeitschrift für Biologie,' vol. 24, p. 383, and vol. 26.

connected through the condenser with leads athwart A at a temperature of 12° C. It is seen that a rhythmical series of changes commenced ·008 second after the single excitation, each change being of such character as to send the mercury away from the time-line. The second change commenced at ·019, the third at ·03 second, &c.

The photograph, Plate 1, fig. 4, is the response when the leads were placed athwart B and the nerve of A excited by a single shock. It is seen that the response is a series commencing ·03 second after the excitation of A, and that each change is of such character as to send the mercury down towards the time-line. A careful inspection shows further the two preceding responses of A and their derivations in the condenser, these being evidenced in the figure by two small upward movements occurring before the main effect at ·01 and ·02 second after the excitation of the nerve.* It thus seems clear that the secondary strip was excited by the two first electrical changes of the primary strip.

Fig. 6.



Exp. 2. A different form of experiment is still more convincing. In this, the leads were placed one athwart the head end of A the other athwart the head end of B, *i.e.*, at the two extreme ends of the combined primary and secondary strips (see fig. 6 in text, second arrangement). The total effect must be the algebraic sum of the responses of both A and B; and obviously that of A will occur first and that of B will come later, and being of opposite sign, will interfere with that of A.

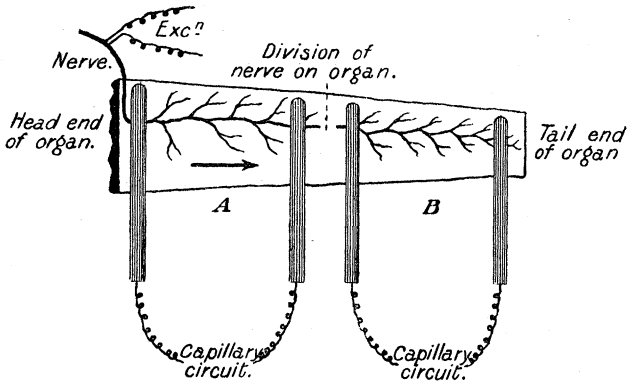
Plate 1, fig. 5, is a fine example of this combined effect at a temperature of 15° C. It is seen that the record commences at ·009 second after the excitation with a movement of the mercury away from the time-line, that this is followed by a second similar effect at ·02 second, and that then the strip B responds causing a downward movement at ·03 second, which is repeated again at ·04 second, to be in its turn overpowered by the upward movement through the continued response of A. It is

* In the reproduction of the photograph these are somewhat blurred.

probable that the response of A being that of the more bulky part of the organ is a larger effect than that of the thinner part B. Such a difference was noted by DU BOIS-REYMOND, and is bound up with the alteration in resistance due to alteration in bulk.

Exp. 3. Finally experiments were made upon another plan. As is well known the nerve of the organ is a single axis-cylinder lying on the internal surface and sending branches into the structure at right angles to its length. If therefore the nerve be divided half way down the organ, the peripheral part beyond the division can no longer respond to stimulation of the more central portion of the exposed nerve. This was carried out upon the nerve-organ preparation of another fish at a temperature of 5° C. (see fig. 7 in text). The results show that the response occurring at ·01 second after excitation is limited to the part A connected with the nerve, *i.e.*, this functional activity is localised in this portion, but that the part beyond the division is excited later through the electrical response of the former portion.

Fig. 7.



The shunted electrometer was first connected directly to the ends of A, *i.e.*, the part on the central side of the nerve division, by leads placed athwart it,—and the nerve entering A was excited outside the organ by a single stimulus.

The character of the response is shown in Plate 1, fig. 6. The rhythmical series of changes commences at ·01 second, the long latency being due to the low temperature; the initial change is indicated by a movement of the mercury from the time-line, and is succeeded by a second similar one at ·026 second, and the third at ·041 second, and so on.

The leads were now placed athwart the ends of B and the nerve of A excited by a single stimulus. The character of the response is shown in Plate 1, fig. 7. It commences much later than that of A, at 0·4 second after excitation, but consists of an exactly similar series of changes.

It is evident from these results that far from the organ being immune to its own shock, even the derivation through an adjacent portion of the tissue is capable of

exciting it and evoking a response; whether this derivation passes in the homodromous direction as in the last series of experiments or in the heterodromous as in the preceding ones.

Since therefore the derivation is capable of stimulating the tissue, it is certain that the more intense current which flows through the actual active strip can excite it and thus renew its activity.

It will be noted that with the derivation, it needed, as far as our observations have gone, two such successive shocks of the response of the primary strip to arouse the secondary one, which accordingly reacted synchronously with the third change, but it is obvious that with the intenser current which must be present in the actual excited tissue which is the seat of the change each single electrical effect may be fully adequate to stimulate it. Thus it appears that one actual causative factor of the peripheral rhythm is the susceptibility of the organ to excitation by its own electrical response. The criticisms advanced by SCHÖNLEIN* in the case of the *Torpedo* do not lay sufficient stress upon the undoubted fact that a portion of organ can be excited by the response of another contiguous part.

This explanation is further supported by comparing the period of delay of the primary strip with the interval of time between any succeeding electrical change in the response and that of its predecessor. The measurements of a considerable number of records give results which may be summed up as follows:—If LP is the latent period of the initial change, D the duration of this change, and I the interval between the termination of the first change and the commencement of the second, then out of thirty-one records, in three cases $LP = D + I$, in fourteen LP was greater than $D + I$ by a time interval varying from $\frac{1}{1000}$ to $\frac{2}{1000}$ second, and in fourteen LP was less than $D + I$ by a time interval varying from $\frac{1}{1000}$ to $\frac{2}{1000}$ second, but reaching in three cases a maximum of about $\frac{7}{1000}$ second, which was practically the time of D itself, so that in these three $LP = I$.

As the initial change is itself of some duration and ends more or less abruptly, its electrical current may excite either at its commencement, its end, or during its development; but if it does so it is obvious that the interval between the cessation of this first change and the commencement of its successor should never be markedly greater than the period of delay of the initial effect, and in the vast majority of instances should be smaller, since the initial effect is further delayed by transmission along the excited nerve from the point of stimulation to the organ.

It will be observed that in no case is this interval greater than the initial period of delay, in three cases it was found to be about the same, whilst in all the others it was less, and that the total time between the commencement of any one change and that of its successor approximates within limits of ·002 second to that which intervenes between the nerve excitation and the initial excitatory change.

* SCHÖNLEIN, "Beobachtungen und Untersuchungen über den Schlag von Torpedo," 'Zeitschrift f. Biologie,' vol. 21, p. 449.

A glance at the records will show further the great regularity in the succession of changes in any one response, and the measurements given in the description of the plates, p. 399, emphasise this.

From this it seems clear that there is nothing in the time records to weaken the belief that each successive development in the peripheral rhythm is due to the exciting effect of the electrical response which immediately preceded it.

It has already been pointed out in the observations made on an isolated strip with the galvanometer and rheotome method, that such a strip responds to an induced current when this is allowed to traverse the organ. Fresh light was thrown on this response by means of the capillary electrometer, and the experimental records of such observations will be now referred to.

Section 4.—*The Excitation of the Organ by the Heterodromous Induced Current.*

In order to pass the induced current through this tissue by the same electrodes as those connected with the leads to the electrometer, and yet avoid the dangers of electrolysis, dislocation of the mercury column, &c., which such a procedure may cause, the following method was employed. Fig. 8 in the text.

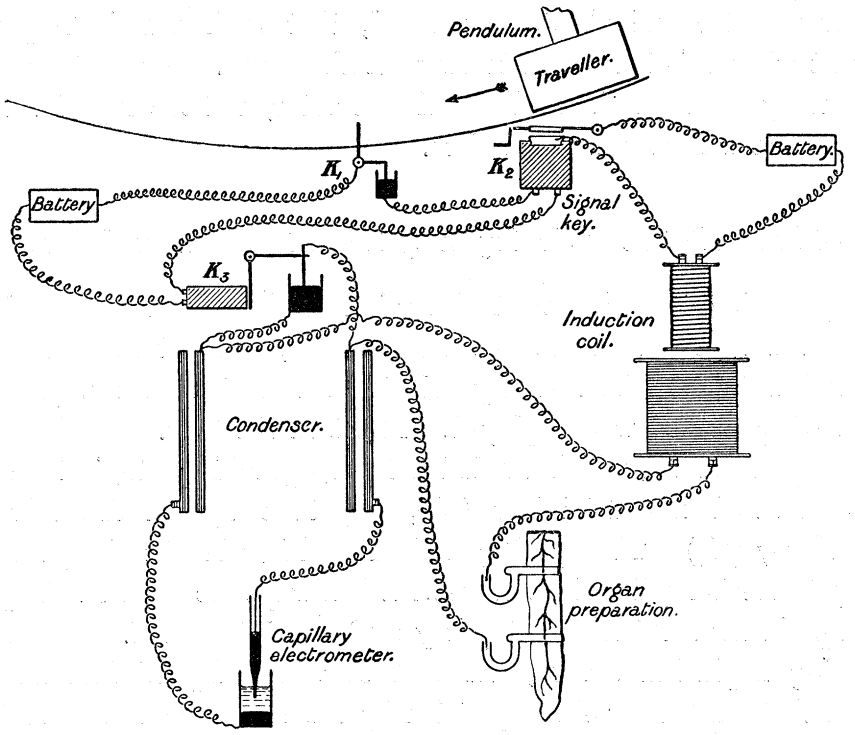
The travelling pendulum, which carried the photographic plate, in its swing broke a specially-constructed mercurial key (K_1), and thus opened the current of the magnetic signal-key (K_2). The opening of the signal-key breaks the primary circuit of the exciting induction coil and its movement is always recorded on the plate. For the present experiment a third shielding-key (K_3) was introduced. This consisted of an arm carrying a platinum wire, the end of which dipped into an adjustable mercurial pool, the arm being held in position by the armature of an electro-magnet arranged so that on breaking the circuit of this magnet the platinum wire was drawn up out of the pool. This shielding key, K_3, was placed so that its magnetic coil should be in the same circuit as that of the key K_2.

The break of K_2 and K_3 is thus simultaneous, but the separation of the armature in K_2 takes place before the complete withdrawal of the platinum wire from the mercury of K_3, the length of wire immersed in the pool being so adjusted that this interval of time should be ·002 second. The circuit was arranged, as in the annexed fig. 8 in the text, from which it will be seen that the condenser is short-circuited by the key K_3, so that on the break of K_2 an induced current will traverse the preparation. After an interval of ·002 second the key K_3 is broken and the condenser plates thus placed in connection with the tissue, so that any electromotive changes occurring after this time will affect the electrometer.

These electromotive changes will include (1) the remainder of the induced current effect, and (2) the electrical response of the organ. Since the exciting induced current must reach a high intensity in order to be adequate for excitation, a perceptible effect due to the slow subsidence of the induced current is seen even when

the condenser is short circuited for $\frac{2}{1000}$ second. The induction current may be arranged to traverse the organ strip either from head to tail, *i.e.*, in the direction of the subsequent response (homodromous), or from tail to head (heterodromous); in both cases the electrometer interpretation of the effect due to the residuum of the induction shock is evidenced by excursions preceding the response, and of definite direction and character.

Fig. 8.



Both currents can excite the tissue, but it appeared that the homodromous must be more intense than the heterodromous in order to secure this excitation, a fact previously referred to in connection with the galvanometer experiments, and interesting since the partial immunity of this organ to electrical currents, unlike that of *Torpedo*,* is evidently more pronounced for currents of a direction similar to those of its own activity.

The records of the response resemble, in their general features, those previously described, but differ, inasmuch as they are fused with the residuum of the induced current.

The response to homodromous stimulation will be referred to in detail later, as it presents certain special features.

* 'Phil. Trans.,' vol. 179, 1888, B, pp. 342, 343.

The Response to the Heterodromous Induction Current.

The organ was excited by the break of a current produced by 5 volts in the primary coil, the core of which was removed and the secondary coil placed fully over it.

The record of the response to heterodromous stimulation in Plate 2, fig. 8, shows first a few oscillations at the break of K_3 and then the rhythmical peripheral response.

The initial response effect shown in the negative is interfered with by the residuum of the exciting shock. It commences ·007 second after the induction current, and is followed by 13 successive similar effects, and probably many others which were not recorded on the plate. The time interval from the commencement of one change to that of its neighbour averaged ·008 second, hence the successive changes occurred at rate of 120 per second. The temperature of the organ was 15° C.

Section 5.—*The Influence of Temperature on the Time Relations of the Heterodromous Response.*

The organ strip was placed upon a glass vessel as a stage capable of being warmed and cooled by running water, and the response to direct excitation by the heterodromous induced current was then recorded when the tissue was at different temperatures. Examples of the alteration in the record are given in Plate 2, figs. 9, 10, and 11.

In Plate 2, fig. 9, the organ was at 5° C. The exciting heterodromous induction current has a complicated residuum shown on the record, and following this is the peripheral organ response. A careful examination showed that the initial effect commenced after a period of delay of ·0092 second, and its duration is ·0029 second; a second effect succeeds it at ·019, *i.e.*, ·01 second after the first, it has a duration of a ·003 second; a third at ·029 and so on, there being eleven such successive developments recorded on the plate, following one another at the rate of 100 per second.

Plate 2, fig. 10, is the record of the response of the organ to the same heterodromous induction current, when at a temperature of about 25° C., the water in the vessel being 30° C.

It is seen that the residuum of the induced current is not perceptible, and that the response consists of a series of electromotive changes occurring in much more rapid succession than in the preceding case.

The initial effect begins ·0035 second after excitation. Its duration and that of each of its successors is ·002 second, the second commences at ·008 second after the induced current, that is, ·0045 second after the commencement of the initial change,

and the same interval occurs for each successive development. The rate at which the effects succeed each other is thus 220 in one second, there being 21 such changes on the plate. Fig. 11, Plate 2, is a record of the response to a similar heterodromous induction current when water at 40° C. was run through the vessel and the tissue warmed to about 35° C. The record shows an extraordinarily rapid rhythm. The initial effect occurs at ·004 second after excitation, its duration is ·0015 second, the second effect commences ·007 after the excitation by the induced current (*i.e.*, ·003 second after the first effect), the third at ·011 and so on, there being on record 22 such successive changes occurring at a rate of 280 per second.

The effect of a rise of temperature in the organ is thus to produce (1) a diminution in the initial period of delay; (2) a more rapid development and shorter duration of each effect; and (3) a more rapid succession of changes. It need scarcely be pointed out that these results afford additional support to those previously referred to, which show that an effective factor in the production of the rhythm is self-excitation; since the change caused by variation of temperature in the latency and character of the initial effect is observed also in each of the successive ones. With regard to the period of delay, two points are of considerable importance. First it will be observed that, even under the most favourable conditions (temperature 35° and direct excitation), there is a perceptible delay, *i.e.*, ·0035 to ·004. This cannot be due to nerve-trunk propagation, since in these experiments the nerve-endings in all the plates were simultaneously stimulated. It is therefore the true expression of the minimum limit in the reaction delay of the organ.

In this respect the observations confirm those of BERNSTEIN in the frog's muscle as to the delay in motorial nerve-endings, which was found to be ·0032 second, but, owing to the intensity and rapid development of the electrical response in an electrical organ, the measurement can in the case of this tissue be effected with far greater certainty than in the case of muscle.*

The second noteworthy fact is involved in that just referred to, and leads to most important conclusions. If the stimulating current excites the organ which it traverses, it is hypothetically possible that it may stimulate either the nerves, or the protoplasmic structure of the plate in which the nerves end, or both the nerves and this structure. The uncomplicated character of such a record as Plate 2, fig. 10, and the close similarity in time relations between the period of delay and that of muscle nerve-endings, appears to us to indicate that, in reality, the first of these suppositions is the only tenable one. This view is supported by the results of careful comparative experiments made upon the same organ at different temperatures, in which the response was evoked by stimulation of the nerve-trunk.

* BERNSTEIN, "Die Erregungszeit der Motorischen Nervenendorgane in den Muskeln." 'DU BOIS, Archiv,' 1882, p. 329.

The comparison is best shown by the following Table :—

DURATION of Initial Period of Delay.

Temperature of organ.	Excitation of nerve outside organ.	Excitation of organ by heterodromous current.
° C.		
30	·0045	·0035
30	·0045	·004
5	·011	·01
5	·011	·0105

It will be observed that the response to excitation of the nerve is only ·0005 second to ·001 second longer than that evoked by the heterodromous induction current traversing the organ. Experiments made especially for the purpose seem to show that, in the nerves of the electrical organ, the rate of propagation was at least as fast as that in the motor nerves of the frog, *i.e.*, 33 metres in 1 second. The discrepancy in time is thus amply accounted for by a nerve-trunk propagation, and, beyond this, there is no fundamental difference between the time-relations of the response as dependent on the mode of stimulation.

The organ protoplasmic plates thus appear to be incapable of direct excitation by induced currents, and it is the nerves, and these only, which respond to such a directly applied stimulus. In further support of this view is the circumstance that, in the electrical organ of Torpedo, there is the same relationship between the period of delay to the two methods of stimulation, nerve-trunk and direct, whilst in the Skate* there is a similar delay to direct excitation. It is well known, too, that curare has but little effect upon the response, which occurs in Torpedo organ even in fully curarised fish ; so also, in the *Malapterurus*, a strip of organ responded to excitation of its nerve after 15 minutes' immersion in either 1 per cent. curare or 1 per cent. atropine solutions, as well as it did before (the latter solution was used on the supposition that, as it affects glands and vagus nerve-endings, it might possibly affect the electrical organ). The organ thus seems, as BOLL first suggested, to owe its excitability to the nerves and nerve-endings which it contains.† In other words, the response being the action of an excitable tissue, is to be regarded as a specific change in the nerves and nerve-endings, and in these only, in which case the plate protoplasm reaction, if it exists, would not be accompanied by the development of a sudden intense electromotive change. What then, it may be asked, is the physiological significance of the nucleated protoplasmic plate? The inquiry is one of great morphological, as well as physiological, interest, but for many reasons cannot be entered into here. It is, however, possible, to regard such a plate rather as the

* GOTCH, *loc. cit.*; SCHÖNLEIN, *loc. cit.* SANDERSON and GOTCH, 'Journal of Physiology,' vol. 9, p. 188. "The Electrical Organ of the Skate," p. 153.

† BOLL, 'Archiv f. Anat. u. Physiol,' 1873.

nutritive support for an appropriate symmetrical arrangement of a vast array of electromotive axis-cylinders and their branches, than as itself a potential electromotive tissue whose potential energy becomes kinetic in response to a nerve change. Whether the former view is sound or not, there can be but little doubt that, in consideration of its obvious inexcitability, the latter view is scarcely tenable in the case of *Malapterurus* organ, and probably the same is true of the *Torpedo*.* This view, rejected by DU BOIS-REYMOND, has been criticised in the case of *Torpedo* by SCHÖNLEIN in his recent publication. He regards the E.M.F. of the plate activity as of the same order as that of muscle, and considers it therefore impossible to suppose that it could arise in connection with nerve structures only. Until, however, the E.M.F. of nerve-ending activity has been further investigated by more exact methods, such as the capillary electrometer offers, it appears to us impossible to draw conclusions from such comparisons.†

Section 6.—*The Response to the Homodromous Induction Current.*

The organ was first excited by a homodromous induction current of the same intensity as that used for the heterodromous, but it was found necessary to increase its intensity, as the resulting response was most uncertain and frequently failed; in this respect the *Malapterurus* organ is unlike that of *Torpedo*.‡ In order, therefore, to increase the strength of the stimulus the core had to be introduced half way into the primary coil, with the result that the prolongation of the induction shock caused a very marked residual condenser effect of its own which, on the opening of the short-circuiting key K_3, caused a considerable downward displacement of the mercury meniscus. Even with this intensity, which was sufficient to cause slight electrolysis in the capillary, the response frequently failed after a few observations had been made, and the risk of injuring the electrometer by using still more intense currents was too great to allow of the further prosecution of the investigation. A few successful records were obtained, with the organ at 5° C. and at 25° C.

They all present the usual record due to a rhythmical response, but the time relations of the initial change are less easy to measure than those of the heterodromous response, owing to the extent of the condenser charges caused by the residuum of the intense homodromous exciting current. The careful examination of the downward displacement due to this in cases where no organ response occurred furnishes the best guide in this connection. It was noticed that the mercury first

* See 'Phil. Trans.,' vol. 179, B (1888), p. 341. GOTCH, "Further Observations on the Electromotive Properties of *Torpedo*."

† SCHÖNLEIN, *loc. cit.* In a more recent publication, SCHÖNLEIN appears to consider the plate itself as a nerve-ending analogous to a motor nerve plate; see 'Electrophysiologie,' BIEDERMANN, vol. 2, p. 838.

‡ In *Torpedo*, the homodromous has been found by most experimenters to be more effectual than the heterodromous exciting current. See GOTCH, 'Phil. Trans.,' *loc. cit.*

dropped from the base line and then approached it in a long sweep. The organ response, if it occurs, will produce a series of excursions in the opposite direction to this long sweeping effect and superimposed upon it as their varying base line.

Plate 2, fig. 12, is a record of such a response obtained at 25° C.; it will be seen that the peripheral rhythm is present, and that the successive changes occurring at a rate of 200 per second are all set upon the induction residuum curve. A remarkable feature is the longer latency of the first visible effect, this being ·013 second as compared with ·0035 second in the case of the heterodromous exciting current. It is quite possible that an effect precedes this one, but if so, it is unrecognizable, owing to the magnitude of the induction residuum; we do not see any indication of it in the record.

Similar responses were obtained at 5° C. Here the rhythm was also marked, being 100 in 1 second, and there was the same prolonged delay between the excitation and the first recognisable response. The delay with this (+) excitation was ·016 as compared with ·009 for the (−) excitation. The prolongation of the delay in these cases constitutes a very remarkable exception to that found with the other methods of stimulation here employed, and its true nature can only be ascertained by experiments especially devised for the purpose. Unfortunately our material gave out before we had measured the curves and realised the importance of further investigation upon this point. We would only, therefore, draw attention to two aspects of the question suggested by this feature of the response to the homodromous current. First, as has been already pointed out and was abundantly confirmed by our observations, there appears to be some difficulty in obtaining a response to the homodromous induced current, and it is probable that this refractory condition of the tissue is connected with the long latency observable when it does respond. A similar effect was observed by SCHÖNLEIN in Torpedo organ when excited with a current which was *ascending* in the nerve-fibres. It is interesting to note that the homodromous current is in the present instance a *descending* one as far as the nerve branches are concerned, hence SCHÖNLEIN'S explanation of an anelectrotonic inhibition does not seem applicable to the present observation.*

Secondly, we only had the opportunity of using, for this direct stimulation, one form of exciting electrical current, namely, an intense induction shock, and it is possible that with other modes of electrical stimulation the result may be different. As was pointed out in Section 3, the organ can respond to a derivation of its own electrical current, whether this passes through it in the homodromous or the heterodromous direction. Our view of the causation of the peripheral rhythm is largely founded on this. There seems, therefore, to be some ambiguity underlying the circumstances which condition the response to the homodromous induced current, an ambiguity which the further investigation of fresh material can alone clear up.

* SCHÖNLEIN, *loc. cit.*

Section 7.—*The Single Initial Response of the Isolated Organ.*

Attention has already been drawn to the circumstance that, in one strip of tissue, the response to nerve trunk excitation was not the usual peripheral rhythm, but the initial first effect only. The occurrence of such a condition afforded us most valuable data as to the behaviour of the capillary electrometer in reply to a single excitatory electromotive change of the organ. A considerable number of records were therefore made at different temperatures, both with the shunted electrometer in direct connection with the organ and with the interposed condenser. As one of the objects in view was the measurement of the E.M.F. of this single change, the special non-inductive lamp-shunt of 80 ohms resistance was used. Four records are reproduced.

Plate 2, fig. 13, is the shunted electrometer effect with the organ at 5° C., the nerve being excited by a single induction current. It will be noticed that the displacement is very considerable, that it commences ·01 second after excitation and lasts until ·021 second, and that the mercury very slowly returns towards its previous level. The curve is just such as is produced on the fast travelling plate with the particular electrometer here used, by a monophasic electromotive change of short duration, the time-relations of the slow return being characteristic for this instrument when the electromotive change ceases.

Plate 2, fig. 14, is the effect of a similar excitation with the organ at 30° C. The period of delay is ·0045 second, the effect lasts until ·0067 second after excitation, and there is the same slow return.

Plate 2, fig. 15, is the record obtained at 5° C. with the unshunted electrometer, the condenser being interposed. The movement of the mercury shows that the condenser plates in connection with the electrometer convert the monophasic electromotive change into a charge in one direction during the onset and rise of E.M.F. due to the tissue response, and into one of opposite sign when this begins to decline. The biphasic character of the condenser record is in harmony with the monophasic character of the shunted electrometer record. (See Section 1.)

As will be seen in this figure, the effect began at ·01 second and was practically over at ·016 second.

Plate 2, fig. 16, is a similar record to the preceding one at 30° C., the effect began at ·007 second and was over at ·009 second.

It is evident from these records that although rise of temperature quickens the time relations of the response, it does not necessarily augment its intensity.

The greater extent of the records at 5° C. may in itself be dependent upon the longer duration of the effect, but a careful examination of the curves shows that the cold one rises more steeply than the warm one, and, therefore, that the E.M.F. of the response of the cold tissue is probably higher than that of the warm tissue.

The above effects were all obtained in response to the excitation of the nerve

outside the organ: a similar single change was observed once or twice in the same strip when excited by the heterodromous induction current, and connected with the condenser; in this strip it was also found that the induced current, even when very intense, failed to excite at all when in homodromous direction.

It is interesting to compare these effects with those produced by charging the condenser with a known E.M.F. Plate 3, fig. 25, is an example of the character of the excursion when, by means of the tertiary key placed ·002 second after the signal key, the condenser plates were placed in connection with a battery of 10 volts. It will be observed that under these circumstances the movement of the meniscus is a very small one.

Section 8.—*Estimation of the E.M.F. and Quantity of the Discharge.*

I. *Physiological Evidence.*

Perhaps the most obvious method of estimating roughly the electromotive force and quantity of the discharge of the *Malapterurus*, is to compare the sensations evoked by its passage through the human body with those produced by currents of known intensity and duration.

To anyone in the habit of handling accumulators, the shocks are suggestive of high potential rather than large quantity. Accordingly, when we had ascertained that the response consisted of a succession of discharges all in the same direction at the rate of about 150 per second, we tried the following experiment: one pole of a series of accumulators was electrically connected with the frame of a recording cylinder, and thus also with the toothed wheel upon its shaft. The experimenter held in one hand the wire from the other pole, and in the other hand a piece of hard brass wire which could be pressed against the revolving cogwheel, so as to give a series of contacts of about the period and duration of the discharges of the *Malapterurus* response. In order that the circuit might be entirely free from self-induction, the accumulators were completely disconnected from all other circuits. A voltmeter was used to measure the E.M.F.

The electrical discharge of the *Torpedo* has been estimated by D'ARSONVAL* as having a voltage of from 8 volts to 17 volts, a current of from 1 ampère to 7 ampères, and a duration of from $\frac{1}{20}$ to $\frac{1}{10}$ of a second.† We found that with 17 volts a current interrupted 150 times per second was just perceptible on the tongue, but not with fingers. With 40 volts the effect reached the knuckles, and with 80 volts it could be felt in the wrists, but not in the elbows even when the hands were wetted.

* 'Comptes Rendus,' vol. 121, 1895, p. 145.

† According to D'ARSONVAL, each discharge consists of from 6 to 10 "partial discharges" at intervals of about $\frac{1}{100}$ second. Evidently his method gave only the average current, and failed altogether to indicate the maximum E.M.F.—September 21, 1896.

Furthermore, the sensation was quite different from that given by the fish discharge, which affects the muscles of the shoulders and the chest, and causes a peculiar numbness of the skin of the hands.

It may be therefore concluded that a potential of 17 volts is totally inadequate to produce the same sensations as the *Malapterurus* discharge, the E.M.F. of which cannot be less than 75 volts and is probably much greater.

II. *Rheotome Experiments.*

It has been ascertained by one of us (G. J. B.) that whereas electrolysis of the acid is instantaneously produced by currents of quite moderate intensity, no such effect follows the discharge of a Leyden-jar into the electrometer, provided its electrical capacity is sufficiently small in relation to that of the capillary.

We accordingly arranged a rheotome so as to connect for $\frac{1}{1000}$ second the electrometer circuit with accumulator cells of 10 volts, and photographed the result. There was no measurable delay (*i.e.*, less than $\frac{1}{10000}$ second) between the communication of the P.D. and the evolution of gas in the capillary.

The same current was then made to charge the outer plates of a pair of condensers, each of about 537 C.G.S. units capacity, the inner plates being connected with the electrometer. The result was a small, sharp excursion, with no sign of electrolysis (see Plate 3, fig. 25). N.B.—The entire circuit being insulated, there is here no return of the meniscus as in the photographs of the organ response.

On increasing the E.M.F. to 26 volts there was still no evolution of gas and the excursion was not nearly so big as those given by the *Malapterurus* response, when the leads from the fish were connected in the same manner with the condensers.

From these experiments we infer that the response of the *Malapterurus* is to be compared rather to a series of discharges from a Leyden-jar than to an interrupted current, and, further, that if the discharge is limited in quantity it must be of correspondingly greater intensity to produce physiological effects exceeding those of an interrupted current of 75 volts.

III. *Evidence deducible from the shape of the Photographed Excursions.*

When a constant difference of potential is communicated to the terminals of a good capillary electrometer, the photographed excursion, as recorded by the pendulum motor, is a curve, having for its equation,* $y = ae^{-c\theta}$, and to each instrument there is a certain time-constant depending on the total resistance, R, of the circuit, given by the formula

$$\mathrm{R} = \mathrm{L} + l + r,$$

where r is the external resistance, l = the resistance of the column of dilute acid, and

* 'Phil. Trans.,' vol. 183 A, p. 91.

L = the "equivalent resistance" of the electrometer (generally between 100,000 and 200,000 ohms).

That is to say, a certain definite time is required for the acting P.D., as indicated by the subnormal to the curve, to fall from a value

$$E = a, \text{ to a value } E = a - b.$$

But if the source of P.D. is of limited capacity, as when a charged condenser is suddenly connected with the electrometer, the resulting curve, though similar in form, is both smaller and shorter, as if the plate had moved more slowly.

It may be easily shown that if y be the vertical height of the excursion produced by a constant source of electromotive force, and if C_1 = the capacity of the condenser, and C_2 = the capacity of the electrometer, then the vertical height of the excursion produced by the condenser charge is

$$y_1 = \frac{C}{C_1 + C_2} y,$$

and, farther, that the time-constant of the excursion is reduced in the same proportion.

But this formula is applicable only when there is no leakage in the circuit either of the condenser or of the electrometer.

This, from the conditions of our experiments, is far from being the case. The preparation itself, and the moisture surrounding it, furnishes a short-circuit by which the charge escapes, and moreover we have as yet no direct evidence as to the rate of development of the electromotive force of the organ response. We therefore propose to reserve the discussion of this problem, which we are now investigating, for a subsequent communication, and confine ourselves here to the statement that inasmuch as the current given by the fish-discharge is practically over in less than $\frac{3}{1000}$ of a second, it seems probable either that the electrical capacity of the organ is much less than that of the electrometer, which was found to be ·55 microfarad, or that it is naturally short-circuited to such a degree as to utilize externally only a very small fraction of the current generated, while in either case the E.M.F. must be considerable.

If we assume, as appears to be the case, a minimum E.M.F. of 75 volts for that present in each excitatory change of the response of an organ 10 centims. in length, then since microscopic examination showed in our specimens an average of 180 plates arranged in series for each centimetre of length, the minimum E.M.F. of each plate would be about ·04 volt, and, most probably, amounts to ·06 to ·07 volt.

Part IV.—The Reflex Response of the Organ investigated with the Capillary Electrometer.

Section 1.—*The Period of Reflex Delay.*

It has already been stated in Part I. that the experiments with the frog nerve-muscle galvanoscope show that the uninjured fish responded readily to mechanical, and less easily to electrical, stimulation of the surface of the skin beyond the limits of the organ, this response being, in the case of the organ, a reflex discharge. That such a response is a reflex one, and not due to excitation of the efferent electrical nerves, is evidenced by the long and variable period of delay which elapses between the excitation and the electrical response, this period having a minimum of ·02 to ·03 second.

It was pointed out that if the stimulus was applied to the surface of the skin over the organ, the resulting electrical response was, as regards its initial effect, not reflex, but due to the stimulation of the efferent nerves of the organ in the immediate neighbourhood of the excited area; this being proved by the fact that there is always a constant short period of delay (from ·004 to ·008 second according to the temperature), identical in character with that found in the case of the isolated organ.

It is evident that by the frog galvanoscope it is impossible to ascertain whether or not such a direct nerve organ response is followed by a reflex one, but the capillary electrometer records show that this may be the case. They thus confirm and extend the results of those observations. A tap on the caudal fin beyond the organ or its electrical excitation caused a reflex response which is evidenced in the records; and it was noted, that whereas such response could only be evoked by an intense electrical stimulus, it was readily produced by a very weak mechanical stimulus, a slight touch with the finger being often quite adequate to evoke it.

Reflex from Skin beyond Organ.—The fish was always caught in the experimental net with wires as previously described, and thus raised out of the water, which was kept at 20° C. It was then excited on the skin either by a strong break induction shock, or by a series of such shocks, or by a slight tap. In the latter case, in order to ensure that the resulting response should come upon the moving photographic plate, the circuit, which was opened by the mercurial key of the pendulum, was made to include both the magnet signal key and an additional magnet key outside the photographing chamber in the immediate neighbourhood of the fish. The armature of this second key carried a light wooden rod, which was so arranged that by its movement it should lightly strike the skin of the fish.

For the investigation of the period of delay this mechanical stimulus, although by

far the most effective one, was found to be not sufficiently trustworthy in point of time, as the moment of the blow with this apparatus could not be ascertained with precision. We have, therefore, discarded these records and taken only the rarer instances in which a response followed the electrical excitation of the skin beyond the organ limits.

The period of delay under these circumstances was very variable in length. Plate 3, fig. 17, shows one of the shortest that we obtained. The capillary was connected directly to the net wires and shunted by a resistance of 100 ohms.

The break of the magnet signal opened the circuit of the primary coil, which comprised a battery of 10 volts, and the secondary coil was placed fully over the primary, this intense induction shock being found necessary to evoke the reflex response. The response is seen to occur after a delay of ·047 second and to consist of several successive monophasic effects (the peripheral organ rhythm).

A similar reflex response was obtained with a similar excitation of the skin surface between the bases of the tentacles and beyond the head limit of the organ.

The mechanical contact of the electrodes itself caused a response in this instance, so that the meniscus was slowly falling to its resting level when the plate passed the slit of the photographing instrument. It was found that after a still longer interval than in the preceding case, namely ·097 second, the reflex response occurred, and consisted of a succession as in the previous example.

It is interesting to compare with these the stimulating effect of a series of electrical currents. For this purpose the magnet signal was connected with an auxiliary key which short-circuited the secondary coil, and the primary coil was arranged with the usual interruptor for faradization, and connected with the battery of 10 volts. It was found that a response could be obtained on faradization when the exciting electrodes were applied to the skin of the tail beyond the organ, but that, though this occurred when the intensity of the repeated stimuli was less than in the preceding case, yet it was still necessary to use a strong series of induction currents, the adequate exciting intensity being only attained by placing the secondary coil three-quarters over the primary. The rate of the interruptor was 50 per second, and, owing to the escape from the exciting into the capillary circuit, it was found necessary to use the capillary condenser method.

A record was obtained with the plate moving more slowly than in the instances previously referred to. The number of stimuli which the tail received were marked on the plate by the slight escape, there being fourteen break and as many make induction currents, but the latter were probably quite inadequate to excite. The response occurred ·44 second after the first and ·25 second after the last excitation; its commencement only was on the record, and showed the usual successive character.

Reflex from Skin over Organ.—The reflex period of delay was found to be considerably shorter when the skin over the organ was stimulated. In these cases, however,

the stimulation almost always evoked a direct nerve organ response, but the records indicate that succeeding this direct response is a second reflex one.

This is well shown in the following examples, which have been selected from several instances to illustrate this and other points. The temperature was kept at 20° C.

In one instance, omitted through lack of space from the plate, the capillary was directly connected with the fish, and shunted by a resistance of 100 ohms. The skin over the organ was excited on the caudal side of the net wires, which were connected with the capillary. The exciting stimulus was the break of the current of 10 volts in the primary coil, the secondary coil being placed fully over the primary. The response was limited to one single monophasic electromotive change, commencing ·006 second after excitation and ending at ·01 second after excitation. It was a direct nerve organ response, and this only.

Plate 3, fig. 18, is the record of the response to a similar single break induced current, the skin over the organ being stimulated on the head side of the net wires, which were connected with the electrometer. The connections between the condenser and the electrometer were "crossed," so that the capillary effects were of the more complicated condenser type, *i.e.*, first towards the time line, then away from it.

A direct nerve organ response is seen commencing at ·0055 second after excitation; it consists of seven successive changes (the peripheral rhythm), and after a short interval is followed by a second response commencing at ·051 second after excitation. This second response is a reflex one, since the interval between its commencement and that of the last change in the direct response is ·013 second, instead of ·005 second, which is the peripheral organ rhythm interval. The reflex response consists of two successive changes; that is, a second development of the organ rhythm.

Plate 3, fig. 19, is another example of the same effect, with similar condenser connections. The skin over the organ was excited as in the preceding observation. The record shows a direct nerve organ response, commencing ·0065 second after excitation, and consisting of two successive changes in the organ; this is followed by an interval during which the meniscus begins to return to its proper level, and at ·023 second after excitation a second response occurs, this being a reflex one with the usual peripheral rhythm. This is the minimal reflex delay we have observed in the capillary records. The rhythm of the second reflex response shows a remarkable break in its regularity, which we consider to be occasioned by a second central discharge, since such an irregularity was not found in the rhythm of the isolated organ. Its commencement at ·033 second after stimulation—that is, ·01 second after the previous reflex—is, in our opinion, far too quick for it to be a second discharge of the same nerve-cell, as will be seen in the next section. We therefore tend to the belief that it is the discharge of the opposite nerve-cell. The further delay of ·01 second would, if this interpretation be correct, indicate the additional delay of a crossed reflex. Finally, as regards the reflex of the same side, the minimal reflex time observed, ·023 second, agrees with that obtained by

the frog galvanoscope; and, allowing ·01 second for the nerve transmission time, and ·005 second for the delay in the organ, gives ·008 second for the central delay which, in the particular structure here investigated, is the delay in a single efferent nerve-cell and its connections in the spinal cord.

Section 2.—*The Character and Rhythm of the Reflex Organ Response.*

The observations previously alluded to with the frog galvanoscope (see Part I.) could not from their nature be considered as affording conclusive evidence in regard to this very important part of the present inquiry. Nor can the far more demonstrative results now to be referred to, in which the capillary electrometer was used, be considered as more than preliminary, but the great interest attaching to this portion of our investigation, and the difficulty of obtaining fresh living material for further inquiry, warrants the publication of such records as we have been able to obtain which bear upon the subject.

The physiological significance of the inquiry as to the multiple character of the reflex organ response will be made clearer by the following considerations. There must be a far more intimate relationship between the response of a peripheral organ and the discharge of its reflex centre in the case of an electrical organ than in that of a muscle.

In the case of a reflex muscular contraction there is abundant evidence to show that neither the rhythm of the mechanical changes, nor that of the electrical response, can be taken as affording conclusive evidence of the rate at which the nerve excitatory changes have reached the motor nerve endings. The excitatory changes must pass through the unknown physiological field which lies between the more excitable ultimate nerve ending and the less excitable muscular substance, and having passed through this, they become transformed. The relationship between the resulting muscular response and the evoking nerve excitatory state is pre-eminently that of a released to a releasing force; the muscle stamps its own character upon its activity, and it is this character rather than that of the releasing or exciting agent which it portrays. Thus, with a weak series of stimuli of even high frequency, a muscle may respond by an initial contraction or by a flickering one, and SANDERSON and BURCH have shown that a special muscular electrical rhythm is evoked in such a reflex as strychnine tetanus.

The electrical organ is not so obviously a terminal peripheral structure, whose activity is released in consequence of the advent of some releasing agency. It has been already pointed out that the similarity of the delay, whether the isolated organ is excited by stimulating its nerve trunk, or by passing the heterodromous current through its whole substance, can only be interpreted as indicating that the nerves and terminal nerve endings are the probable seat of the intense electrical response.

On these grounds we think that the investigation of the rhythm of the reflex organ response is of great general importance, since it brings us far nearer than any

existing method of inquiry towards the solution of the question as to the rate of nervous discharge from efferent nerve cells. The importance of the present investigation in *Malapterurus* is further increased by the circumstance that in this fish the efferent nervous channel is reduced structurally to great simplicity through its consisting of one nerve cell and one efferent nerve fibre on each side. The rate of the organ rhythm, as found in reflex activity and as determined by that activity, is thus a very near approach to, if not an actual experimental record of, the rate of nervous discharge of a single efferent cell. No other known reflex structure offers at once a reflex response easily recorded and of great intensity, whose phases are directly translateable into nerve excitatory states, and a mechanism such that all nerve excitatory states have emerged from one efferent cell on each side of the central nervous system.

We made a very large number of observations upon this subject, but the difficulty of obtaining comparable reflex effects is notorious, and is greatly increased in the case of the *Malapterurus* by the extreme variability of the organ response. Hence, on many points, our information is still incomplete.

It was necessary to employ some form of stimulus which should adequately arouse the central nervous system, and to use a method of recording the response which should distinguish between the peripheral organ rhythm and a succession of reflex responses such as would be caused by a succession of excitatory changes issuing from the efferent electrical nerve cell, and propagated to the organ by the electrical nerve fibre. The best form of stimulus we found to be a mechanical one of a more or less prolonged character, and the simplest was that of squeezing the flanks of the fish between the fingers and the hand. In order to obtain a photographic record of the response, it was necessary that the discharge brought about by the squeeze should occur when the pendulum plate was passing the projection arrangement of the instrument. This was effected by causing the pendulum to signal to the individual manipulating the fish the moment when it is necessary to squeeze. In this way good reflex effects were obtained, and were recorded on slow moving plates, the pendulum being specially adapted to move past the slit at the rate of about 1 centim. in $\frac{1}{10}$ second.

The differentiation between the peripheral and the central rhythm seemed to us at first a difficult matter. In our earlier experiments we employed for the purpose an electrometer of very considerable capillary bore. The inertia of the mercury column was such that it was unable to follow the rapid oscillations of the peripheral rhythm; and each group of oscillatory responses caused an unbroken movement of the meniscus. A number of records were obtained with this electrometer, shunted by a large resistance, and connected direct to the wires of the net which contained the fish, and the fish itself squeezed on the flank. The record showed, in a typical case, three large oscillations, the second occurring about ·2 second after the first, and the third about ·2 second after the second. A considerable number of observations were made of this character, many of the records being taken on

a slowly moving cylinder driven by clock-work, and carrying a sheet of sensitized bromide paper.

It was however found that, with a suitably arranged circuit, the more sensitive capillary recorded both the peripheral and central rhythms, and that the rapidity and absolute regularity of the peripheral organ rhythm, and the comparative slow rate of the central discharge, afforded ample means for their differentiation in the records. The subsequent records were, therefore, all made with this latter instrument.

In examining these, the first striking feature is the extremely variable character of the organ response. In some cases, it was simply the initial single electromotive change, in others, the single response with the peripheral rhythm, and in others, a series of such responses.

This variability of reflex effect was shown also by the differences in both the intensity and the duration of the peripheral rhythm. Thus, Plate 3, fig. 20, is the reflex response to a squeeze of the organ when connected directly to the sensitive electrometer shunted by a low resistance, 20 ohms. The time trace below is $\frac{1}{8}$ second for a full double vibration, and the response is seen to consist of seven successive effects; the multiple character is due to the peripheral organ rhythm, and is clearly seen on the record, being such as would be produced and probably was produced in this instance by a single discharge from the central efferent cells.

Plate 3, fig. 21, is a reflex response obtained under similar conditions, but with a shunt of 30 ohms. In this case, the peripheral organ rhythm is of enormous extent, there being 27 successive changes recorded, and indications of five others beyond the limit of the record. The response is, however, as regards its central origin, still a single one, such as could be evoked by a single nerve stimulus, and thus probably indicates a single intense central discharge.

In Plate 3, fig. 22, the reflex response under similar conditions consists of two such thrilling electromotive changes, the first showing a more extensive peripheral rhythm than the second. The latter commenced about ·27 second after the commencement of the first. Plate 3, fig. 23 is an example of three such successive multiple effects, the interval between the commencement of the first and that of the second being ·27 second; that between the second and third being ·31 second. Another record of a similar observation, which, owing to electrolysis is not a good one for reproduction, showed three successive multiple organ-responses taken on the same rate of moving surface. The second response occurred about ·2 second after the first, and the third about ·19 second after the second, this last being far more intense and with a more prolonged organ rhythm than its predecessors. Finally, Plate 3, fig. 24, is an example of a triple response obtained when the condenser was interposed between the fish and the electrometer, the arrangement of the condenser connection being of the "crossed kind." The condenser brings out far more effectively the individual electromotive changes of the peripheral organ rhythm in each response. The second multiple response occurs ·092 second after the first and the third ·085 second after

the second. In this case the vibrations of the 500 fork are given on the original negative in the base line, and there are 46 such vibrations between the first and the second, and 42 between the second and the third.

These last two cases are the most rapid successions of responses we have been able to obtain. A comparison between these results and those given with the Frog-galvanoscope (Part I., Section 3) will show how closely the results of the two methods agree. It is evident, from the consideration of both sets of records, that the reflex central rhythm is one which very rapidly fails, since we have never succeeded in obtaining any record of more than five multiple responses occurring after one another at a rate of from $\frac{1}{12}$ to $\frac{1}{3}$ of a second. The fish will often discharge again after a few seconds, if the skin pressure is maintained, but this response is frequently only a single one. On the other hand the intensity of the response itself and the number of successive developments of the peripheral organ rhythm is not susceptible to fatigue in the same way. The response may be very powerful, although such as would be evoked by only a single stimulus, and this even after the fish has been subjected to the squeeze treatment for a considerable number of times.* This fact has become familiar to us, as to Du Bois-Reymond, by many prolonged experimental demonstrations, particularly those in which a large number of people have successively obtained, by the same method, the discharge through the hand, as for instance at the Conversazione of the Royal Society, and that of the British Association at Ipswich, where living specimens of *Malapterurus* were shown.

An analysis of those reflex records in which the members of a group of responses recur at the more rapid intervals, shows the following time interval between the successive members of the group :—

·085 sec.	·092 sec.	·096 sec.	·098 sec.	·110 sec.
·130 ,,	·140 ,,	·150 ,,	·15 ,,	·19 ,,
·19 ,,	·2 ,,	·2 ,,	·2 ,,	·23 ,,
·23 ,,	·25 ,,	·27 ,,	·31 ,,	·35 ,,

The recurrence of members at intervals of from $\frac{1}{2}$ to 1 sec. or more, although a very familiar experience, is not worth referring to in detail.

The results as to the reflex activity of the organ may be now summarised as follows :—

(1) The periodicity of the reflex response to the central nerve cell activity is exceedingly variable. (2) The minimal time observed in a few cases between the first member of a reflex response and its successor is $\frac{1}{12}$ second. (3) The central discharge is often of such character that the organ gives only one such member in its reflex response, this having of course its own peripheral rhythm. (4) Between these

* See Du Bois-Reymond, 'Gesammelte Abhandlugen,' II., p. 618.

extreme limits the more general result is that a second member occurs after the first at about $\frac{1}{4}$ second. (5) The number of successive independent members of the response to any given stimulation of the skin, recurring at intervals of from $\frac{1}{12}$ to $\frac{1}{4}$ second, is very limited, being at most five or six, and generally two or three. (6) The intensity of each individual member of the reflex response varies with the frequent repetition of the sensory stimulation far less than the above periodicity, but may in any reflex be either great or small varying with the amount of the sensory stimulation. (7) The periodicity of the members in any group is much affected by previous reflex activity. Responses, which, in a perfectly fresh fish, number four or five members, are reduced to groups of one or two if the experiments are long continued and at greater intervals.

Various questions of considerable general interest are raised by these conclusions. It is evident that the essential features of this reflex response are its variable periodicity, the susceptibility of this periodicity to fatigue, and the relation between the intensity of the cell discharge and that of the afferent stimulus.

The activity of a single efferent nerve cell, apart from groups of such cells, has not up to the present been investigated, but we claim that the results here given express the mode of action in the single electrical cell of the *Malapterurus*, and, possibly, that of many or all efferent nerve cells. The maximum periodicity of discharge, ten to twelve per second, is curiously like that which has been attributed by different authors (SCHÄFER, HORSLEY, and others) to the groups of anterior cornual cells in the spinal cord.* The experiments of LOVÈN in the case of strychnised muscle have often been put forward as showing that the reflex muscular electrical periodicity of eight per second in the strychnia spasm, is an indication of a like number of discharges from the central nervous system,† and according to DELSAUX this muscular periodicity may be as low as five per second!‡ Whether this be so or not, a rate of this order appears to be that of the single electrical nerve cell.

The susceptibility to fatigue showing itself in slower central rhythm rather than in diminished intensity of central discharge, is another marked functional feature of this single efferent cell or its connections on the efferent side. The similar variability in the duration of the central delay, seems to point to the fatigue and delay phenomena having an analogous structural and physiological basis. This basis must be regarded, therefore, rather as an alteration, lowering, of central conductivity, causing retarded or blocked propagation than as a decrease in central excitability.

Can these characteristics be extended to all efferent cells? It is obvious that such a generalisation must be made with the utmost caution, especially if it involves new aspects of central functional activity. What these are will be now considered. If

* SCHÄFER, 'Journal of Physiology,' vol. 7, p. 116, and others.

† LOVEN, 'Centralblatt f. d. Med.,' 1881.

‡ DELSAUX, 'Travaux du Lab. de Liège,' vol. 4, 1892; see also SANDERSON, 'Journal of Physiology,' vol. 18.

the characters of the discharge from the single electrical cell are those of all efferent cells, then the persistence of a central rapid discharge in muscular and other reflexes would imply that the activity of all the members of the groups of cells is not simultaneously evoked, but would find its analogy rather in company than in battalion volley-firing. In this way, the extremely rapid but variable central discharge from the thousands of nerve cells of *Torpedo* or *Gymnotus* might be produced. It seems, in the light of the present results, highly improbable that each nerve cell in these fish continues discharging at the rate of eighty to one hundred per second, which is the possible rate of response of the *Torpedo* and *Gymnotus* organ to the reflex central activity. The minimum central delay of ·008 second in the single *Malapterurus* electrical nerve cell may well be a true expression of central propagation time from the afferent to the efferent side of all efferent nerve cells, since this generalisation conflicts with no existing facts. The further susceptibility to fatigue shown by increased delay, is a phenomenon which not improbably occurs in all other similar nerve structures, and though often masked by the number of cells and the number of fresh central paths along which the central discharge can take place, this alteration in conductivity may be, and we suggest probably is, a fundamental characteristic of the physiological mood of the ingoing side of each efferent cell. In other words, central activity would, on this hypothesis, be succeeded by localised transient decrease in central conductivity.

The increase in the rapidity of central conduction which appears to exist in the case of muscular reflexes, can, if this fatigue characterises every efferent cell, still be explained. For a diversion of the ingoing nerve-change into other and fresh paths is rendered possible in all reflexes except the special one which forms the subject of this investigation, since in other reflexes a large number of groups of cells are concerned, and a large number of paths from the afferent to the efferent side are thus offered.

These are some of the new aspects which are involved in the extension of the fundamental characteristics of the single electrical cell to all efferent nerve cells.

The Malapterurus and Torpedo Compared.—The susceptibility to central fatigue is characteristic of all living uninjured electrical fish, but since the isolated organ of such fish does not show any such rapid exhaustion in consequence of stimulation of its efferent nerve, the seat of the fatigue must be in the central nervous system and not in the peripheral organ. In *Torpedo*, the responses due to reflex central discharge were found both by MAREY and by one of us (F. G.) to recur at a rate of 100 per second, gradually running down to 50 or less. This could not be the expression of a peripheral organ-rhythm, since the particular recording instrument used, an electromagnetic signal, was found to be incapable of following such peripheral rhythm, but responded by a single movement to the discharge evoked in the organs when the nerves of the fish were exposed and stimulated immediately after destruction of the electrical lobe in the medulla (F. G.). It is interesting to note that a similar delicate

electromagnetic signal showed no appreciable movement when connected with the *Malapterurus.*

Although the *Torpedo* central discharge thus appears to recur at a very rapid rate, the susceptibility of this central periodicity to fatigue, though present, appears to be less marked than in the case of the *Malapterurus.* On the other hand, the intensity of the individual organ response in the last-named fish is but little affected by a central fatigue which has so sensibly influenced the central periodicity. The efferent cell discharge, when it does occur, may still be very pronounced. In connection with this there is the suggestive fact of the striking difference in the structure of the central nervous mechanism. The *Torpedo,* with its large electrical lobes, containing thousands of nerve cells, giving rise to 80,000 efferent electrical nerve fibres, forms an extraordinary contrast to the *Malapterurus* with its two nerve cells and two nerve fibres.

Finally, the results referred to in this section, throw some light on the efficiency for its purpose of the organ activity. It is well known that a series of electrical currents occurring in rapid succession, and all similarly directed (monophasic) is of great potency in stimulating physiological tissues, and the possession of an organ capable of producing these furnishes a powerful armament either for attack or defence. In the *Torpedo* and the *Gymnotus* this essential feature of the weapon, the production of currents of similar sign in rapid succession, appears to be mainly achieved by a correspondingly rapid series of central nerve discharges to the organ, and the structural mechanism for carrying out this purpose is thus largely dependent for its efficiency upon the condition of the nervous system. In the *Malapterurus* the organism has been more completely adapted to attain this end by the excitable nature of the peripheral organ itself, so that to one central discharge of the nervous system the organ can reply with a succession far more rapid (280 per second) than that of the central discharge of the *Torpedo,* and as the discharge of the weapon is thus made to a great extent self-firing, the necessity of rapid central nerve-activity is less essential. The possession of such a marked tendency to self-excitation may be fairly considered as the result of a development in the excitability of the peripheral organ which has coincided with the want of development of a more elaborate central structural mechanism, and the end is thus achieved more cheaply, that is, with less expenditure of nerve activity. The correlation of structure and function is strikingly displayed in all electrical organs, but in none more than in *Malapterurus electricus.*

Summary of Conclusions.

The conclusions arrived at by the authors from the observations on the isolated organ and uninjured living fish may be summarised as follows :—

(1) The isolated organ responds to electrical excitation of its nerve by monophasic electromotive changes indicated by electrical currents which traverse the tissue from

the head to the tail-end; this response commences from ·0035 second at 30° C. to ·009 second at 5° C. after excitation, the period of delay for any given temperature being tolerably constant.

(2) The response occasionally consists of a single such monophasic electromotive change (shock) developed with great suddenness, and subsiding completely in from ·002 second to ·005 second, according to the temperature; in the vast majority of cases the response is multiple, and consists of a series of such changes recurring at perfectly regular intervals, 5, 10, 15, or 20 times (peripheral organ rhythm); the interval between the successive changes varies from ·004 second at 30° C. to ·001 second at 5° C., but is perfectly uniform at any given temperature throughout the series.

(3) Such a single or multiple response (in the great majority of cases the latter) can be also evoked by the direct passage of an induced current through the organ and its contained nerves, in either direction, heterodromous or homodromous.

(4) The time-relations of the response are almost identical, whether this is evoked by nerve-trunk (indirect) stimulation or by the passage of the heterodromous induced current.

(5) There is no evidence that the electrical plate substance can be excited by the induced current apart from its nerves, *i.e.*, it does not possess independent excitability.

(6) The organ and its contained nerves respond far more easily to the heterodromous than to the homodromous induced current, and the period of delay in the case of the latter response is appreciably lengthened.

(7) The peripheral organ rhythm (multiple response) varies from about 100 per second at 5° C. to about 280 per second at 35° C.

(8) One causative factor in the production of the peripheral rhythm is the susceptibility of the excitable tissue to respond to the current set up by its own activity (self-excitation).

(9) In the uninjured fish mechanical or electrical excitation of the surface of the skin beyond the limits of the organ, evokes a reflex response with a long delay (·03 second to ·5 second); this reflex response consists of groups of shocks, each group showing the peripheral organ rhythm, but separated from its neighbour by a considerable interval of time (reflex or central rhythm).

(10) In the uninjured fish electrical excitation of the skin over the organ evokes a response which may consist of a direct peripheral organ effect followed by such a reflex effect.

(11) The minimal total reflex delay at 20° C. is ·023 second, giving a central excitatory time of about ·01 second.

(12) The reflex or central rhythm in our specimens showed a maximum rate of 12 per second, and an average rate of from 3 to 4 per second.

(13) The number of separate groups in the reflex response recurring at the intervals mentioned in the preceding paragraph was in our fish limited to from 2 to 5.

(14) The E.M.F. of each single change in an organ response depends upon the number of effective plates with their nerves, and in 10 centims. of excited organ cannot possibly be less than 75 volts, and is probably much nearer 150 volts. As in our specimens the number of plates in series in 1 centim. of organ was 180 ; this gives a minimum possible E.M.F. of ·04 volt and a probable E.M.F. of ·07 volt for each plate.

(15) Since each lateral half of the organ is innervated by the axis-cylinder branches of one efferent nerve cell, and the specific characters of the reflex response of the organ express far more closely than those of muscle the changes in central nerve activity, the authors further conclude that the reflex characteristics are those of the activity of a single efferent nerve cell.

The single efferent nerve cell, the activity of which is thus for the first time ascertained, shows :—

(*a*) A minimum period of delay of ·08 to ·01 second.

(*b*) A maximum rate of discharge of 12 per second.

(*c*) An average rate of discharge of 3 to 4 per second.

(*d*) A susceptibility to fatigue showing itself in the discharge failing after it had recurred from 2 to 5 times at the above rates.

Description of Plates.

The figures in the plates are facsimile reproductions of the photographed excursions of a downward pointing capillary electrometer. In each case the rate of movement of the plate is indicated by a tuning fork which, in the majority of instances, made 500 D.V. per second, the shadows producing the serrated circular arc at the bottom of the figure. Above this is the shadow of the signal key, the upward movement marking the moment of electrical stimulation.

Above this again is the record of the excursions; the shadow of the mercury appears dark in the figure, and in all cases (see fig. 4 in the text) an upward movement of the shadow corresponds to an upward movement of the meniscus, *i.e.*, away from the point of the capillary.

Plate 1, fig. 1, is the record of the excursions produced when the isolated *Malapterurus* organ was connected by electrodes, in contact with its ends, to the electrometer, shunted by 100 ohms, and the nerve of the organ excited 1 centim. before its entry by a single break induction shock. The response consists of a series of monophasic effects, showing the regularity of the peripheral organ rhythm.

Fig. 2 is a record with the same preparation, but with the condenser connection of the electrometer ; the nerve was excited by a single break induction shock.

Fig. 3 is the record with the condenser electrometer of the response to a single nerve excitation of the head half of the organ immediately after it had been cut in two.

Fig. 4. In this case (the organ being already cut in two) the head half was excited by its nerve, and only the tail half connected with the electrometer through the condenser. The tail half was turned end for end and placed in contact with the head half. The currents due to the head-half response traversed the tail half, and two small excursions preceding the main effect indicate their derivations. The secondary response of the tail half coincides with the third of these, and is shown by the large reversed excursions of the mercury.

Fig. 5 is the record of the condenser electrometer when both strips lay between the contacts, *i.e.*, that give rise to both the effects shown in fig. 3 and in fig. 4. The nerve to the head half was excited by a single induced current, and the record shows the presence and interference of the two responses.

Figs. 6 and 7 are the respective records of the shunted electrometer when the nerve was excited before its entry into the head end of the organ, and had previously been divided half-way along the length of the preparation. The first (fig. 6) is the response of the head half, that in actual connection with the excited nerve, the second (fig. 7) is the response of the part of the organ beyond the cut. Note the difference in the period of delay.

Plate 2, figs. 8, 9, 10, and 11, are the records of the condenser-electrometer when a heterodromous induced current had traversed and excited the whole length of the organ strip with which the condenser was connected. The organ was at 5° C., 15° C., 25° C., and 35° C., respectively. The response is preceded by an effect due to the residuum of the induced current, the greater part of which was excluded from the condenser by a special key (see text).

Fig. 12 is a record in which the organ responded to such an homodromous current, the organ being at 25° C.

Figs. 13 and 14 are instances of the less frequently-observed cases in which a single excitation of the nerve evokes a single monophasic electromotive change in the organ. The records are those of the shunted electrometer, the organ being at 5° C. and 30° C. respectively.

Figs. 15 and 16 are similar instances of this single organ effect, the records being those of the condenser electrometer and the organ at 5° C. and 30° C. respectively.

Plate 3, fig. 17, is the shunted electrometer record of a reflex response of the organ. The excitation was a single induced current through the skin over the caudal fin beyond the organ limit; it shows the long reflex delay.

Figs. 18 and 19 are records obtained with the electrometer and condenser, the latter with crossed connections. They both show a direct multiple response to a single excitation of the skin over the organ, but in each this is followed by a reflex

response, the commencement of which succeeds the conspicuous break in the otherwise regular rhythm. In fig. 19 are two such breaks indicating two reflex responses.

Figs. 20, 21, 22, and 23 are all records, on a slow rate, of the excursions of the shunted electrometer produced by reflex responses. These were brought about by squeezing the fish in the hand. Each reflex response is seen to exhibit the regular peripheral organ rhythm; that in fig. 21 is very large; in the later ones two, and in one case three, such responses are seen. The time record is $\frac{1}{8}$ second D.V. Fig. 24 is the record of a reflex response when the condenser method with crossed connections was employed. There are three responses shown, each with the peripheral organ rhythm; the rate of the plate was timed by the 500 fork, the fine vibrations of which are easily seen on the negative.

Fig. 25 is the record of the extent of the excursion produced in the sensitive capillary electrometer here used by its connection with a charge of 10 volts in the condenser.

The accurate time-relations and minute details of these records are given in the annexed tables. In these the following abbreviations, &c., are made use of:—

(1) *Connection with Preparation.*—D = distance between organ contracts. T = temperature of organ.

(2) *Excitation.*—P = battery in connection with primary induction coil. Coil = position of secondary coil on graduated scale of Kronecker's inductorium.

(3) *Electrometer Shunt* = connection of organ to each side of a specified resistance (either a coil or a non-inductive resistance composed of incandescent lamps) acting as a short circuit for the electrometer.

Condenser = connection of preparation to inner plates of condenser and of outer plates of this to electrometer.

Crossed Condenser = crossed connection between condenser and electrometer so that excursion is reversed in direction.

(4) *Numbers.*—The unit to which the numbers refer is ·0001 second, and the number given indicates the measurement in $\frac{1}{10000}$ second of the point specified from the rise of the signal key shadow and thus from the moment of excitation. (The numbers in brackets refer to excursions due to escape of excitation current.)

(5) *Signs.*—$\uparrow$ = movement of capillary meniscus upwards, *i.e.*, away from tip; $\downarrow$ = movement downwards. The sign $\rightarrow$ indicates that from this period to the next change the E.M.F. is practically nil.

PLATE 1.

Fig. 1. (No. 128.)*

(1) Isolated organ strip, 10 centims. long. D = 1 centim. T = 15° C.
(2) Excitation, P = 4 volts. Coil = 4000. X on nerve, 1 centim. outside organ (head end).
(3) Electrometer, shunt = 100-ohm coil.

85	125	165	205	245	290	310	360	385	425
↑	→	↑	→	↑	→	↑	→	↑	→
460	505	530	570	605	650	685	700	755	800
↑	→	↑	→	↑	→	↑	→	↑	→
830	870	905	950	985	1025	1060	1115	1140, &c.	
↑	→	↑	→	↑	→	↑	→	↑	

Average period, ·0076 second.

Fig. 2. (No. 127.)

(1) Same as in fig. 1.
(2) Same as in fig. 1.
(3) Condenser connection.

80	115	170	195	250	275	325	350	395	420
↑	↓	↑	↓	↑	↓	↑	↓	↑	↓
470	490	540	567	615	640	690	715	765	790
↑	↓	↑	↓	↑	↓	↑	↓	↑	↓
840	865	910	940	990	1015	1065	1090, &c.		
↑	↓	↑	↓	↑	↓	↑	↓		

Average period, ·0076 second.

Fig. 3. (No. 147.)

(1) Isolated organ, cut across; leads on head portion. D = 3 centims.
(2) Same as in fig. 1.
(3) Condenser connections.

80	112	185	200	295	325	400	430	502	535
↑	↓	↑	↓	↑	↓	↑	↓	↑	↓
615	645	720	750	830	860	935	965	1065	
↑	↓	↑	↓	↑	↓	↑	↓	↑	

Average period, ·0109 second.

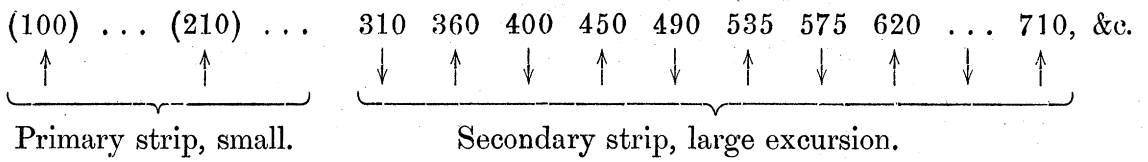
* These numbers refer to the actual sequence of the experiments.

Fig. 4. (No. 151.)

(1) Isolated organ, cut across; leads on caudal portion, which is reversed. D = 3 centims.

(2) Same as fig. 3.

(3) Same as fig. 3.



Average period, ·0088 second.

The numbers in brackets correspond to small excursions produced by the primary strip. The secondary strip comes into action with the third discharge of the primary.

Fig. 5. (No. 152.)

(1) Isolated organ, cut across, with caudal half reversed; leads one on head half and one on caudal half. D = 6 centims.

(2) and (3) Same as in fig. 4.

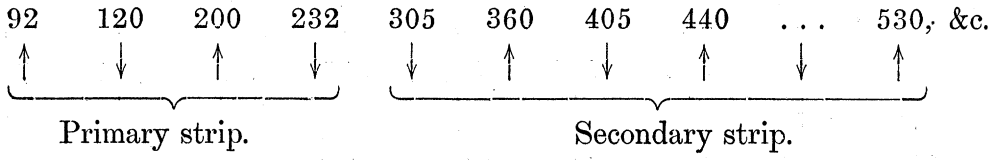


Fig. 6. (No. 208.)

(1) Isolated organ, with section across nerve, leads head side of section. D = 2 centims.

(2) Same as in fig. 5.

(3) Electrometer, with shunt = 80-ohm lamp.

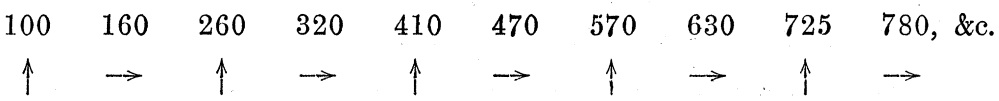


Fig. 7. (No. 209.)

(1) Same as in fig. 6, but leads tail side of section. D = 2 centims.

(2) Same as in fig. 6.

(3) Same as in fig. 6.

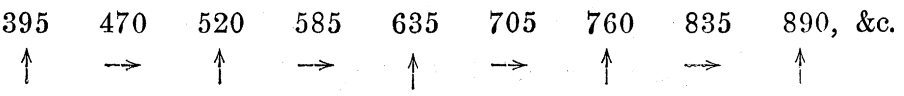


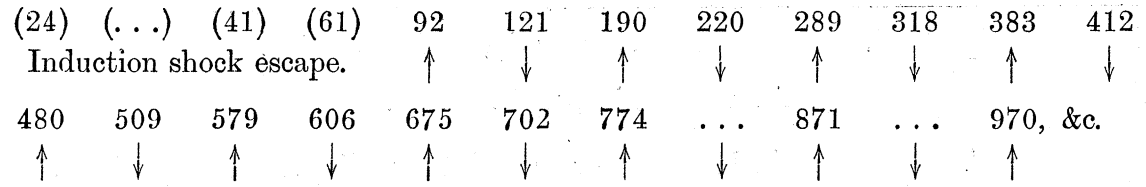
PLATE 2.

Fig. 8. (No. 218.)

(1) Isolated organ strip, 3 centims. long, contacts at ends. T = 5° C.

(2) X by heterodromous induced current. P = 5 volts. Coil = 12000. X-electrodes joined to contacts.

(3) Condenser, kept short-circuited by shielding-key for ·002 second.

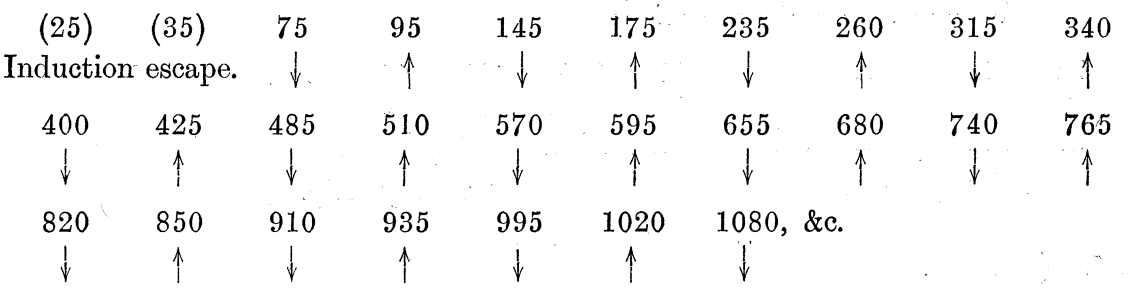


Average period, ·0097 second.

Fig. 9. (No. 213.)

(1) Same as fig. 8, but T = 15° C.

(2) and (3) As in fig. 10, *i.e.*, by heterodromous direct excitation.

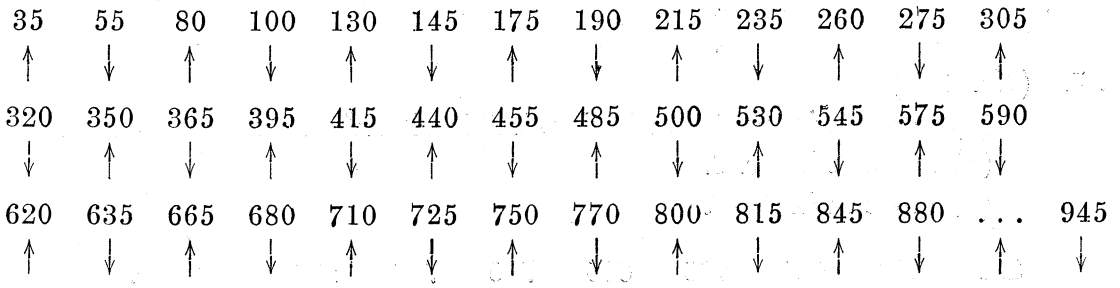


Average period, ·0083 second.

Fig. 10. (No. 219.)

(1) Same as fig. 9, but T = 25° C.

(2) and (3) Same as in fig. 9.



Average period, ·0045 second.

Fig. 11. (No. 224.)

(1) Same as in fig. 10, but T = 35° C.

(2) and (3) Same as in fig. 10.

(29)	40	57	71	83	113	130	150	164	189	200	222
↓	↑	↓	↑	↓	↑	↓	↑	↓	↑	↓	↑
234	256	270	293	305	330	341	362	378	400	414	435
↓	↑	↓	↑	↓	↑	↓	↑	↓	↑	↓	↑
450	471	484	508	520	542	567	578	592	615	629	651
↓	↑	↓	↑	↓	↑	↓	↑	↓	↑	↓	↑
663	689	700	722	...	760	...	795	...	830, &c.		
↓	↑	↓	↑	↓	↑	↓	↑	↓	↑		

Average period, ·0038 second.

Fig. 12. (No. 221.)

(1) Isolated organ strip. T = 35° C.

(2) Homodromous induced current. P=5 volts. Coil=12,000, with core in.

(3) Condenser connection.

Response of organ to homodromous induced current.

(35)	...	135	...	185	...	235	...	280	...	330	...	425
↓		↑	↓	↑	↓	↑	↓	↑	↓	↑	↓	↑
...	475	...	525	...	575	...	622	...	675	...	720	...
↓	↑	↓	↑	↓	↑	↓	↑	↓	↑	↓	↑	↓
775	...	820	...	870	...	915	...	970	...	1020	...	1070, &c.
↑	↓	↑	↓	↑	↓	↑	↓	↑	↓	↑	↓	↑

Average period, ·0050 second.

Fig. 13. (No. 199.)

(1) Organ preparation. D = 6 centims. T = 5° C.

(2) Nerve excitation outside organ. P = 5 volts. Coil = 5000.

(3) Electrometer with shunt = 80-ohm lamp.

105	210
↑	→

Single response.

Fig. 14. (No. 200.)

(1) Same as in fig. 13, but T = 30° C.

(2) and (3) As in fig. 13.

45	67
↑	→

Single response.

Fig. 15. (No. 194.)

(1) Same as in fig. 13. T = 5° C.
(2) Same as in fig. 13.
(3) Electrometer, condenser connections.

(25) 105 ↑ 160 ↓

Single response.

Fig. 16. (No. 196.)

(1) Same as in fig. 15, but T = 30° C.
(2) Same as in fig. 15.
(3) Electrometer, condenser connections.

(30) 70 ↑ 90 ↓

PLATE 3.

Fig. 17. (No. 90)

(1) Living uninjured fish in net. D = 1 centim. T = 20° C. Reflex response.
(2) Excitation on tail, beyond organ. P = 5 volts. Coil = 12,000.
(3) Electrometer, shunt, 100-ohm coil.

475 ↑ 507 → 545 ↑ 575 → 605 ↑ 635 → 670 ↑ 700 → 740 ↑, &c.

Average period, ·0066 second.

Fig. 18. (No. 103.)

(1) Living fish, as in fig. 17. Both direct and reflex response.
(2) Excitation of skin over organ, 3 centims. on head side of net-wires.
(3) Electrometer, crossed condenser connection.

55 ↓ 80 ↑ 105 ↓ 125 ↑ 150 ↓ 170 ↑ 195 ↓ 215 ↑ 240 ↓ 265 ↑ 295 ↓ 317 ↑ 347 ↓

Direct response.

Interval → 475 ↓ 510 ↑ 530 ↓ 555 ↑ 580 ↓

Reflex response.

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

Fig. 6.

Fig. 7.

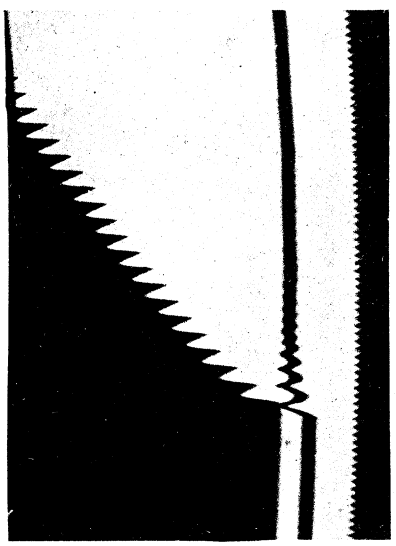


Fig. 10.

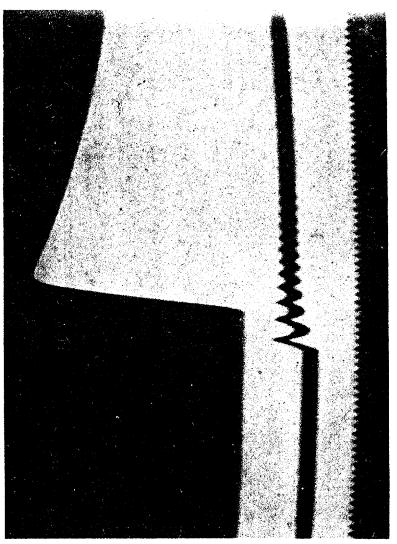


Fig. 13.

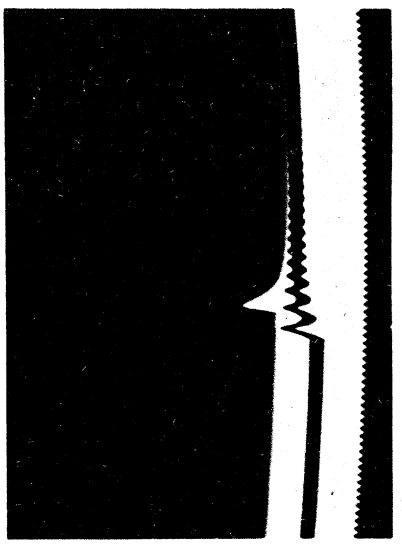


Fig. 16.

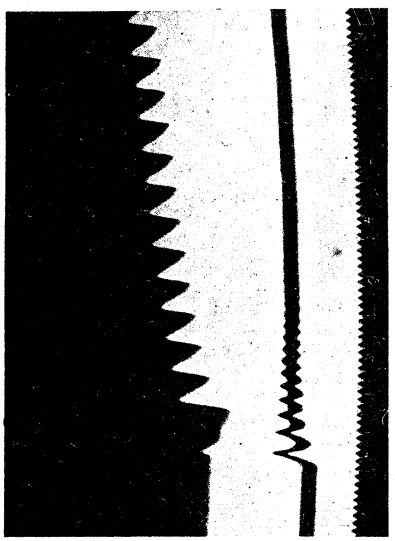


Fig. 9.

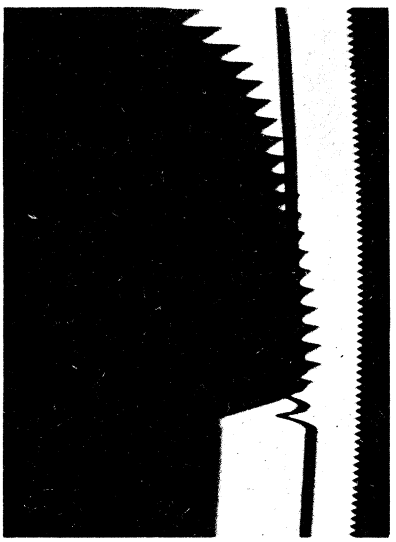


Fig. 12.

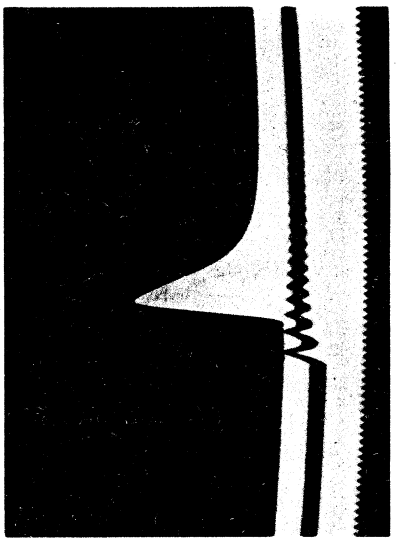


Fig. 15.

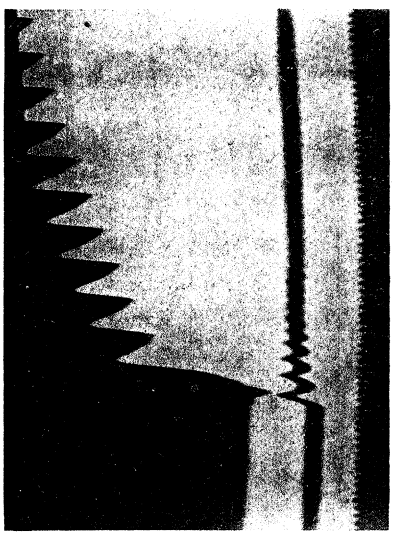


Fig. 8.

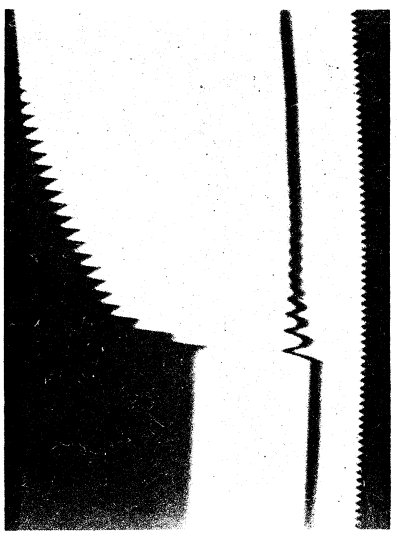


Fig. 11.

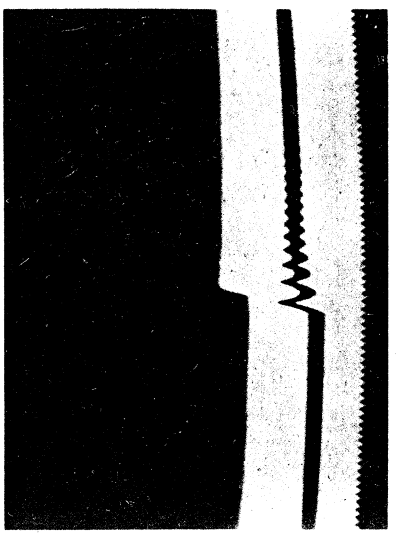


Fig. 14.

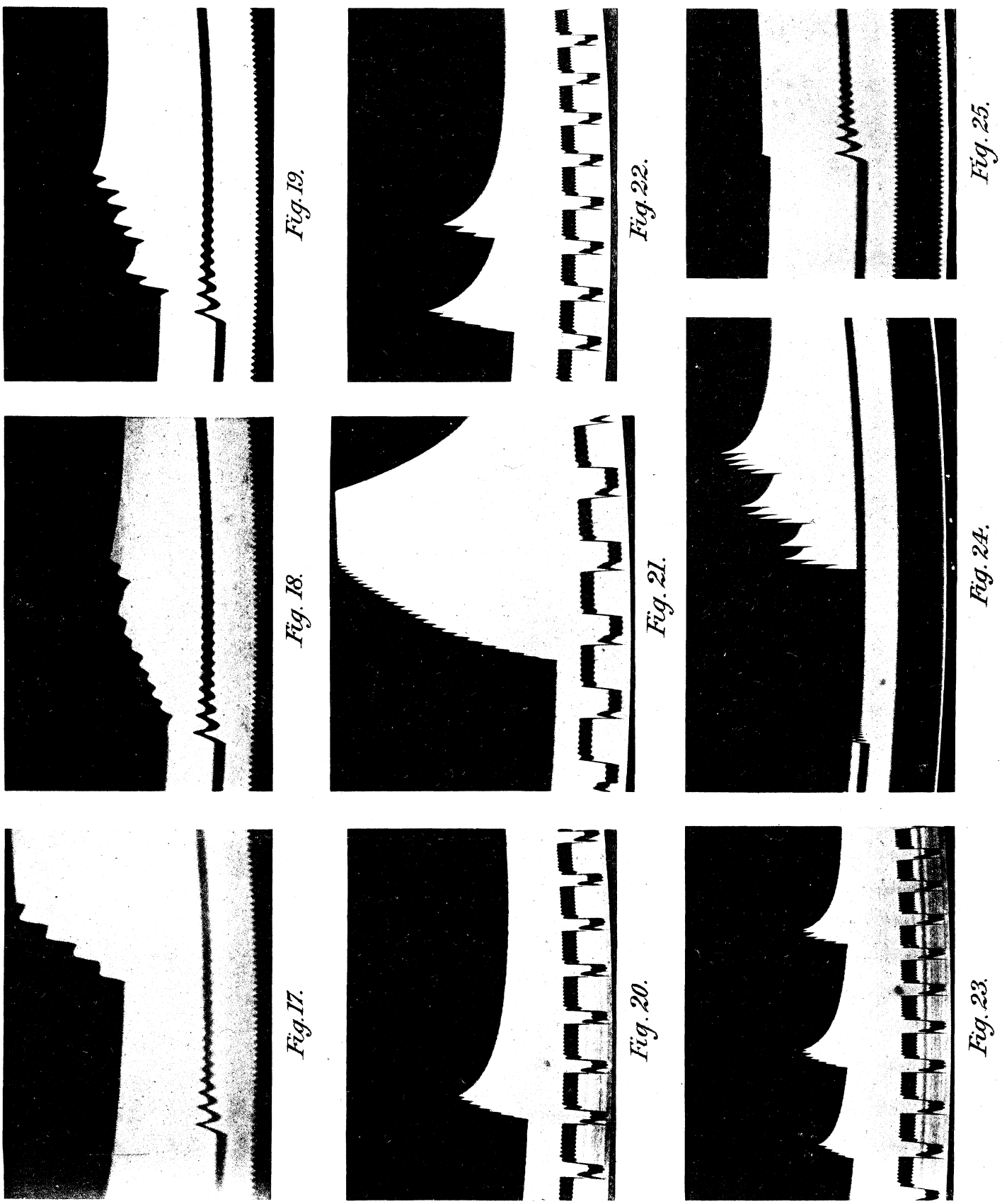


Fig. 17.

Fig. 18.

Fig. 19.

Fig. 20.

Fig. 21.

Fig. 22.

Fig. 23.

Fig. 24.

Fig. 25.

Fig. 19. (No. 108.)

(1) Living fish, as in fig. 18. Both direct and reflex responses.

(2) Excitation as in fig. 18.

(3) Electrometer, crossed condenser connections.

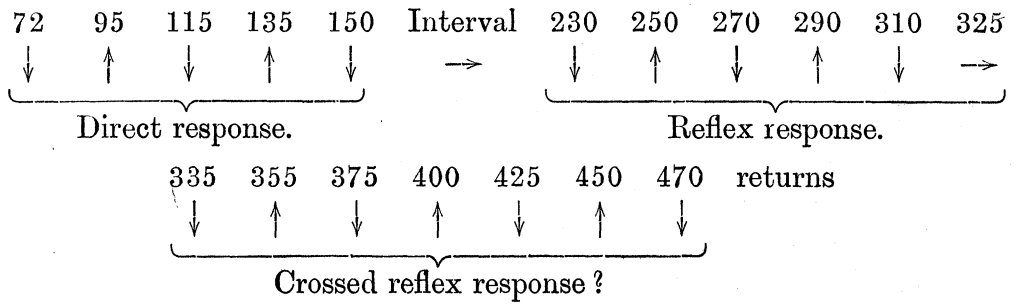


Fig. 20. (No. 179.)

(1) Same as in fig. 17.

(2) Excitation by prolonged squeeze of flank by hand.

(3) Electrometer = the downward-pointing, quick-action, sensitive capillary; shunt = 20-ohm coil; slow rate; time marker, $\frac{1}{8}$ second.

One reflex response of seven shocks (peripheral organ rhythm).

Fig. 21. (No. 184.)

(1), (2), and (3) as in fig. 20.

One reflex response of thirty-two shocks (twenty-seven visible, and five indicated on negative).

Average period = ·0070 second (peripheral rhythm).

Fig. 22. (No. 181.)

(1), (2), and (3) as in fig. 20.

Two reflex responses, the first with six apices, followed after an interval of ·25 second by a second with three apices.

Fig. 23. (No. 180.)

(1), (2), and (3) as in fig. 20.

Three reflex responses; the second begins ·26 second after the first, and the third ·31 second after the second.

Fig. 24. (No. 56.)

(1) and (2) as in fig. 20.

(3) Electrometer = crossed condenser connections.

Three reflex responses. Very slow rate of plate. Time record (500-fork) barely discernible without a lens.

Fig. 25. Excursion produced by action of mercurial shielding-key (K_3 in fig. 8 in text) in suddenly charging the condenser to a potential difference of 5 volts.

Overshooting of the meniscus very slight. No leakage in electrometer circuit, and therefore no return to zero.

Delay due to K_3 = ·002 second.

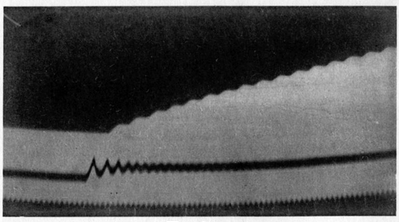


Fig. 1.

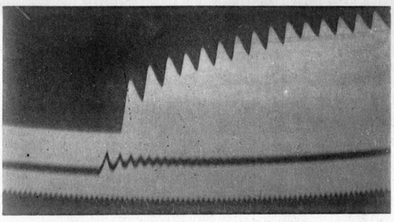


Fig. 2.

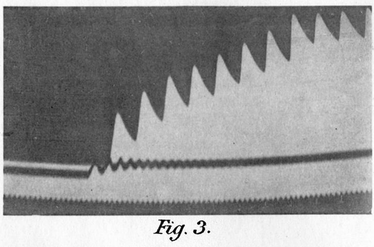


Fig. 3.

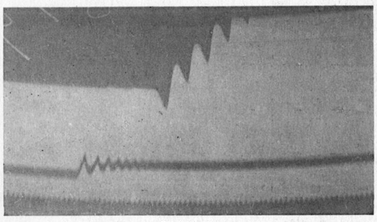
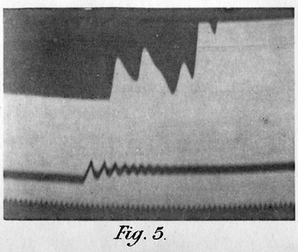


Fig. 4.



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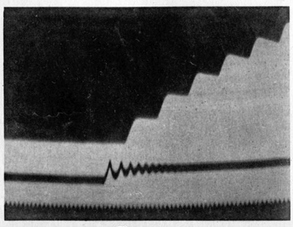


Fig. 6.

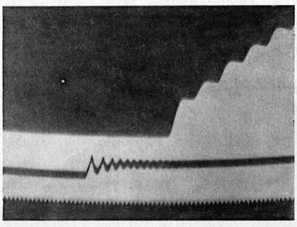


Fig. 7.

PLATE 1.

Fig. 1. (No. 128.)*

(1) Isolated organ strip, 10 centims. long. D = 1 centim. T = 15° C.
(2) Excitation, P = 4 volts. Coil = 4000. X on nerve, 1 centim. outside organ (head end).
(3) Electrometer, shunt = 100-ohm coil.

85	125	165	205	245	290	310	360	385	425
↑	→	↑	→	↑	→	↑	→	↑	→
460	505	530	570	605	650	685	700	755	800
↑	→	↑	→	↑	→	↑	→	↑	→
830	870	905	950	985	1025	1060	1115	1140, &c.	
↑	→	↑	→	↑	→	↑	→	↑	

Average period, ·0076 second.

Fig. 2. (No. 127.)

(1) Same as in fig. 1.
(2) Same as in fig. 1.
(3) Condenser connection.

80	115	170	195	250	275	325	350	395	420
↑	↓	↑	↓	↑	↓	↑	↓	↑	↓
470	490	540	567	615	640	690	715	765	790
↑	↓	↑	↓	↑	↓	↑	↓	↑	↓
840	865	910	940	990	1015	1065	1090, &c.		
↑	↓	↑	↓	↑	↓	↑	↓		

Average period, ·0076 second.

Fig. 3. (No. 147.)

(1) Isolated organ, cut across; leads on head portion. D = 3 centims.
(2) Same as in fig. 1.
(3) Condenser connections.

80	112	185	200	295	325	400	430	502	535
↑	↓	↑	↓	↑	↓	↑	↓	↑	↓
615	645	720	750	830	860	935	965	1065	
↑	↓	↑	↓	↑	↓	↑	↓	↑	

Average period, ·0109 second.

Fig. 4. (No. 151.)

(1) Isolated organ, cut across; leads on caudal portion, which is reversed. D = 3 centims.
(2) Same as fig. 3.
(3) Same as fig. 3.

(100) ...	(210) ...	310	360	400	450	490	535	575	620	... 710, &c.
↑	↑	↓	↑	↓	↑	↓	↑	↓	↑	↓ ↑
Primary strip, small.		Secondary strip, large excursion.								

Average period, ·0088 second.

The numbers in brackets correspond to small excursions produced by the primary strip. The secondary strip comes into action with the third discharge of the primary.

Fig. 5. (No. 152.)

(1) Isolated organ, cut across, with caudal half reversed; leads one on head half and one on caudal half. D = 6 centims.
(2) and (3) Same as in fig. 4.

92	120	200	232	305	360	405	440	...	530, &c.
↑	↓	↑	↓	↓	↑	↓	↑	↓	↑
Primary strip.				Secondary strip.					

Fig. 6. (No. 208.)

(1) Isolated organ, with section across nerve, leads head side of section. D = 2 centims.
(2) Same as in fig. 5.
(3) Electrometer, with shunt = 80-ohm lamp.

100	160	260	320	410	470	570	630	725	780, &c.
↑	→	↑	→	↑	→	↑	→	↑	→

Fig. 7. (No. 209.)

(1) Same as in fig. 6, but leads tail side of section. D = 2 centims.
(2) Same as in fig. 6.
(3) Same as in fig. 6.

395	470	520	585	635	705	760	835	890, &c.
↑	→	↑	→	↑	→	↑	→	↑

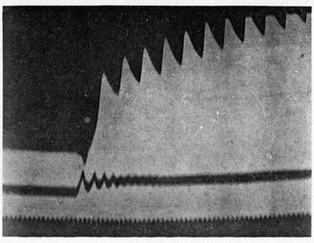


Fig. 8.

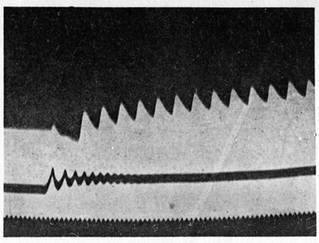
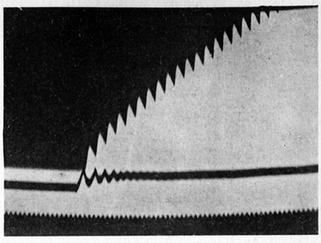


Fig. 9.



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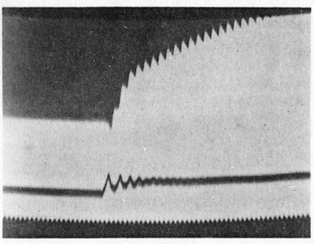


Fig. 11.

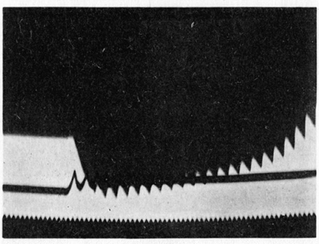


Fig. 12.

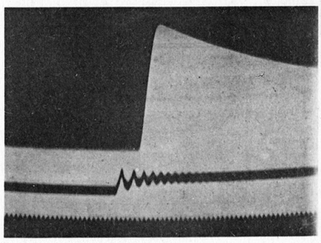


Fig. 13.

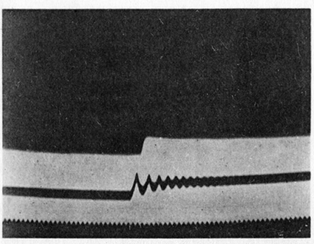


Fig. 14.

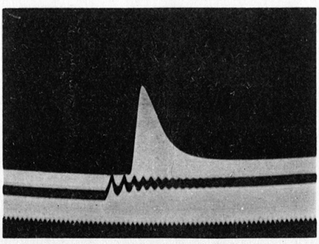


Fig. 15.

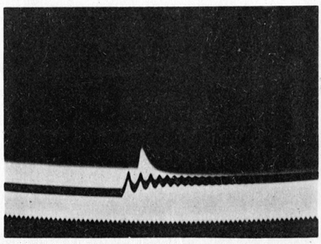


Fig. 16.

PLATE 2.

Fig. 8. (No. 218.)

(1) Isolated organ strip, 3 centims. long, contacts at ends. T = 5° C.
(2) X by heterodromous induced current. P = 5 volts. Coil = 12000.
X-electrodes joined to contacts.
(3) Condenser, kept short-circuited by shielding-key for ·002 second.

(24) (. . .) (41) (61) 92 121 190 220 289 318 383 412
Induction shock escape. ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓
480 509 579 606 675 702 774 . . . 871 . . . 970, &c.
↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑

Average period, ·0097 second.

Fig. 9. (No. 213.)

(1) Same as fig. 8, but T = 15° C.
(2) and (3) As in fig. 10, *i.e.*, by heterodromous direct excitation.

(25) (35) 75 95 145 175 235 260 315 340
Induction escape. ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑
400 425 485 510 570 595 655 680 740 765
↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑
820 850 910 935 995 1020 1080, &c.
↓ ↑ ↓ ↑ ↓ ↑ ↓

Average period, ·0083 second.

Fig. 10. (No. 219.)

(1) Same as fig. 9, but T = 25° C.
(2) and (3) Same as in fig. 9.

35 55 80 100 130 145 175 190 215 235 260 275 305
↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑
320 350 365 395 415 440 455 485 500 530 545 575 590
↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓
620 635 665 680 710 725 750 770 800 815 845 880 . . . 945
↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓

Average period, ·0045 second.

Fig. 11. (No. 224.)

(1) Same as in fig. 10, but T = 35° C.
(2) and (3) Same as in fig. 10.

(29) 40 57 71 83 113 130 150 164 189 200 222
↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑
234 256 270 293 305 330 341 362 378 400 414 435
↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑
450 471 484 508 520 542 567 578 592 615 629 651
↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑
663 689 700 722 . . . 760 . . . 795 . . . 830, &c.
↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑

Average period, ·0038 second.

Fig. 12. (No. 221.)

(1) Isolated organ strip. T = 35° C.
(2) Homodromous induced current. P=5 volts. Coil=12,000, with core in.
(3) Condenser connection.
Response of organ to homodromous induced current.

(35) . . . 135 . . . 185 . . . 235 . . . 280 . . . 330 . . . 425
↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑
. . . 475 . . . 525 . . . 575 . . . 622 . . . 675 . . . 720 . . .
↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓
775 . . . 820 . . . 870 . . . 915 . . . 970 . . . 1020 . . . 1070, &c.
↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑ ↓ ↑

Average period, ·0050 second.

Fig. 13. (No. 199.)

(1) Organ preparation. D = 6 centims. T = 5° C.
(2) Nerve excitation outside organ. P = 5 volts. Coil = 5000.
(3) Electrometer with shunt = 80-ohm lamp.

105 210
↑ →

Single response.

Fig. 14. (No. 200.)

(1) Same as in fig. 13, but T = 30° C.
(2) and (3) As in fig. 13.

45 67
↑ →

Single response.

Fig. 15. (No. 194.)

(1) Same as in fig. 13. T = 5° C.
(2) Same as in fig. 13.
(3) Electrometer, condenser connections.

(25) 105 160
↑ ↓

Single response.

Fig. 16. (No. 196.)

(1) Same as in fig. 15, but T = 30° C.
(2) Same as in fig. 15.
(3) Electrometer, condenser connections.

(30) 70 90
↑ ↓

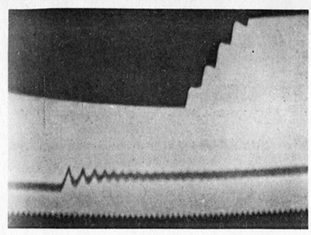


Fig. 17.

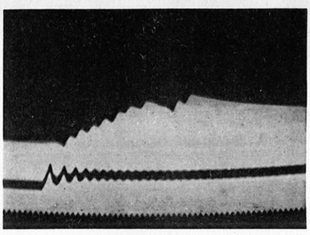


Fig. 18.

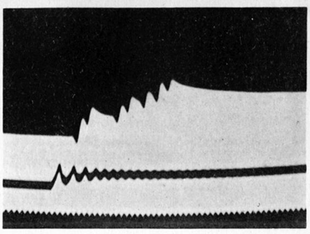


Fig. 19.

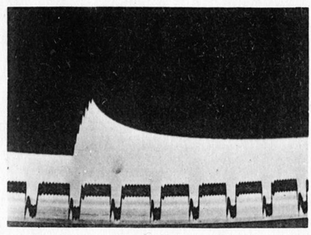


Fig. 20.

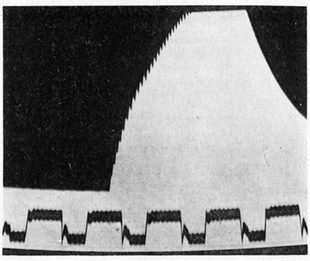
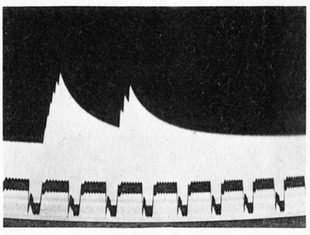


Fig. 21.



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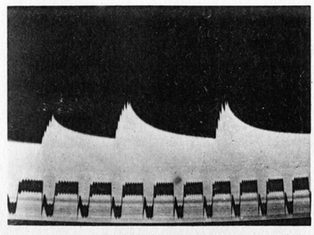

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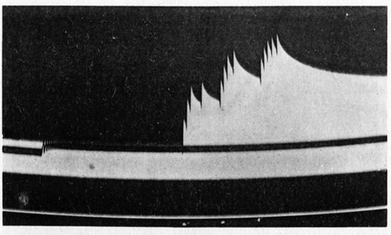

Fig. 24.

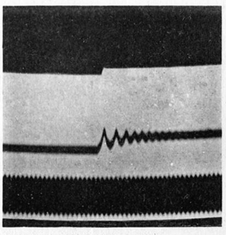

Fig. 25.

PLATE 3.

Fig. 17. (No. 90.)

(1) Living uninjured fish in net. D = 4 centim. T = 20° C. Reflex response.
(2) Excitation on tail, beyond organ. P = 5 volts. Coil = 12,000.
(3) Electrometer, shunt, 100-ohm coil.

475 ↑ 507 → 545 ↑ 575 → 605 ↑ 635 → 670 ↑ 700 → 740 ↑ &c.

Average period, ·0066 second.

Fig. 18. (No. 103.)

(1) Living fish, as in fig. 17. Both direct and reflex response.
(2) Excitation of skin over organ, 3 centims. on head side of net-wires.
(3) Electrometer, crossed condenser connection.

55 ↓ 80 ↑ 105 ↓ 125 ↑ 150 ↓ 170 ↑ 195 ↓ 215 ↑ 240 ↓ 265 ↑ 295 ↓ 317 ↑ 347 ↓

Direct response.

Interval → 475 ↓ 510 ↑ 530 ↓ 555 ↑ 580 ↓

Reflex response.

Fig. 19. (No. 108.)

(1) Living fish, as in fig. 18. Both direct and reflex responses.
(2) Excitation as in fig. 18.
(3) Electrometer, crossed condenser connections.

72 ↓ 95 ↑ 115 ↓ 135 ↑ 150 ↓ Interval → 230 ↓ 250 ↑ 270 ↓ 290 ↑ 310 ↓ 325 →

Direct response. Reflex response.

335 ↓ 355 ↑ 375 ↓ 400 ↑ 425 ↓ 450 ↑ 470 ↓ returns

Crossed reflex response?

Fig. 20. (No. 179.)

(1) Same as in fig. 17.
(2) Excitation by prolonged squeeze of flank by hand.
(3) Electrometer = the downward-pointing, quick-action, sensitive capillary; shunt = 20-ohm coil; slow rate; time marker, $\frac{1}{3}$ second.

One reflex response of seven shocks (peripheral organ rhythm).

Fig. 21. (No. 184.)

(1), (2), and (3) as in fig. 20.

One reflex response of thirty-two shocks (twenty-seven visible, and five indicated on negative).

Average period = ·0070 second (peripheral rhythm).

Fig. 22. (No. 181.)

(1), (2), and (3) as in fig. 20.

Two reflex responses, the first with six apices, followed after an interval of ·25 second by a second with three apices.

Fig. 23. (No. 180.)

(1), (2), and (3) as in fig. 20.

Three reflex responses; the second begins ·26 second after the first, and the third ·31 second after the second.

Fig. 24. (No. 56.)

(1) and (2) as in fig. 20.
(3) Electrometer = crossed condenser connections.

Three reflex responses. Very slow rate of plate. Time record (500-fork) barely discernible without a lens.

Fig. 25. Excursion produced by action of mercurial shielding-key (K_3 in fig. 8 in text) in suddenly charging the condenser to a potential difference of 5 volts.

Overshooting of the meniscus very slight. No leakage in electrometer circuit, and therefore no return to zero.

Delay due to K_3 = ·002 second.