

# Researches on the Electric Discharge of the Isolated Electric Organ of *Astrape* (Japanese Electric Ray) by Means of Oscillograph.

By

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*With 30 Plates.*

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## Contents.

	Page
I. Introduction. ... ..	1
II. Description of the fish, and preparation of the organ. ... ..	3
III. Plan of the experiments. ... ..	6
IV. Formula expressing the discharge curve. ... ..	14
V. Relation between the form of stimulus and the discharge caused by it, ...	26
VI. Discharge by two successive stimuli. ... ..	42
VII. Fatigue phenomenon. ... ..	65
VIII. Speed of propagation of excitation through the nerve. ... ..	70
IX. Miscellaneous problems... ..	72
Summary. ... ..	77
Appendix. Tables of experimental data and calculated numbers. ...	80

## I. Introduction.

It is now some twenty years since the discharge curves of electric fishes began to be investigated by such physiologists as Gotch, Schönlein, Garten, Koike, Cremer and others. The method of Gotch consisted in tracing the curve, point by point, by means of a ballistic galvanometer, a single point being determined by each discharge. Schönlein applied Bernstein's rheotome; Garten and Koike used the capillary electrometer and the string

galvanometer, whereas Cremer employed his string electrometer. Although the method of experiments used by Gotch was certainly the most ingenious at that time, the curves obtained are not sufficiently accurate to be analysed quantitatively. The method of Schönlein is inferior to that of Gotch, for the form of the discharge curves obtained by his method cannot fail to be much affected by the fatigue of the tissues. As the capillary electrometer, the string galvanometer and the string electrometer cannot faithfully follow so quick a change in the electromotive force as happens in the case of the discharge phenomena in question, the curves obtained by them are only qualitative.

In April 1906, in conjunction with Mr. S. Oinuma, now *Igakuhakushi*, the author began his experiments on the same subject by means of an oscillograph in the Physiological Institute of the Imperial University of Tōkyō. In the course of this investigation, his collaborator went to Europe, and the author was then obliged to continue the experiments alone.

The electric fish used by us was one of the electric rays called *Astrape japonica*, which was brought from Misaki, a fishing town in Sagami peninsula. Perhaps on account of the imperfectness of our aquarium, the fish could not be kept in a healthy state except for a few months in Spring and Autumn; and in these most favourable periods, even a single fish sometimes could not be obtained. On account of these and other hindrances, and although lengthy and exhaustive experiments were continued up to 1910, the problems first proposed could not be thoroughly investigated. The results so far obtained by these experiments are now presented in this paper.

With regard to the form of the discharge curve which will be discussed in § IV., it is very interesting to note that some physiological phenomena can be explained from the standpoint of the theory of probability. It is a known fact that many quantities characterising a class of animals or plants are subject to individual variations; and if the observations are taken on a sufficiently large number of individuals of the same class, the values representing any of these characteristics distribute themselves, among the number of

individuals taken, in such a manner that the variation appears to occur in accordance with the law of errors. Since now the tissues of an organism consist of a large number of structural elements, it is natural to suppose that a characteristic belonging to these elements varies in different individuals according to a similar law. Then, it may be remarked, that the treatment of the physical phenomenon in a tissue must be based on the principle of probability, and especially in the treatment from the standpoint of the "all or none"\* theory, the application of this principle must be effective and indispensable, for a physical phenomenon exhibited by a tissue must be the integral effect of the phenomena occurring in each of the component elements.

## II. Description of the Fish, and Preparation of the Organ.

The structure of the electric organ in *Astrape japonica* was recently described in detail by K. Ishimori<sup>†</sup>, and therefore need not be entered into here. However, a few points having direct bearing on the present investigations may here be recorded.

The external aspect of the fish and its electric organs are represented in Plate I. The length of the mature fish is about 25 cm.,

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\* Lucas inferred from his investigation on the contraction of a skeletal muscle, *M. cutaneus dorsi*, of the frog (Journal of Physiology, Vol. 38, 1909), that, when a stimulus greater than a certain threshold value is given to a single nerve-fibre, the excitation evoked in it appears to have a definite value independent of the intensity of the stimulus. Then, it seems very probable that, with regard not only to a nerve but to tissues in general, the excitation evoked at a point in the excitatory elements follows the so-called "all or none" law. In other words, there exist only two alternatives, *i. e.*, whether the excitation does occur in a definite intensity or not at all,—no intermediate value being possible. In this view, the propagation of the excitation should take place by the successive action of the excited point towards its neighbour, the propagation in reverse direction being impossible in virtue of the existence of the refractory period. The energy of the excitation of each portion should be supplied by some chemical change in it, and therefore its intensity should depend on the physiological state of that portion only. A case may occur, that an excitation is enfeebled on its way to propagation, by passing through a portion in an abnormal state, to such a degree as is incapable of evoking the excitation of the neighbouring portion. Then the farther propagation is impossible and stops there. For proper understanding of the discussions throughout this paper, it is necessary to keep these considerations in mind.

† Beiträge zur Physiologie. Festschrift zu Ehren der 25 Jährigen Lehrtätigkeit von Kenji Osawa.

measured from head-end to tip of tail. The electric organ is present in a pair in the form of large flat bodies, situated one on each side and lateral mainly to the head and the branchial regions. The upper and lower surfaces of the organ are in direct contact with the integument of the fish. Each organ is an assemblage of vertical hexagonal prisms about 200 in number. The height of the prisms measures 1-1.5 cm. Each prism consists of a pile of disc-like body called the *electric plate* numbering about 400. The plates consist each of a clear jelly-like mass inclosing a number of large nuclei and are surrounded as well as separated from one another by a connective-tissue layer in which the nerves and the blood vessels find their course. From the *Lobus electricus* of the brain, there arise on each side five special nerves, the electric nerves, which supply the organ in question. Distally the nerves undergo successive branching, finally to terminate in fine network on the ventral side of each electric plate. In the discharge of electricity the side of the plate just mentioned is always negative, while the dorsal side without the nerve-endings is positive.

Before explaining the plan of the experiments, we shall describe the method of preparing the organ for the purpose. Except when the spontaneous discharge was to be studied, the organ was separated from the body and the whole or a part of it was used according to circumstances. When the fish was brought from the aquarium to the laboratory, in order to avoid the setting in of fatigue, the brain was extracted by applying a cork-borer to the head and then striking its upper end with a hammer. The spinal cord was next destroyed by pushing a wire into the spinal canal. Having thus avoided the reflex action of the nervous centre, the organ was separated from the fish.

The electric discharge of the organ is evidently a very complex phenomenon, for it must be the integral effect of unit discharges of the electric plates. When a stimulus is given at a point in the nerve-trunk, the excitation is distally transmitted through nerve-fibres of different lengths, and as the speed of transmission through them is finite, it should arrive at the different electric plates not simultaneously but at different periods. Hence it is



advantageous, for the investigation of the discharge curve, to stimulate the organ not through the nerve-trunk but directly, so that each plate may receive the stimulus at the same instant. For the direct stimulation of the muscle, it is customary to use *curara* in order to benumb the nerve-endings. In the case of the electric organs, however, there is known no such drug that can be used with the same effect. Hence the term *direct stimulation* used in this paper in relation to the electric organ has a somewhat different meaning from that used in the case of a muscle. Though the stimulating electric current is sent directly through the electric organ, the stimulus is probably in the main imparted to it through the nerve-fibres distributed in it. Nevertheless, in that way the condition of simultaneous stimulation can be better fulfilled than when the stimulation is given through the nerve-trunk. Moreover, when the nerve-trunk is left attached to the organ, the discharge current flowing through the nerve-trunk is very liable to act as a second stimulus and to cause a *secondary discharge* of considerable magnitude, by which a tertiary discharge is called forth, and so on. This makes the phenomenon very complex. But, in the case of direct stimulation of the organ, if the nerve-trunk be carefully taken away from the organ, and if its temperature be kept sufficiently low, there will result only a very weak secondary discharge (Plate I., Fig. 2). In accordance with these considerations, we employed direct stimulus in general, except when the property of the nerve was to be investigated. In the former case the five trunks of the nerves were cut off as near as possible to the organ, and the whole or a part of it was utilised. In the latter case, when the stimulus was to be sent through the nerve-trunk, about a quarter of the organ with one nerve-trunk was employed.

### III. Plan of Experiment.

The diagram of the plan of the experiment is represented in Fig. 1.

The oscillograph used by us was that designed by Duddell and made by The Cambridge Scientific Instrument Company, and that which is known as the high frequency type. The period of strips in an undamped state measures about  $1/10000$  sec. By means of this instrument, an alternating current having a period 50 times that of the strips may be photographed without an appreciable error.\* As the duration of a discharge of the organ measures about  $1/100$  sec., the curve obtained by this instrument may be relied on for quantitative analysis. As the instrument is designed for an alternating current, it has a pair of strips, one for the current and the other for the applied E. M. F. In our experiments, when the organ was stimulated directly, only one of them was employed, the stimulating current and the resulting discharge current being made to flow through the same strip; and when the stimulus was sent through the nerve-trunk, one of the strips was used for the stimulus and the other for the discharge. The fact that both the stimulus and the discharge may be photographed upon one and the same film is very convenient for accurate work. The sensitivity of the oscillograph is about 26 mm. for 0.1 ampere, the film being at a distance of 50 cm. from it. The resistance of each strip is about 8 ohms.

The light source  $Q$  for illuminating the oscillograph consists of a hand-regulating arc lamp of 15 amperes, the image of which is formed on a slit  $s$  by a lens  $L$ .

The registering drum  $D$  is supported within a camera and has a circumference of 50 cm. (Plate III., Fig. 1). This is revolved by a small motor  $M$  of  $1/30$  H.P. The number of revolutions used was 5–20 per. sec., according to circumstances. A photographic film was wound around the drum and kept in position by means of two india-rubber rings which keep each side of the film pressed

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\* Zeitschrift für Instrumenten Kunde, S. 240, Bd. 21, 1901.

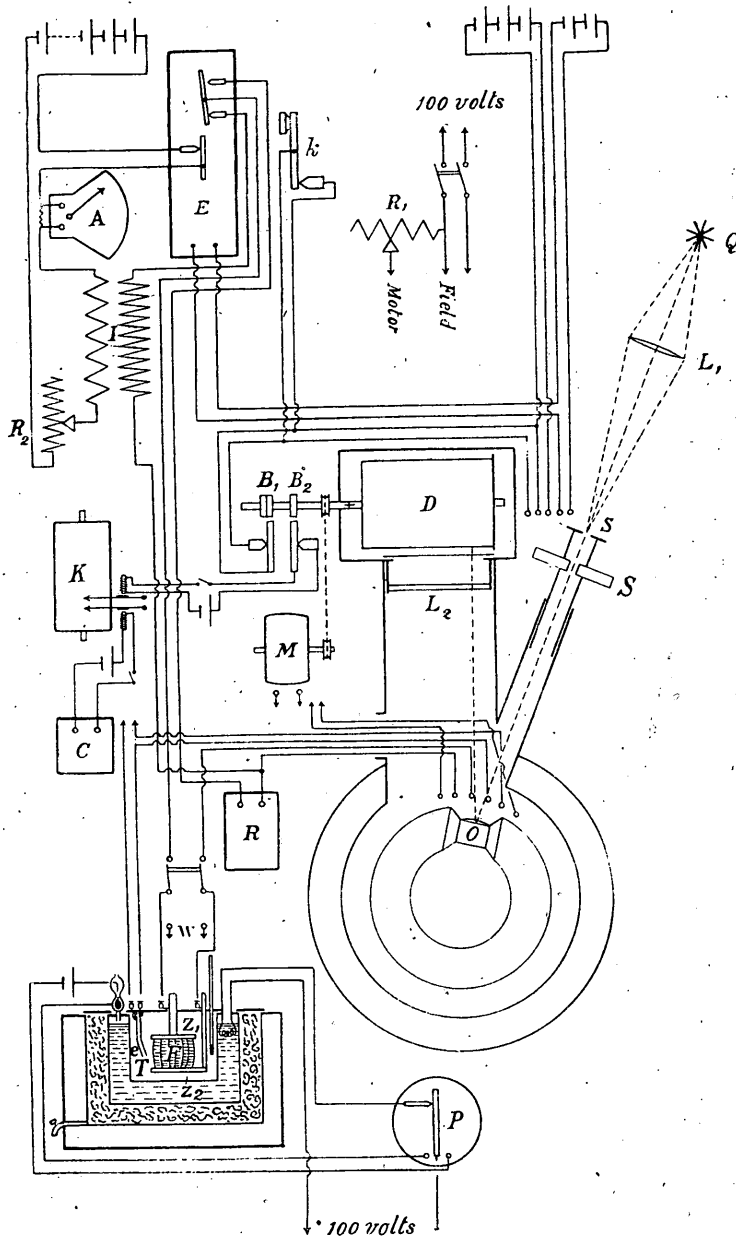


Fig 1. The Plan of Experiment.

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|-------------------------------------|--------------------------------------|-------------------------------------|--|
| <i>O</i>                            | Oscillograph.                        | <i>Z<sub>1</sub>, Z<sub>2</sub></i> | Zinc electrodes for electric organ.                          |
| <i>Q</i>                            | Arc lamp.                            | <i>P</i>                            | Relay for thermostat.  |
| <i>L<sub>1</sub></i>                | Converging lens.                     | <i>E</i>                            | Stimulation-apparatus.                                       |
| <i>s</i>                            | Slit.                                | <i>I</i>                            | Induction coil.  |
| <i>S</i>                            | Shutter.                             | <i>A</i>                            | Ammeter.   |
| <i>L<sub>2</sub></i>                | Cylindrical lens.                    | <i>R<sub>1</sub></i>                | Regulating resistance for primary current of induction coil. |
| <i>D</i>                            | Registering drum.                    | <i>k</i>                            | Morse key.   |
| <i>M</i>                            | Motor.                               | <i>K</i>                            | Chronograph.   |
| <i>B<sub>1</sub>, B<sub>2</sub></i> | Break-circuit contrivances.          | <i>C</i>                            | Chronometer.   |
| <i>F</i>                            | Organ-preparation.                   | <i>R</i>                            | Resistance box.  |
| <i>T</i>                            | Thermostat.                          | <i>W</i>                            | To Kohlrausch bridge.  |
| <i>e</i>                            | Electrodes for indirect stimulation. |                                     |  |

firmly against the drum and also by a thin piece of bamboo which presses the two overlapping ends of the film. When the stand supporting the drum is pulled, the axis of the drum is disconnected from its driving shaft by means of a special contrivance (Plate IV., Fig. 1, *a*), and the drum with its stand may be taken out of the camera, the operation being accomplished in the dark without any trouble.

On the shaft of this registering apparatus, there are two break-circuit contrivances like that of a chronometer (Plate IV., Fig. 1, *b*<sub>1</sub> *b*<sub>2</sub>; Fig. 2), one for the chronograph by which the number of revolutions of the drum is measured, and the other for the shutter described below.

A kymograph *K* made by Zimmermann, with accompanying time-markers, was used as the chronograph, the record being obtained on smoked paper. When the speed of the rotation of this instrument is increased to its maximum, the number of revolutions of the registering drum may be accurately determined to three figures.

The organ-preparation was supported between two zinc plates that served as electrodes. To secure a good contact, and also to avoid the effect of polarisation, if such existed, the surfaces of the zinc plates were covered with kaolin paste, soaked with a saturated solution of zinc sulphate, and then with a layer of the same material kneaded with a physiological solution of sodium chloride.

Since it is found that the form of the discharge curve is much affected by the change of temperature, the organ is put into an electrically regulated thermostat. As the favourable range of temperature for our investigation was found to be 8°C.—15°C., and because in the warm season this range of temperature is lower than that of the room, the thermostat must be so designed as to ensure that a constant temperature lower than the surrounding temperature be maintained. For this purpose the author constructed a special thermostat shown in Fig. 1. The moist chamber, in which the organ supported by the zinc electrodes is put, is surrounded by a jacket of transformer oil, in which a toluene regulator and an

electrically-heated resistance are immersed. Outside of this comes a layer of ice, and the whole is protected from external heat by an air jacket. The thermostat works well for 6—7 hours without any fresh supply of ice.

Next we shall describe the construction of a shutter designed by the author (Plate II.). The function of this shutter is as follows. (*a*) When a certain place on the film just comes to receive light from the oscillograph, the shutter opens, (*b*) then the stimulation-apparatus is set in work, whereby the organ is excited and the oscillograph prints the motion due to the stimulation and the discharge current, and (*c*) when the drum has made just one revolution after the shutter first opened, it is made to close so as to protect the film from unnecessary exposure to light. The operations *a* and *c* are accomplished by sending to the electro-magnets on the shutter instantaneous breaks of current, which occur once in each revolution of the registering drum. Fig. 4 in Plate IV. represents the construction of the shutter. It consists essentially of two almost identical aluminium sectors *A* and *B*, placed one behind the other with a circular hole in each of them, and two electro-magnets *A'* and *B'*, one for each sector. When the sectors, by means of cords, are pulled to the left against the action of the springs, and there held in position by the detents attached to the armatures of the electro-magnets, the shutter is ready for action. When the current is broken for an instant, at the break-circuit contrivance attached to the shaft above mentioned, only the electro-magnet *A'* belonging to the front sector is put into action and the sector *A* is released and turns to the right, and then a free passage of light through the shutter is admitted, (operation *a*). By a simple mechanism attached to the front sector, the electric connection is changed automatically, without interrupting the current in the operation, so that at the next break of the current, which takes place after one revolution of the drum, the back sector is released and the passage of light is intercepted (operation *c*). The contrivances for these operations are illustrated diagrammatically in Fig. 2. The mechanism of the operation *b* will be described under the paragraph of the

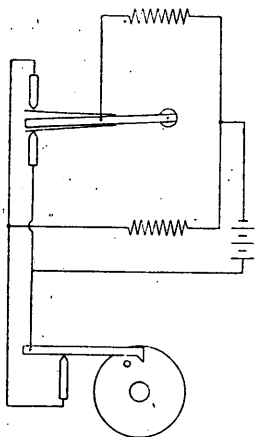


Fig 2. Connections of shutter.

stimulation-apparatus. The shutter does not work unless a Morse key *k* is pressed which serves as a shunt to the break-circuit contrivance. By adjusting the phase of the break with reference to the drum, the shutter may be opened when any desired position on the film comes to receive light from the oscillograph. For the sake of economy of time and of film, a series of discharges are photographed in order on one film, by thus shifting the phase of break with reference to the drum. The shutter may be used as a time-shutter if desired, when it is connected to the ordinary Morse key as shown in Fig. 3.

Before describing the stimulation-apparatus, we shall explain the form of stimulus used in our experiments. The stimulation ordinarily used was an induced current in the

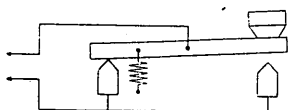


Fig. 3. Connection of Morse key for time-shutter.

secondary circuit of a Du Bois Raymond's induction coil usually employed by physiologists. When the primary current is suddenly opened, the secondary current

increases from zero to a maximum value in a very short period, and then decreases exponentially to zero. By shunting the secondary current at a desired instant in its decreasing stage, it can be made to decrease to zero suddenly. Such a current was ordinarily used as our stimulus in direct stimulation. In many experiments the strength and the duration of such a secondary stimulating current were changed and their influence upon the discharge curve was investigated. The oscillogram in Plate I. (Fig. 2) shows a form of such stimulus followed by the discharge current of the organ in response to it. Here we may remark that we can see in this oscillogram how well the shutter works. In the indirect stimulation, however, the induced current caused by an instantaneous contact in the primary circuit of the induction coil is ordinarily used. This forms a stimulus of very short duration as shown in Fig. 4. For brevity we shall hereafter call such

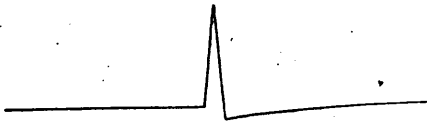


Fig. 4. Momentary stimulus.

a stimulus the *momentary stimulus*. Sometimes it was required to experiment with two such momentary stimuli separated by a given interval of time.

In the direct stimulation of the organ, the secondary of the induction coil, the organ and the oscillograph must be connected in a series. But when the discharge is to be photographed, it is necessary to exclude the secondary coil from the circuit and to introduce a proper resistance if required. For, if the secondary coil is in the circuit, its enormous self-induction influences and modifies the form of the discharge curve, so that, after a stimulus is given, the exclusion of the secondary coil is necessary.

To fulfil the requirements above mentioned, a stimulation-apparatus represented in Plate III. and Plate V. was designed. A brief description of the apparatus will be given below.

A small car *A* having three wheels *B* on each side lies on a pair of cylindrical rails *C*. The rails have grooves in their upper and lower sides to guide the motion of the wheels. A helical spring is wound round each rail and pushes the car to the left end of the rails. An armature made of laminated iron is fixed to the right end of the car. An electro-magnet fixed on the right end of the apparatus, whose core consists of a bundle of soft iron wires, attracts the armature and keeps the car at the right end of the rails against the action of the helical springs. The current of the electro-magnet flows through the breaking contrivance of the shutter. When the shutter is opened (operation *a* before mentioned), the electro-magnet releases the car (operation *b*) and the latter is pushed away along the rails by the action of the helical springs. The car has a knocking contrivance on its lower side called a *knocker*, whose function will be explained later on. In order to protect the car from damage caused by a strong collision against the stop at the end of its leftward motion, a special device is attached to the stop. This consists of a pair of jaws closed by a strong spring. When the car comes against the stop, a plate forming part of the car plunges into the jaws and dissipates

its energy by friction. Behind the electro-magnet, there is a circuit-breaker for opening the current of the electro-magnet. To its lever, an armature made of laminated iron is fixed, so that when the armature is pushed against the electro-magnet, the contact on the upper end of the lever makes the current by means of which this armature as well as the armature fixed to the car is kept in position at the same time, and the magnetic circuit is thus closed through these armatures and the cores of the electro-magnet. The service of this contrivance is twofold. When the current through the electro-magnet is broken at the shutter, this armature, together with that of the car, is released, and the magnetic circuit is broken at once, so that, on account of the increase of the demagnetising force, the electro-magnet loses its magnetism very soon. This is essential for the quick and unfailing action of the stimulation-apparatus. The second service of this contrivance is evident, for when once the circuit is opened at this place, it does not close again.

On the base-board of the stimulation-apparatus and under the rails before mentioned, lie three grooves each furnished with a millimetre-scale along its length and each parallel to the rails. Into these grooves fits any one or a combination of small mechanisms, which are put into action by the knocker attached to the car. The position of these mechanisms can be read to one-tenth of a millimetre by means of verniers attached to them.

One of these mechanisms is called a *circuit-breaker* and is used for breaking the primary circuit of the induction coil. Plate V., Fig. 2 shows the construction of the circuit-breaker. The circuit is to be broken at the contact between a knock-down lever *l* and the platinum point of an adjustable screw *s*. The lever *l* is kept vertically and pressed firmly against the screw by a holder *h* by means of a spring. When the car moves leftwards, the knocker kicks down the lever *l* and the contact is broken. The peculiar form of the end of the lever and of the holder protects the former from making a second contact with the screw.

Plate V., Fig. 3 is another mechanism which we shall call the *connection-changer*. The rôle of this is to short circuit the secondary



coil at the proper instant after the primary current is broken and then to exclude the secondary coil from the oscillograph circuit. Since the latent period of the discharge measures about  $80 \times 10^{-4}$  sec., this change of connection may be made without disturbing the discharge current. Referring to the figure, *A* and *B* are two springs attached to an arm of a T-shaped lever. At first, the spring *A* is in contact with *A'*. In this case the organ, the oscillograph and the secondary of the induction coil are in a series. When the knock-down lever is kicked, the spring *B* comes into contact with *B'* and then *A* parts from *A'*. At the moment when *B* touches *B'*, the secondary coil is short circuited, and when *A* parts from *A'*, it is excluded from the oscillograph circuit. Then the organ, the oscillograph and an appropriate inductionless resistance are in a series, ready to receive the response of the organ. *C* is a catcher of the knock-down lever to prevent it from rebounding. The mechanism here mentioned is the final form used by the author. In the earlier experiments mercury contacts were employed, but the trembling of the surfaces of the mercury which generally formed a very complex stimulus could not be avoided. Next we attempted simply to cut the secondary current instead of short circuiting the secondary coil, but the spark at the instant of breaking the circuit, prevented the instantaneous decrease of the current. After such experiences, the author was convinced that it is very dangerous to presume on the form of the stimulus by theoretical considerations only; actual experimental evidence is indispensable. Plate V., Fig. 4 is a contrivance for giving two successive momentary stimuli with any desired interval of time. Two electric contacts are made between the ends of the levers and the knocker of the car. Usually such stimuli are given to the nerve and consequently in this case the connection-changer is not necessary. The distance of the two points of contacts may be adjusted from zero to 25 mm. and may be read to one-tenth of a millimetre by means of a vernier.

These mechanisms are fitted into the grooves fixed on the base-board of the apparatus. The grooves being provided with millimetre-scales, their positions may be read to one-tenth of a

millimetre by means of verniers. When in good working-condition, the length of one millimetre on this apparatus corresponds to  $4.4 \times 10^{-4}$  sec.

#### IV. Formula Expressing the Discharge Curve.

From the oscillogram in Plate I., we see that the discharge curve, caused by a direct stimulus, resembles the probability curve of Gauss, except that it is not symmetrical with respect to the maximum ordinate. After some assumptions, a formula is obtained for expressing the curve that agrees very closely with the experimental curve.

In the first place it is assumed that the discharge of each electric plate, caused by a single stimulus, is of very short duration. It is a known fact that only the first small time-interval of a closing current influences the height of the discharge curves, and this will be discussed more fully afterwards. When this fact is considered, it will not be unnatural to suppose, that a stimulus of such short duration causes a discharge of an instantaneous nature. In the second place it is assumed that the interval between the stimulus and the discharge of a single plate in response to it, which interval may be called the *latent period of a single plate*, may have various values, and among them there is a certain value, which predominates in number, so that other values deviate more or less from it according to the law of errors, though in a somewhat modified form. This predominating latent period may be called the *modal latent period*, which, as will be explained afterwards, represents the interval between the stimulus and the instant corresponding to the maximum point of the discharge curve. In biological phenomena there exist many instances which are governed by a law that involves the idea of probability. The phenomenon of contingency and of correlation treated by Pearson and others are such examples. Here it is simply assumed that a similar relation exists in the quantity—the *latent period of a single plate*.

In Gauss's probability curve, the freedom of deviation from its most probable value is symmetrical with respect to it. In the

discussion here, the discharge of any single plate cannot of course occur before a stimulus is given, so that the freedom of deviation from the modal value can never be symmetrical. There must exist a certain instant before which the discharge can never occur. We shall call this instant the *origin of the discharge*. This origin may be at the instant of stimulation or it may be later.

To adapt the present case to that of Gauss's it is assumed that the equivalent elementary interval with respect to the deviation is proportional to the interval between the origin and that instant.

Denoting the latent period of a single plate by  $x$ , the above assumption gives

$$\Delta x = kx,$$

$$i. e. \quad \Delta \log x = k,$$

where  $k$  is a proportional constant. This means that, when the logarithm of  $x$  is taken as the measure of the abscissa, the case becomes identical with that of Gauss's.

The well known curve of probability is expressed by

$$y = Ae^{-b^2x^2}, \dots\dots\dots (1)$$

where the origin of  $x$  is at the maximum of  $y$ . Transforming the origin to  $-x_0$ , then

$$y = Ae^{-b^2(x-x_0)^2}$$

is obtained. Substituting the logarithm of  $x$  and of  $x_0$  instead of them, the above reduces to

$$y = Ae^{-b^2 \log \frac{x}{x_0}} \dots\dots\dots (2)$$

Since the total electromotive force at any instant must be proportional to the number of plates simultaneously discharged at that instant, then, when  $y$  is taken as the electromotive force at a point on the discharge curve and  $x$  as the time-interval measured from the origin of the discharge to that point, the curve expressed by the above formula ought to represent the discharge curve obtained by the oscillograph.

Before entering into an examination of experimental curves, the method for determining the constants  $A$ ,  $b^2$  and  $x_0$  must be treated.

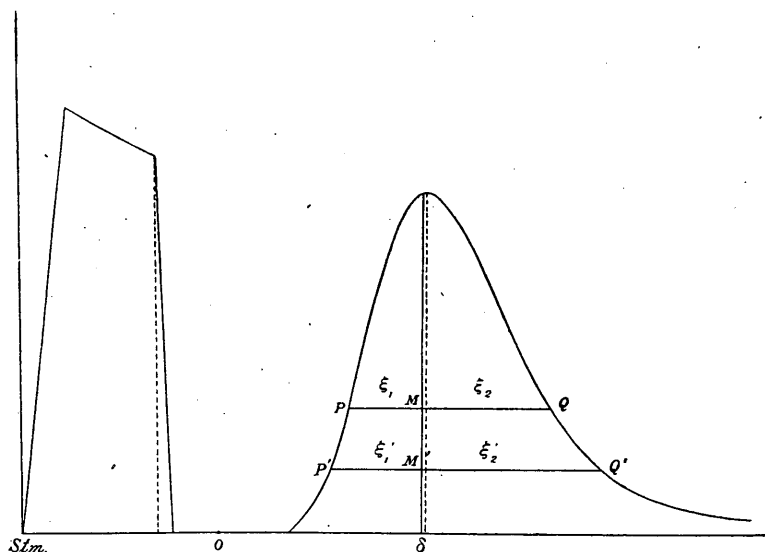


Fig. 5.

To determine  $x_0$ , take two points  $P$  and  $Q$  with the abscissae  $x_1$  and  $x_2$  on the curve in question on its ascending and descending branches where the values of  $y$  are equal. Then it is obvious that

$$\frac{x_2}{x_0} = \frac{x_0}{x_1} \quad \text{or} \quad x_1 x_2 = x_0^2. \dots\dots\dots (3)$$

Let  $M$  be the intersection of  $PQ$  with the maximum ordinate of the curve. Measure  $PM$  and  $QM$ , which may be called  $\xi_1$ ,  $\xi_2$ , then

$$(x_0 - \xi_1)(x_0 + \xi_2) = x_0^2,$$

or

$$x_0 = \frac{\xi_1 \xi_2}{\xi_2 - \xi_1}. \dots\dots\dots (4)$$

Thus we can determine the value of  $x_0$ , so that the position of the origin is made known. Then we can calculate  $b^2$  by the following formula,

$$b^2 = \frac{\log_{10} A - \log_{10} y}{(\log_{10} x - \log_{10} x_0)^2} \times 0.4343, \dots\dots\dots (5)$$

where  $x$  and  $y$  are the co-ordinates of  $P$  or  $Q$ .

Since the denominator of the fraction of  $x_0$  in (4) is very small, errors incurred in measuring  $\xi_1$  and  $\xi_2$  influence very much the value of  $x_0$ . Evidently the error due to  $\xi_2 - \xi_1$  is made smaller, the lower the points  $P$  and  $Q$  are taken; but near the foot of the curve on its descending branch, there exists probably secondary discharge, and therefore we cannot take  $P$  and  $Q$  too low. It may be shown that in the calculation of  $b^3$ , it is least affected by the error in  $y$ , caused by the error on the position of the  $x$ -axis, when  $y$  is equal to  $Ae^{-1}$ . So also, for the determination of  $x_0$ , we prefer the points  $P$  and  $Q$  whose heights are equal to  $Ae^{-1}$ . Since it is very difficult to accurately determine the position of the maximum ordinate, and since the error in its determination influences the difference  $\xi_2 - \xi_1$  doubly, we must make full allowance for the existence of an error of not insignificant importance in  $x_0$  due to this cause. To eliminate this error as far as possible, we take another pair of points  $P'$  and  $Q'$  of equal heights and calculate  $x_0$  as above. If the values of  $x_0$  in the two cases do not coincide, let us assume that the discrepancy is due solely to the error of the position of the maximum ordinate, say  $\delta$ . Correcting for this amount and equating the values of  $x_0$  in the two cases, we have

$$\delta = \frac{\xi_1' \xi_2' (\xi_2 - \xi_1) - \xi_1 \xi_2 (\xi_2' - \xi_1')}{2(\xi_2' \xi_1' - \xi_2 \xi_1)}, \dots\dots\dots (6)$$

where the terms of the second order are neglected.

First the agreement between the theoretical and the experimental curve was examined on Oscillogram No. 54 (Plate XIII.). This was a series of experiments for finding the relation between the magnitude of the stimulation current and the discharge in response. The stimuli were direct and their durations were taken pretty long in order to avoid the effect of small changes in them.

The following are the data of the experiment:—

Oscillogram No. 54.

Object of experiment:      Relation between the intensity of  
the stimulation current and the  
magnitude of the discharge.

Date of experiment: Nov. 6, 1909.

Organ: Left organ (whole) of a fish of middle size.

Temperature of the organ:  $8.5^{\circ}$ — $7.2^{\circ}\text{C}$ .

Resistance of the organ: About 240 ohms.

Reading on the first rail of the stimulation-apparatus (circuit-breaker): 64.0 mm.

Reading on the second rail of the stimulation-apparatus (connection-changer): 60.0 mm.

No. of stimulus in order of time.	1	2	3	4	5	6	7	8
Primary current of induction coil in amp.	1.5	2.0	2.5	3.0	3.5	4.0	4.5	4.95
Number of revolutions of registering drum.	6.51	6.38	6.50	6.53	6.40	6.18	6.00	6.36

The ordinates of the points on the curves were measured for every one mm. of abscissa on the oscillogram, and they were plotted on a section paper, the value of the abscissa being converted to the unit of  $10^{-4}$  sec. (Plate VI.). The following table shows the constants obtained by applying the method above described on the reproduced curves:—

TABLE I.

No.	L. P. in $10^{-4}$ sec.	M. L. P. obs. in $10^{-4}$ sec.	$\delta$ in $10^{-4}$ sec.	M. L. P. corr. in $10^{-4}$ sec.	$A$ in mm.	$b^2$	$x_0$ in $10^{-4}$ sec.
1	76.8	107.5	Too low to be measured.		1.6		
2	79.2	106.4			5.0		
3	73.9	107.8	+ 0.68	108.5	10.1	4.60	59.2
4	71.9	107.1	+ 1.12	108.2	17.3	4.69	59.8
5	73.6	109.6	— 0.10	109.5	26.7	5.63	64.2
6	69.7	108.5	+ 1.40	109.9	35.7	5.37	60.8
7	68.3	106.6	+ 1.06	107.7	44.8	4.49	54.8
8	67.5	109.9	+ 1.46	111.4	55.6	5.95	61.8

L. P. means *latent period* (ordinary usage).

M. L. P. means *modal latent period*.

Full details of calculations are given in the Appendix.

Referring to the table we see that the value of the modal latent period is tolerably constant in spite of the wide changes of the magnitude of the stimulus, while the latent period decreases with the height of the discharge curve. The small increase of the modal latent period may be due to the progressive decrease of temperature, as is given in the data of the experiment. In this case it is a remarkable fact, that  $\delta$  is always positive except in Curve No. 5, and the constancy of the modal latent periods corrected becomes rather worse than that of the observed modal latent periods. The values of  $x_0$  and of  $b^2$  vary with the increase of the height of the stimulus and the values of  $b^2$  are equal to 5.0 in order of magnitude. Here we may remark; that it is very difficult to determine accurately the value of  $x_0$ , but  $b^2$  may compensate for the error of  $x_0$  in the final result. So we cannot put too much weight on the changes of the value of  $x_0$  and of  $b^2$ . At any rate we calculated the values of  $y$  for every one-thousandth of a second, from the values of constants in the table, and plotted these calculated values on the reproduced curves. These are shown in Plate VI. The agreement between the calculated and the observed curves is very satisfactory except for a small part on both feet of the curves, where the calculated points are in general lower than the observed. The discrepancy on the descending foot may be due to the superposed secondary discharge.

Next Oscillogram No. 37 (Plate XIII.) was examined. This was a series of experiments for investigating the relation between the duration of the stimulating current and the magnitude of the discharge. The durations of the stimuli were very small compared with those of Oscillogram No. 54. The curves on the oscillogram were measured and reproduced in the same way as in No. 54 (Plate VII.).

In this series of experiments, the previous method for the determination of  $x_0$  failed to give consistent values to  $x_0$  on account of the smallness of  $\xi_2 - \xi_1$ , or, in other words, the values of  $x_0$  were greater than those of No. 54. After many laborious trials, we at last found that, when we took the origin of the discharge at the beginning of the stimulus, the square root of the product of  $x_1$  and

$x_2$  for any value of  $y$ , agreed very closely with the observed modal latent period. So assuming that the origin of discharge was at the beginning of the stimulus, we calculated as in No. 54.

The following table shows the constants of the curves:—

TABLE II.

Oscillogram No. 37. Left organ (whole) of a fish, the same preparation as No. 35 and No. 36.

Temperature of the organ: 11° C.

No.	M. L. P. obs. in $10^{-4}$ sec.	Mean of $\sqrt{x_1 x_2}$ .	$b^2$ .	$A$ in mm.
1	123.0	122.0	23.7	31.5
2	124.2	124.6	25.8	30.8
3	125.7	126.6	27.1	28.3
4	126.7	127.4	27.4	27.5
5	125.4	126.6	26.1	25.0
6	128.2	128.2	27.0	23.3
7	129.5	129.2	26.3	19.0
8	127.5	128.2	27.8	12.5

The data and the details of the observed and the computed numbers given in the Appendix.

Here the modal latent period is tolerably constant as in No. 54, having a tendency to increase a little with the progress of the experiment. The constant  $b^2$  increases with the decrease of the breadth of the stimulus \*or the height of the discharge.\*

Calculating with these constants the values of  $y$  for every one-thousandth of a second, and plotting the values obtained on the reproduced curves, the agreement of the points is very satisfactory as we may see in the figures (Plate VII.).

\* For the sake of brevity, let us call the duration of the stimulating current the *breadth of stimulus*, the maximum intensity of it the *height of stimulus*, and the maximum electromotive force of the discharge the *height of discharge*.



Oscillogram No. 40 (Plate XVII.), which is the same kind of experiment as No. 37 and in which the breadths of the stimuli are very small, was examined and the constants were calculated as in No. 37 (Plate VIII.).

The following is the table of the constants obtained:—

TABLE III.

Oscillogram No. 40. Left organ, the same preparation as No. 38.

Temperature of the organ: 11.5° C.

No.	M. L. P. obs. in 10 <sup>-4</sup> sec.	Mean of $\sqrt{x_1 x_2}$ .	$b^2$ .	$A$ in mm.
1	121	121.6	20.0	44.5
2	119	119.6	20.8	41.0
3	120	120.4	20.6	40.0
4	120	120.2	20.4	38.0
5	122	122.2	21.8	39.0
6	122	122.8	23.2	33.5
7	122	122.0	22.2	35.6
8	122	123.4	22.9	39.5

The data and the details of the observed and the computed numbers are given in the Appendix.

Here the modal latent period is constant again, and  $b^2$  seems to increase with the decrease of the height of the discharge. The agreement between the calculated and the observed curves is shown in Plate VIII. The values of  $b^2$  in No. 37 and No. 40 are equal to 20 in order of magnitude.

Thus having proved the close agreement of the theoretical formula with the experimental curves, we shall next seek the source of the discrepancy between the constants of No. 54 and those of No. 37 and No. 40. In the foregoing considerations, we did not take into account the effect of the stimulus due to the break of the current

at all. The stimulus used in these experiments consisted of the closing and the opening-stimulus.\* The stimulus on the break of the current must be due to the recovery from some sort of polarisation, though not limited to electrical polarisation, caused by the current. It is not therefore unreasonable to suppose that, the closer the opening-stimulus is to the closing-stimulus, the smaller is the effect of the former. Moreover, when we consider the existence of the refractory period, we may suppose the effect of the opening-stimulus neglected when the breadth of the stimulus is sufficiently small. Comparing Oscillograms No. 37 and No. 40 with No. 54, we find that the breadths of the stimuli in No. 54 are greater than those in No. 37 and in No. 40. Examining many other oscillograms, we see that, where the breadth of the stimulus is great, the unsymmetry of the curve is manifest. Hence we may conclude that the anomaly in No. 54 must be due to the superposition of the effect of the opening-stimulus.

In No. 54 we see that, when we take the magnitude of the latent period into consideration, the actual commencement of the discharge by the opening-stimulus must be a little later than the culmination of the curve. Hence assuming that the discharges caused by the closing-stimuli had their origins at the beginning of the stimuli and the ascending branches of the curves were wholly due to them, we calculated  $b^2$  from their respective co-ordinates  $x$ , and  $y$ . These values of  $b^2$  corresponding to each curve in No. 54 are represented in the following table. Let us denote such  $b^2$  by  $b_0^2$ .

TABLE IV.

No.	$x_0$ in $10^{-4}$ sec.	$b_0^2$	No.	$x_0$ in $10^{-4}$ sec.	$b_0^2$
1	107.5	—	5	109.6	18.8
2	106.4	—	6	108.5	19.8
3	107.8	20.8	7	106.6	24.3
4	107.1	21.1	8	109.9	26.5

\* In this paper, the stimulus on the growth of the stimulating current is called the *closing-stimulus*, and the stimulus on the decay of the current is called the *opening-stimulus*, whether the current is derived directly from the battery or is induced by an induction coil.

Here we see that the values of  $b_0^2$  thus obtained agree in order of magnitude with those of No. 37 and No. 40. To prove that our consideration was correct, we took Curve No. 7 in No. 54, and using the new constants we calculated the values of  $\gamma$  for every 1/1000 sec. Plotting the calculated values on the experimental curve, we see that they fall so very closely on the ascending branch, that even the disagreement previously observed at the beginning of the curve disappears; while the descending branches separate from each other widely. The experimental and the calculated curves are shown in Plate IX. Calculating the differences of the ordinates of points on the descending branches of the two curves for every 4/10000 sec., we have drawn a residual curve which would no doubt be caused by the opening-stimulus only. The residual curve thus found is plotted on the same Plate. Having assumed the origin of the residual curve to be at the instant of breaking of the stimulating current and having found the value corresponding to  $x_0$  by the formula  $x_0 = \sqrt{x_1 x_2}$ , we calculated the value of  $b^2$  corresponding to the new curve, and we found that it was equal in order of magnitude to that of the main curve. The constants thus found for the residual curve were  $A=10.0$ ,  $b^2=17.2$  and  $x_0=100.8$ . Calculating the values of  $\gamma$  for every 1/1000 sec. by using these constants, and plotting them on the residual curve, we see that the agreement is rather wonderful. The value of  $x_0$  of this curve is a little smaller than that of the main curve, but if we consider that the effective instant of the closing-stimulus is a little later than the beginning of the stimulus, we have reason to suppose that the modal latent periods are equal.

Tables V. and VI. show the constants obtained on Oscillograms No. 62 and No. 63, where broad stimuli are used. Oscillograms No. 62, No. 63 and No. 64 (Plate XVI.) form a set of experiments for finding the relation between the intensity of the stimulus and the magnitude of the discharge. The breadth of the stimulus is greatest in No. 62, medium in No. 63 and smallest in No. 64. The temperature of the organ was 13.5°C.

TABLE V.

No. 62.

No.	$x_0$ in $10^{-4}$ sec.	M. L. P. in $10^{-4}$ sec.	$b^2$ .	$b_0^2$ .	$A$ in mm.
1	46.5	82.0	2.69	12.8	33.7
2	45.0	83.5	3.76	11.9	26.6
3	55.3	83.5	5.10	11.0	19.7
4	90.5	90.5	5.96	11.3	13.7
5	80.5	88.0	9.48	10.7	8.7
6	64.5	84.1	5.05	12.4	4.6
7	—	—	—	—	2.3

TABLE VI.

No. 63.

No.	$x_0$ in $10^{-4}$ sec.	M. L. P. in $10^{-4}$ sec.	$b^2$ .	$b_0^2$ .	$A$ in mm.
1	45.8	84.1	3.28	14.5	25.3
2	44.1	74.2	3.35	14.0	19.3
3	54.5	84.0	4.96	14.0	14.3
4	44.1	83.5	2.84	13.8	10.4
5	53.8	86.0	4.47	13.8	6.4
6	53.0	83.7	4.93	14.7	3.4
7	89.7	86.5	12.4	14.7	1.5
8	—	—	—	—	—
9	38.8	83.0	2.08	14.1	24.4

In these tables the numbers in the columns denoted by  $b_0^2$  are the values of  $b^2$  calculated on the assumption that the origin of the discharge is at the beginning of the stimulus. Here again the values of  $b^2$  seem to vary with the decrease of the height of the stimulus. But the variation of  $b^2$  in No. 54, No. 62 and No. 63 should be apparent, and it shows that the effect of the opening-

stimulus is small when the closing-stimulus is very great or when the opening-stimulus is very small. The increase of  $b^2$  in No. 37 and No. 40 with the decrease of the breadth of the stimulus would show that the narrower the stimulus the smaller the effect of the opening-stimulus.

The last curve in Plate VIII. shows that the formula may be applied to the discharge caused by an *indirect* stimulus, if a small part of the organ is taken. The figure represents a curve reproduced from Oscillogram No. C. 3. which is not shown in this paper. The constants obtained by the ordinary way are :—

No. C. 3.

$$A = 55.4 \text{ mm.},$$

$$x_0 = 57.6 \times 10^{-4} \text{ sec.},$$

$$b^2 = 5.83,$$

$$\text{M. L. P.} = 162.2 \times 10^{-4} \text{ sec.}$$

The temperature of the organ was  $10.5^\circ \text{C}$ . The stimulus was indirect and descending. From the order of magnitude of the constants, we may suppose that the discharge is not simple. It seems to the author that the opening-stimulus had some effect on the response curve.

From the above discussion we find that :—

i.) When the discharge is simple, the time-curve of the electromotive force of it may be represented by the formula  $y = Ae^{-b^2 \log^2 \frac{x}{x_0}}$ , where the origin of the discharge is at the stimulus.

ii.) The departure from the above law, as in No. 54, may be considered to be apparent, the superposition of the discharge by the opening-stimulus changing the values of the constants.

iii.) The modal latent period of a simple discharge remains constant in spite of the change of the magnitude of the stimulus.

iv.) The value of  $b^2$  seems to vary a little with the height of the discharge, but the relation is not clear on account of the overlapping of the errors of the same order of magnitude.

v.) It is very doubtful whether the so-called latent period has a definite meaning. It should be a function of the sensitivity of the instrument by which it is determined.

## V. Relation between the Form of Stimulus and the Discharge Caused by It.

The relation between the form of the electric stimulus and the excitation in a nerve caused by it, has been investigated by many physiologists. Some give a formula representing the relation which contains a function of an unknown form. König's formula is such an example and is expressed by

$$E = \int_0^t F(t) \frac{di}{dt} dt,$$

where  $E$  denotes the excitation evoked, and  $i$  the instantaneous value of the stimulating current at a time  $t$  which is measured from the commencement of the stimulating current. According to him  $F(t)$  is a function of an unknown form that acts as a decrement factor and that has a finite value only when  $t$  is very small.

In 1892 Hoorweg,\* in his experiments on the stimulation of a condenser discharge, found a relation connecting the potential difference, by which the condenser was charged, the resistance of the conductor in the circuit, and the capacity of the condenser that caused minimal shock in a nerve. He deduced from it a general expression representing the relation between the electric stimulus and the excitation caused by it. His formula is expressed by

$$E = a \int_0^t i e^{-\beta t} dt, \dots \dots \dots (7)$$

where  $a$  and  $\beta$  are constants. According to his opinion the elementary excitation evoked in a nerve at an instant is proportional to the strength of the current  $i$  at that instant, in opposition to the prevailing opinion in which it depended on the rate of change of the current  $i$ .  $e. \frac{di}{dt}$ ; and as a decrement factor he introduced  $e^{-\beta t}$ . Although many authors opposed his formula, it is the only one that is expressed by a definite function. He afterwards tried to deduce

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\* Plüger Archiv, Bd. 52, S. 87, 1892.

his formula from the hypothesis of Nernst, but his solution of the differential equation does not satisfy the initial condition of uniform concentration. The main defects of his formula are: (1) the definition, explaining how the excitation in a nerve is measured, is very obscure; (2) since his formula is deduced from the experimental data at a point of minimal excitation, it is not possible to extend it into the region of finite excitation.

In 1910 Hill,\* following Nernst's hypothesis and introducing the assumption of Lapicque, found excitation formulae in several cases of electric stimuli. Since his consideration is based on the theory of "all or none" first proposed by Gotch, the formulae have a somewhat different meaning from that of Hoorweg. They represent the progression of a local change which on attaining a definite value causes an actual excitation. At any rate, in the case of a constant current, his formula contains the exponential function as the term that varies with the duration of stimulating current. According to the "all or none" theory the magnitude of the response depends on the number of elementary portions that receive a stimulus greater than the threshold value to evoke the response. The number may depend on the distribution of the current in a tissue or on the variety of the elementary portions whose minimal stimuli are different from one another. In the former case, the relation between the electric stimulus and its response reduces to a mere physical problem, and as in the latter case to that of some kind of probability.

Since it was considered that the discharge of an electric organ is the best means for the investigation of such problems, many experiments in these subjects were made. Let us here explain the superiority of the discharge as a means for the investigation of the general properties of excitation in tissues. The means ordinarily used are muscular contraction and negative variation in a nerve or in a muscle. In the former case very troublesome factors of elasticity and viscosity (if the latter term may be allowed) in a muscle complicate the phenomena. On the contrary, the negative variation is an ideal means for the purpose, but to obtain its record we are obliged

\* The Journal of Physiology, Vol. 40, p. 101, 1910.

at present to use such an instrument as the capillary electrometer or the string galvanometer. As we remarked at the beginning of this paper, such an instrument does not give a true picture of the electromotive force as in this case, unless the change of the electromotive force is very slow as in a cardiogram. Some people try to correct the curve obtained on these instruments by finding the inclination of the tangent to the curve from point to point. But since a small error in the measurement of the inclination may cause a considerably great error in the correction, especially when the inclination approaches  $\frac{\pi}{2}$ , it is dangerous to rely on the result obtained by analysing the curve thus corrected, even if it be allowed that the principle of the correction is right. On the contrary, the electromotive force of the discharge of an electric organ is very large and therefore in this case we may employ such an ingenious instrument as the oscillograph, in which, if used with proper care, correction is unnecessary. Moreover the stimulus must be very strong for exciting the organ so that even a subminimal stimulus may be recorded by the same instrument. It must, however, be admitted that the record due to the abrupt change of current is not so correct as that of the discharge. The only difficulty met with was our local trouble in obtaining fish.

Returning to the problem: we made many experiments regarding the magnitude of the electric stimulus and the same of the corresponding discharge. The experiments were made in the main with direct stimulation, and its form was that described in § III. As it was more convenient to make the picture of the stimulus on the oscillogram on the same side of the zero line as that of the discharge, the direction of the stimulating current was always homodrome. By changing the strength of the current of the primary of the induction coil, or by shifting the position of the circuit-breaker with regard to that of the connection-changer on the stimulation-apparatus, stimuli having different strengths and equal durations, or stimuli having different durations and equal strengths, were given to the organ and the resulting discharges were investigated.



Assuming that the opening-stimulus, when very near to the closing-one, has not an appreciable effect on the discharge curve, its influence was not considered in the first plan of the experiment. But in examining the discharge curve very minutely, as in the preceding section, we found that it may be influenced more or less by the opening-stimulus. If that be the case, in the experiment for the relation between the duration of the current and the magnitude of the corresponding discharge, the maximum electromotive force of a discharge may, for two reasons, diminish with the decrease of the duration on account of the opening-stimulus: (1) since the opening-stimulation would be due to the recovery from some kind of polarisation, the magnitude of its effect may be due to the duration of the current that flowed before; and (2) when a stimulus occurs immediately after another it has a smaller effect, being influenced by the preceding one—a phenomenon to be discussed later. Though I believe, after the result of the analysis of No. 37 and of No. 40 in the preceding section, that the decrease of the maximum electromotive force is due mainly to the decrease of the duration of the current of the closing-stimulus, it is very difficult to know how much the opening-stimulus affects the discharge-height. Therefore without making any assumption, we shall now regard the set of our stimuli to be a single stimulus as a whole and deal with its relation to the corresponding response. In the preceding section we see that a discharge curve has three parameters to characterise its form, *i. e.*  $A$ ,  $b^2$  and  $x_0$ . Since, as we see, the changes of  $b^2$  and  $x_0$  with respect to the stimulus are not conspicuous, we shall use  $A$  as the measure of the excitation. The area of the curve, which, if we assume the theory of “all or none,” would correspond to the number of the electric plates discharged, may be found by integrating the formula of the discharge curve *i. e.*

$$\text{Area} = \int_0^{\infty} A e^{-b \log^2 \frac{x}{x_0}} dx = \frac{\sqrt{\pi}}{b} A x_0 e^{\frac{1}{4b^2}} \dots \dots \dots (8)$$

Indeed it was tried to use the area as the measure of the excitation in the reduction of some of our experiments, but it did not give a result much differing from that of  $A$  in general. Therefore leaving

this problem to more precise investigations, we shall now confine ourselves to the discussion of the relation of  $A$  to the stimulus.

Tables in regard to many experiments for the stimuli with equal breadths and different heights are given next, and graphs representing the relation between the height of the stimulus and the height of the discharge are drawn in Plate X. Fig. 1, 2, 3. Here we may remark that a small error must be taken into account for the height of the stimulus measured on the oscillogram, because even our oscillograph does not follow such an abrupt increase of current as that observed in our stimulating current.

TABLE VII.

Oscillograms No. 35 and No. 36 (Plate XIV.).

Temperature of the organ:  $11.0^{\circ}\text{C}$ .

Resistance of the organ: 130 ohms.

No.	Height of Stim. in mm.			Height of discharge in mm.		
	No. 35.	No. 36.	Mean.	No. 35.	No. 36.	Mean.
1	34.7	35.4	35.1	17.0	17.3	17.2
2	41.2	41.7	41.5	25.0	24.0	24.5
3	47.0	47.2	47.1	31.0	30.1	30.6
4	52.3	53.3	52.8	37.5	37.0	37.3
5	58.0	58.7	58.4	40.8	40.3	40.6
6	62.0	63.3	62.7	43.3	44.5	43.9
7	68.5	69.0	68.8	48.0	48.0	48.0

TABLE VIII.

Oscillogram No. 38 (Plate XV.).

Temperature of the organ:  $11.5^{\circ}\text{C}$ .

No.	Height of Stim. in mm.	Height of dis- charge in mm.	No.	Height of Stim. in mm.	Height of dis- charge in mm.
1	26.8	11.0	4	45.7	41.5
2	33.2	20.8	5	51.5	47.0
3	39.2	32.8	6	64.2	58.5

TABLE IX.

Oscillograms No. 42 and No. 43.

Temperature of the organ:  $11.5^{\circ}\text{C}$ .

No.	Height of stimulus. in mm.			Height of discharge in mm.		
	No. 42.	No. 43.	Mean.	No. 42.	No. 43.	Mean.
1	12.5	13.5	13.0	2.5	2.5	2.5
2	19.5	19.5	19.5	3.5	3.5	3.5
3	26.0	26.5	26.3	10.0	8.5	9.3
4	32.0	33.0	32.5	20.5	17.5	19.0
5	39.0	38.5	38.8	29.5	24.5	27.0
6	45.0	46.0	45.5	38.0	33.5	35.8
7	51.0	52.0	51.5	43.7	40.5	42.1
8	58.0	58.5	58.3	48.0	48.8	48.4
9	63.5	63.5	63.5	51.0	55.0	53.0

TABLE X.

Oscillogram No. 54 (Plate XIII.).

Temperature of the organ:  $8.5^{\circ}$ — $7.2^{\circ}\text{C}$ .

Resistance of the organ: 240 ohms.

No.	Height of Stim. in mm.	Height of discharge in mm.
1	19.0	1.5
2	25.5	5.0
3	31.5	10.0
4	38.0	17.3
5	44.3	26.5
6	50.2	35.8
7	56.8	45.5
8	64.5	56.0

TABLE XI.

Oscillograms No. 55 and No. 56 (Plate XV.).

Temperature of the organ: 10.4° C.

Resistance of the organ: 240 ohms.

No.	Height of Stim. in mm.			Height of discharge in mm.		
	No. 55.	No. 56.	Mean.	No. 55.	No. 56.	Mean.
1	70.0	67.0	68.5	48.5	46.0	47.3
2	63.0	63.0	63.0	39.0	40.0	39.5
3	58.0	56.8	57.4	32.5	32.5	32.5
4	51.5	50.5	51.0	22.5	23.7	23.1
5	45.0	44.5	44.8	15.5	17.3	16.4
6	38.5	37.5	38.0	9.5	10.5	10.0
7	—	32.0	—	—	6.2	—
8	25.0	25.5	25.3	0.8	2.5	1.8
9	68.0	66.0	67.0	45.5	45.7	45.6

TABLE XII.

Oscillograms No. 62, No. 63 and No. 64 (Plate XVI.).

Temperature of the organ: 13.5° C.

Resistance of the organ: 190 ohms.

No.	No. 62.		No. 63.		No. 64.	
	Stim. in mm.	Discharge in mm.	Stim. in mm.	Discharge in mm.	Stim. in mm.	Discharge in mm.
1	63.7	33.7	62.3	25.3	63.3	24.0
2	57.7	26.6	56.5	19.3	57.4	17.4
3	50.8	19.7	50.3	14.3	50.6	12.5
4	44.3	13.7	44.4	10.4	45.6	9.2
5	38.7	8.7	38.5	6.4	38.2	5.5
6	31.7	4.6	31.4	3.4	31.8	3.2
7	25.6	2.3	25.4	1.5	25.5	1.4
8	—	—	62.6	24.4	63.5	22.5

Here in general we used very broad stimuli to avoid the effect due to the difference of their breadths. In No. 35 and No. 36 the preparation of the organ was the same, and in the former case the stimuli were given in the increasing order of height and in the latter in the decreasing order so as to eliminate the progressive change in the organ. The two curves (Plate X., Fig. 1) representing them run very closely to each other, the latter being somewhat lower than the former. This shows that the progressive change, which might be due to the decay of the organ or slow cooling of the same, was very small during the experiments. The mean curve of No. 35 and No. 36 is shown in Plate X., Fig. 2. This may be considered to be the true course of the curve when there exists no progressive change. Oscillograms No. 42 and No. 43 are of a set of experiments of the same kind as the above. The preparation was the same as that of No. 40 and No. 41, which were a set of experiments for the investigation of the relation between the breadth of a stimulus and the corresponding height of the discharge, and which will be discussed later. The stimuli are in the increasing order of height in No. 42, and in the reverse order in No. 43. Here we see that the curves (Plate X.) representing them do not coincide; showing the existence of a progressive change, so that the discharges became relatively smaller with the course of the experiments. Assuming that the progressive change was uniform, the mean curve may represent the true course of the curve. Oscillograms No. 55 and No. 56 (Plate X.) are of experiments of the same kind. Here we have a check on each film, which shows that the effect of the progressive change was very small. In the figure, the check points are marked with  $\odot$ . Oscillograms No. 38 and No. 54 have no check for the progressive change (Plate X., Fig. 3). Oscillograms No. 62, No. 63 and No. 64 (Plate X., Fig. 3) relate to a series of experiments in which stimuli given were in the decreasing order with respect to their heights, having a check on each film. The breadths of the stimuli are different in the three films, broadest in No. 62, and narrowest in No. 64.

Tracing the general course of these several curves we see that they converge to the origin of the co-ordinates. The height of the

discharge increases very slowly from zero. Then comes a steep increase of the height of the discharge, where the curve has an inflexion point and then becomes concave with respect to the axis of the abscissa. By direct stimulations we could not arrive at the upper part of the curve on account of the very large stimulation current required. Nevertheless, it is very probable that the curve approaches an asymptotic value of the ordinate which may easily be attained in the case of indirect stimulation. Thus the curve forms an S-shape analogous to that, found by Waller, relating to the negative variation in the nerve. Here we may remark that it is very doubtful whether the words *minimal* and *subminimal stimulus* as customarily used have any definite meaning. By the word *minimal stimulus* or *liminal current*, is certainly meant the stimulus by which the response becomes just sensitive to a certain instrument. Of course, if we acknowledge the truth of the "all or none" theory, there certainly exist the minimal and the maximal stimulus in the literal meaning. But that which is ordinarily obtained by experiment would not be the true *minimal* stimulus, *i. e.* not for the response of *a unit* element. Now, if we take the height of the discharge as a measure of the excitation, the proportionality between the current and the response in Hoorweg's formula does not hold good for the finite range of the discharge. It is not clear whether the inclination of the tangent to the curve at the origin is equal to zero or not. If the latter is the case, the proportionality in the very small portion at the beginning of the curve, in agreement with the formula of Hoorweg, is nothing but the general property of any curve, that a small portion of it may be regarded as a straight line. Many trials were made to formulate the relation extending to the finite region of the stimulus, but the results were not satisfactory. As we remarked before, if we may assume that the magnitude of a discharge is due to the number of elements evoked by the stimulus, and that the number depends on the variety of the elementary portions whose minimal stimuli are different from one another, then the curve representing the relation between the strength of the stimulus and the area of the discharge should be the integral curve of the

category of a probability curve. Since I cannot ascertain the proper method of analysing the curve from the standpoint of this hypothesis, I am not able to give the rigorous proof for it. But it is obvious that, qualitatively, the course of the experimental curve agrees with this view.\* I am now working on this principle; I only refer to it here, and shall leave the problem for a later report.

Next we shall treat the relation between the breadth of the stimulus and the height of the discharge. With reference to the problem, the film first examined was that of No. 37, an analysis of which was made in the preceding section. The organ-preparation was the same as that of No. 35 and No. 36, in which we knew that the effect of the progressive change was very small. Assuming Hoorweg's decrement factor to be true and not taking into consideration the effect of the opening-stimulus separately, which Hoorweg, in his condenser investigation, also ignored, we examined whether his factor held good in our case. According to his formula the excitation  $E$  caused by our stimulus is equal to

$$\int_0^t aie^{-\lambda t}e^{-\beta t}dt = \frac{ai}{\lambda + \beta} \{1 - e^{-(\lambda + \beta)t}\},$$

where  $i$  represents the maximum current in the secondary of the induction coil,  $\lambda$  is a constant determined by the self-induction and the resistance of the secondary circuit, and where  $e^{-\beta t}$  means Hoorweg's decrement factor. Of course, in our stimulus there is a steep rising portion of the current before its maximum, which is not considered here. But in treating of the variation only, the part common to all stimuli has no influence on the result, if we take the origin of the time at a proper instant. Hence measuring the time from a suitable origin the formula becomes

$$E = a \frac{i}{\lambda + \beta} \{1 - e^{-(\lambda + \beta)(t - t_0)}\},$$

which, for the sake of brevity, we write

\* A trial examination was made on the curves of Oscillogram No. 54. The curve representing the relation between the height of the stimulus and the area of the resulting discharge curve was graphically differentiated by drawing the tangents to the curve, point by point, and by finding the corresponding rates of increase of the ordinates with respect to the abscissa. Then it was found that the differential curve might be expressed by a formula analogous to that of the discharge curve given in the previous section.

$$E = B \{1 - e^{-\gamma(t-t_0)}\}. \dots\dots\dots(9)$$

After laborious trials  $B$ ,  $\gamma$  and  $t_0$  were found from the plotted curve of No. 37 (Plate XI., Fig. 1). As the breadth of the stimulus, we took the interval between its beginning and the instant of abrupt decrease of the current. Though our oscillograph would not give a true picture for such a quick change of current as our stimulus, it does not influence the value of the stimulation-breadth taken as above. The result of the experiment and the corresponding calculated values are given in the next table, and represented graphically in Plate XI., Fig. 1.

TABLE XIII.

Oscillogram No. 37.

Temperature of the organ: 11.0°C.

Resistance of the organ: 130 ohms.

Formula used in calculation:  $y = 34.0 \times (1 - 10^{-0.0862(t-5.1)})$

No.	M. L. P. in $10^{-4}$ sec.	Breadth of Stim. in $10^{-4}$ sec.	Height of discharge obs. in mm.	Height of discharge calc. in mm.	Diff.
1	124.2	18.2	31.5	31.5	0.0
2	122.7	16.1	30.8	30.2	+ 0.6
3	125.4	14.2	28.3	28.4	- 0.1
4	126.7	13.0	27.5	26.9	+ 0.6
5	127.1	11.8	25.0	25.0	0.0
6	126.5	11.3	23.3	24.1	- 0.8
7	127.9	9.1	19.0	18.8	+ 0.2
8	127.7	7.7	12.5	13.9	- 1.4

As we see in the table and in the figure, the agreement of the observed with the calculated values is very satisfactory.

Oscillogram No. 58 (Plate XVII.) is an example in which the breadths of the stimuli were too large, so that the heights of the discharges showed a nearly constant value. In this oscillogram, it may be seen that the height of the discharge never becomes smaller with the increasing stimulation-breadth, even



when the beginning of the opening-discharge appears later than the summit of the discharge curve. This shows that the variation of the discharge-height with respect to the stimulation-breadth is not the effect of the opening-stimulus, but is due to the variation of the duration of the closing-stimulation current.

Next we examined Oscillograms No. 40 and No. 41 (Plate XVII.): These are a series of experiments on the same preparation as No. 42 and No. 43. In No. 40 the stimuli were given in the decreasing order of breadth and in No. 41 in the reverse order. For the breadth of the stimulus in this case, we took the breadth on the bottom of the graph, for the measurement as in No. 37 was very difficult to ascertain accurately. In this case, it was found that the heights of the stimuli differed a little from one another. Since the small differences in the heights of the stimuli exceedingly influence the heights of the discharges, the latter were reduced into those corresponding to their respective stimuli having an equal height 44.5 mm. The proportional constants in these calculations were derived from the mean curve of No. 42 and No. 43. Here the stimulation-apparatus did not work well on account of the contraction of the wooden part, by which the two rails were bent a little. So the breadth of the stimuli did not decrease regularly. Moreover, on plotting the points on a section paper, it became clear that some progressive change had occurred during the experiments, so that the points on the figure arranged themselves in a very complex manner. Therefore we assumed a fatigue factor  $e^{-na}$ , where  $n$  represents the number of the order of a discharge, the first discharge being regarded as zero. The numbers observed and calculated are given in the next table and the graph is represented in Plate XI., Fig. 2.

TABLE XIV.

Oscillograms No. 40 and No. 41.

Temperature of the organ: 11.5 °C.

Formula used in calculation:

$$\text{No. 40, } y = 48.0 \times 10^{-0.00691n} \{1 - 10^{-0.0429(l-0)}\},$$

$$\text{No. 41, } y = 46.9 \times 10^{-0.00601n} \{1 - 10^{-0.0429(l-0)}\}.$$

## No. 40.

No.	M. L. P. in $10^{-4}$ sec.	Breadth of Stim. in $10^{-4}$ sec.	Height of discharge obs. in mm.	Height of discharge calc. in mm.	Diff.
0	121	28.0	44.5	45.0	-0.5
1	119	18.4	39.9	39.7	+0.2
2	120	19.8	39.1	40.1	-1.0
3	120	17.4	37.6	37.8	-0.2
4	122	19.2	38.2	38.6	-0.4
5	122	15.0	33.5	34.6	-1.1
6	122	14.3	35.0	33.3	+1.7
7	122	11.6	29.7	29.7	0.0

## No. 41.

No.	M. L. P. in $10^{-4}$ sec.	Breadth of Stim. in $10^{-4}$ sec.	Height of discharge obs. in mm.	Height of discharge calc. in mm.	Diff.
0	118	13.9	35.9	35.0	+0.9
1	119	13.1	33.7	33.6	+0.1
2	120	15.7	36.0	35.9	+0.1
3	119	17.0	36.7	36.6	+0.1
4	120	18.8	36.4	37.4	-1.0
5	125	17.5	38.6	36.0	+2.6
6	118	23.0	38.6	38.7	-0.1
7	120	22.4	38.4	37.9	+0.5

The details of the data are given in the Appendix.

Next, Oscillograms No. 59, No. 60 and No. 61 are of a series of experiments of the same kind made on the same organ, in which the heights of the stimuli are different in the three films. In each series, the experiments were in decreasing order with respect to the breadths of the stimuli. On each film, a check was taken at the end of the experiments, and it was found that there were

progressive changes. So, using  $e^{-na}$  as a fatigue factor, in which  $a$ 's were calculated from the checks, and finding the other constants by laborious trials, the corresponding values of  $A$  were calculated. These results are given in the next tables (Plate XI., Fig. 3):—

TABLE XV.

Oscillograms No. 59, No. 60 and No. 61. (Plate XVIII.).

Temperature of the organ: 13.5 °C.

Referring to the accompanying figure,  $AF'$  in No. 59,  $AC'$  in No. 60 and  $AF'$  in No. 61 were taken for the stimulation-breadths.

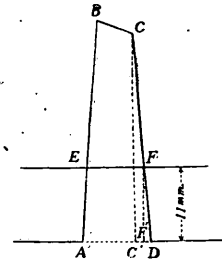


Fig. 6.

Formula used in calculation:

$$\text{in No. 59, } y = 21.3 \times 10^{-0.00373n} \{1 - 10^{-0.0560(t-2)}\},$$

$$\text{in No. 60, } y = 32.1 \times 10^{-0.0121n} \{1 - 10^{-0.0935(t-2)}\},$$

$$\text{in No. 61, } y = 38.8 \times 10^{-0.01319n} \{1 - 10^{-0.0623(t-2)}\}.$$

No. 59.

No.	M. L. P. in $10^{-4}$ sec.	Breadth of Stim. in $10^{-4}$ sec.	Height of discharge obs. in mm.	Height of discharge calc. in mm.	Diff.
0	90.0	27.3	20.5	20.5	0.0
1	91.7	19.4	19.5	18.9	+0.6
2	89.5	19.8	19.3	18.8	+0.5
3	91.2	19.3	18.1	18.5	-0.4
4	88.6	16.7	17.4	17.5	-0.1
5	88.1	14.9	17.0	16.5	+0.5
6	83.0	8.1	11.0	11.0	0.0
7	86.9	27.4	19.3	19.3	0.0

## No. 60.

No.	M. L. P. in $10^{-4}$ sec.	Breadth of Stim. in $10^{-4}$ sec.	Height of discharge obs. in mm.	Height of discharge calc. in mm.	Diff.
0	84.5	26.4	32.0	32.0	0.0
1	84.0	22.0	30.8	31.0	-0.2
2	82.9	19.0	29.7	30.0	-0.3
3	80.9	17.3	29.0	29.0	0.0
4	—	—	—	—	—
5	87.4	17.1	27.5	27.4	+0.1
6	78.0	14.8	26.0	26.2	-0.2
7	83.5	27.1	26.3	26.4	-0.1

## No. 61.

No.	M. L. P. in $10^{-4}$ sec.	Breadth of Stim. in $10^{-4}$ sec.	Height of discharge obs. in mm.	Height of discharge calc. in mm.	Diff.
0	83.1	29.4	38.0	38.0	0.0
1	79.5	21.2	36.9	36.1	+0.8
2	84.0	19.9	36.0	35.4	+0.6
3	81.5	18.1	34.6	34.3	+0.3
4	—	—	—	—	—
5	83.0	16.4	32.0	32.8	-0.8
6	85.0	13.8	30.4	30.4	0.0
7	79.2	25.8	36.0	35.6	+0.4

In the calculation, we assumed that the values of  $t_0$  are equal in the three cases. But as we see in the tables, the measurements of the breadths were not ascertained in the same way. Hence the values of  $t_0$  must differ in these three cases. Indeed we attempted to find the more correct values of  $B$ ,  $r$ ,  $t$ , and  $\alpha$  by applying the method of least squares to the residuals of the approximate values obtained by the trial method, and to compare the values of these constants

for various heights of the stimuli. But the coefficients of the normal equations became very different in order of magnitude, and perhaps for this reason, no significant values could be obtained. Hence we abandoned these calculations, and we shall leave the problem without any presumption upon the variations of the constants with regard to the height of the stimulus, until we shall have had an opportunity of obtaining more trustworthy results free from progressive changes.

In short, except No. 37, the results of the experiments were not perfect; but taking into consideration the difficulty of the measurement of the small duration of the stimulus, and the influence of the troublesome factor of the progressive change, these results rather prove the correctness of the decrement factor of Hoorweg.

Next we shall give an experiment of indirect stimulation, in which momentary stimuli of different heights were given. The relation between the height of the stimulus and the height of the corresponding discharge is given in the next table and in Plate X., Fig. 3.

TABLE XVI.

Oscillogram No. 49 (Plate XXVIII.).

Temperature of the organ: 8.2°C.

Additional resistance inserted in series: 200 ohms.

The stimuli given: Descending.

(The stimulus of Curve No. 1 was ascending by accident.)

No.	L. P. in $10^{-4}$ sec.	M. L. P. in $10^{-4}$ sec.	Height of Stim. in mm.	Height of discharge in mm.
1	142	173	4.0	9.0
2	} Too low for measurement.		6.0	0.5
3			7.0	1.0
4	162	185	9.0	2.3
5	162	188	11.0	8.3
6	159	185	12.5	15.0
7	156	189	13.0	17.0
8	156	189	14.0	18.3

The course of the curve representing the relation between the height of the stimulus and the height of the discharge resembles that of the direct stimulus. Here we may remark that the modal latent periods have very consistent values except in Curves No. 1, No. 2 and No. 3, in which, since the curves are very low, the measurements were very inaccurate.

In closing this section, the results of our experiments are summarised as follows:—

i.) The height of the discharge  $A$  slowly increases with the increasing intensity of the stimulation current from zero.

ii.) Then it increases very steeply, where it passes an inflexion point; and then approaches an asymptotic value.

iii.) With respect to the duration of the stimulating current, Hoorweg's decrement factor seems to be correct, but it is not clear whether the constant  $\beta$  in it does really depend on the strength of the stimulating current or not.

## VI. Discharges by Two Successive Stimuli.

Already in one of the preliminary experiments, we discovered that when two successive stimuli not too far apart in time from each other are given to the nerve, the discharge by the second stimulus shows greater delay compared with the normal. A pair of momentary stimuli which were caused by a contrivance on the shaft of the registering drum were sent periodically, *i.e.* once in each revolution, to the nerve. At first only the preceding one of the pair, then the succeeding, and finally the pair together were sent through the nerve. These were photographed on the same film. The second stimulus was so given that, if the two discharges appeared at the normal delay, the second discharge should appear in a position superposed on the descending branch of the first. But from the film we saw, on the contrary, that the second discharge occurred after the first had been over.

For the precise investigation of the phenomenon, we constructed a special contrivance in our stimulation-apparatus, by means of which two consecutive momentary stimuli separated by a desired

interval of time may be given. The details of the mechanism were explained in § III. and illustrated in Plate V., Fig. 4. As for the strength of the stimuli, care was always taken to obtain the maximal discharges. The sense of the stimulating current was mainly descending, the distance of the two electrodes being about 3 mm. This comes from the consideration that, in a descending stimulus, the excitation in the nerve evoked by the closing-stimulus, occurs at the cathode which is nearer to the organ than the anode and therefore the excitation is evoked in an undisturbed part in the nerve and propagates to the organ without any obstacle, while the excitation caused by the opening-stimulus occurs at the anode and it is arrested by the cathodic block from propagating to the organ. On the contrary, if we use an ascending stimulus, not only it has frequently been observed that the excitation due to the closing stimulus propagates to the organ, though greatly enfeebled in passing the anode; but the excitation by the opening-stimulus must be affected by the stimulating current which flowed before that instant. In short the result in the case of the descending current should be more simple.

Returning to the problem, the influence of the first stimulus to the second consists of two parts: namely (1) the effect on the modal latent period of the second discharge, (2) the effect on the height of the second discharge. The former effect almost disappears when the second stimulus departs from its predecessor about one-hundredth of a second, while the latter remains a little later. These may be the effects of some kind of fatigue that recovers itself in a small fraction of a second. We shall call the phenomena the *temporary fatigue*.

Oscillograms No. 74 and No. 75 (Plate XIX.) are a series of experiments for such phenomena. Two stimuli, separated by various intervals of time, were given at a point on a nerve, and the influences of the first stimulus on the second discharge were measured accurately. The following table shows the numbers deduced from these oscillograms:—

TABLE XVII.

Oscillograms No. 74 and No. 75.

Temperature of the organ: 14.5°C.

No. 74.

No.	Interval between two Stim. in 10 <sup>-1</sup> sec.	Ratio of 2nd M. L. P. to 1st.	Height of 1st discharge in mm.	Height of 2nd discharge in mm.	Ratio of 2nd height to 1st.
1	120.5	1.000	53.0	39.0	0.736
2	110.4	1.015	51.5	41.5	0.806
3	99.5	1.030	48.5	45.5	0.989
4	90.2	1.023	48.0	49.0	1.020
5	79.9	1.063	47.0	48.5	1.030
6	72.5	1.100	46.0	46.7	1.015
7	63.2	1.120	46.0	45.5	0.990
8	55.8	1.175	45.0	42.0	0.935

No. 75.

No.	Interval between two Stim. in 10 <sup>-1</sup> sec.	Ratio of 2nd M. L. P. to 1st.	Height of 1st discharge in mm.	Height of 2nd discharge in mm.	Ratio of 2nd height to 1st.
9	43.9	1.301	45.0	24.7	0.550
10	33.6	1.411	43.3	4.5	0.104
11	34.7	1.411	41.5	4.5	0.109
12	27.4	—	42.5	?	—
13	14.9	—	41.8	?	—
14	9.1	—	41.2	—	—
15	3.0	—	42.5	—	—
16	0.0	—	41.5	—	—

N. B.:—In this paper, for the sake of brevity, the word *latent period* or *modal latent period* is used to represent the interval between the stimulus and the commencement (observed) of the discharge or between the stimulus and the instant of the maximum electromotive force respectively, whether the stimulus is direct or indirect, *i. e.* the values of them are inclusive of the time for the propagation of the nerve-excitation.



Full details of the data and the computed numbers are given in the Appendix.

The numbers in the table are plotted in Plate XII., Fig. 1. Referring to Curve 1, the abscissa represents the interval between two momentary stimuli in  $10^{-4}$  sec., and the ordinate represents the ratio of the two modal latent periods subtracted by one, *i. e.* the excess of the delay of the second discharge with respect to the first. Here we see that the ordinate decreases exponentially with the increase of the abscissa. We assume the curve to be expressed by exponential function  $y = Me^{-\lambda t}$ , and determine the value of  $M$  and of  $\lambda$ , in which we may find  $M = 1.74$ ,  $\lambda = 409$ . Calculating the values of  $y$  from the formula, and plotting these numbers on the experimental curve, we see that they agree very well within the limits of the experimental errors.

The other curve in the figure is that of the heights of the second discharges. To eliminate the individual errors of each experiment, the ratio of the height of the second discharge to that of the first is taken as ordinate. Referring to the curve we see that, even in  $1/100$  sec. from the first stimulus, the height of the second discharge is smaller than the normal. Proceeding towards the origin from this point it increases even greater than the normal, and then decreases quickly to an almost imperceptible height where the second stimulus enters the so-called refractory period. The refractory period in this experiment is measured to be  $32.0 \times 10^{-4}$  sec. In this experiment it is not certain whether in the refractory period the response does not occur absolutely, or whether some small responses continue to exist up to the origin of the coordinates. Indeed there exist many small discharges that cannot be distinguished from the discharge of the higher order of the preceding experiment. To clear this point further investigations will be necessary.

The increase of the height of the second discharge towards the origin seems to be paradoxical at first sight. But on examining the film, we can find that when the second discharge is great, the second stimulus is at an instant corresponding to a point on the ascending branch of the first discharge, so that the second discharge

overlaps the *secondary discharge* of the first stimulus. Hence we see that the apparent increase of the height may be due to the summation effect of the secondary discharge. To make this fact clearer, we may refer to the following table:—

TABLE XVIII.

Oscillogram No. 74.

From the first set of curves the interval between the first stimulus and the summit of the secondary discharge may be found to be  $193.2 \times 10^{-4}$  sec.

No.	Ratio of two heights.	Interval between first stimulus and summit of second discharge, in $10^{-4}$ sec.
1	0.736	226
2	0.806	214
3	0.989	208
4	1.020	201
5	<u>1.030</u>	<u>193</u>
6	1.015	191
7	0.990	183
8	0.935	185

In this table we see that the maximum ratio between the height of the second discharge and that of the first, occurs when the summit of it just coincides in position with that of the secondary discharge.

Oscillogram No. 65 (Plate XX.) is another series of experiments of the same kind. The corresponding numbers are tabulated in the next table and plotted in Plate XII., Fig. 2.

TABLE XIX.

Oscillogram No. 65.

Temperature of the organ: 13.5 °C.

No.	Interval between two Stim. in $10^{-4}$ sec.	Ratio of 2nd M. L. P. to 1st.	Height of 1st discharge. in mm.	Height of 2nd discharge. in mm.	Ratio of 2nd height to 1st.
1	133	1.790	24.5	9.0	0.367
2	—	—	22.6	17.8	0.788
3	110	0.970	21.5	19.0	0.885
4	97	1.025	21.0	19.0	0.925
5	88	1.130	20.3	18.0	0.900
6	—	—	20.0	15.0	0.750
7	69	1.230	19.5	16.0	0.820
8	60	1.300	19.9	11.0	0.553
9	49	1.480	18.8	3.9	0.207

The general course of the curve is similar to the preceding. On the right hand side, the arrangement of the points is not so regular as in No. 74—No. 75, especially the position of the last point in the figure deviates exceedingly from the others. But on examining the oscillogram, we see that the second discharge occurs after the secondary discharge of the first. Thus the second stimulus was influenced by the first discharge which acted as a preceding stimulus. Here we may find that  $M = 3.00$ ,  $\lambda = 376$  and the refractory period  $= 46.0 \times 10^{-4}$  sec. The values of  $y$  calculated from these constants are plotted on the figure. The interval of time, in which the value of  $y$  becomes one half, may be called the period of recovery of the temporary fatigue. In the preceding two experiments the period of recovery is equal to  $17.0 \times 10^{-4}$  sec. in the former and  $18.5 \times 10^{-4}$  sec. in the latter, the temperature being 14.5 °C. and 13.5 °C. respectively.

With respect to the height of the second discharge, we may remark that it decreases with the decreasing interval between the two stimuli. But, if we take the ratio of the height of the second

discharge to that of the first, we can see that it has a maximum value as in No. 74—No. 75. In this oscillogram the interval between the first stimulus and the summit of the secondary discharge may be measured from the first set of the discharges, and as this value we obtain  $223 \times 10^{-4}$  sec. Here we see again that the maximum of the ratio of the height of the second discharge to that of the first occurs when its summit just coincides with that of the secondary discharge. The relation is shown in the following table:—

TABLE XX.

Oscillogram No. 65.

Interval between the first stimulus and the summit of the secondary discharge:  $223 \times 10^{-4}$  sec.

No.	Ratio of two heights.	Interval between first stimulus and summit of second discharge, in $10^{-4}$ sec.
1	0.367	348
2	0.788	226
3	0.885	229
4	0.925	222
5	0.900	225
6	0.750	222
7	0.820	217
8	0.553	215
9	0.207	220

Now since it was not plain to me whether the seat of the phenomena is in the nerve or in the organ, an experiment was made to determine the question. By giving a pair of stimuli with a fixed interval between them, and by inserting proper resistance in the discharge circuit, we carried out a series of experiments with equal stimuli and different heights of discharges. Changing the magnitude of discharges by varying the resistance, the delay of the second discharge with respect to the first was measured. The following table shows the results.

TABLE XXI.

Oscillogram No. 84 (Plate XX.).

No.	Resistance inserted in ohm.	Interval between two Stim. in $10^{-4}$ sec.	Ratio of two M. L. P.
I. {	0	30.0	1.14
	200	30.6	1.16
	300	30.2	1.17
II. {	0	21.8	1.27
	200	24.6	1.24
	300	24.9	1.25
III. {	0	15.4	1.46
	200	14.6	1.67
	300	23.2	1.36

In each set of the experiments, the ratios of the two modal latent periods were found to be nearly equal. The disagreement in the third set must have occurred in virtue of the differences of the interval between the stimuli as shown in the table. So we have to conclude that the temporary fatigue, so far as it is defined by the prolongation of the modal latent period, is not the result of the discharge.

In December 1909, Lucas\* reported the same phenomenon in a somewhat different way. According to his paper, experiments were made on the negative variation in the sartorius muscle of the frog. The instrument used by him was a capillary electrometer and the curve obtained was corrected by the method of Burch. As the time of reference he always took the latent period *i. e.* the interval between the stimulus and the commencement of its response. Even when he measured the interval between the stimulus and the summit of the response curve in his later paper, he subtracted a constant value in order to obtain the latent period. For my part, to measure on a curve the commencement of the response

\* The Journal of Physiology, Vol. 39, p. 331.

is not only very inaccurate, but it is doubtful whether the so-called latent period measured on a graph has any definite meaning. For example the theoretical curve discussed in § IV., which has its commencement at the stimulus, may give some finite value for the so-called latent period, if it is measured as is usually done on the experimental curve. The response in a muscle or in a nerve may differ in its property from the discharge of an electric organ, though I am inclined to think that the form of the negative variation depends on a similar cause to ours. As a matter of fact, the modal latent period so-called by us, gives more consistent values among themselves than latent periods either in our case, as always observed before, or in the case of the negative variation in a muscle, as was shown in the paper by Lucas. Whatever it may be, he said in his paper: "It is found that the second electric response begins at a constant time after the beginning of the first, whether the stimulus by which it is provoked occurs immediately after the end of the refractory period or considerably later. If the second stimulus occurs immediately after the end of the refractory period the latency of the resulting electric response may be many times the normal. As the second stimulus is made later the latency of the resulting response becomes proportionately less. Only when the second stimulus occurs so late that it would otherwise have a latency less than the normal does the second response depart from its fixed time of occurrence." He also shows that the nearer the second stimulus approaches the end of the refractory period, the smaller the resulting response becomes.

After this paper appeared, Gotch\* reported his analysis of a similar phenomenon on the negative variation in the sciatic nerve of the frog, and concluded that: "I. The electrical response of the excised sciatic nerve of the frog to a second stimulus may show a great increase in delay as compared with the response to the preceding stimulus. II. This increase of delay is augmented in proportion as the second stimulus approaches the end of the period of complete inexcitability (refractory period) which is developed

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\* The Journal of Physiology, Vol. 40, p. 250, 1910.

during the first response, but becomes imperceptible if the second stimulus occurs at a sufficient interval after the first." He reported the effect of temperature upon the phenomenon and also gave the discussion about the locality of this peculiarity. More recently Lucas \*reported his researches on the locality of the same phenomenon by his ingenious method, and concluded that it is an after effect of the disturbance propagating through a nerve or a muscle. In this paper he plotted many curves which represent the relation between the interval of the two stimuli and the same from the first stimulus to the commencement of the second response, and not only did he accept the behaviour of the delay of the second response agreeing with that of Gotch, so that he modified his first statement, but he found that the interval between the first stimulus and the second response becomes greater in some cases, when the second stimulus is brought very near to the refractory period. Quoting his words: "In the more complex cases with which I have dealt, namely the excitation of nerve and the recording of the consequent electric response in the innervated muscle, it appears that a new phenomenon must be recognised; the electric response becomes still later when the second stimulus is brought very near to the first. This suggests an important difference associated with the passage of the propagated disturbance through successive tissues having unlike time relations." Now we shall reproduce here two figures of such kind given in his paper.

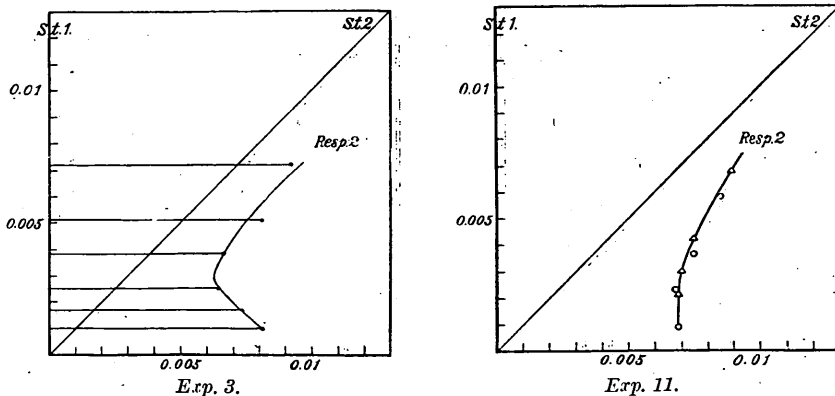


Fig. 7.

\* The Journal of Physiology, Vol. 41, p. 68, 1910.

Here the ordinate represents the interval between the two stimuli, and the abscissa the same between the first stimulus and the commencement of the second response. The length of the abscissa measured from the straight line inclined at  $45^\circ$  to the axis, represents the interval between the second stimulus and the commencement of the second response. The curves have a minimum with respect to the abscissa.

Now from the numbers given in the tables in Lucas's paper, which are reproduced below, I constructed two curves representing the relation between the interval from the second stimulus to the commencement of the second response and the interval between the two stimuli (Plate XII.). Then it was found that the newly reduced curves were simply exponential in agreement with our results. Of course, in this case, the ordinate shows the absolute value of the so-called latent period instead of the ratio of the two modal latent periods. But since the values were obtained by subtracting a constant value which may be considered to be the interval between the beginning of the response and its summit, the nature of the curve must be the same as if it were drawn in our way.

The tables found in the paper of Lucas are given below.

TABLE XXII.

Exp. 3 and Exp. 11 by Lucas. The Journal of Physiology, Vol. 41, p. 337 and p. 399.

Exp. 3. Sciatic-gastrocnemius preparation. Frog. Temp.  $17.5^\circ\text{C}$ .

Obs.	Time first stimulus to second stimulus.	Time first stimulus to second response.	Time second stimulus to second response.
A.	.0010 sec.	.0081 sec.	.0071 sec.
B.	.0017	.0074	.0057
C.	.0025	.0064	.0039
D.	.0038	.0066	.0028
E.	.0051	.0081	.0030
F.	.0072	.0092	.0020



The times of the beginning of the second responses are estimated on the assumption that the response begins always at a fixed time (0.0031) before it attains its maximum P. D.

Ex. 11. Gastrocnimius-sciatic preparation. Frog. Temp. 17.5 °C.

B. Time of commencement of second response calculated from time of its maximum P.D. (as the interval between the commencement of the curve and its summit, .0022 sec. is taken)

I. With second stimulus at same point as first.

Obs.	Time first stimulus to second stimulus.	Time first stimulus to beginning of second response.	Time second stimulus to beginning of second response.
A.	.0021 sec.	.0069 sec.	.0048 sec.
B.	.0030	.0070	.0040
C.	.0042	.0074	.0032
D.	.0067	.0093	.0026

II. With second stimulus 11 mm. nearer to muscle than first.

Obs.	Time first stimulus to second stimulus.	Time first stimulus to beginning of second response.	Time second stimulus to beginning of second response.
E.	.0015 sec.	.0069 sec.	.0054 sec.
F.	.0029	.0067	.0040
G.	.0042	.0074	.0032
H.	.0064	.0084	.0020

Correcting by time of conduction .0006.

Obs.	Time first stimulus to second stimulus.	Time first stimulus to beginning of second response.	Time second stimulus to beginning of second response.
E.	.0009 sec.	.0069 sec.	(.0060) sec.
F.	.0023	.0067	(.0045)
G.	.0036	.0074	(.0038)
H.	.0058	.0084	(.0026)

The numbers enclosed in the brackets are calculated by the present author.

From these data we calculated  $M$  and  $\lambda$ . The values of the normal latent period could not be discovered in his paper and we therefore found them as follows:—

Taking three ordinates  $y_1$ ,  $y_2$  and  $y_3$  on the figure (Plate XII.) with equal intervals in succession, we put

$$\begin{aligned}y_1 &= l + b, \\y_2 &= l + mb, \\y_3 &= l + m^2b,\end{aligned}$$

where  $l$  is the normal latent period and  $m$  a constant to be determined by the period of recovery. So in Exp. 3 we may find  $l=0.0019_s$  and  $m=0.40_s$ , the interval between the successive ordinates being  $0.0024_s$  sec. From these values we obtain  $M=0.0098$ ,  $\lambda=646$ . The numbers calculated from the data are plotted on the curve by the mark  $\cdot$  (Plate XII., Fig. 3 and Fig. 4). In experiment 11 we get  $l=0.0016_s$  and  $m=0.48$ , the interval between the successive ordinates being  $0.0024$  sec. and using these constants, we obtain  $M=0.0058$ ,  $\lambda=300$ . Taking the value of  $0.0031$  in exp. 3 and of  $0.0022$  in Exp. 11 as the interval between the summit and the commencement of the response, we may calculate the values of  $M$  and of  $\lambda$  in the same units as in our case. These constants are given below:—

Exp. 3.	$M = 2.25,$
	$\lambda = 646,$
Exp. 11.	$M = 2.66,$
	$\lambda = 300.$

In Plate XII. we see that the agreement between the experimental and the calculated curves is very good. From these results, we may say that our exponential law for the recovery of the temporary fatigue holds good in the results obtained by Lucas on the gastrocnemius-sciatic preparation of the frog.

Now denoting the interval between the stimuli by  $t$ , and the normal latent period by  $l$ , the interval between the first stimulus

and the commencement of the second response is given by

$$t + lMe^{-\lambda t} + \frac{l^2}{2}$$

This has a minimum with respect to  $t$  at

$$t_m = \frac{1}{\lambda} \log_e \lambda Ml.$$

The values of  $t_m$  at this minimum are evaluated as follows:—

Experiment by Lucas:

No. 3. 0.0029 sec.

No. 11. 0.0020

Experiment by the author:

No. 74—No. 75. 0.0049<sub>5</sub>

No. 65. 0.0069<sub>5</sub>

Thus we see that the existence of the minimum is a consequence of the exponential property of the recovery, and therefore little weight should be placed on this minimum. Since, as we see, the minimum occurs very near to the end of the refractory period, it would sometimes not be discovered in an experimental result. It is very probable then that the so-called irresponsible period reported by Lucas in his first paper was an apparent phenomenon appearing for the reason that the observations were restricted in the vicinity of this minimum, where the variation becomes zero.

The corresponding phenomenon to the supernormal increase of the height of the second discharge was observed by Samojloff\* on the electric response of a muscle indirectly stimulated. Recently Adrian and Lucas† interpreted the phenomenon by the summation of two successive disturbances propagating through a nerve-ending. They considered that a propagated disturbance whose propagation is stopped at the nerve-ending by its decrement, if alone, is successfully transmitted through the block, when the like disturbance passed before. In our case, it seems rather probable that the supernormal magnitude of the second discharge is not the

\* Arch. f. (Anat. u.) Physiol., Suppl., 1908.

† The Journal Physiology, Vol. 44, p. 68, 1912.

direct effect of the disturbance evoked by the first stimulus, but it is the effect of the first discharge acting as a stimulus. In this view we must assume that the maximal disturbance in a nerve-trunk cannot cause the maximal discharge of the organ. The possibility of the fact may be considered in several ways. For instance, some elementary portions of an end-organ, say electric plates or muscle fibres, cannot be excited by the disturbance through a nerve, on account of the enormous decrement of the nerve-endings of those individuals, or else the disturbances in some nerve-fibres are too small to be transmitted to the end-organ for the same cause. In our experiment, when we take a part of an organ with a nerve-trunk attached, there certainly exist electric plates which do not receive the supply of the nerve-fibres from the trunk through which stimuli are given. Such plates cannot be excited by stimulating the nerve-trunk, but can be excited by the discharges of the electric plates belonging to that nerve-trunk. Then, when the discharge of such secondary nature is superposed on the discharge evoked by the second stimulus, the result must be the increase of the magnitude of the second discharge. If we may allow that the electric response of muscle may act as a stimulus, then the same interpretation may be applied in the case of muscle.

Our experiments hitherto described were made in such cases as the discharge evoked by the first stimulus had an asymptotic values in practice. Without presuming the law of "all or none" it is very important to examine the case when the discharge is so-called submaximal. We have three series of such experiments that were obtained accidentally. These are Oscillograms No. 50, No. 47 and No. 51.

In Oscillogram No. 50 (Plate XXI.), when two stimuli separated by an interval  $77.5 \times 10^{-4}$  sec., the response by the second cannot be observed. When they approach  $66.3 \times 10^{-4}$  sec., we see a low discharge scarcely distinguishable from the secondary. Then they approach nearer *i. e.* to  $55.0 \times 10^{-4}$  sec. and the second discharge appears on the descending branch of the first discharge. When they approach each other still nearer *i. e.*  $29.9 \times 10^{-4}$  sec., the second

comes on the ascending branch of the first. At last when the interval between the two becomes  $16.4 \times 10^{-4}$  sec., the discharges coalesce into a single one. Here since the position of the second summit would be displaced on account of its lying on the inclined branch of the first, we cannot measure the modal latent period accurately and therefore we also measured the interval between the stimulus and the commencement of the curve. The next table shows the numbers obtained on the oscillogram.

TABLE XXIII.

Oscillogram No. 50.

Temperature of the organ:  $8.2^{\circ}\text{C}$ .

No.	Interval between Stim. in $10^{-4}$ sec.	L. P. of 1st discharge in mm.	L. P. of 2nd discharge in mm.	Ratio of two L. P.
1	77.5	69.0	No response.	
2	66.3	70.0	71.5	1.02
3	55.0	71.0	70.5	0.99
4	44.2	71.0	65.0	0.92
5	29.9	70.0	65.0	0.93
6	16.4	65.0	Coalesce into a single curve.	
7	5.8	—		

No.	M. L. P. of 1st discharge in mm.	M. L. P. of 2nd discharge in mm.	Ratio of two M. L. P.
1	81.0	—	—
2	82.0	—	—
3	82.0	78.0	0.95
4	79.0	75.5	0.96
5	—	—	—
6	—	—	—
7	—	—	—

As a mere experimental result, it seems that before the so-called refractory period there exists a period in which the response *may occur*. The modal latent period or the latent period of the second discharge seems to decrease even to a smaller value than that of the first for some value of the interval between the two stimuli. Indeed the shortening of the latent period from the normal is equal to 6 mm. in the maximum length on the oscillogram. But in other experiments we know that, while the modal latent period gives very consistent values, the latent periods differ widely according to the height of the curve. It will not therefore be useless to calculate roughly the value of the displacement of the summit of the second discharge curve on account of its lying on the descending branch of the first. Suppose a discharge curve  $y = Ae^{-b^2 \log^2 \frac{x}{x_0}}$  superposed on an inclined straight line

$$y = (p-x)\tan\varphi.$$

Then the resultant curve is expressed by

$$y = (p-x)\tan\varphi + Ae^{-b^2 \log^2 \frac{x}{x_0}}.$$

Differentiating the expression with respect to  $x$ , and equating the result to zero, we have

$$\tan\varphi + 2Ab^2 \log \frac{x}{x_0} \cdot \frac{1}{x} e^{-b^2 \log^2 \frac{x}{x_0}} = 0.$$

A value of  $x$  satisfying the equation must be that for the maximum value of  $y$ .

Let the displacement of the summit be represented by  $\delta$ , which, in the first approximation, may be considered very small when compared with  $x_0$ . Putting  $x = x_0 - \delta$  in the above expression and neglecting the higher orders of  $\frac{\delta}{x_0}$  than the first, we have

$$\delta = \frac{x_0^2 \tan\varphi}{2Ab^2} \dots\dots\dots (10)$$

Taking the third experiment in the oscillogram No. 50, we may put very roughly

$$x_0 = 29 \text{ mm.},$$

$$b^2 = 10.7,$$

$$A = 4 \text{ mm.}$$

and

$$\tan \varphi = \frac{1.5}{10} \text{ at most,}$$

where the value of  $x_0$  and of  $b^2$  are determined from the first experiment. From these data we may get 1.4 mm. as the value of  $\delta$ . Referring to the table, the difference of the two apparent modal latent periods in that experiment is equal to 4.0 mm. So giving full allowance to the effect of  $\delta$ , the difference needs not be smaller than 2.6 mm. The value cannot be considered to be an error of measurement.

Oscillogram No. 47 (Plate XXI.) is another example of the same kind, and the numbers obtained on this film are tabulated in the next table.

TABLE XXIV.

Oscillogram No. 47.

Temperature of the organ: 8.5 °C.

No.	Interval of two Stim. in $10^{-4}$ sec.	M. L. P. of 1st discharge in $10^{-4}$ sec.	M. L. P. of 2nd discharge in $10^{-4}$ sec.	Height of 1st discharge in mm.
1	79.1	174	233	31.0
2	69.4	171	235	31.2
3	58.1	172	248	30.8
4	45.0	175	—	29.0
5	37.6	174	—	29.5
6	28.9	173	188 ?	27.0
7	8.3	176	—	33.2
8	0.0	—	—	33.2

Here the modal latent period of the first discharge is tolerably constant. In the first three, the modal latent period of the second discharge increases a little with the decrease of the interval

between the two stimuli. When the interval becomes  $45.0 \times 10^{-4}$  sec. the second discharge seems to disappear. When it is diminished to  $37.6 \times 10^{-4}$  sec. the second discharge becomes perceptible on the descending branch of the first discharge, but the modal latent period cannot be measured, although it is certain that it is made smaller. When the interval becomes  $28.9 \times 10^{-4}$  sec. the modal latent period of the superposed second discharge may roughly be determined to be  $190 \times 10^{-4}$  sec. Finally, the interval becoming  $8.3 \times 10^{-4}$  sec., the two discharges coalesce into a single one. From this onwards, the height of the first discharge becomes greater than those of the preceding, thus showing the summation of the second discharge.

Oscillogram No. 51 (Plate XXI.) is a series of the experiments of the same type. Here we may find as the ratios of the second modal latent period to the first the values of 1.00, 0.98, 0.95 and 0.93 for 4th, 5th, 6th and 7th curve respectively.

Let us now discuss the results with reference to the theory of "all or none." As the stimulus is submaximal, a part of the nerve fibres is excited by the first stimulus and the other part is not excited, but only receiving the subminimal stimulus. Let us call the former the first part and the latter the second part. When the second stimulus, which is also subminimal to the second part, is in the refractory period and on the outside of the *summation interval*\* so-called by Lucas, which must be assumed to be smaller than the refractory period, the second response cannot occur. But when the second stimulus enters into the summation interval it excites the second part in concordance with the first stimulus, while it does not excite the first part. Hence the experimental results can be explained. For the correctness of this interpretation, it must be allowed that the refractory period in this case is greater than  $77.5 \times 10^{-4}$  sec. and the summation interval is greater than  $66.3 \times 10^{-4}$  sec. The latter number is very great compared with the same measured by Lucas on the motor nerve to the gastrocnemius muscle of the frog which was equal to  $5 \times 10^{-4}$  sec. Whether the modal latent

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\* The Journal of Physiology, Vol. 39, p. 461.



period; measured from the second stimulus, belonging to two subminimal stimuli may take a value smaller than the normal or not is a question which appeared on Oscillograms No. 50 and 51, and worth while investigating hereafter.

Next we shall give an example of summation of two discharges in response to a closing and an opening-stimulus (Plate XXII., Oscillogram No. 70). Stimuli of the same type as those used in the direct stimulation were given to a nerve-trunk with a proper shunt, by which the stimulation current through the nerve remains submaximal and yet the current flowing through the oscillograph was sufficiently large to trace its form. The experiment was made for another purpose *i. e.* for the comparison of the intensity of the stimulating current and the magnitude of the resulting discharge. At first the stimulating current was increased step by step for five successive experiments. Then the duration of the stimulation current was changed, and commencing with the smaller current, it was increased step by step in the five succeeding experiments in an exactly similar way. In the latter half, the forms of stimuli were not good, and we have not therefore used them in the analysis. The following table shows the numbers measured on the oscillogram.

TABLE XXV.

Oscillogram No. 70.

No.	Height of Stim. in mm.	L. P. of 1st discharge in $10^{-4}$ sec.	L. P. of 2nd discharge in $10^{-4}$ sec.	Ratio.	M. L. P. of 1st discharge in $10^{-4}$ sec.	M. L. P. of 2nd discharge in $10^{-4}$ sec.	Ratio.
1	11.0	96.5	101.8	1.055	113.9	119.0	1.045
2	23.3	88.0	101.5	1.150	112.0	115.2	1.030
3	35.5	81.3	103.0	1.270	109.8	111.5	1.015
4	47.0	79.0	100.2	1.270	108.5	108.5	1.000
5	Out of film.	79.5	102.5	1.290	109.0	109.0	1.000

Since the duration of the stimulating current did not exceed  $21 \times 10^{-4}$  sec., it must be allowed that the opening-stimulus had occurred before the end of the refractory period due to the

closing-stimulus, and therefore the response to the opening-stimulus must be due to the nerve-fibres that were not excited by the closing-stimulus. Referring to Oscillogram No. 70, we see that when the intensity of the stimulating current is very weak, the discharge by the opening stimulus is higher than that by closing. When the intensity of the stimulating current is made larger, the discharge due to the closing-stimulus becomes larger while the same due to the opening-stimulus becomes first larger and then smaller. Putting the base for the explanation of this phenomenon upon the theory of "all or none," when the stimulating current is sufficiently strong so that all the plates are discharged by the set of two stimuli, the area of the superposed resultant curve, which corresponds to the number of the plates discharged,\* must be constant. In this view we measured the values proportional to the areas of the curves on the oscillogram by weighing the pictures cut out from bromide paper, and then multiplying each of them by its respective interval corresponding to one-millimetre of the abscissa, we got the values proportional to the number of the plates discharged. These values are given in the next table.

TABLE XXVI.

No	Weight of picture cut out, in mgr.	1 mm. of abscissa corresponds to, in $10^{-4}$ sec.	Product.
1	32.4	3.45	112
2	41.3	3.39	140
3	44.1	3.38	149
4	45.4	3.29	149
5	45.8	3.31	151

\* When we take a small part of the organ as in our experiments, the resistances of all individual columns may be considered to be equal to one another. Let the resistance of one column be denoted by  $r$ , the current flowing through each of the columns at an instant by  $i_1, i_2, i_3, \dots, i_n$  respectively, the resistance of the external conductor by  $R$ , and the current flowing through it by  $I$ . Let the electromotive force of an elementary discharge of a plate be  $e$ , and the number of

The above table shows that the area of the discharge curve becomes constant when the stimulus is made strong enough. While the experimental result gives support for the theory of "all or none," it seems to reveal two new facts: (1) the opening-stimulus can evoke its response, which could not be caused on closing the same stimulating current, or, otherwise, the opening-stimulus may be summed up into something that occurred at the anode on closing the current: (2) the delay of the second discharge is longer than the normal. The cause of the second phenomenon is not clear. It may be seen that the modal latent period measured on the oscillogram seems rather to have normal value *i.e.* not prolonged. But since the second summit lies upon the inclined branch of the first discharge curve, the displacement of the apparent summit towards the stimulus is not small. On calculating the displacement by the formula  $\delta = \frac{x_0^2 \tan \phi}{2At^2}$ , it may be found that the displacement is not smaller than 2 mm. on the film. Therefore the prolongation of the modal latent period of the discharge by opening-stimulus seems certainly to exist.

Before closing this section we have two more oscillograms of allied problem to be explained. Since I thought that the rhythmic response of a nerve or of a muscle to high frequency stimuli, might be the effect of the refractory period, a few experiments were made regarding that subject. Oscillograms No. 67 and No. 85 (Plate XXIII.) represent the results obtained. In No. 67 the make and break of the high frequency of the primary circuit of an induction coil was made by a contrivance like the commutator

the plates discharging per second at an instant in each column be  $n_1, n_2, n_3, \dots, n_m$  respectively. Then by Kirchhoff's law, we have

$$cn_1e = RI + ri_1,$$

$$cn_2e = RI + ri_2,$$

$$cn_3e = RI + ri_3,$$

$$cn_me = RI + ri_m,$$

where  $I = i_1 + i_2 + i_3 + \dots + i_m$ , and  $c$  is a proportional constant.

By adding each side of the equations, we have

$$ce \sum_{1}^m n_m = (R + r) I,$$

and therefore

$$\int_{t=0}^{t=\infty} \sum_{1}^m n_m dt = \frac{R+r}{ce} \int_{t=0}^{t=\infty} I dt.$$

*i.e.* the total number of the plates discharged is proportional to the area of the curve.

of a dynamo, and the nerve-trunk attached to the organ was stimulated by the induced current. For this and the other ends, our shutter was so constructed that, when we made proper connections, the stimulating current could flow only when the shutter opened (Plate IV., *c*). The number of the momentary stimuli given amounts to 885 per sec. In this case the stimuli varied a little in their strength, and hence another experiment No. 85 was made in which the induction coil was not used. Here, as stimulus, a current from eight accumulators was interrupted by the same contrivance as No. 67, no induction coil being used. The stimuli were regular, and their number amounted to 1412 per sec. As may be seen in the oscillograms, the discharges were not so regular as to account for one determinate period, being a series of high and low superposed discharges. This might be the case because the stimuli were not maximal, though in the beginning part it seems to be so. From many other experiments it seems to me, that the liminal value of the stimulus for the maximal response in the nerve increases with the temporary fatigue, and by this assumption the irregularity of the discharges may be easily interpreted. Hence assuming that the stimuli were sufficiently strong at the beginning, we may take as the period of response, the interval between the first and the second discharge, and we get as its value  $117 \times 10^{-4}$  sec. in No. 85, the temperature of the organ being  $15^{\circ}\text{C}$ . For the more advanced discussion the more precise analysis should be necessary, and hence we here allude to this as a mere experimental result.

The summary of this section is:—

i.) When two successive stimuli separated by an interval a little greater than the refractory period are given at a point in a nerve of the electric organ, the modal latent period of the second discharge is prolonged with regard to the normal.

ii.) The recovery of this prolongation follows an exponential law with respect to the interval between the two stimuli.

iii.) The prolongation of the modal latent period of the second discharge is accompanied by the variation of the maximum electromotive force of the second discharge.

iv.) The electromotive force increases probably from zero when the second stimulus separates more and more from the end of the refractory period and when at a certain interval between the two stimuli it becomes even greater than the normal and then decreases again.

v.) The abnormal increase of the electromotive force may be interpreted as the summation effect of the second discharge and the secondary discharge of the first stimulus.

vi.) The second discharge caused by two successive submaximal stimuli given at a point in the nerve may be superposed on the first discharge, and the modal latent period of the second discharge seems to be even smaller than the normal at a certain interval between the two stimuli.

vii.) The discharge by an opening-stimulus given in the nerve may be superposed on that by closing-stimulus.

viii.) Phenomena vi. and vii. may give support for the theory of "all or none," but for this we must assume new subordinate properties of the nerve which is worth while investigating hereafter.

## VII. Fatigue phenomenon.

Fatigue phenomenon was investigated in two different ways.

(1) The registering drum was rotated very slowly by connecting the shaft of it with the clockwork of a kymograph, and successive momentary stimuli about 25 in a second were given to the nerve and the deviation of the strip of the oscillograph was photographed on a film. The periphery speed of the drum being about 1 cm. per sec., a discharge curve reduces to a straight line and the locus of its summit forms the so-called fatigue curve.

(2) The drum was rotated rapidly and two stimuli in each revolution were given to the nerve so that they might be photographed at two fixed places on the film. The stimulus consists of the induced current of an induction coil, which was caused by the make and break of the primary current flowing for a very short interval during which a peg on the shaft makes instantaneous contact with a stationary conductor (Plate IV., Fig. 1). The direc-

tion of the stimulating current was in general descending on closing the primary circuit. But in one case the ascending and the descending stimuli were alternately given to the nerve by a proper contrivance on the shaft of the registering drum (Plate IV., Fig. 3). In another case the stimuli were given directly to the organ. Here, as remarked at the outset of this paper, the induction coil must be excluded from the circuit during the discharge of the organ. This was accomplished by a proper contrivance belonging to the shaft of the registering drum (Plate IV., Fig. 3)

Beginning with the former case, the fatigue curve resembles very closely that of muscle. Oscillograms No. 1, No. 2 (Plate XXIV.), No. 3, No. 4 and No. 5 (Plate XXV.) show such curves. In No. 1, which shows the typical form of the fatigue curve, the electromotive force increases a little during a few discharges at the outset of the fatigue, and passing over a maximum, it decreases almost exponentially. The rate of decrease increases after passing the maximum, then decreases gradually, again increases a little and then decreases again. Thus repeating the same type of variation, in such a way that the locus of the top of the discharge curve forms a mild wave form, the nerve or the organ is tired out. Two low loci on the bottom of the oscillogram are those of the secondary and of the tertiary discharge. The marks of regular intervals on the bottom are those of a second. Here we may remark that the tops of the discharge curves form a smooth curve at the beginning of the fatigue, but when in deep fatigue their heights become very irregular (Oscillogram No. 2).

Oscillograms No. 3, No. 4 and No. 5 (Plate XXV.) form a series of experiments. Oscillogram No. 4 was taken at an interval of one hour after No. 3, and Oscillogram No. 5 at 40 min. after No. 4. The number of stimuli is about 25 per sec. Here we see, that the fatigue may be partially recovered by a repose of the stimulation so that there must be two kinds of fatigue, namely that which can be recovered and that which cannot be recovered. I am of opinion that, that part of the fatigue which can be recovered is the same as the temporary fatigue of the nerve discussed in the

previous section, and that which cannot be recovered is due to the alteration in the organ or in the nerve. Of course, the interval between two consecutive stimuli is very large compared with the period of recovery discussed in the former section, but there is still a fatigue, for not only small residuals of the fatigue may accumulate in such cases, but also a part of the nerve trunk may still be in deep fatigue on account of the stimulation by the discharge of the higher order, when a succeeding stimulus is given. As we remarked in the preceding section, when the fatigue advances, the liminal value for the maximal stimulus increases in nerve, so that the stimulus of the given magnitude, which is sufficiently maximal at the outset of the fatigue, becomes submaximal, and a little variation in its magnitude may cause the discharge of a different magnitude. May not this be the cause of the irregularity of the discharge in the tired state?

In regard to the increase of the contraction at the outset of fatigue in muscle, Fröhlich interprets the phenomenon as the apparent effect of the prolongation of the wave length of the contraction propagating through a muscle. He thinks that, the fact that the same phenomenon could not be observed in negative variation, gives support to his theory. But since a similar interpretation fails to apply in our case, it is probably incorrect. In view of our experimental results, it seems to me that the phenomenon is analogous to the abnormal increase of the electromotive force of the second discharge discussed in the preceding section. In that section, we explained the phenomenon as the effect of the superposition of the second discharge on the secondary discharge. Here, of course, the principal discharge evoked by the succeeding stimulus is very far from the secondary discharge, but it may be superposed with a discharge of one of the higher orders. To express my idea clearly, suppose a discharge followed by a series of higher orders, to be evoked by one of the stimuli separated by a fixed interval of time as in the experiment. When the fatigue advances, the modal latent period is prolonged gradually, as may be observed in the fatigue investigations of the other form, and the secondary, the tertiary discharge *et seq.* delay in propor-

tion to the intervals between these and the stimulus, so that the discharges of the higher orders chase the succeeding stimulus. At the instant at which one of the discharges of the higher orders just comes at the principal discharge due to the succeeding stimulus, the height of the discharge must be increased. By this consideration not only the first maximum of the fatigue curve may be explained, but its wave form may be interpreted also. In the case of muscle, ability for response of the higher order may be observed in the so-called tetanic state which, in my opinion, is caused by a series of responses successively evoked by the preceding electric response acting as a stimulus on the tissue in a highly excitable state. This view may be supported by the fact that the decrease of the proper period with the rise of temperatures follows the same law as that of the increase of the speed of propagation through the nerve.\* Then may not the same interpretation be applied to the case of muscle? Concerning this point further investigation should be necessary. Here we describe this as an interpretation which seems to be true in so far as our experiment goes.

Next we shall explain another form of fatigue oscillogram. Oscillograms No. 6, No. 78 and No. 78' (Plate XXVI.) show such experiments. From these oscillograms we see that, when the fatigue advances, the modal latent period is prolonged and the height of the discharge curve decreases. Oscillogram No. 7 (Plate XXVII.) is an example in which the discharges appeared in a very complex manner. Perhaps the discharge was affected by the tertiary discharge belonging to the preceding set, but no satisfactory explanation has been obtained. The following explanation looks somewhat probable. The discharges due to the opening-stimuli at first appeared, then those due to the closing-stimuli were superposed on their ascending branches, and finally in the advanced stage of the fatigue, only those by the closing-stimuli remained. For the sake of correctness of this consideration, it must be assumed that the modal latent period belonging to the open-

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\* { Dittler and Tichomirow. Pflüger Archiv, Bd. 125, S. 117.  
 { Dittler and Oinuma. Pflüger Archiv, Bd. 139, S. 293.



ing-stimulus was greater than the normal. In these experiments the direction of the stimulating current was generally descending on closing the primary circuit, but in the above case the stimulating current was ascending. If the above phenomenon may be explained by Pflüger's contraction law in the muscle-nerve preparation, it must be recognized that the value of the maximal stimulus with respect to the nerve increases with the progression of the fatigue and hence the same stimulating current will be strong at first, then it will become medial and finally weak with respect to the nerve. If the above explanations be correct, here again we have evidence that the value of the maximal stimulus with respect to the nerve increases with the progression of the fatigue.

Oscillogram No. 8 (Plate XXVI.) shows the case in which the stimulating currents are ascending and descending alternately. This oscillogram shows that the fatigue phenomenon is not the consequence of the polarisation at the electrodes. Oscillograms No. 78 and No. 78' (Plate XXVI.) show the fatigue by the descending and by the ascending stimuli respectively.

Oscillogram No. 9 (Plate XXVII.) is an example of the fatigue phenomenon by the direct stimulations. In this case, it is a remarkable fact that, although the modal latent period is prolonged with the progression of the fatigue, the descending branches of the discharge curves coincide with one another into a line. Since the discharges in the two sets of curves have the very same aspect, notwithstanding the stimuli are different in their breadths, the responses must be due to the closing-stimuli only,—the case when the closing-stimuli are strong enough to evoke the maximal discharges. Therefore the oscillogram shows the fatigue phenomenon in the case when the stimuli are direct and simple.

The principal point of this section is that the increase of the magnitude of the response at the outset of the fatigue exists in the case of the electric organ as well as in muscle. Therefore the explanation by Fröhlich in the case of muscle cannot be considered correct.

### VIII. Speed of Propagation of Excitation through the Nerve.

Since the time relation can be measured very accurately by our method, some experiments were made regarding the speed of the propagation through the nerve-trunk.

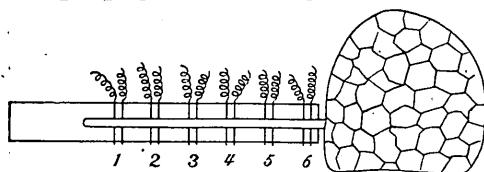


Fig. 8. Nerve-organ preparation with six pairs of the electrodes.

Oscillogram No. C. 5 (Plate XXVIII.) shows an experimental result regarding the uniformity of the speed along the nerve-trunk. On an ebonite plate about 1 cm.

in breadth, six pairs of electrodes were fixed as shown in the accompanying figure. The distance between the electrodes in a pair was 1 mm. and the distances between the corresponding points of such consecutive pairs were 5 mm. A nerve-trunk with a part of an organ was laid on this plate along its length and the momentary stimuli were sent to the points on the nerve in the order of 1, 2, 3, 4, 5, 6 and 2, the last one being for the check. The following numbers were obtained on this oscillogram:—

TABLE XXVII.

Oscillogram No. C. 5.

No additional resistance.

Temperature of the organ : 11.6 °C.

No. of electrodes.	Time stimulus to beginning of discharge in mm.	Number of revolutions of registering drum.	1 mm. corresp. to, in $10^{-4}$ sec.	Time stimulus to beginning of discharge in $10^{-4}$ sec.	5 and 6 of 2nd column interchanged*
1	81.4	13.23	1.515	123.0	
2	66.0	13.04	1.533	101.3	
3	60.9	12.79	1.565	95.5	
4	58.3	13.17	1.520	88.6	
5	50.3	13.27	1.508	76.0	83.0
6	48.7	12.13	1.650	80.4	73.5
2	60.0	11.70	1.710	102.3	

\* In 5 and 6 the electrodes should have been interchanged by accident, therefore for their values we used the numbers in the last column.

The modal latent periods could not be measured, for the summits of the curves were on the outside of the film. Therefore the time between the stimulus and the beginning of the discharge was measured.

In Plate X. a graph representing the time between the stimulus and the beginning of the discharge with regard to the position of the electrodes is drawn. In this figure we see that the check point lies very closely on the curve. This shows that the experiment was not affected by any progressive change. The points 2, 3, 4, 5 and 6 arrange themselves on a straight line, while the point 1 falls on the upward side of the line. This shows that between the points 2 and 6 in the nerve, the speed of propagation was uniform whether the point concerned was near to or far from the stimulated point. As the value of the speed, we obtained 7.31 metres per sec., the temperature of the nerve being 11.6 °C. The discrepancy of the point No. 1 must have its cause in the alteration or decay of the nerve at that portion which occurred near the excised end of the nerve. This becomes very obvious when we examine the oscillogram, for there we see that the discharge curve corresponding to No. 1 is very low compared with the other discharges, while the stimulus is not smaller than the others. The prolongation of the latent period of the discharge evoked by a stimulus given at a point near the excised end of the nerve, may be explained by one of the following assumptions. (1) The speed of propagation in the portion near the excised end of the nerve altered by its injury is smaller than the normal. (2) The local latent period at the nerve-ending or in the organ, *i.e.* the interval between the instant, at which the disturbance arrived at the nerve-ending, and that of the beginning of the discharge is greater when the disturbance in the nerve is smaller. (3) The speed of propagation of the nerve excitations differing in magnitude has different values, the stronger the larger. (4) The local latent period at the point of stimulation is greater when that portion of the nerve is altered. The cases (2) and (3) cannot be considered to be true from the standpoint of

the "all or none" theory. Moreover Oscillogram No. 49 denies these assumptions, for the modal latent periods of the discharges are equal, though the magnitude of the discharges varies very widely. Then the cause of the prolongation must be due either to (1) or to (4). The causes (1) and (4) cannot be separated in our former experiments. I am, however, inclined to believe that the cause would be that of (1).

*N. B.*—Oscillogram No. 49 is an experiment intended to find the relation between the strength of the stimulus and the height of the discharge as shown in § V. The latent periods and the modal latent periods are given again in the following table:—

Table XXVIII.

No.	Height of discharge in mm.	Latent period in $10^{-4}$ sec.	Modal latent period in $10^{-4}$ sec.
1	9.0	142	173
2	0.5	Too low to be measured accurately.	
3	1.0	Too low to be measured accurately.	
4	2.3	162	185
5	8.3	162	188
6	15.0	159	185
7	17.0	156	189
8	18.3	156	189

(The stimulus of No. 1 was ascending by accident.)

Here we see that the latent period decreases with the increase of the height of the discharge and therefore, when our eyes are restricted to L. P., it seems that the speed of the propagation of the excitation increases with the increase of the height of the stimulus. But when our eyes are turned to the modal latent periods, we see that they give tolerably constant value, and show no regular variations with the increasing strengths of the stimuli. This shows that the speed of the propagation through the nerve in the normal state does not depend on the strength of the stimulus or on the magnitude of the excitation. Also this experiment shows that the so-called latent period is not suitable to be used as the time of reference for exact work.

### IX. Miscellaneous problems.

Oscillograms No. 53 and No. 100 (Plate XXIX.) represent photographs of spontaneous discharges of a living fish. At first we tried to open our shutter by the first discharge of the fish and to photograph the motion of the strips of the oscillograph caused by

the succeeding discharges. The shutter could be opened as desired, but the discharge curve could not be obtained. So laying a living fish on a wooden board having a hole of the shape of the organ for an electrode, and applying a pair of electrodes to the dorsal and the ventral side of the organ by my hands, the registering drum was rotated. Judging the proper instant, which could be readily known by the behaviour of the fish before its discharge, the shutter, used as time-shutter, was opened. When the discharges occurred, which were perceived by the shocks felt, the shutter was closed. In the two oscillograms taken under different conditions, we see that a shock always consists of two discharges followed by a very low one, the second discharge being a little smaller than the first. The proper period of the discharges of a living *malapterurus* and its variation by the change of the temperature were investigated by Koike \* with the string galvanometer. In his results a shock consists of many periodic discharges, which Garten and Koike thought to be the effect of rhythmic central excitations. In our experiment, the kind of fish was different from his, and in his experiment the fish was placed in water whereas ours was placed in air. Therefore it is not strange that the results do not agree in the two experiments. But in the face of our experimental results, perhaps the second and the succeeding discharges would be of a secondary nature, for a similar phenomenon *i. e.* two large discharges followed by a very low one was frequently observed in many experiments of the indirect stimulation given to the preparation of the isolated nerve-organ.

We shall next show two experiments regarding the discharge by the stimulating current of long duration in the ascending or in the descending direction. Oscillograms No. 76 and No. 77 (Plate XXX.) are two such experiments. These are the results with different preparations. The original object of these experiments was to test Hoorweg's consideration that the opening stimulus was the effect of the polarisation current flowing through the shunt ordinarily used for the regulation of the stimulation current. The result was of course negative. But on examining the

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\* Zeitschrift für Biologie, Bd. 54, 1910.

oscillograms precisely, we found that the stimulating current of long duration sent through the nerve influences the strength and the modal latent period of the succeeding discharge in a peculiar way. The experiments were performed by closing the stimulation circuit and by shunting it at the proper instant. These operations can be made by our stimulation apparatus by using two connection changers, one of which is a mercury key of earlier design. The current was directly derived from eight storage cells. The numbers obtained from these oscillograms are tabulated in the following table:—

TABLE XXIX.

Oscillograms No. 76 and No. 77.

Stimulus : Indirect.

Temperature of the organ :  $14.5^{\circ}$

No. 76.

No.	Direction of stimulating current.	Duration of current in $10^{-4}$ sec.	Modal latent period in $10^{-4}$ sec.	Height of discharge in mm.
1	Ascending.	169.9	110.7	20.0
2	Ascending.	304.0	110.0	18.5
3	Descending.	300.0	113.5	8.0
4	Descending.	172.0	120.4	2.0

## No. 77.

No.	Direction of stimulating current.	Duration of current in $10^{-4}$ sec.	Modal latent period in $10^{-4}$ sec.	Height of discharge in mm.
1	Descending.	18.7	129.3	Out of
2	Descending.	124.8	133.3	film.
3	Ascending.	166.0	213.9	47.5
4	Ascending.	43.7	148.2	46.5
5	Ascending.	23.0	138.5	53.5
6	Descending.	21.2	130.5	59.0

The modal latent periods of 1 and 2 in No. 77 were found by the formula  $x_0 = \sqrt{x_1 x_2}$ . Since the stimulus was indirect, it must be allowed that the values of the modal latent period thus found may be somewhat larger than the correct values.

In the descending stimulus, the discharge occurs by the closing-stimulus and in the ascending by the opening-stimulus. The positive direction of the ordinate on the oscillograms shows the descending stimulus.

In No. 77, the modal latent period of the third experiment shows extraordinary prolongation. The discharge was caused by an ascending stimulation current of tolerably long duration and the preceding discharge was that due to the descending current. The succeeding discharges were evoked by the stimulus of the same direction and the result was that, the shorter the duration the shorter the modal latent periods, though it is longer than the normal. The prolongation may be interpreted either as the effect of some local change caused by the ascending stimulating current of long duration, of which the longer the duration, the greater is the prolongation; or as the influence of the preceding stimulus which is recovered by repeating the opposite current. The former is more probable if the observation is limited to this film only, but in the discharge evoked by the stimulus of the same direction in Oscillogram No. 76, it cannot be observed that the modal latent period is prolonged. The number of the series of experiments of the above kind is only two, and therefore we cannot give a definite conclusion.

In Oscillogram No. 71 (Plate XXII.), similar prolongations of the modal latent periods may be observed in the experiments of the ascending-stimulus which were made after a series of experiments of the descending-stimulus. But there is no proof that the prolongation was the influence of the previous descending stimulus.

TABLE XXX.

Oscillogram No. 71.

No.	Height of stimulus in mm.	Height of discharge in mm.	Modal latent period in $10^{-4}$ sec.
1	12.0	26.0	96.5
2	23.0	24.5	92.7
3	34.0	24.0	97.4
4	46.0	24.0	94.0
5	—	23.0	91.5
6	—	18.0	106.3
7	45.0	18.0	110.0
8	34.0	16.0	107.5
9	10.0	20.5	99.0

Here the stimuli of No. 1.—No. 5 and that of No. 9 were descending, and those of No. 6, No. 7 and No. 8 were ascending.

In the oscillograms we may observe that when the modal latent period exhibits its prolongation, it is always accompanied by the decrease of the magnitude of the corresponding discharge, although the converse is not true always. We may remark here that this law applies to all cases whether the cause of prolongation is the temporary fatigue or any other alteration in the nerve, or that of an unknown cause like that above described. On the contrary, when the magnitude of the discharge is small on account of the smallness of the stimulus, the prolongation does not appear. This shows that, when the prolongation appears, the nerve-fibres are changed in its state and in consequence the discharge becomes small, *i. e.* every "all" of an excitation itself in the nerve fibres becomes



small, and perhaps the number of disturbances in the nerves which can pass through the decrement of nerve-endings or of some altered part in the nerve becomes less ; and when the prolongation does not appear, the smallness of the discharge is caused on account of a small part of nerve fibres in a trunk being excited. Thus the phenomenon gives support to the "all or none." theory.

#### Summary.

Since several new phenomena have been brought to light after the analyses of the oscillograms, and since at present we have not an opportunity to confirm them by further experiments, we are obliged to leave many problems as not positively decided. We shall conclude this paper, by summarising the results.

1) A formula expressing the time relation of a simple discharge may be got from the theory of probability and is expressed by

$$y = A e^{-b^2 \log^2 \frac{x}{x_0}},$$

where  $y$  denotes the electromotive force at time  $x$  measured from a certain fixed moment,  $b^2$  and  $x_0$  being constants.

2) In the case of the direct stimulus of short duration, the origin of time in this formula is in agreement with the instant of stimulation.

3) When the direct stimulation is of a longer duration, the discharge in response to it may be analysed into two simple discharges corresponding to the closing and to the opening-stimulus, and each of them may be represented by the above formula, having its origin at the instant of the corresponding stimulus.

4) Taking the value of  $A$  as the measure of the excitation, the relation between the intensity of a stimulating current and the excitation in response forms an S-shaped curve which rises from the zero-stimulus very slowly, then quickly, and after passing an inflexion point on its way, finally approaches asymptotically a constant maximal value.

5) With regard to the relation between the duration of a stimulating current and the excitation in response, Hoorweg's decrement factor seems to hold good.

6) When a stimulation is given to a nerve, there remains a fatigue which recovers in a very short interval, and which is called the *temporary fatigue* by the author.

7) The fatigue is characterised by

- a) The prolongation of the modal latent period of the discharge in response to a stimulus given in the interval influenced by that fatigue.
- b) The decrease in the intensity of the discharge denoted by  $A$  in the discharge formula.

8) The time relation of the recovery of this fatigue measured by the excess of the modal latent period of the second discharge compared with the same of the first may be expressed by an exponential function  $Me^{-\lambda t}$ , and this law of the recovery holds good also in the case of similar results obtained by Lucas in nerve-muscle preparation.

9) The abnormal increase in the intensity of the second of the discharges, evoked by two successive stimuli, may be interpreted by the superposition of the secondary discharge.

10) The behaviour of the discharges in response to the two submaximal indirect stimuli, separated by an interval shorter than the refractory period, gives support to the "all or none" theory.

11) In this case, a new phenomenon is probably involved, *i.e.* the shortening of the modal latent period of the discharge, caused by the summation of the two subminimal stimuli.

12) The discharges in response to submaximal closing and opening-stimulus indirectly given may superpose, and the modal latent period corresponding to the opening-stimulus shows the prolongation in the modal latent period. In this case also, the phenomenon may be explained by the "all or none" theory, together with the assumption that the subminimal stimulus may cause some local change, which is made apparent from the prolongation of the modal latent period of the succeeding discharge and which is not yet otherwise confirmed.

13). The fatigue curve in the case of the electric organ very closely resembles that of the contraction of muscle. In both-

cases, there exist the so-called *staircase* phenomenon and the other details in a similar way, and this fact indicates the failure of Fröhlich's explanation in the case of muscle.

14) The speed of propagation of the excitation is uniform throughout the nerve-trunk whether the point concerned is near to or far from the stimulated point, if the nerve is in the normal state.

15) In the altered part of a nerve, near its periphery end, the speed of propagation becomes smaller and is accompanied by the decrease of the intensity of the corresponding discharge.

16) A spontaneous discharge curve of the living fish *Astrape* consists always of two peaks, sometimes followed by a very low irregular one. The second and the following discharge may be considered to be the secondary discharge, *etc.* evoked by the first.

17) The prolongation of the modal latent period from its normal value, of whatever cause it may be, is necessarily accompanied by the enfeeblement of the discharge, while the feeble discharge evoked by the weak stimulus does not indicate the same prolongation.

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In closing this paper, I wish to express my best thanks to Prof. K. Osawa, Director of the Physiological Institute, whose liberality enabled me, for such a long period, to carry out in the Institute, these costly experiments. Also cordial thanks are due to Dr. S. Oinuma who was my zealous collaborator at the beginning of these researches, who kindly collected and placed at my disposal the literature relating to the subjects discussed in this paper, and who gave me many valuable advices.

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## APPENDIX.

## Tables of Experimental Data and Calculated Numbers.

(Table I.—V. are those for the form of the discharge curve.)

TABLE I.

Oscillogram No. 54.

Date of experiment:

Nov. 6, 1909.

Object of experiment:

Relation between the intensity of a stimulating current and the magnitude of the corresponding discharge.

Preparation:

Left organ (whole) of a fish of middle size.

Temperature of the organ:

8.5°–7.2° C.

Resistance of the organ:

240 ohms.

Reading on the stimulation-apparatus:

Circuit-breaker: 64.0 mm.

Connection-changer: 60.0 mm.

No.	Current through primary circuit of induction coil in amp.	Number of revolutions of registering drum per sec.	1 mm. of oscillogram corresponds to, in 10 <sup>-4</sup> sec.	Height of stimulus in mm.	Height of discharge in mm.
1	1.50	6.51	3.07	19.5	1.6
2	2.00	6.38	3.13	25.7	5.0
3	2.50	6.50	3.08	31.8	10.1
4	3.00	6.53	3.06	38.0	17.3
5	3.50	6.40	3.13	44.7	26.7
6	4.00	6.18	3.24	50.0	35.7
7	4.50	6.00	3.33	57.0	44.8
8	4.95	6.36	3.14	65.5	55.6

No.	Latent period		Modal latent period	
	in mm.	in $10^{-4}$ sec.	in mm.	in $10^{-4}$ sec.
1	25.0	76.8	35.0	107.5
2	25.3	79.2	34.0	106.4
3	24.0	73.9	35.0	107.8
4	23.5	71.9	35.0	107.1
5	23.5	73.6	35.0	109.6
6	21.5	69.7	33.5	108.5
7	20.5	68.3	32.0	106.6
8	21.5	67.5	35.0	109.9

Co-ordinates of the points on the discharge curve for every 2 mm. of  $x$  on the oscillogram.

Curve No. 3.		
$x$ in mm.	$x$ in $10^{-4}$ sec.	$y$ in mm. Beginning of stimulus.
0.0	0.0	
24.0	73.9	0.0
5.0	77.0	0.5
7.0	83.2	2.1
9.0	89.3	4.9
31.0	95.5	7.7
3.0	101.6	9.5
5.0	107.8	10.1
7.0	114.0	9.7
9.0	120.1	8.8
41.0	126.3	7.4
3.0	132.4	6.1
5.0	138.6	4.8
7.0	144.8	3.4
9.0	150.9	2.7
51.0	157.1	1.8
3.0	163.2	1.3
5.0	169.4	1.1
7.0	175.6	0.7
9.0	181.7	0.3
Summit of the curve.		
35.0	107.8	10.1

Curve No. 4.		
$x$ in mm.	$x$ in $10^{-4}$ sec.	$y$ in mm. Beginning of stimulus.
0.0	0.0	
23.5	71.9	0.0
25.0	76.5	1.2
7.0	82.6	3.8
9.0	88.7	8.6
31.0	94.9	13.5
3.0	101.0	16.5
5.0	107.1	17.3
7.0	113.2	16.6
9.0	119.3	15.0
41.0	125.5	12.8
3.0	131.6	10.4
5.0	137.7	8.1
7.0	143.8	6.2
9.0	149.9	4.6
51.0	156.1	3.4
3.0	162.2	2.5
5.0	168.3	1.7
7.0	174.4	1.3
9.0	180.5	1.0
Summit of the curve.		
35.0	107.1	17.3

Curve No. 5.		
$x$ in mm.	$x$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0	Beginning of stimulus.
23.5	73.6	0.0
25.0	78.3	2.4
7.0	84.5	7.0
9.0	90.8	14.2
31.0	97.0	21.1
3.0	103.3	25.3
5.0	109.6	26.7
7.0	115.8	25.3
9.0	122.1	22.2
41.0	128.3	18.5
3.0	134.6	14.5
5.0	140.9	11.0
7.0	147.1	8.3
9.0	153.4	6.0
51.0	159.6	4.5
3.0	165.9	3.3
5.0	172.2	2.4
7.0	178.4	2.0
9.0	184.7	1.6
Summit of the curve.		
35.0	109.6	26.7

Curve No. 6.		
$x$ in mm.	$x$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0	Beginning of stimulus.
21.5	69.7	0.0
23.0	74.5	1.6
5.0	81.0	4.5
7.0	87.5	11.5
9.0	94.0	22.8
31.0	100.4	31.5
3.0	106.9	35.5
5.0	113.4	35.1
7.0	119.9	31.4
9.0	126.4	26.3
41.0	132.8	20.6
3.0	139.3	15.7
5.0	145.8	11.5
7.0	152.3	8.5
9.0	158.8	6.1
51.0	165.2	4.6
3.0	171.7	3.5
5.0	178.2	2.8
7.0	184.7	2.4
9.0	191.2	2.2
Summit of the curve.		
33.5	108.5	35.7

Curve No. 7.		
$x$ in mm.	$x$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0	Beginning of stimulus.
20.5	68.3	0.0
3.0	76.6	3.2
5.0	83.3	9.3
7.0	89.9	22.7
9.0	96.6	35.7
31.0	103.2	43.6
3.0	109.9	44.8
5.0	116.6	40.7
7.0	123.2	33.9
9.0	129.9	26.5
41.0	136.5	20.0
3.0	143.2	14.6
5.0	149.9	10.2
7.0	156.5	7.5
9.0	163.2	5.4
51.0	169.8	4.1
3.0	176.5	3.3
5.0	183.2	2.3
7.0	189.8	2.1
Summit of the curve.		
32.0	106.6	45.0

Curve No. 8.		
$x$ in mm.	$x$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0	Beginning of stimulus.
21.5	67.5	0.0
23.0	72.2	1.1
5.0	78.5	3.8
7.0	84.8	9.2
9.0	91.1	22.0
31.0	97.3	37.5
3.0	103.6	52.2
5.0	109.9	55.5
7.0	116.2	53.4
9.0	122.5	46.4
41.0	128.7	38.1
3.0	135.0	29.4
5.0	141.3	21.8
7.0	147.6	16.3
9.0	153.9	11.9
51.0	160.1	8.5
3.0	166.4	6.3
5.0	172.7	4.7
7.0	179.0	3.8
9.0	185.3	3.0
Summit of the curve.		
35.0	109.9	55.5

From the values given in the above tables, the curves from No. 3 to No. 8 were reproduced on section papers whose one division is equal to two millimetres. These curves are shown in Plate VI. For the ordinates, one division of the section paper represents one millimetre of the original; and for the abscissa, one division represents  $2 \times 10^{-4}$  sec. On these curves,  $\xi_1$ ,  $\xi_2$  and  $\xi_1'$ ,  $\xi_2'$  were measured; and from these values,  $\delta$ ,  $x_0$  and  $b^2$  were calculated. The following table shows these values. As the unit of  $y$ ,  $\xi_1$ ,  $\xi_2$ ,  $y_1'$ ,  $\xi_1'$  and  $\xi_2'$ , one division of the section paper is taken.

No.	$y$ .	$\xi_1$ .	$\xi_2$ .	$y'$ .	$\xi_1'$ .	$\xi_2'$ .	$\delta$ in $10^{-4}$ sec.	M.L.P. correct. in $10^{-4}$ sec.	$x_0$ in $10^{-4}$ sec.	$b^2$ .
1										
2				Too low to be used.						
3	3.5	10.9	18.5	1.4 <sub>5</sub>	13.4	26.1	+0.6 <sub>8</sub>	108.5	59.2	4.60
4	6.2	10.6	18.4	3.1	12.9	25.1	+1.1 <sub>2</sub>	108.2	59.8	4.69
5	9.8	11.3	17.2	4.3 <sub>5</sub>	14.1	24.8	-0.1 <sub>0</sub>	109.5	64.2	5.63
6	13.0	10.0	17.2	6.5	12.5	24.0	+1.4 <sub>0</sub>	109.9	60.8	5.37
7	16.5	9.8	17.1	8.2	12.1	24.0	+1.0 <sub>6</sub>	107.7	54.8	4.49
8	20.5	9.7	16.4	10.1	12.4	23.4	+1.4 <sub>6</sub>	111.4	61.8	5.95

By using these constants, the ordinates of each curve for every  $1/1000$  sec. were calculated. These are shown in the next table.



$x$ in $10^{-4}$ sec.	$y$ in mm. (calculated).					
	No. 3.	No. 4.	No. 5.	No. 6.	No. 7.	No. 8.
0.0	Origin of discharge.					
10.0	0.0 <sub>0</sub>	0.0 <sub>0</sub>	0.0 <sub>0</sub>	0.0 <sub>0</sub>	0.0 <sub>0</sub>	0.0 <sub>0</sub>
20.0	0.0 <sub>4</sub>	0.2	0.0 <sub>1</sub>	0.0 <sub>5</sub>	0.5	0.0 <sub>3</sub>
30.0	1.1	1.6	0.9	2.4	8.8	2.5
40.0	5.0	8.2	7.3	13.9	28.8	18.1
50.0	8.9	14.8	18.4	29.1	43.3	42.6
60.0	10.1	17.3	25.9	35.7	43.4	55.3
70.0	8.8	15.4	25.7	32.1	34.4	50.7
80.0	6.5	11.5	20.6	23.8	23.7	37.4
90.0	4.4	7.8	14.4	15.6	14.9	24.0
100.0	2.7	4.8	9.0	9.4	8.9	14.1
110.0	1.6	2.9	5.4	5.4	5.1	7.7
120.0	0.9	1.7	3.1	3.0	2.9	4.1
130.0	0.5	1.0	1.7	1.6	1.6	2.1
140.0	0.3	0.5	0.9	0.9	0.9	1.0
150.0	0.2	0.3	0.5	0.4	0.5	0.1

These values are plotted in Plate VI. by the marks  $\circ$ .

TABLE II.

Oscillogram No. 37.

Date of experiment: Oct. 23, 1909.

Object of experiment: Relation between the duration of a stimulating current and the magnitude of the resulting discharge.

Temperature of the organ: 11.0° C.

Resistance of the organ: 130 ohms.

No.	Readings on stimulation-apparatus.		Number of revolutions of registering drum per sec.	1 mm. of oscillogram corresponds to, in 10 <sup>-4</sup> sec.
	Circuit-breaker.	Connection-changer.		
1	64.0 mm.	54.8 mm.	6.60	3.03
2	63.8	„	6.59	3.03
3	63.6	„	6.79	2.95
4	63.4	„	6.94	3.88
5	63.2	„	7.28	2.75
6	63.0	„	7.27	2.75
7	62.8	„	7.66	2.61
8	62.6	„	7.77	2.58

No.	Stimulation breadth		Modal latent period		A.
	in mm.	in 10 <sup>-4</sup> sec.	in mm.	in 10 <sup>-4</sup> sec.	
1	6.0	18.2	40.6	123.0	31.5
2	5.3	16.1	41.0	124.3	30.8
3	4.8	14.2	42.6	125.7	28.3
4	4.5	13.0	44.0	126.7	27.5
5	4.3	11.8	45.6	125.4	25.0
6	4.1	11.3	46.7	128.2	23.3
7	3.5	9.1	49.5	129.5	19.0
8	3.0	7.7	49.5	127.5	12.5

Co-ordinates of the points on the discharge curves for every  
2 mm. of  $x$  on the oscillogram.

Curve No. 1.		
$x$ in mm.	$x$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0	Beginning of stimulus.
26.0	78.8	0.0
8.0	84.8	1.6
30.0	90.9	4.4
2.0	97.0	9.0
4.0	103.0	15.0
6.0	109.1	22.4
8.0	115.1	29.0
40.0	121.2	31.5
2.0	127.3	30.0
4.0	133.3	25.8
6.0	139.4	20.6
8.0	145.4	15.0
50.0	151.5	10.6
2.0	157.6	7.0
4.0	163.6	4.6
6.0	169.7	2.8
8.0	175.7	2.0
60.0		
Summit of the curve.		
40.6	123.0	31.5

Curve No. 2.		
$x$ in mm.	$x$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0	Beginning of stimulus.
27.0	81.8	0.0
8.0	84.8	1.4
30.0	90.9	2.6
2.0	97.0	6.4
4.0	103.0	11.6
6.0	109.1	18.4
8.0	115.1	25.6
40.0	121.2	30.0
2.0	127.3	30.0
4.0	133.3	26.8
6.0	139.4	22.0
8.0	145.4	16.8
50.0	151.5	12.0
2.0	157.6	8.0
4.0	163.6	5.4
6.0	169.7	3.4
8.0	175.7	2.2
60.0	181.8	1.8
Summit of the curve.		
41.0	124.3	30.8

Curve No. 3.		
$x$ in mm.	$x$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0	Beginning of stimulus.
28.0	82.6	0.0
30.0	88.5	1.0
2.0	94.4	3.6
4.0	100.3	7.0
6.0	106.2	12.0
8.0	112.1	18.8
40.0	118.0	25.0
2.0	123.9	28.0
4.0	129.8	27.6
6.0	135.7	24.4
8.0	141.6	20.0
50.0	147.5	15.0
2.0	153.4	10.4
4.0	159.3	6.8
6.0	165.2	4.4
8.0	171.1	2.8
60.0	177.0	1.8
Summit of the curve.		
42.6	125.7	28.3

Curve No. 4.		
$x$ in mm.	$x$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0	Beginning of stimulus.
29.0	83.5	0.0
32.0	92.2	2.4
4.0	97.9	5.4
6.0	103.7	9.0
8.0	109.4	14.2
40.0	115.2	20.2
2.0	122.0	25.4
4.0	126.7	27.5
6.0	132.5	26.0
8.0	138.2	22.6
50.0	144.0	18.2
2.0	149.8	13.6
4.0	155.5	9.4
6.0	161.3	6.6
8.0	167.0	4.4
60.0	192.8	3.2
2.0	178.6	2.0
Summit of the curve.		
44.0	126.7	27.5

Curve No. 5.		
$x$ in mm.	$x$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0	Beginning of stimulus.
30.0	82.3	0.0
2.0	88.0	1.0
4.0	93.5	2.8
6.0	99.0	5.2
8.0	104.5	9.4
40.0	110.0	14.0
2.0	115.5	19.6
4.0	121.0	24.0
6.0	126.5	24.8
8.0	132.0	23.8
50.0	137.5	20.6
2.0	143.0	16.4
4.0	148.5	12.6
6.0	154.0	9.0
8.0	159.5	6.0
60.0	165.0	4.0
2.0	170.5	2.4
4.0	176.0	1.4
Summit of the curve.		
45.6	125.4	25.0

Curve No. 6.		
$x$ in mm.	$x$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0	Beginning of stimulus.
30.0	82.3	0.0
2.0	88.0	1.0
4.0	93.5	2.2
6.0	98.0	4.6
8.0	104.5	7.8
40.0	110.0	11.6
2.0	115.5	16.8
4.0	121.0	21.6
6.0	126.5	23.2
8.0	132.0	22.8
50.0	137.5	20.4
2.0	143.0	16.6
4.0	148.5	13.2
6.0	154.0	9.8
8.0	159.5	6.6
60.0	165.0	4.6
2.0	170.5	3.2
4.0	176.0	2.0
Summit of the curve.		
46.7	128.2	23.3

Curve No. 7.		
$x$ in mm.	$x$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0	Beginning of stimulus.
33.0	86.1	0.0
4.0	88.7	0.6
6.0	94.0	2.2
8.0	99.2	3.8
40.0	104.4	5.8
2.0	109.6	8.8
4.0	114.8	13.0
6.0	120.1	16.4
8.0	125.3	18.8
50.0	130.5	19.0
2.0	135.7	17.6
4.0	140.9	15.2
6.0	146.2	12.4
8.0	151.4	9.6
60.0	156.6	7.0
2.0	161.8	5.2
4.0	167.0	3.4
6.0	172.3	2.0
Summit of the curve.		
49.5	129.5	19.0

Curve No. 8.		
$x$ in mm.	$x$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0	Beginning of stimulus.
35.0	90.3	0.0
6.0	92.9	1.2
8.0	98.0	2.4
40.0	103.2	3.8
2.0	108.4	5.6
4.0	113.5	8.0
6.0	118.7	10.6
8.0	123.0	11.8
50.0	129.0	12.4
2.0	134.2	11.6
4.0	139.3	10.0
6.0	144.5	8.4
8.0	149.6	6.4
60.0	154.8	4.8
2.0	160.0	3.2
4.0	165.1	2.0
Summit of the curve.		
49.5	127.5	12.5

From the values given in the above tables, the curves from No. 1 to No. 8 were reproduced on section papers in the exactly same way as in No. 54. These curves are shown in Plate VII. On these curves  $x_1$  and  $x_2$  for several values of  $y$  were measured. Then the mean of  $\sqrt{x_1 x_2}$  for every curve was found and compared with the value of the modal latent period observed. The units of  $x_1$ ,  $x_2$  and  $y$  are one division of the section paper. Using the mean of  $\sqrt{x_1 x_2}$  as the value of  $x_0$  we calculated  $b^2$ .

No.	$y$ .	$x_1$ .	$x_2$ .	$\sqrt{x_1 x_2}$ .	$y'$ .	$x_1'$ .	$x_2'$ .	$\sqrt{x_1' x_2'}$ .	$y''$ .	$x_1''$ .	$x_2''$ .	$\sqrt{x_1'' x_2''}$ .
1	11.6	50.0	74.9	61.1	6.0	46.6	79.8	61.0	21.0	53.7	69.4	61.0
2	11.4	51.4	75.8	62.4	6.0	48.0	80.7	62.2	20.0	55.2	70.4	62.4
3	10.4	52.4	76.7	63.4	5.0	48.5	81.7	63.0	19.0	56.3	71.3	63.5
4	10.1	52.3	77.1	63.6	5.0	48.8	82.7	63.5	19.0	57.0	71.5	63.9
5	9.2	52.2	76.8	63.4	5.0	49.0	81.0	63.0	17.0	56.3	71.3	63.5
6	8.6	52.7	77.7	64.0	4.0	49.0	83.6	64.0	15.0	56.8	72.8	64.3
7	7.0	53.4	78.5	64.8	4.0	50.0	82.9	64.4	13.0	57.5	72.7	64.6
8	4.6	52.8	77.5	64.0	2.0	48.2	82.5	(63.1)	8.0	56.6	72.6	64.1

The number in the bracket was not taken in the calculation of the mean.

No.	Mean of $\sqrt{x_1 x_2}$ .	$x_0$ thus found, in $10^{-4}$ sec.	$b^2$ .
1	61.0	122.0	23.7
2	62.3	124.6	25.8
3	63.3	126.6	27.1
4	63.7	127.4	27.4
5	63.3	126.6	26.1
6	64.1	128.2	27.0
7	64.6	129.2	26.3
8	64.1	128.2	27.8

By using the constants given in the above tables, the ordinates of the curves for every 1/1000 sec. were calculated. These values are shown in the next table.

$x$ in $10^{-4}$ sec.	$y$ in mm. (calculated).							
	No. 1.	No. 2.	No. 3.	No. 4.	No. 5.	No. 6.	No. 7.	No. 8.
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
70.0	0.0 <sub>2</sub>	0.0	0.0	0.0	0.0	0.0	0.0	0.0
80.0	0.5	0.2	0.2	0.1	0.1	0.1	0.1	0.0 <sub>3</sub>
90.0	3.5	2.0	1.2	1.0	1.1	0.8	0.7	0.4
100.0	12.5	9.2	6.4	5.6	5.8	4.5	3.5	2.3
110.0	24.5	20.6	16.6	15.3	14.8	12.4	9.6	6.5
120.0	31.3	29.7	26.2	24.3	23.2	20.7	16.4	11.1
130.0	28.6	29.4	27.8	27.2	24.5	23.2	18.8	12.4
140.0	20.1	21.7	21.5	21.5	19.1	18.9	16.0	10.1
150.0	11.5	12.9	13.0	13.2	11.6	12.0	10.6	6.3
160.0	5.5	6.1	6.4	6.8	5.8	6.2	5.7	3.2
170.0	2.3	2.6	2.7	2.8	2.5	2.9	2.6	1.4
180.0	0.8	0.9	1.0	1.0	0.7	1.0	1.1	0.5
190.0	0.2	0.3	0.3	0.3	0.3	0.0 <sub>3</sub>	0.4	0.2
200.0	0.0	0.1	0.1	0.2	0.1	0.0	0.1	0.1



TABLE III.

Oscillogram No. 40.

Date of experiment:

Nov. 24, 1909.

Object of experiment:

The relation between the duration of a stimulating current and the magnitude of the discharge.

Temperature of the organ:

11.5° C

Resistance of the organ:

—

Current of the primary of the induction coil:

3.5 amperes.

No.	Readings on stimulation-apparatus.		Number of revolutions of registering drum per sec.	1 mm. on oscillogram corresponds to, in 10 <sup>-4</sup> sec.
	Circuit-breaker.	Connection-changer.		
1	65.0 mm.	54.8 mm.	7.00	2.86
2	64.2	„	6.93	2.88
3	63.8	„	6.77	2.96
4	63.6	„	6.99	2.86
5	63.4	„	6.67	3.00
6	63.2	„	6.67	3.00
7	63.0	„	6.99	2.86
8	62.8	„	7.05	2.84

No.	Stimulation-breadth		Modal latent period		A.
	in mm.	in 10 <sup>-4</sup> sec.	in mm.	in 10 <sup>-4</sup> sec.	
1	9.8	28.0	42.5	121	44.5
2	6.4	18.4	41.4	119	41.0
3	6.7	19.8	40.7	120	40.0
4	6.1	17.4	42.2	120	39.0
5	6.4	19.2	40.7	122	39.0
6	5.0	15.0	40.8	122	33.5
7	5.0	14.3	42.5	122	35.6
8	4.1	11.6	43.0	122	29.5

Co-ordinates of the points on the discharge curves for every 2 mm. of  $x$  on the oscillogram.

Curve No. 1.		
$x$ in mm.	$x$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0	Beginning of stimulus.
18.7	53.5	0.0
19.7	56.3	0.0
21.7	62.1	0.3
3.7	67.8	1.0
5.7	73.5	1.4
7.7	79.2	2.3
9.7	84.9	4.4
31.7	90.7	8.5
3.7	96.4	16.5
5.7	102.1	25.1
7.7	107.8	34.1
9.7	113.5	41.0
41.7	119.3	44.3
3.7	125.0	43.6
5.7	130.7	49.8
7.7	136.4	34.0
9.7	142.1	27.6
51.7	147.9	21.0
3.7	153.6	15.6
5.7	159.3	11.3
7.7	165.0	8.1
9.7	170.7	5.9
61.7	176.5	4.4
3.7	182.2	3.6
5.7	187.9	3.4
7.7	193.6	3.6
9.7	199.3	4.2
71.7	205.1	4.7
Summit of the curve.		
42.5	121.2	44.5

Curve No. 2.		
$x$ in mm.	$x$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0	Beginning of stimulus.
22.0	63.4	0.0
26.0	74.9	0.9
8.0	80.6	3.1
30.0	86.4	6.0
2.0	92.2	10.9
4.0	97.9	18.5
6.0	103.7	26.5
8.0	109.4	35.0
40.0	115.2	39.6
2.0	121.0	40.9
4.0	126.7	38.0
6.0	132.5	32.9
8.0	138.2	26.3
50.0	144.0	20.1
2.0	149.8	14.6
4.0	155.5	10.6
6.0	161.3	7.5
8.0	167.0	5.5
60.0	172.8	4.0
2.0	178.6	3.2
Summit of the curve.		
41.4	119.0	41.0

Curve No. 3.		
$x$ in mm.	$x$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0	Beginning of stimulus.
23.5	69.6	0.0
5.5	75.5	1.9
7.5	81.4	2.7
9.5	87.3	6.0
31.5	93.2	11.1
3.5	99.1	18.3
5.5	105.1	27.1
7.5	111.0	35.5
9.5	116.9	39.2
41.5	122.8	39.8
3.5	128.8	36.6
5.5	134.7	31.3
7.5	140.6	24.3
9.5	146.5	17.9
51.5	152.4	12.7
3.5	158.4	8.9
5.5	164.3	6.2
7.5	170.2	4.5
9.5	176.1	3.5
Summit of the curve.		
40.7	120.5	40.0

Curve No. 4.		
$x$ in mm.	$x$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0	Beginning of stimulus.
23.9	68.4	0.0
5.9	74.1	1.2
7.9	79.8	2.4
9.9	85.5	4.3
31.9	91.3	8.2
3.9	97.0	14.0
5.9	102.7	21.8
7.9	108.4	29.8
9.9	114.1	36.0
41.9	119.8	39.0
3.9	125.4	37.4
5.9	131.3	33.0
7.9	137.0	27.4
9.9	143.0	21.4
51.9	148.4	15.4
3.9	154.2	11.1
5.9	159.9	7.2
7.9	165.6	5.0
9.9	171.3	3.6
61.9	177.0	2.6
Summit of the curve.		
42.2	120.7	39.0

Curve No. 5.		
$x$ in mm.	$x$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0	Beginning of stimulus.
21.1	63.3	0.0
4.1	72.3	0.8
6.1	78.3	1.4
8.1	84.3	2.8
30.1	90.3	6.0
2.1	96.3	11.8
4.1	102.3	18.8
6.1	108.3	27.8
8.1	114.3	34.7
40.1	120.3	38.9
2.1	126.3	38.5
4.1	132.3	34.8
6.1	138.3	28.2
8.1	144.3	21.5
50.1	150.3	15.5
2.1	156.3	10.7
4.1	162.3	6.3
6.1	168.3	4.8
8.1	174.3	3.3
60.1	180.3	3.8
Summit of the curve.		
40.8	122.4	39.0

Curve No. 6.		
$x$ in mm.	$x$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0	Beginning of stimulus.
25.0	75.0	0.0
7.0	81.0	1.7
9.0	87.0	3.9
31.0	93.0	6.3
3.0	99.0	11.5
5.0	105.0	17.9
7.0	111.0	25.8
9.0	117.0	31.7
41.0	123.0	33.5
3.0	129.0	31.9
5.0	135.0	27.1
7.0	141.0	21.9
9.0	147.0	15.2
51.0	153.0	11.3
3.0	159.0	7.9
5.0	165.0	5.3
7.0	171.0	3.7
9.0	177.0	2.7
61.0	183.0	2.7
Summit of the curve.		
40.8	122.4	33.5

Curve No. 7.		
$x$ in mm.	$t$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0	Beginning of stimulus.
24.1	68.9	0.0
6.1	74.6	0.0
8.1	80.4	1.4
30.1	86.1	4.4
2.1	91.8	6.1
4.1	97.5	11.3
6.1	103.2	18.2
8.1	109.0	26.5
40.1	114.7	32.3
2.1	120.4	35.3
4.1	126.1	34.5
6.1	131.8	31.0
8.1	137.6	25.5
50.1	143.3	19.8
2.1	149.0	14.8
4.1	154.7	10.0
6.1	160.4	6.5
8.1	166.2	4.3
60.1	171.9	3.5
Summit of the curve.		
42.5	122.0	35.6

Curve No. 8.		
$x$ in mm.	$t$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0	Beginning of stimulus.
26.5	75.3	0.0
8.5	80.9	1.6
30.5	86.6	2.2
2.5	92.3	4.7
4.5	98.0	8.8
6.5	103.7	14.2
8.5	109.3	20.6
40.5	115.0	26.2
2.5	120.7	29.5
4.5	126.4	28.0
6.5	132.1	25.0
8.5	137.7	20.5
50.5	143.4	16.0
2.5	149.1	12.0
4.5	154.8	8.5
6.5	160.5	6.0
8.5	166.1	4.0
60.5	171.8	2.6
2.5	177.5	1.8
Summit of the curve.		
43.0	122.2	29.5

From the values given in the above tables, the curves No. 1—No. 8 were reproduced on section papers in the same way as in No. 37. These curves are shown in Plate VIII. In these curves,  $x_1, x_2$  for several values of  $y$  were measured. Then the mean of  $\sqrt{x_1 x_2}$  for every curve was found and compared with the observed value of the modal latent period. The unit of  $x$  and of  $y$  are one division of the section paper. Using the mean of  $\sqrt{x_1 x_2}$  as the value of  $x_0$ , we calculated  $b_2$ .

No.	$y$ .	$x_1$ .	$x_2$ .	$\sqrt{x_1 x_2}$ .	$y'$ .	$x_1'$ .	$x_2'$ .	$\sqrt{x_1' x_2'}$ .	Mean of $\sqrt{x_1 x_2}$ .	$x_0$ thus found in $10^{-4}$ sec.	$b_2$ .
1	16.3	48.3	76.1	60.6	8.2	45.1	82.5	61.0	60.8	121.6	20.0
2	15.0	47.9	74.5	59.5	7.5	44.4	80.7	59.5	59.5	119.6	20.8
3	14.6	48.3	75.1	60.2	7.3	44.4	81.0	60.2	60.2	120.4	20.6
4	14.2	48.5	75.0	60.3	7.1	44.3	80.8	59.8	60.1	120.2	20.4
5	14.3	49.5	75.7	61.2	7.2	45.9	80.8	60.9	61.1	122.2	21.8
6	12.3	50.0	75.6	61.5	6.2	46.0	81.7	61.3	61.4	122.8	23.2
7	13.0	49.5	75.5	61.1	6.5	46.0	80.4	60.8	61.0	122.0	22.2
8	10.7	49.6	75.4	61.2	5.4	45.8	81.0	61.0	61.1	123.4	22.9

From the constants given in the above tables, the ordinates of the curves for every 1/1000 sec. were calculated. These values are shown in the next table.

$x$ in $10^{-4}$ sec.	$y$ in mm. (calculated).							
	No. 1.	No. 2.	No. 3.	No. 4.	No. 3.	No. 6.	No. 7.	No. 8.
0.0			Beginning of stimulus.					
60.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
70.0	0.1	0.1	0.1	0.1	0.0 <sub>4</sub>	0.0 <sub>2</sub>	0.0 <sub>4</sub>	0.0 <sub>2</sub>
80.0	1.4	1.4	1.3	1.3	0.8	0.5	0.7	0.5
90.0	7.3	7.6	7.0	7.0	5.1	3.6	4.6	3.6
100.0	21.0	21.3	19.9	19.6	16.4	12.8	15.0	11.9
110.0	36.4	35.5	33.8	32.9	30.7	25.3	28.1	22.9
120.0	44.4	41.0	40.0	38.6	38.7	33.1	35.4	29.3
130.0	40.7	35.5	35.4	33.7	35.9	31.0	31.8	27.0
140.0	29.9	24.5	25.0	24.0	26.0	22.5	23.4	19.3
150.0	18.5	14.1	14.8	14.2	15.5	13.2	13.8	11.2
160.0	9.9	7.0	7.5	7.3	8.0	6.6	7.0	5.6
170.0	5.3	3.1	3.4	3.3	3.6	2.7	3.1	2.4
180.0	2.1	1.3	1.4	1.4	1.5	1.1	1.2	0.9
190.0	0.8	0.5	0.5	0.5	0.6	0.5	0.5	0.3
200.0	0.3	0.2	0.2	0.2	0.3	0.1	0.2	0.1

TABLE IV.

Oscillogram No. 54, curve No. 7 and its residual curve.

$$y = 44.8 e^{-4.49 \log^2 \frac{x-32.4}{54.8}}$$

$$y_0 = 44.8 e^{-21.3 \log^2 \frac{x}{106.6}}$$

$$y = 10.0 e^{-17.2 \log^2 \frac{x}{100.8}}$$

$x$ in $10^{-4}$ sec.	$y$ in mm.	$y_0$ in mm.	$y-y_0$ in mm.
106.0	44.6	44.8	0.2
112.0	43.6	42.2	1.4
6.0	41.0	37.6	3.4
120.0	37.3	31.9	5.4
4.0	33.0	25.8	7.2
8.0	28.6	19.9	8.7
132.0	24.4	14.8	9.6
6.0	20.6	10.7	9.9
140.0	17.1	7.4	9.7
4.0	14.0	5.0	9.0
8.0	11.5	3.3	8.2
152.0	9.3	2.1	7.2
6.0	7.5	1.3	6.2
160.0	6.0	0.8	5.2
4.0	4.8	0.5	4.3
8.0	3.8	0.3	3.5
172.0	3.0	0.2	2.8
6.0	2.4	0.1	2.3
180.0	1.8	0.0 <sub>6</sub>	1.7
4.0	1.5	0.0 <sub>8</sub>	1.5
8.0	1.2	0.0 <sub>1</sub>	1.2
192.0	0.9	0.0 <sub>0</sub>	0.9

$x$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0
70.0	0.9
80.0	4.0
90.9	8.1
100.0	10.0
110.0	8.8
120.0	5.9
130.0	3.3
140.0	1.6
150.0	0.7
160.0	0.3

TABLE V.

Oscillogram No. C. 3.

Date of experiment:

May 13, 1910.

Preparation:

About a quarter of the organ with  
one nerve-trunk.

Temperature of the organ:

10.5° C.

Stimulus:

Indirect momentary stimulus.

One millimetre on the film  
corresponds to: $1.64 \times 10^{-4}$  sec.



Co-ordinates of the points on the discharge curve for every 2 mm. of  $x$  on the oscillogram.

$x$ in mm.	$x$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0	Beginning of stimulus.
78.0	128.0	0.0
82.0	134.5	2.4
4.0	137.9	5.4
6.0	141.1	10.4
8.0	144.4	19.4
90.0	147.6	29.0
2.0	151.0	39.0
4.0	154.2	47.0
6.0	157.5	52.4
8.0	160.8	55.0
100.0	164.0	55.0
2.0	167.3	53.6
4.0	170.6	50.8
6.0	173.8	47.0
8.0	177.1	42.8
10.0	180.4	38.4
2.0	183.7	33.8
4.0	187.0	29.0
6.0	190.2	24.6
8.0	193.5	20.4
20.0	196.9	16.8
2.0	200.0	13.4
4.0	203.4	11.0
6.0	206.6	8.6
8.0	210.0	6.8
30.0	213.2	5.6
2.0	216.4	4.4
4.0	219.8	3.4
6.0	223.0	2.4
8.0	226.4	2.0
40.0	229.6	1.4
148.0	242.8	0.0
Summit of the curve.		
99.0	162.3	55.4

The values of the ordinates for every  $\frac{1}{1000}$  sec., calculated by the formula

$$y = 55.4 e^{-5.88 \log^2 \frac{x}{57.6 \times 10^{-4}}}$$

$x$ in $10^{-4}$ sec.	$y$ in mm.
0.0	0.0
30.0	4.3
40.0	25.5
50.0	49.3
60.0	54.9
70.0	44.4
80.0	29.5
90.0	17.3
100.0	9.3
110.0	4.8
120.0	2.4
130.0	1.2
140.0	0.6

$$\delta = +0.84.$$



TABLE VII.

Oscillograms No. 40 and No. 41.

Date of experiment:

Oct. 24, 1909.

Preparation:

Left organ (whole). (The same organ as No. 38 and No. 39.)

Temperature of the organ:

11.5° C.

Primary current:

3.5 amperes.

The formula employed: No. 40  $y = 48.0 \times 10^{-n \times 0.0601} \{1 - 10^{-0.29(-n)}\}$  $y = 46.9 \times \quad \quad \quad$ 

No. 40.

No.	Reading of position of C. B. in mm.	Reading of position of C. Ch. in mm.	Breadth of stimulus (AD) in mm.	Number of revolutions per sec.	1 mm. on film corresponds to, in 10 <sup>-4</sup> sec.
1	65.0	54.8	9.8	7.00	2.86
2	64.2	„	6.4	6.93	2.88
3	63.8	„	6.7	6.77	2.96
4	63.6	„	6.1	6.99	2.86
5	63.4	„	6.4	6.67	3.00
6	63.2	„	5.0	6.67	3.00
7	63.0	„	5.0	6.99	2.86
8	62.8	„	4.1	7.05	2.84

No.	Height of stimulus in mm.	Breadth of stimulus in 10 <sup>-4</sup> sec.	Height of discharge in mm.	Height of discharge reduced to Stm. 44.5, in mm.	Height of discharge calculated, in mm.	Difference.
1	44.5	28.0	44.5	44.5	45.0	-0.5
2	45.0	18.4	40.5	39.9	39.7	+0.2
3	44.8	19.8	39.5	39.1	40.1	-1.0
4	45.0	17.4	38.2	37.6	37.8	-0.2
5	45.1	19.2	39.0	38.2	38.6	-0.4
6	44.5	15.0	33.5	33.5	34.6	-1.1
7	45.0	14.3	35.6	35.0	33.3	+1.7
8	44.0	11.6	29.1	29.7	29.7	+0.0

(C. B. Circuit-breaker.

C. Ch. Connection-changer.)

## No. 41.

No.	Reading of position of C. B. in mm.	Reading of position of C. Ch. in mm.	Breadth of stimulus (AD) in mm.	Number of revolutions per sec.	1 mm. on film corresponds to, in $10^{-4}$ sec.
1	62.8	54.8	4.2	6.05	3.31
2	63.0	„	4.0	6.12	3.27
3	63.2	„	4.8	6.12	3.27
4	63.4	„	5.5	6.47	3.08
5	63.6	„	6.0	6.38	3.14
6	63.8	„	5.3	6.08	3.29
7	64.2	„	7.2	6.25	3.20
8	65.0	„	7.1	6.35	3.16

No.	Height of stimulus in mm.	Breadth of stimulus in $10^{-4}$ sec.	Height of discharge in mm.	Height of discharge reduced to Stm. 44.5, in mm.	Height of discharge calculated, in mm.	Difference.
1	45.0	13.9	36.5	35.9	35.0	+0.9
2	44.5	13.1	33.7	33.7	33.6	+0.1
3	45.0	15.7	36.6	36.0	35.9	+0.1
4	45.5	17.0	38.0	36.7	36.6	+0.1
5	45.0	18.8	37.0	36.4	37.4	-1.0
6	45.0	17.5	39.2	38.6	36.0	+2.6
7	44.8	23.0	39.0	38.6	38.7	-0.1
8	45.0	22.4	39.0	38.4	37.9	+0.5

TABLE VIII.

Oscillograms No. 59, No. 60 and No. 61.

Date of experiment: Nov. 10, 1909.

Preparation: Left organ (whole).

Temperature of the organ: 13.5°

Resistance of the organ: About 200 ohms.

Current in primary:

No. 59: 3 amperes.

No. 60: 4 „

No. 61: 5 „

Formula employed:

$$\text{No. 59} \quad y = 21.3 \times 10^{-n \cdot 0.0373} \{1 - 10^{-0.0560(t-2)}\},$$

$$\text{No. 60} \quad y = 32.1 \times 10^{-n \cdot 0.0121} \{1 - 10^{-0.0935(t-2)}\},$$

$$\text{No. 61} \quad y = 38.8 \times 10^{-n \cdot 0.0319} \{1 - 10^{-0.0623(t-2)}\}.$$

No. 59.

No.	Reading of position of C. B. in mm.	Reading of position of C. Ch. in mm.	Breadth of stimulus (AF) in mm.	Number of revolutions per sec.	1 mm. on film corresponds to, in 10 <sup>-4</sup> sec.	Height of stimulus in mm.
1	62.0	62.0	8.2	6.00	3.33	38.0
2	61.0	„	6.1	6.28	3.18	37.5
3	60.8	„	5.4	5.46	3.66	37.2
4	60.6	„	5.5	5.70	3.51	37.9
5	60.4	„	4.9	5.87	3.41	38.1
6	60.2	„	4.3	5.77	3.46	37.5
7	60.0	„	2.3	5.67	3.53	32.8
8	62.0	„	8.2	5.98	3.34	37.5

No.	Breadth of stimulus in 10 <sup>-4</sup> sec.	Height of discharge in mm.	Height of discharge reduced to Stm. 37.5, in mm.	Height of discharge calculated. in mm.	Difference.	Height of discharge calculated by neglecting fatigue factor.
1	27.3	21.0	20.5	20.5	0.0	20.5
2	19.4	19.5	19.5	18.9	+0.6	19.0
3	19.8	19.0	19.3	18.8	+0.5	19.1
4	19.3	18.5	18.1	18.5	-0.4	19.0
5	16.7	18.0	17.4	17.5	-0.1	18.1
6	14.9	17.0	17.0	16.5	+0.5	17.3
7	8.1	6.3	11.0	11.0	0.0	11.6
8	27.4	19.3	19.3	19.3	0.0	20.5

## No. 60.

No.	Reading of position of B. C. in mm.	Reading of position of C. Ch. in mm.	Breadth of stimulus (AC) in mm.	Number of revolutions per sec.	1 mm. on film corresponds to, in $10^{-4}$ sec.	Height of stimulus in mm.
1	62.0	62.0	11.9	9.00	2.22	50.0
2	61.0	„	9.7	8.83	2.27	50.0
3	60.8	„	8.5	8.91	2.24	50.5
4	60.6	„	8.1	9.40	2.13	50.0
5	60.4	„	—	8.89	2.25	—
6	60.2	„	8.0	9.33	2.14	50.8
7	60.0	„	6.4	—	—	50.0
8	62.0	„	11.7	8.61	2.32	50.0

No.	Breadth of stimulus in $10^{-4}$ sec.	Height of discharge in mm.	Height of discharge reduced to Stm. 50.0, in mm.	Height of discharge calculated in mm.	Difference.	Height of discharge calculated by neglecting fatigue factor
1	26.4	32.0	32.0	32.0	0.0	32.0
2	22.0	30.8	30.8	31.0	-0.2	31.9
3	19.0	30.2	29.7	30.0	-0.3	31.7
4	17.3	29.0	29.0	29.0	0.0	31.5
5	—	—	—	—	—	—
6	17.1	28.3	27.5	27.4	+0.1	37.4
7	14.8	26.0	26.0	26.2	-0.2	31.0
8	27.1	26.3	26.3	26.4	-0.1	32.0

No. 61.

No.	Reading of position of C. B. in mm.	Reading of position of C. Ch. in mm.	Breadth of stimulus (AF') in mm.	Number of revolutions per. sec.	1 mm. on film corresponds to, in $10^{-4}$ sec.	Height of stimulus in mm.
1	62.0	62.0	12.6	8.59	2.33	Could not be measured.
2	61.0	„	9.5	8.96	2.23	
3	60.8	„	8.7	8.74	2.29	
4	60.6	„	8.8	9.73	2.06	
5	60.4	„	—	9.35	2.14	
6	60.2	„	7.9	9.67	2.07	
7	60.0	„	7.1	10.25	1.95	
8	62.0	„	12.7	9.84	2.03	

No.	Breadth of stimulus in $10^{-4}$ sec.	Height of discharge in mm.	Height of discharge calculated in mm.	Difference.	Height of discharge calculated by neglecting fatigue factor.
1	29.4	38.0	38.0	0.0	38.0
2	21.2	36.9	36.1	+0.8	36.4
3	19.9	36.0	35.4	+0.6	35.9
4	18.1	34.6	34.3	+0.3	35.0
5	—	—	—	—	—
6	16.4	32.0	32.8	-0.8	33.9
7	13.8	30.4	30.4	0.0	32.1
8	25.8	36.0	35.6	+0.4	37.4

TABLE IX.

Oscillograms No. 74—75.

Date of experiment:

Nov. 17, 1909.

Preparation:

A quater of an organ with one  
nerve-trunk.

Temperature of the organ:

14.5°.

No.	Distance betw. two contacts on stimulation- apparatus in mm.	Number of revolutions per sec.	1 mm. on film corre- sponds to, in 10 <sup>-4</sup> sec.	Interval between two stimuli in mm.	Interval between two stimuli. in 10 <sup>-4</sup> sec.	M. L. P. of first Disch. in mm.	M. L. P. of second Disch. in mm.
1	26.0	5.98	3.35	36.0	120.5	31.5	31.5
2	24.0	6.06	3.30	33.5	110.4	32.0	32.5
3	22.0	6.18	3.24	30.7	99.5	32.5	33.5
4	20.0	6.22	3.22	28.0	90.2	33.5	34.3
5	18.0	5.84	3.43	23.3	79.9	31.0	33.0
6	16.0	6.05	3.31	21.9	72.5	32.5	35.7
7	14.0	6.17	3.24	19.5	63.2	33.0	37.0
8	12.0	6.11	3.28	17.0	55.8	33.5	39.4
9	10.0	6.34	3.16	13.9	43.9	33.0	43.0
10	8.0	6.57	3.05	11.0	33.6	34.0	48.0
11	6.0	6.62	3.02	11.5	34.7	34.0	48.0
12	4.0	6.58	3.04	9.0	27.4	34.0	—
13	2.0	6.71	2.98	5.0	14.9	34.0	—
14	1.0	6.60	3.04	3.0	9.1	34.5	—
15	0.5	6.67	3.00	1.0	3.0	35.0	—
16	0.2	6.92	2.90	Coincide.	0.0	35.5	—

No.	Ratio of two M. L. P.	Interval between first Sam. and second discharge. in mm.	Ditto in 10 <sup>-4</sup> sec.	Height of first Disch. in mm.	Height of second Disch. in mm.	Ratio of two heights.
1	1.000	67.5	226	53.0	39.0	0.736
2	1.015	66.5	214	51.5	41.5	0.806
3	1.030	64.2	208	48.5	45.5	0.989
4	1.023	62.3	201	48.0	49.0	1.020
5	1.063	56.3	193	47.0	48.5	1.030
6	1.100	57.6	191	46.0	46.7	1.015
7	1.120	56.5	183	46.0	45.5	0.990
8	1.175	56.4	185	45.0	42.0	0.935
9	1.301	56.9	180	45.0	24.7	0.550
10	1.411	59.0	180	43.3	4.5	0.104
11	1.411	59.5	180	41.5	4.5	0.109
12	—	—	—	42.5	?	?
13	—	—	—	41.8	?	?
14	—	—	—	41.2	—	—
15	—	—	—	42.5	—	—
16	—	—	—	41.5	—	—



TABLE X.

Oscillogram No. 65.

Date of experiment:

Nov. 10, 1909.

Preparation:

Part of an organ with one nerve-trunk.

Temperature of the organ:

13.5° C.

Stimulus:

Ascending.

No.	Distance betw. two contacts on stimulation-apparatus in mm.	Number of revolutions per sec.	1 mm. on film corresponds to, in 10 <sup>-4</sup> sec.	Interval between two stimuli in mm.	Interval between two stimuli in 10 <sup>-4</sup> sec.	M. L. P. of first Disch. in mm.	M. L. P. of second Disch. in mm.
1	26.0	6.34	3.16	42.0	133	38.0	68.0
2	24.0	6.57	3.04	—	—	39.6	—
3	22.0	6.55	3.05	36.0	110	40.0	39.0
4	20.0	6.20	3.22	30.0	97	38.0	39.0
5	18.0	6.27	3.19	27.6	88	38.0	43.0
6	16.0	6.36	3.14	—	—	37.5	—
7	14.0	6.47	3.09	22.2	69	39.0	48.0
8	12.0	6.55	3.06	19.6	60	39.0	50.8
9	10.0	6.54	3.06	16.0	49	39.0	56.0

No.	Ratio of two M. L. P.	Interval between 1st Stim. and 2nd Disch. in mm.	Ditto in 10 <sup>-4</sup> sec.	Height of first Disch. in mm.	Height of second Disch. in mm.	Ratio of two heights.
1	1.790	110.0	348	24.5	9.0	0.367
2	—	74.4	226	22.6	17.8	0.788
3	0.975	75.0	236	21.5	19.0	0.885
4	1.025	69.0	222	21.0	19.0	0.925
5	1.130	70.6	225	20.3	18.0	0.900
6	—	71.0	222	20.0	15.0	0.750
7	1.230	70.2	217	19.5	16.0	0.820
8	1.300	70.4	215	19.9	11.0	0.553
9	1.480	72.0	220	18.8	3.9	0.207

K. FUJI.

RESEARCHES ON THE ELECTRIC DISCHARGE OF THE ISOLATED ELECTRIC ORGAN  
OF *ASTRAPE* BY MEANS OF OSCILLOGRAPH.

PLATES.

- I.— III., Photographs.  
IV.— V., Drawings of instruments.  
VI.— XII., Curves.  
XIII.—XXX., Oscillograms.

### Abbreviations used in Plates.

Stim. or Stm.:	Stimulus.
Resp.:	Response.
C. Stim.:	Closing-stimulus.
O. Stim.:	Opening-stimulus.
E. T.:	Equivalent time <i>i. e.</i> time interval corresponding 1 mm. of abscissa on oscillogram.
$S_m, {}_1S_m, {}_2S_m$ :	All these abbreviations represent "Stimulus." Figures in suffix show the order of experiment with respect to time. Where two successive stimuli were used, ${}_1S_m$ represents the predecessor in those of the $m$ th experiment, and ${}_2S_m$ the successor in the same set.
$R_m, {}_1R_m, {}_2R_m$ :	All these abbreviations represent "Response". The numbers in prefix and suffix show the correspondence of the response to the stimulus having the same respective affixes.
2ry D.:	Secondary discharge.
3ry D.:	Tertiary discharge.

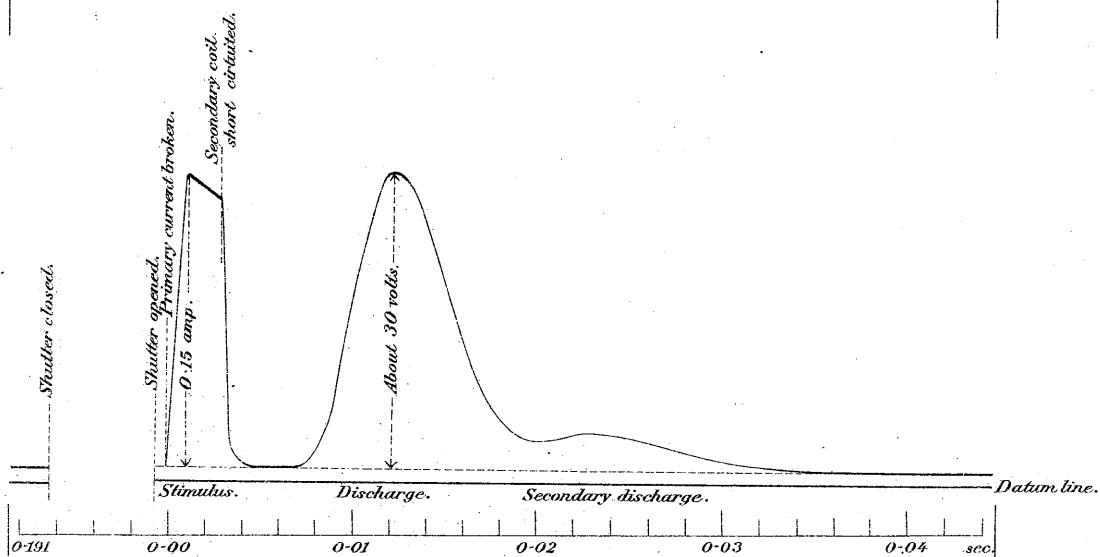
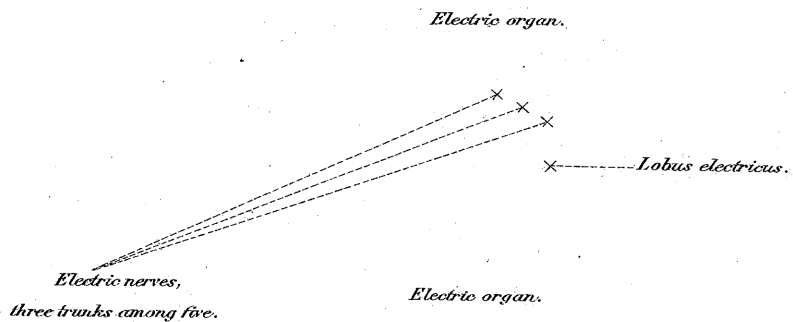
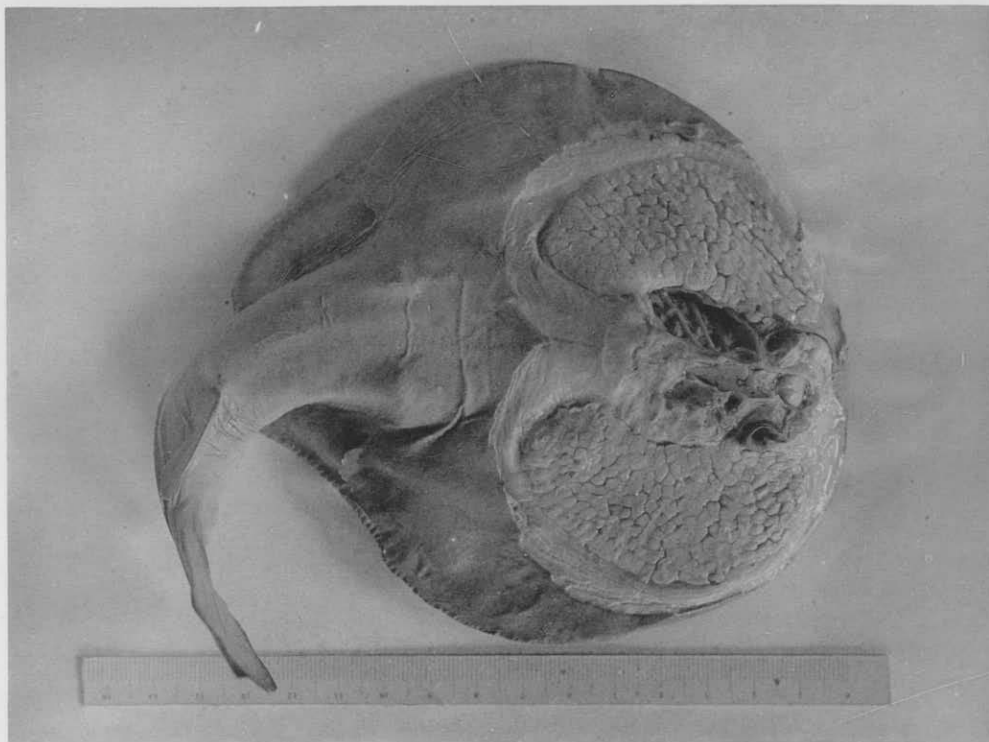


Fig. 1.

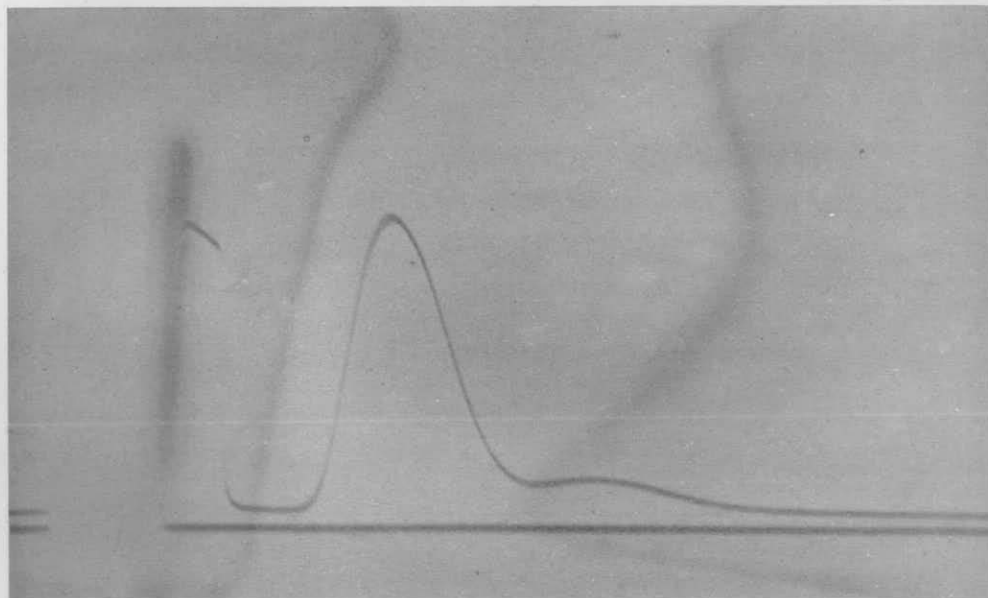
*Astrape japonica.*



Anterior part of the skin has been removed to show the electric organs and the electric nerves.

Fig. 2.

A direct stimulus and the resulting discharge.



K. Fuji: Researches on the Electric Discharge of the Isolated Electric Organ of *Astrape* (Japanese Electric Ray) by Means of Oscillograph.

Shutter.

Fig. 1.

Front view.

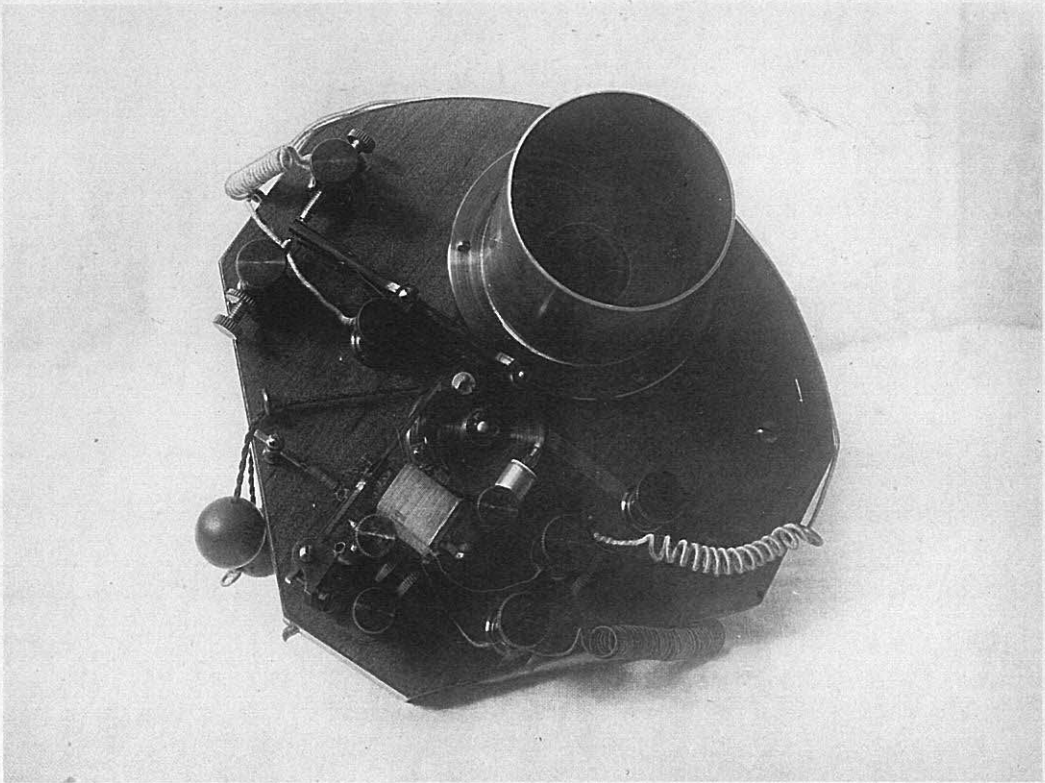


Fig. 2.

Back view.

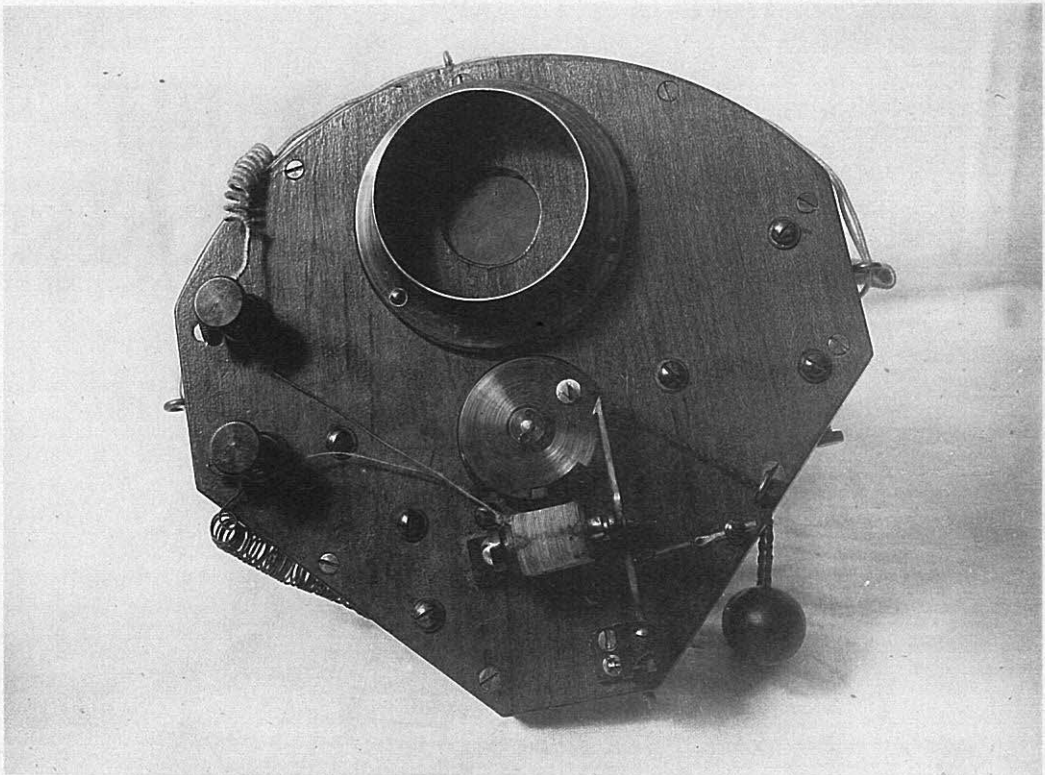


Fig. 1.

Registering apparatus (cover removed).

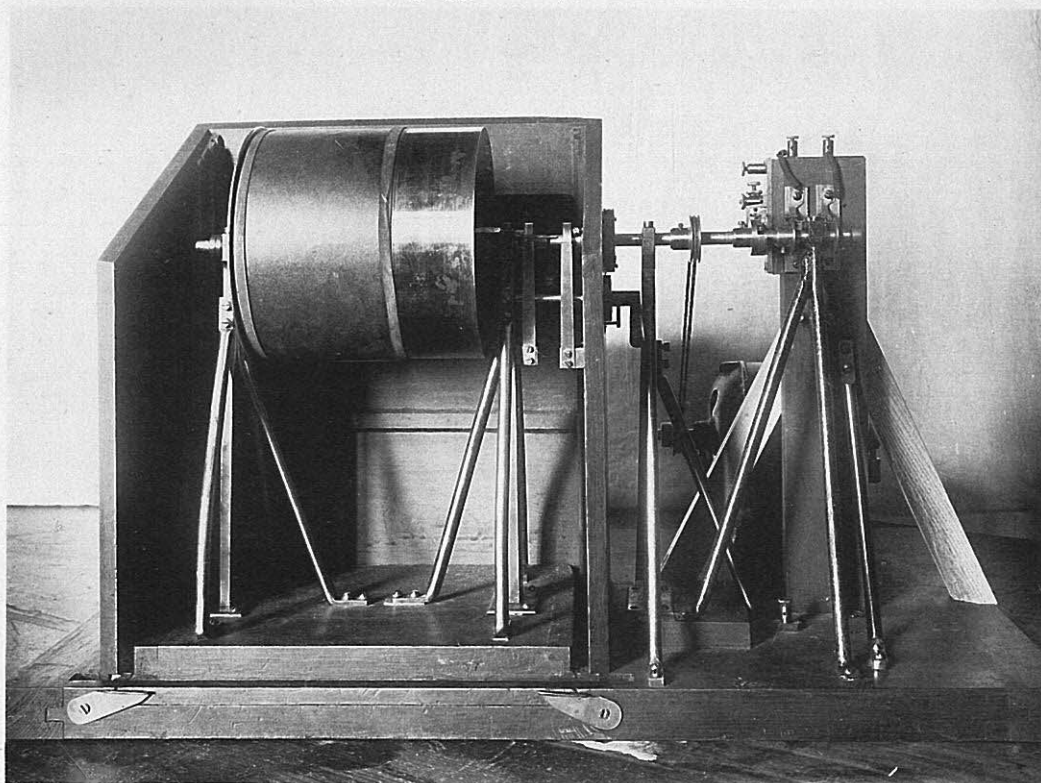
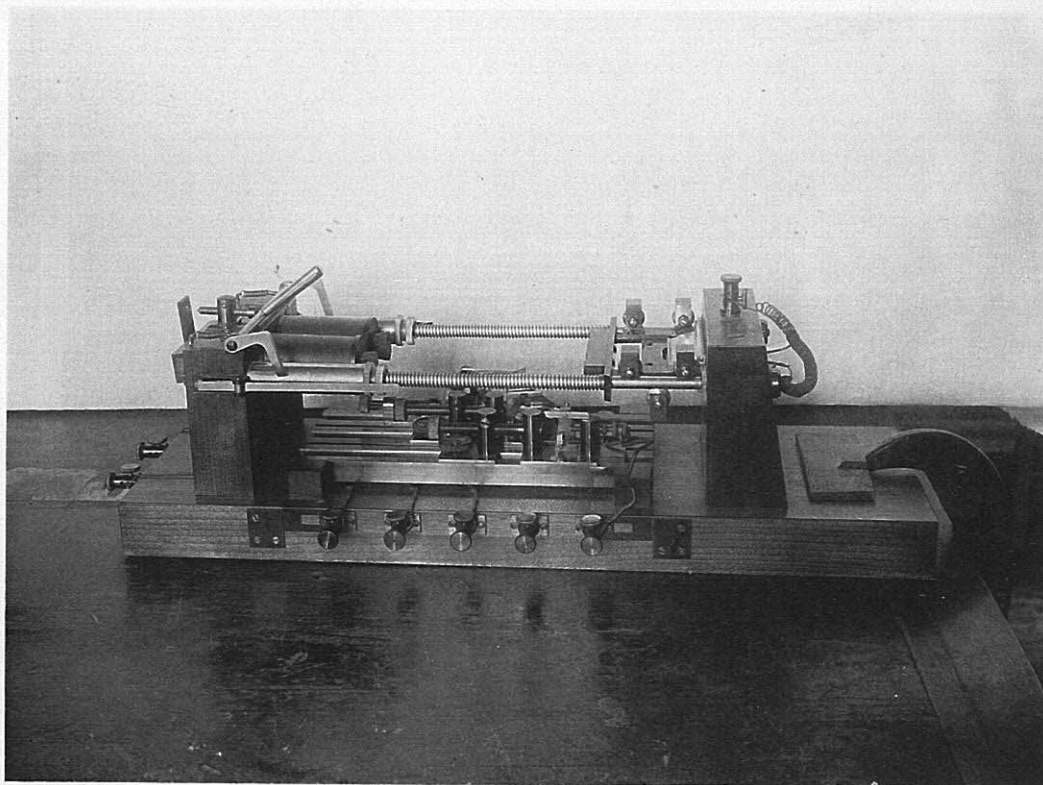


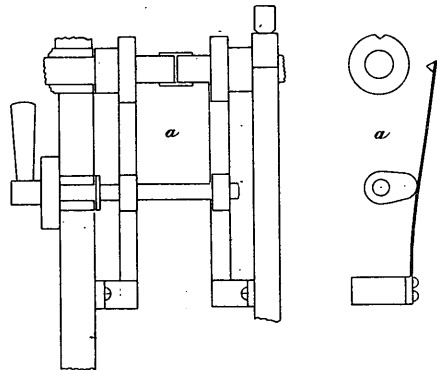
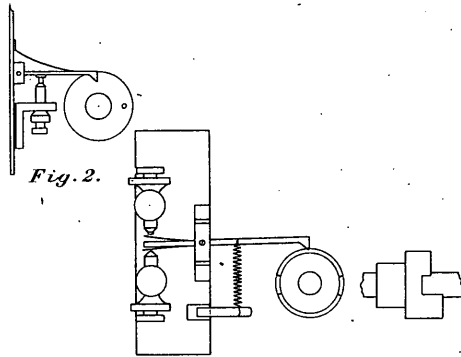
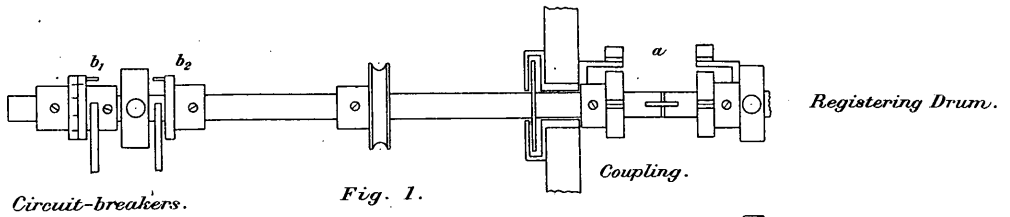
Fig. 2.

Stimulation-apparatus clamped to a table.



K. Fuji: Researches on the Electric Discharge of the Isolated Electric Organ of *Astrape*  
(Japanese Electric Ray) by Means of Oscillograph.

*Driving Shaft of the Registering Drum and Its Accessories.  
( $\frac{2}{5}$  Actual Size.)*



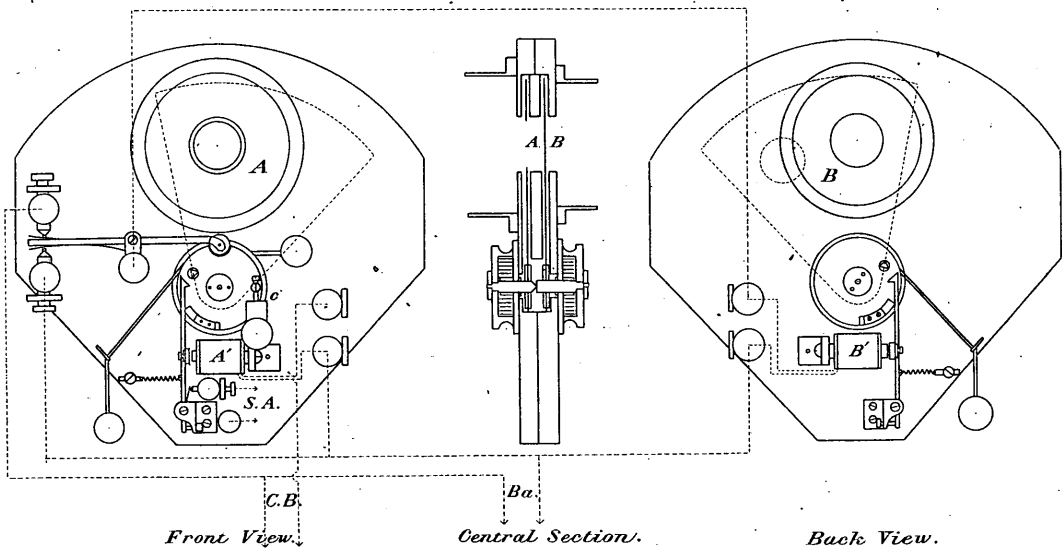
*Fig. 3.*

*Fig. 1. Driving Shaft and Its Coupling.*

*Fig. 2. Circuit-breaker.*

*Fig. 3. Connection-changer.*

*Shutter. ( $\frac{2}{5}$  Actual Size.)*

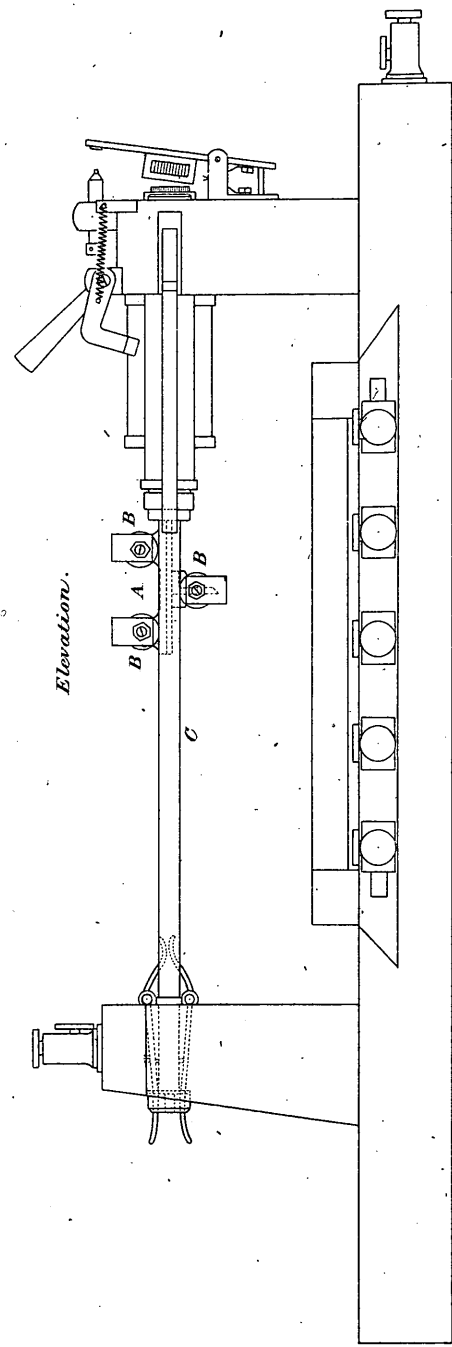


*Fig. 4.*

K. Fuji: Researches on the Electric Discharge of the Isolated Electric Organ of *Astrape* (Japanese Electric Ray) by Means of Oscillograph.



Stimulation-apparatus and Its Accessories.  
( $\frac{2}{3}$  Actual Size.)



Plan.

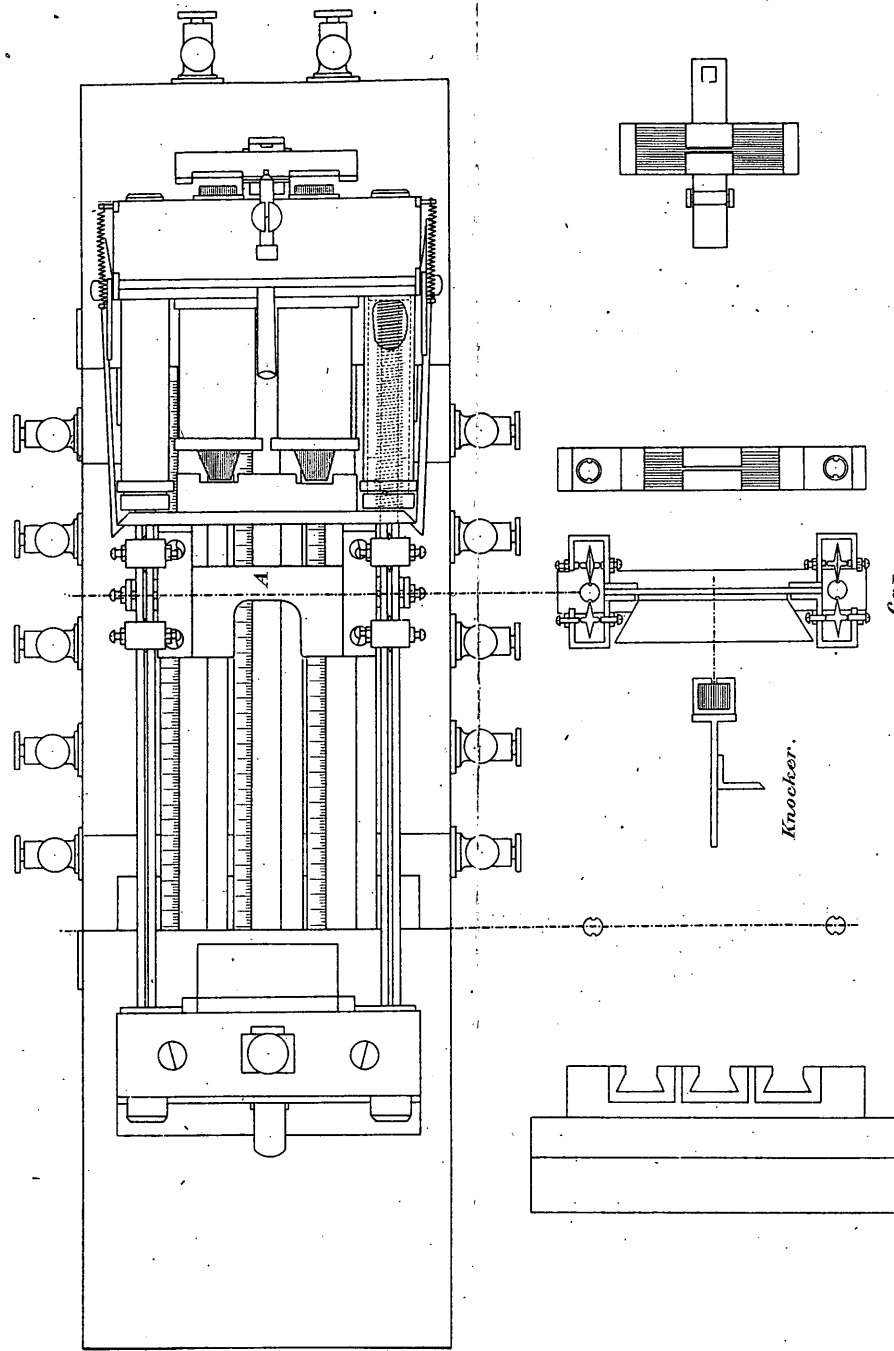


Fig. 1.

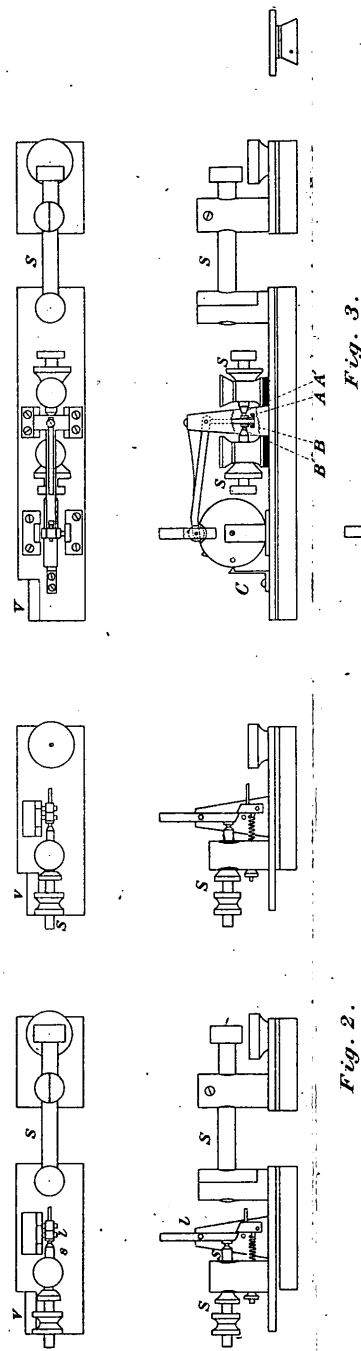
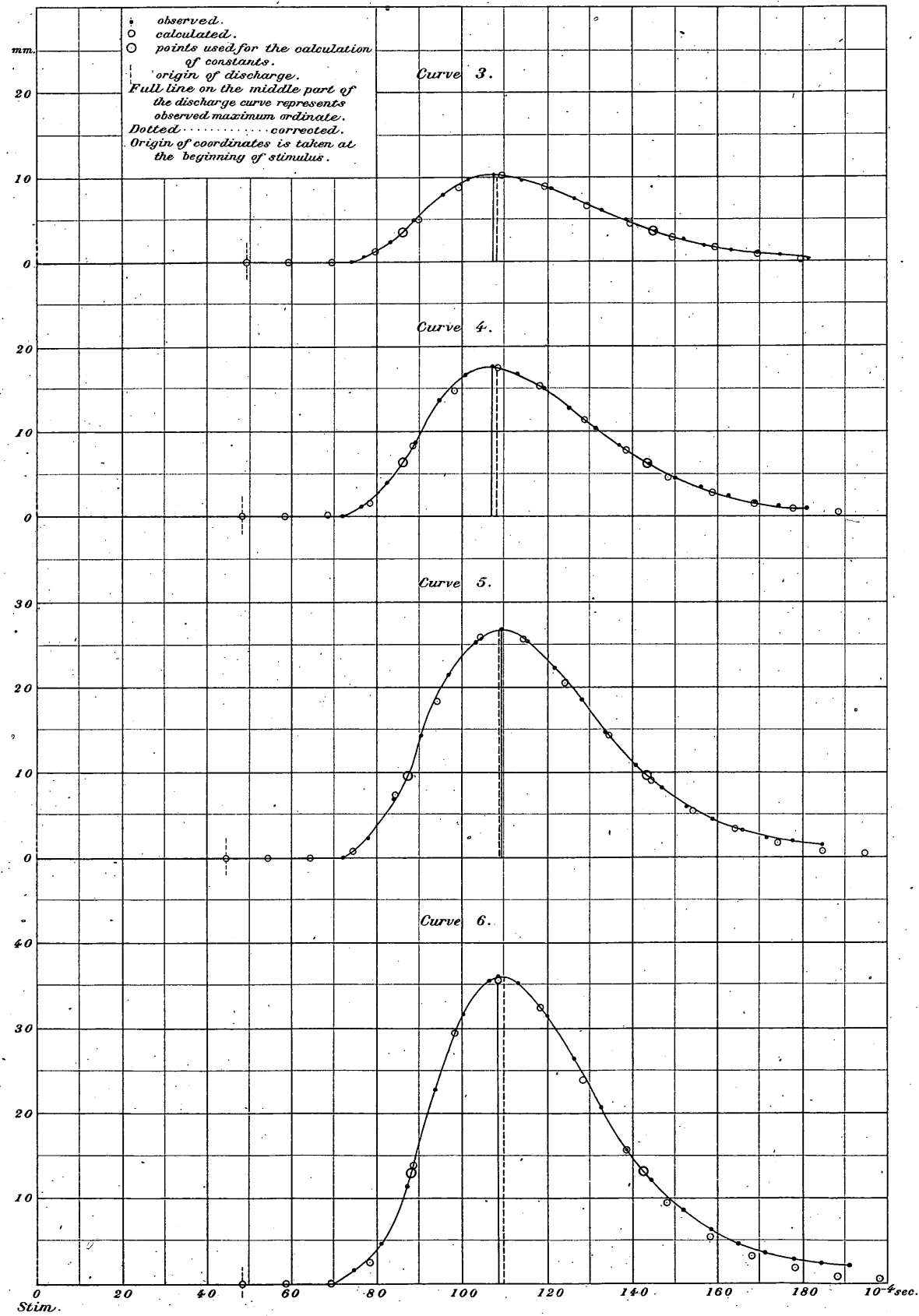


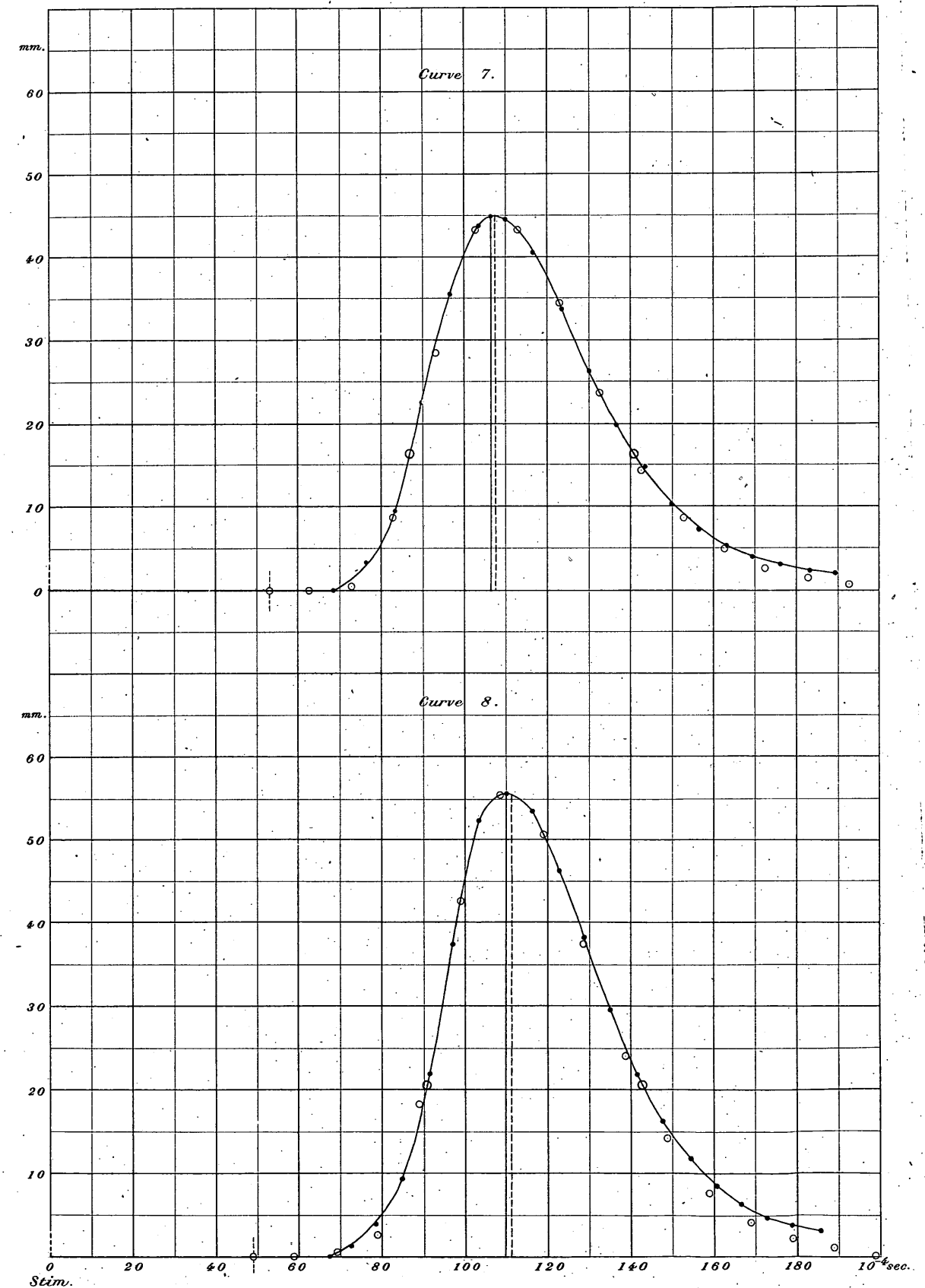
Fig. 1. Stimulation-apparatus.  
Fig. 2. Circuit-breakers.  
Fig. 3. Connection-changer.  
Fig. 4. Contrivance for Two Momentary Stimuli.  
S's Represent Screws.  
V's Represent Verniers.

Fig. 4.

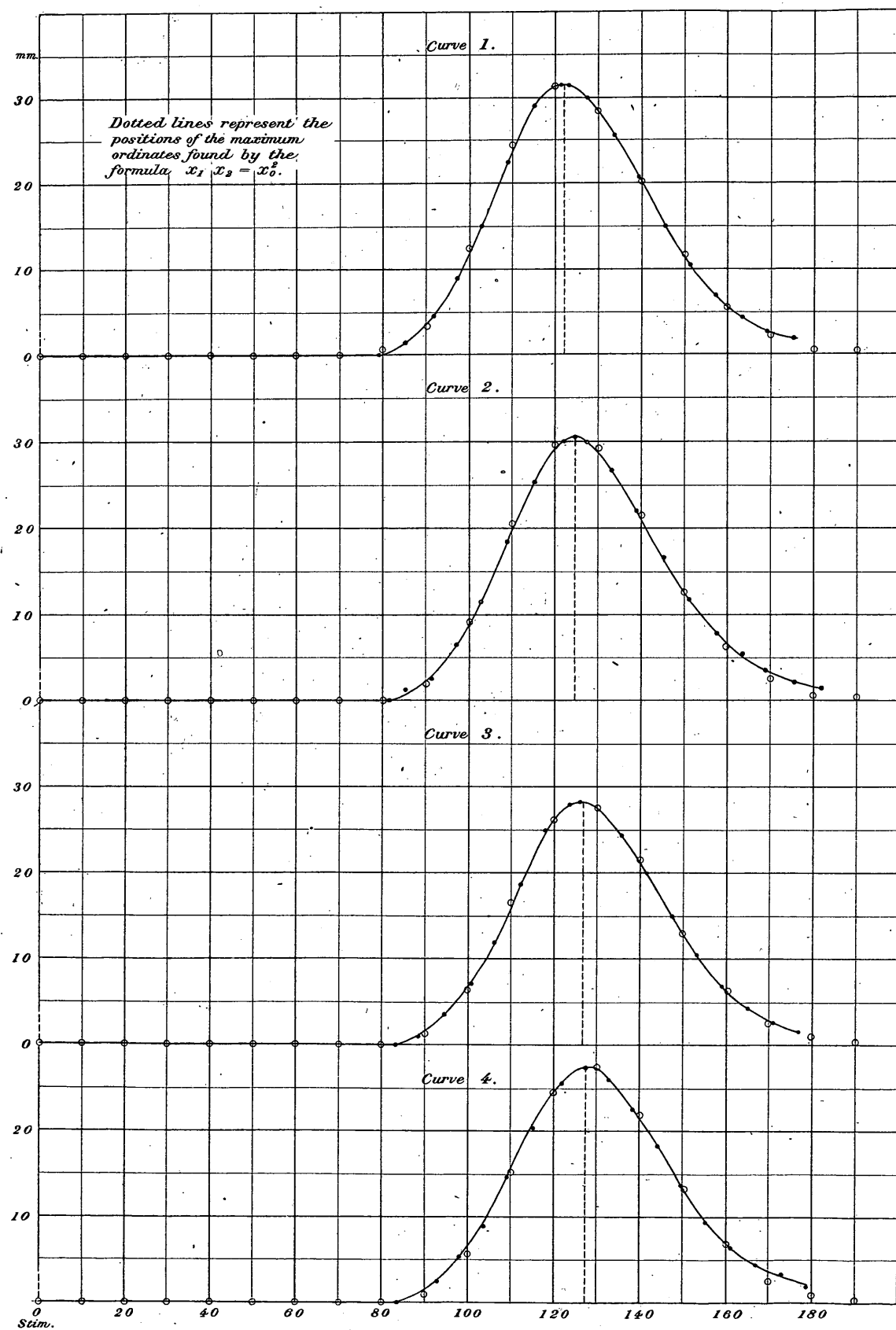
Oscillogram No. 54.



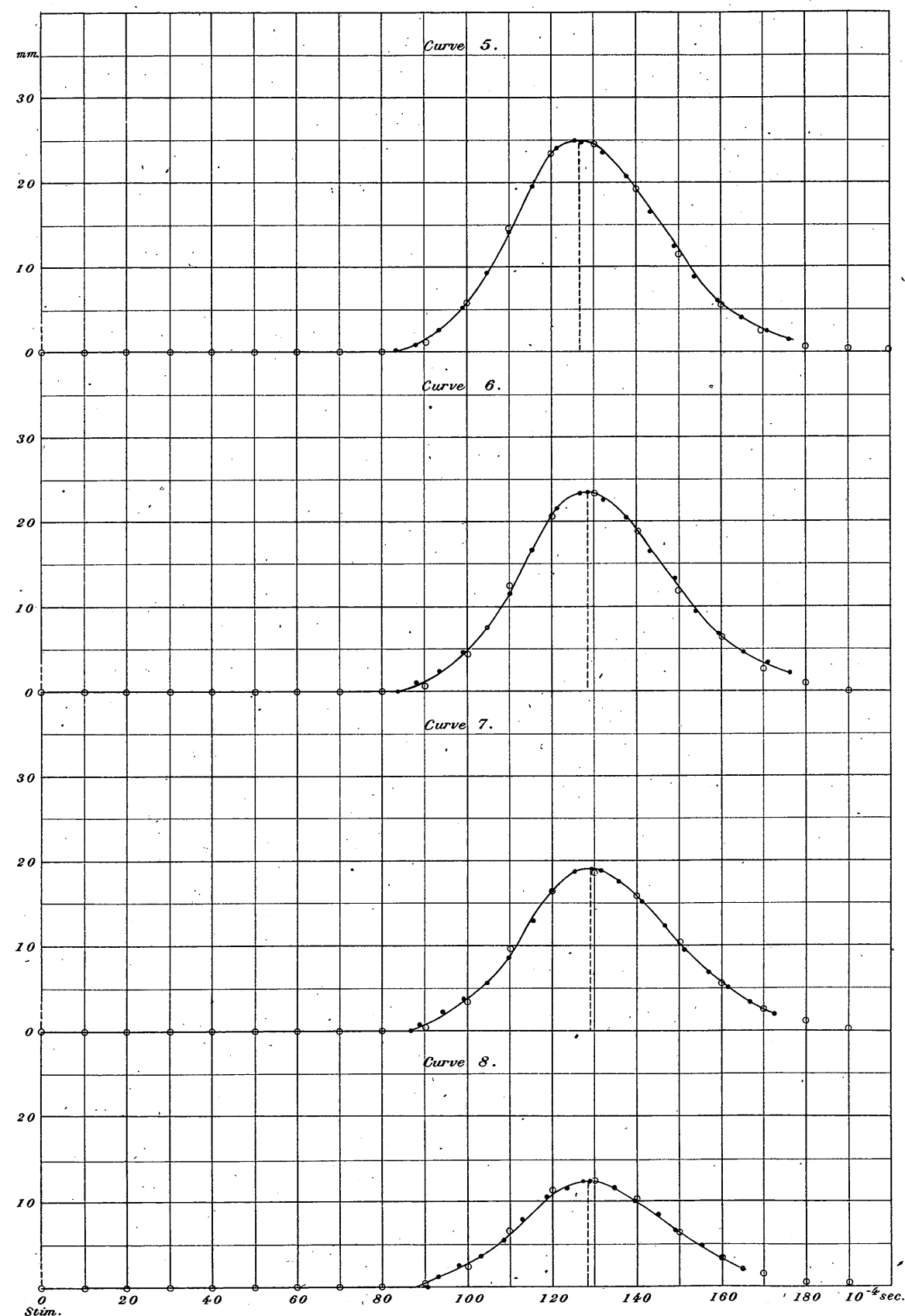
(Reduced to  $1/15$  of Actually Used Scale.)



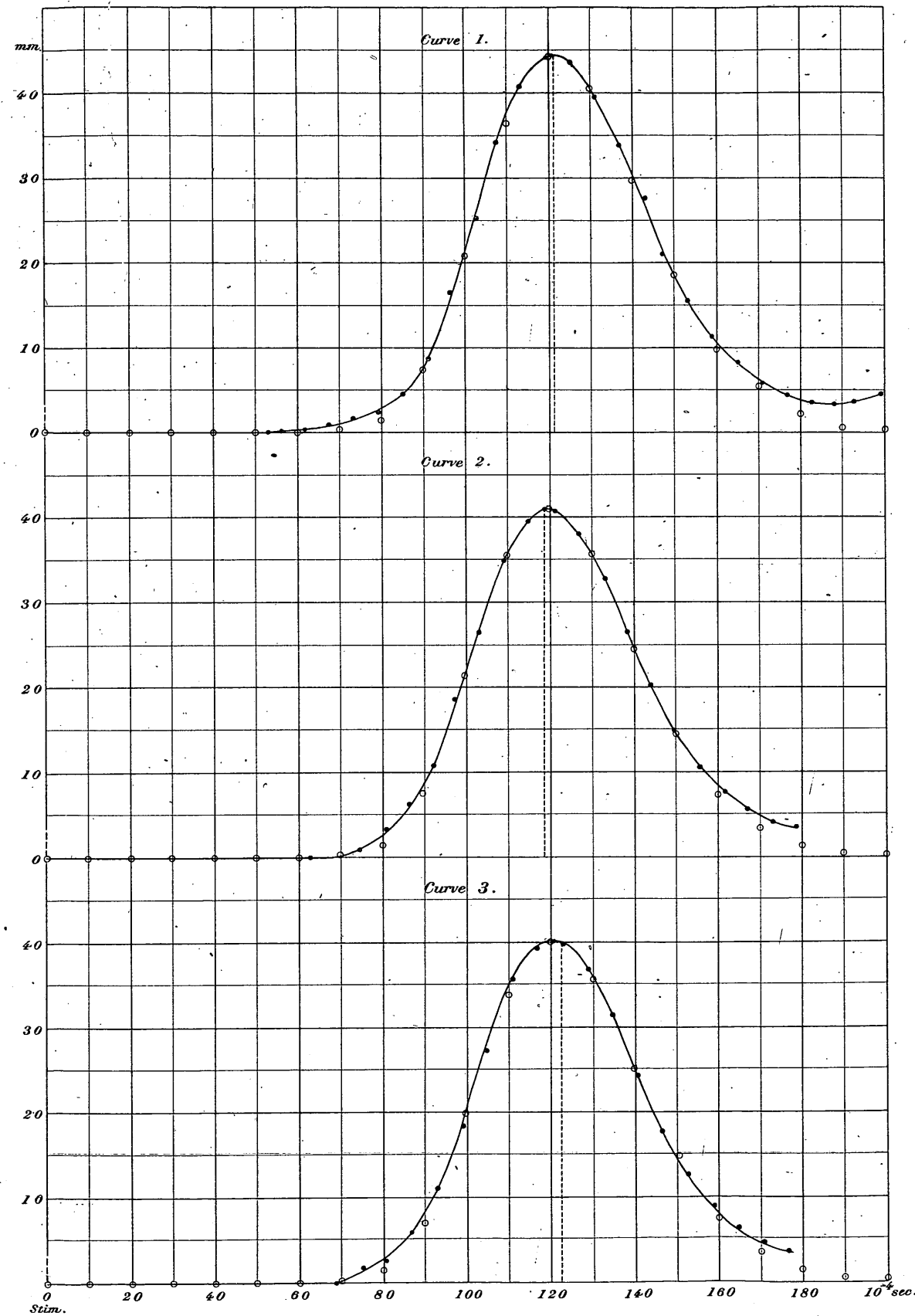
Oscillogram No. 37.



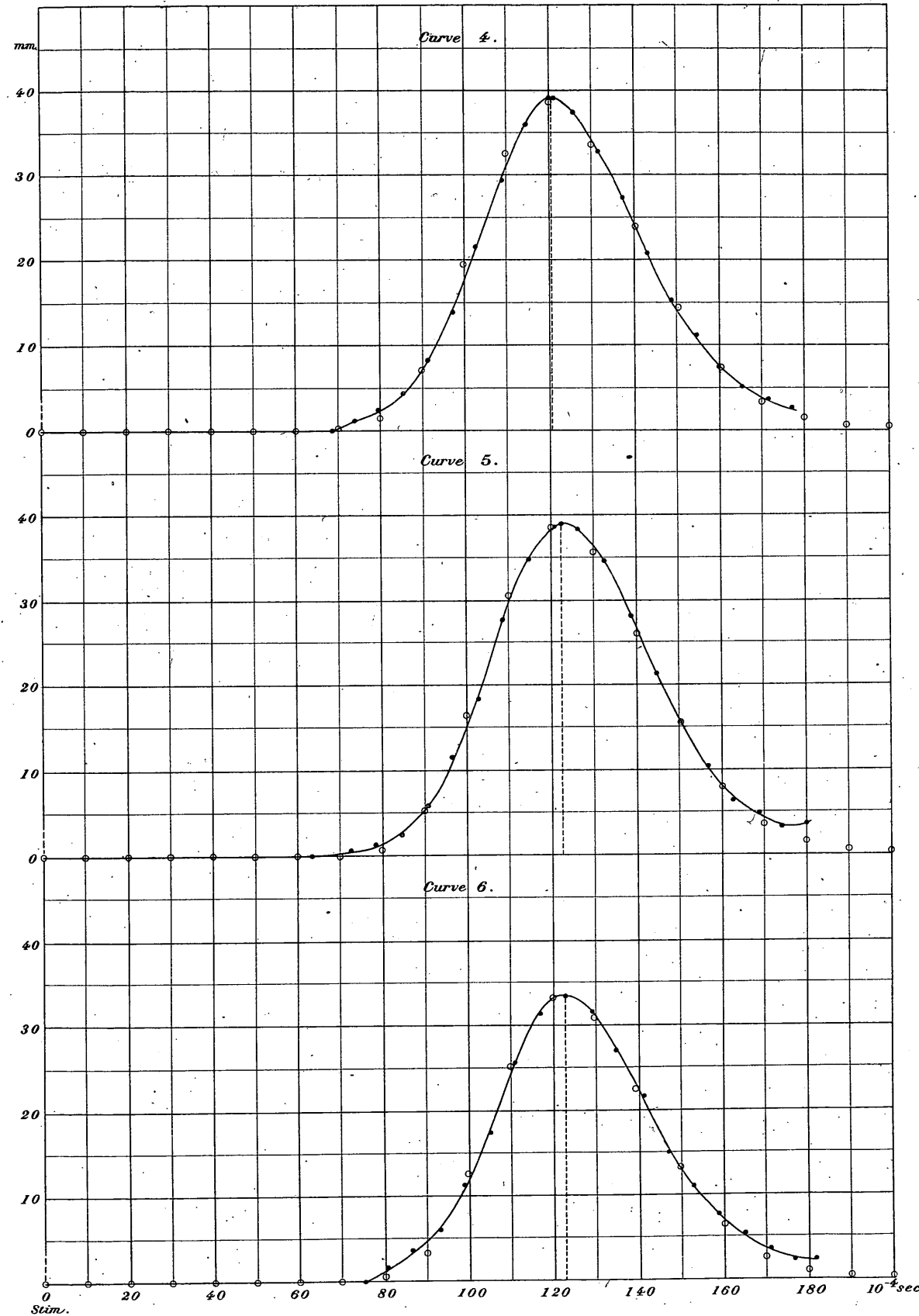
(Reduced to  $11/15$  of Actually Used Scale.)



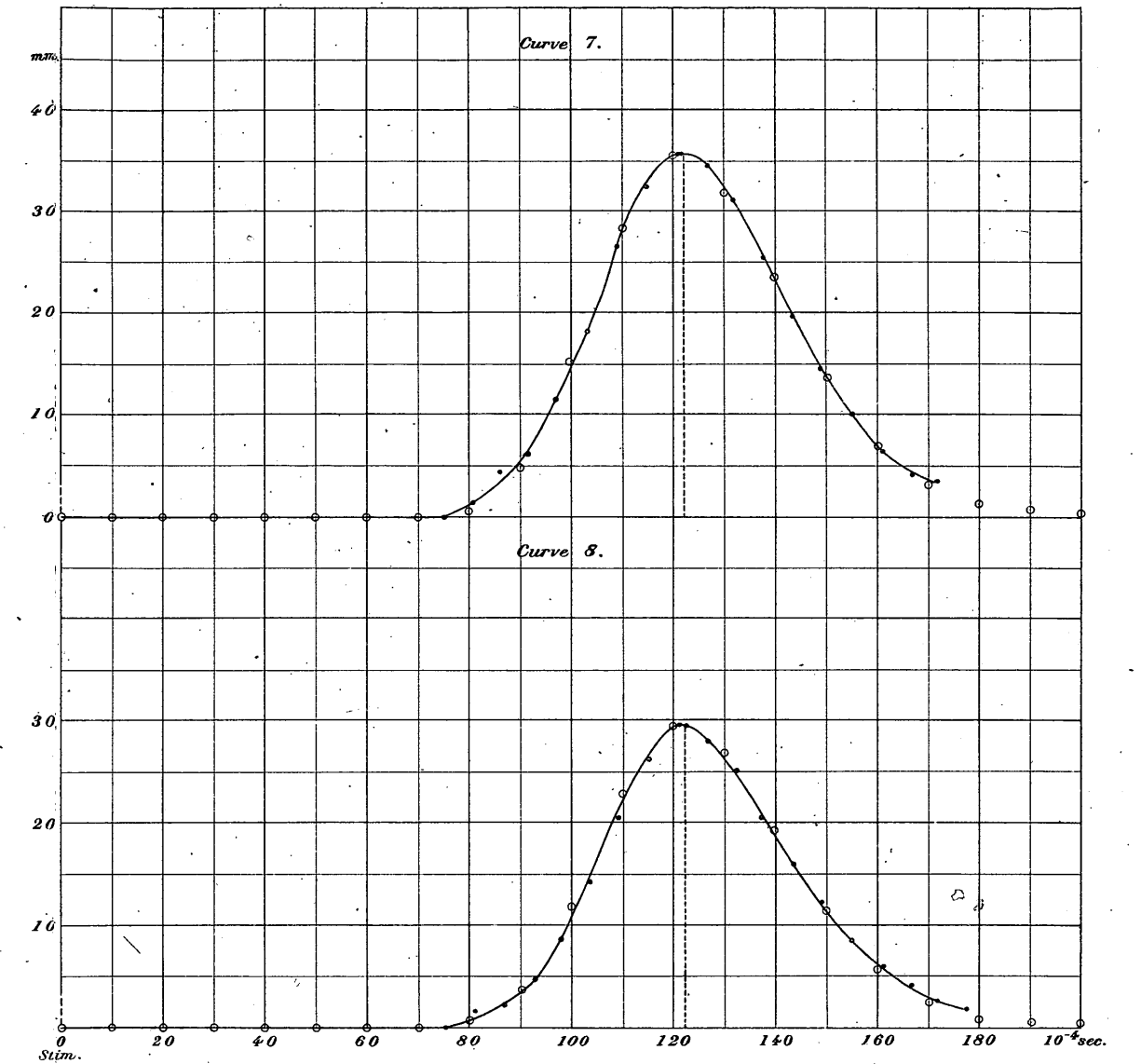
Oscillogram No. 40.



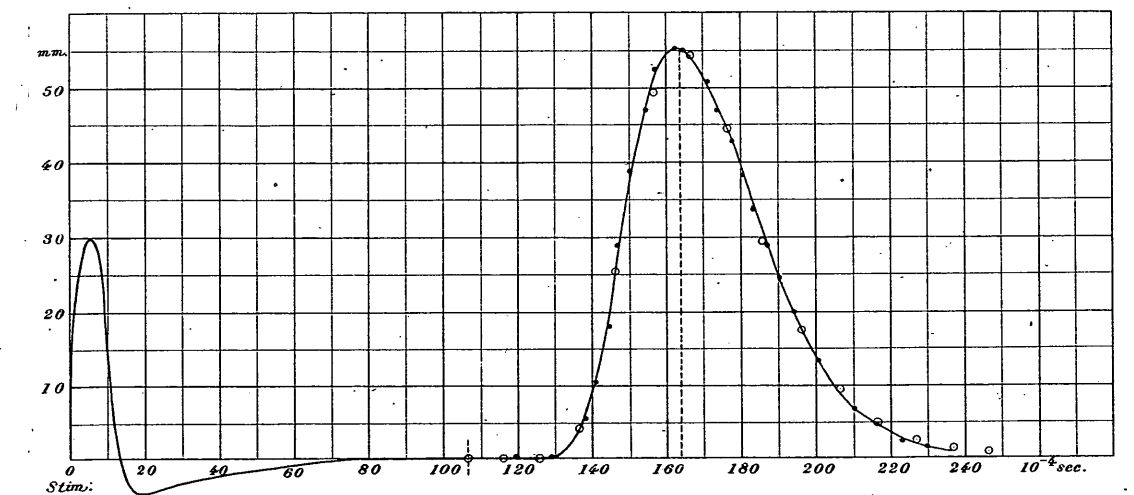
(Reduced to  $11/15$  of Actually Used Scale.)

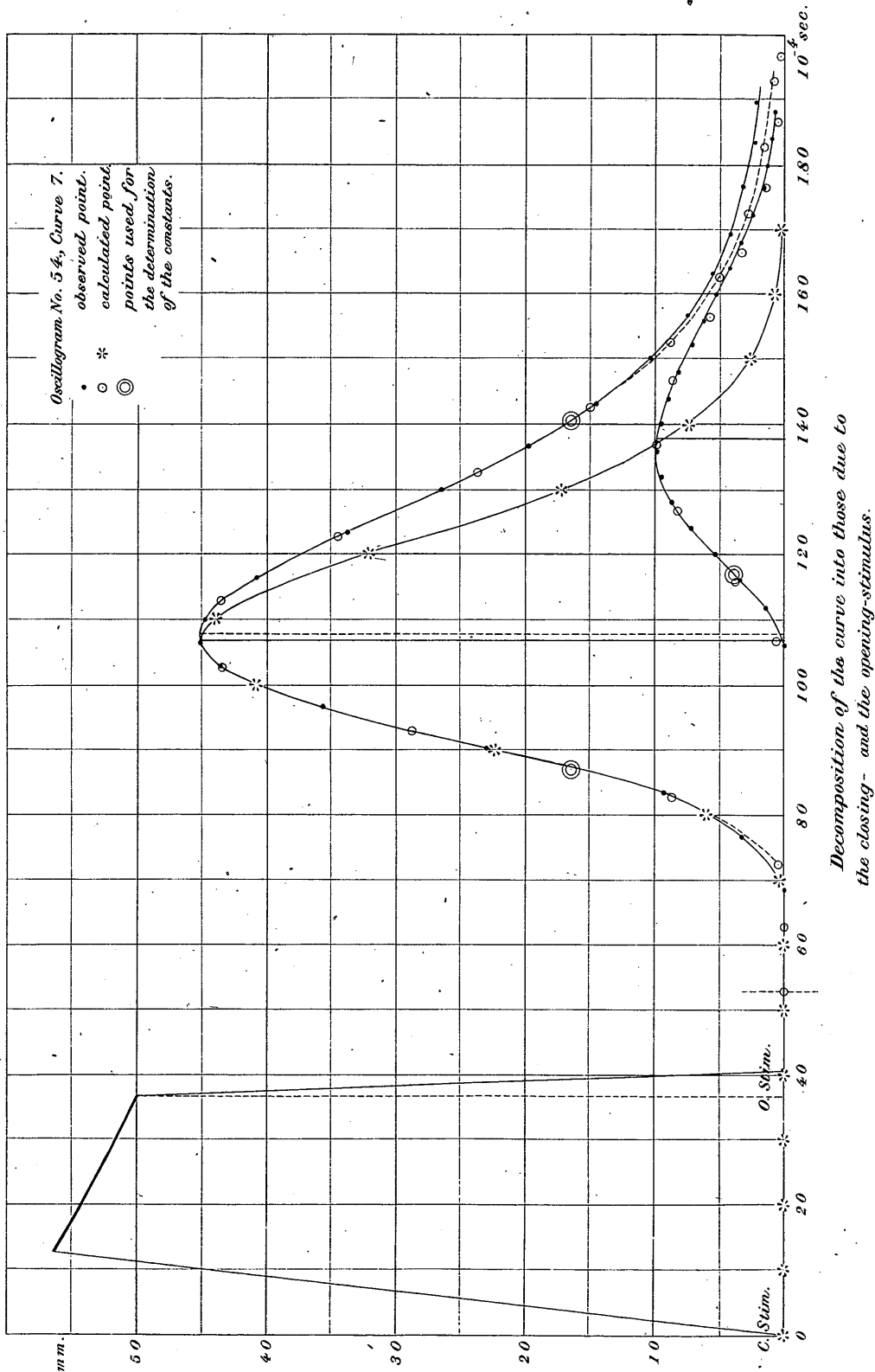


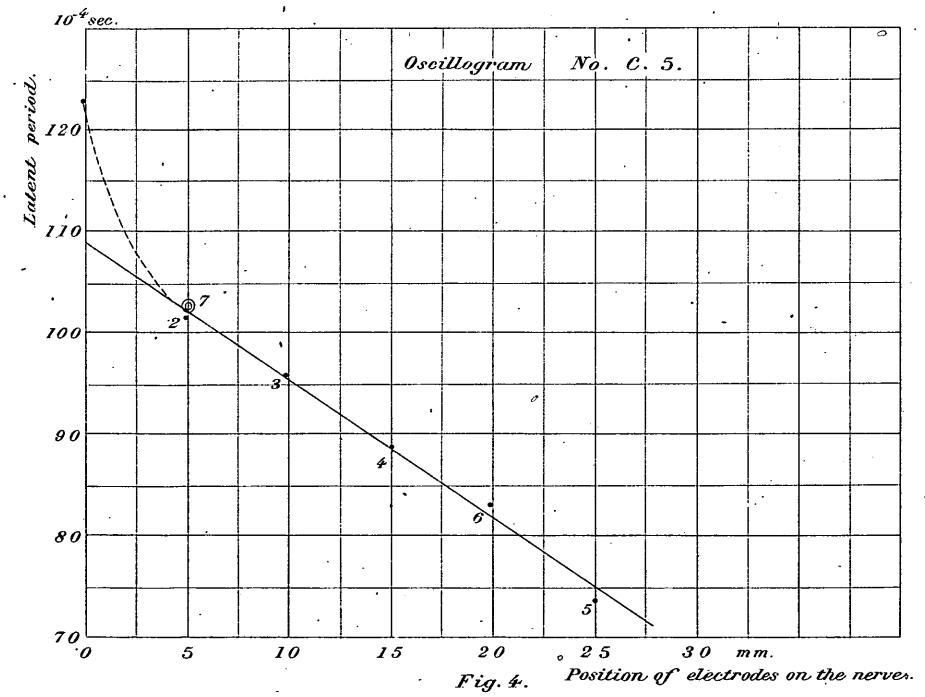
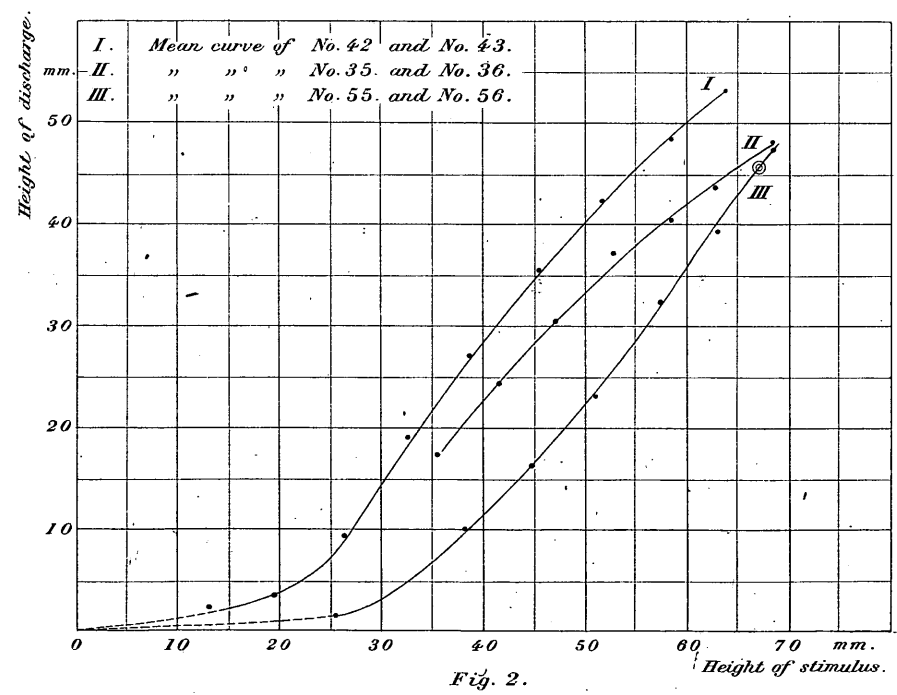
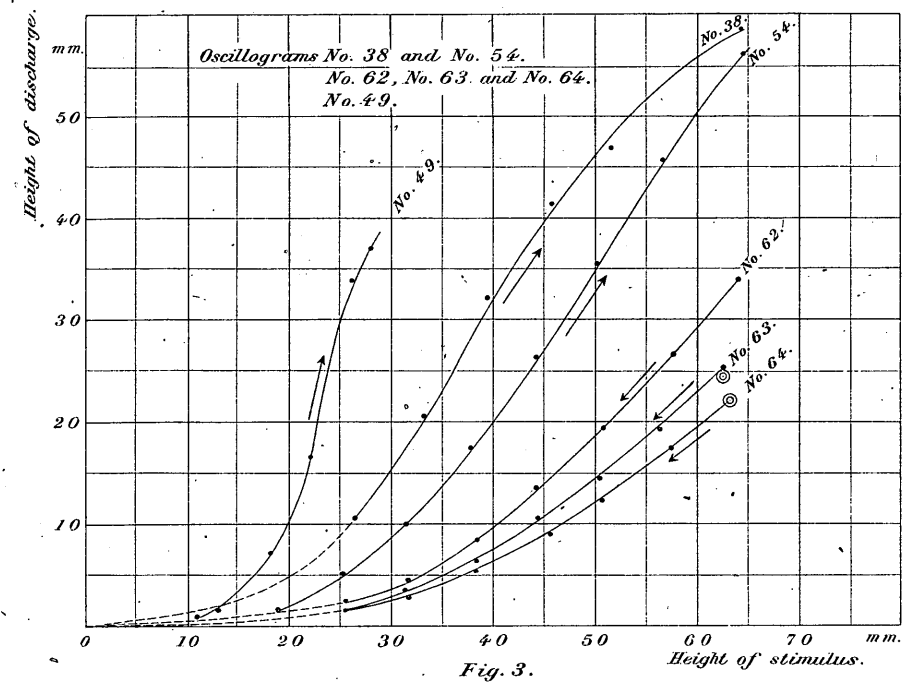
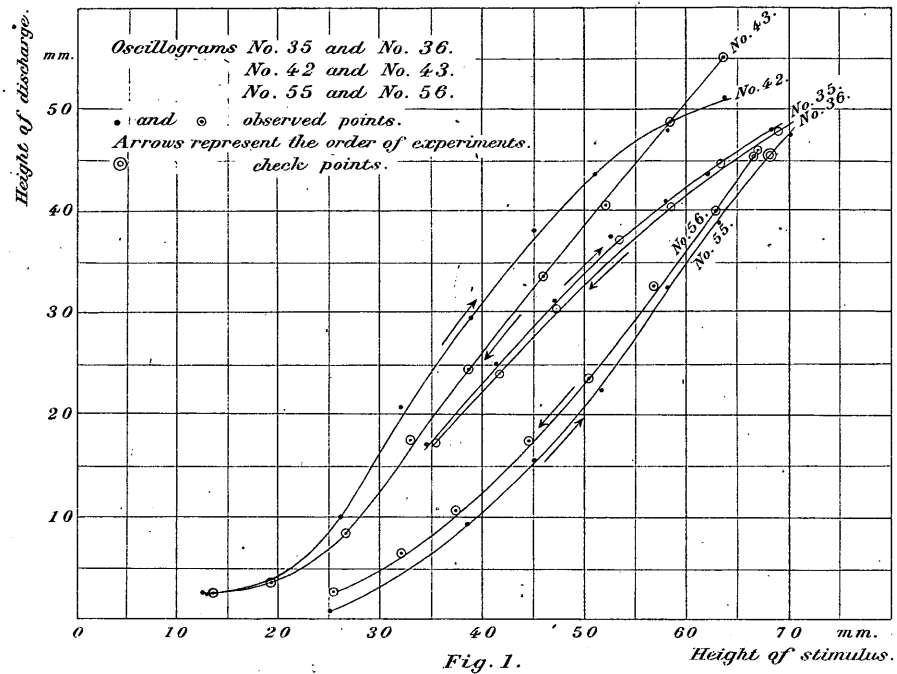
Curve 7.



Oscillogram No. C. 3.  
(Reduced to  $1/2$  of Actually Used Scale.)







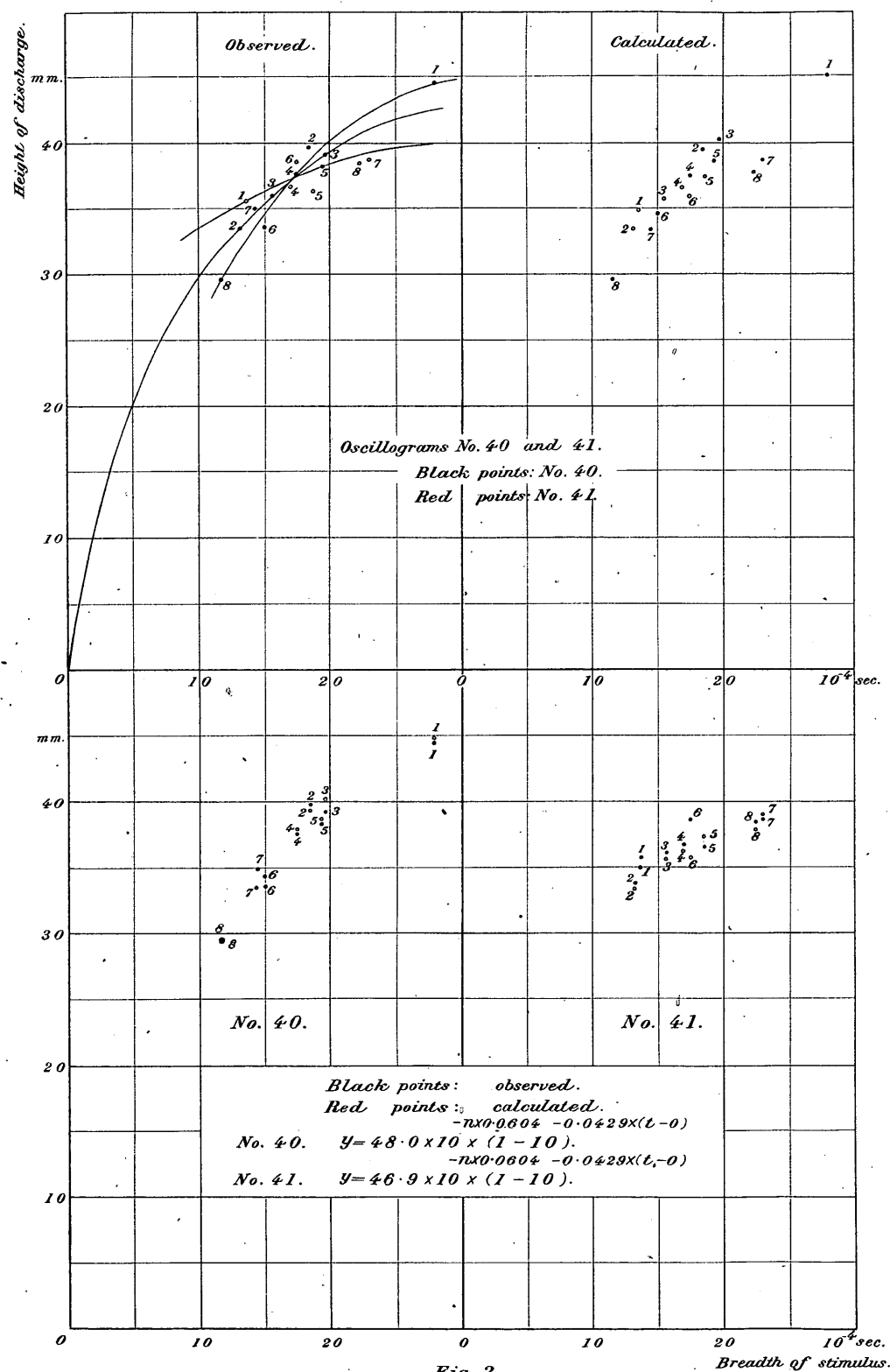


Fig. 2.

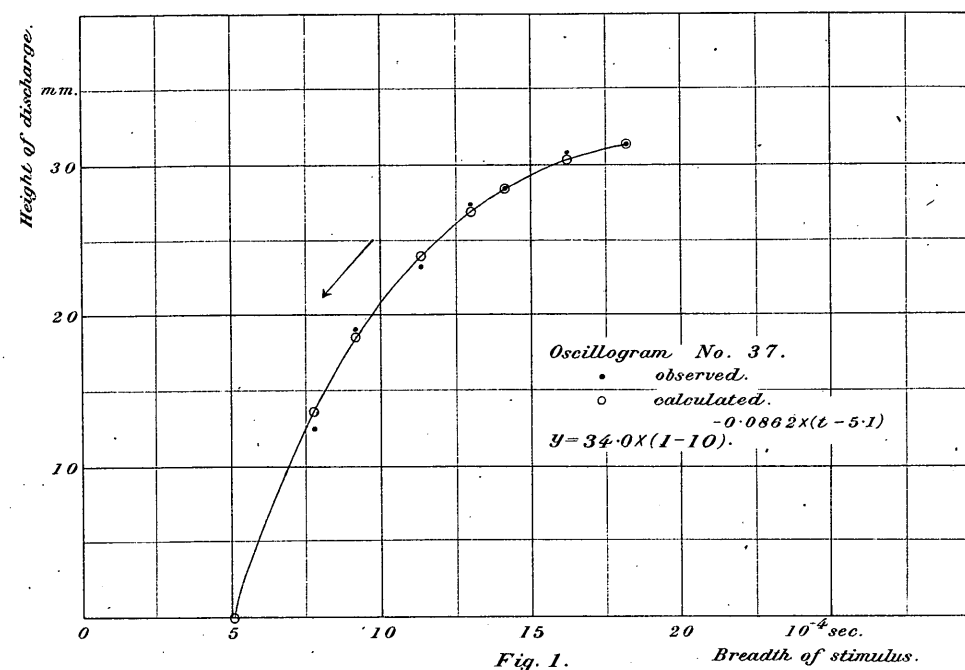


Fig. 1.

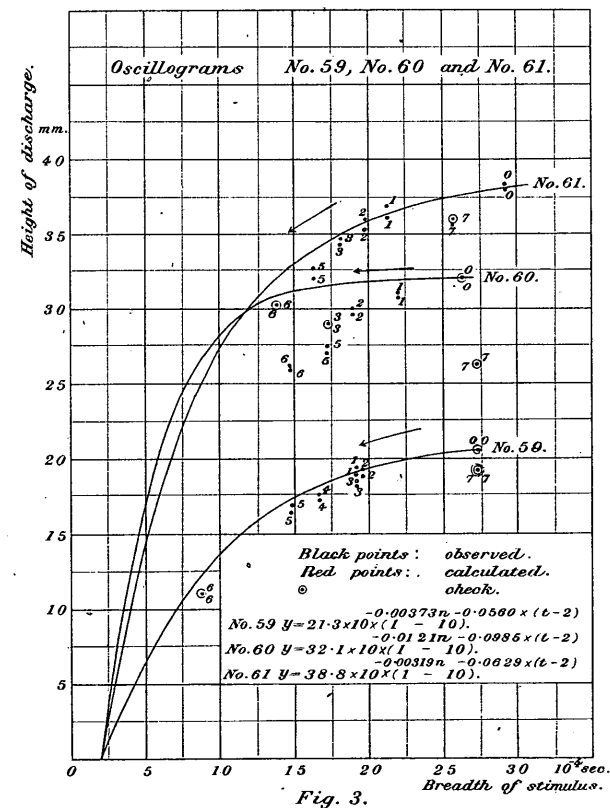


Fig. 3.

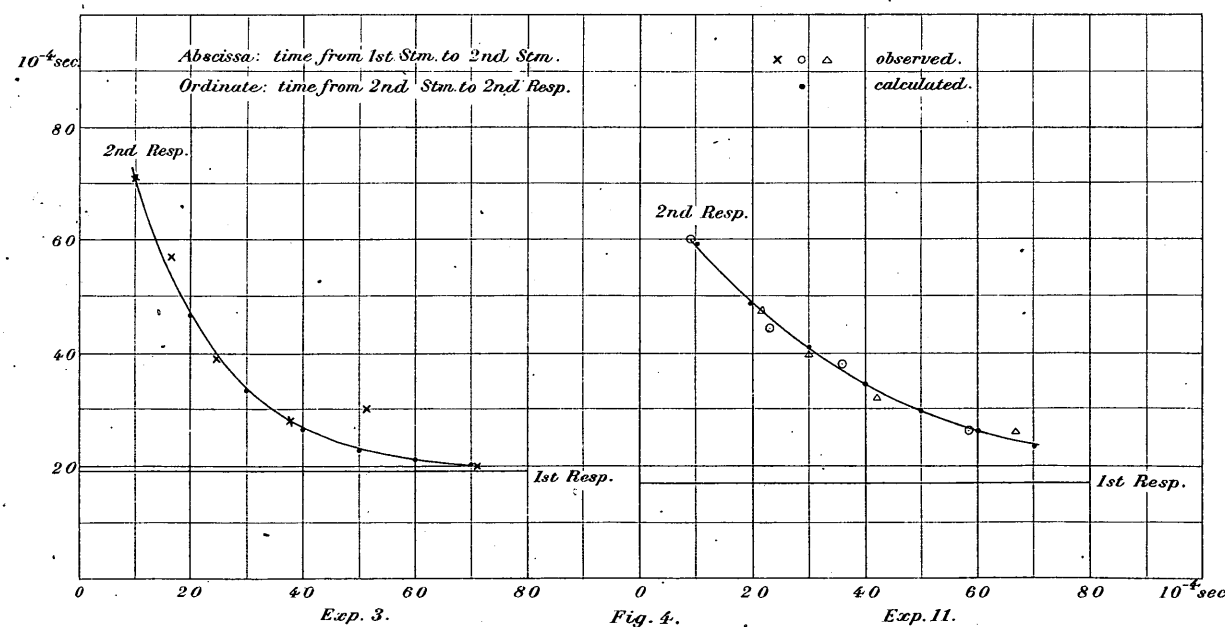
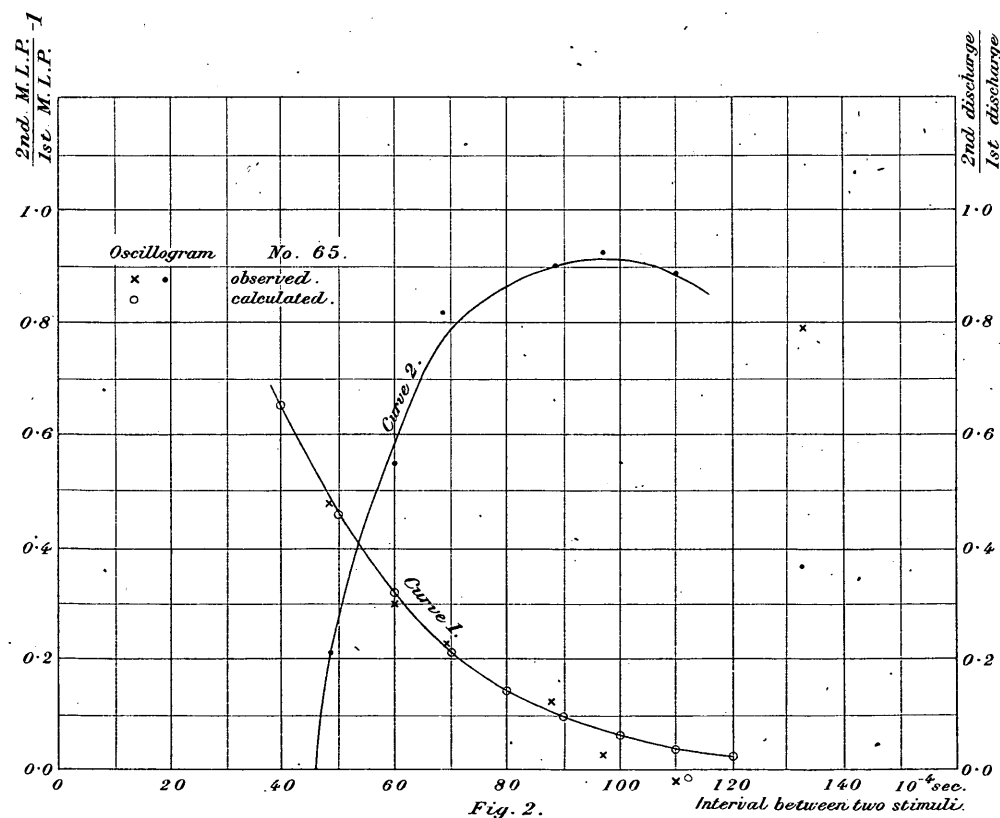
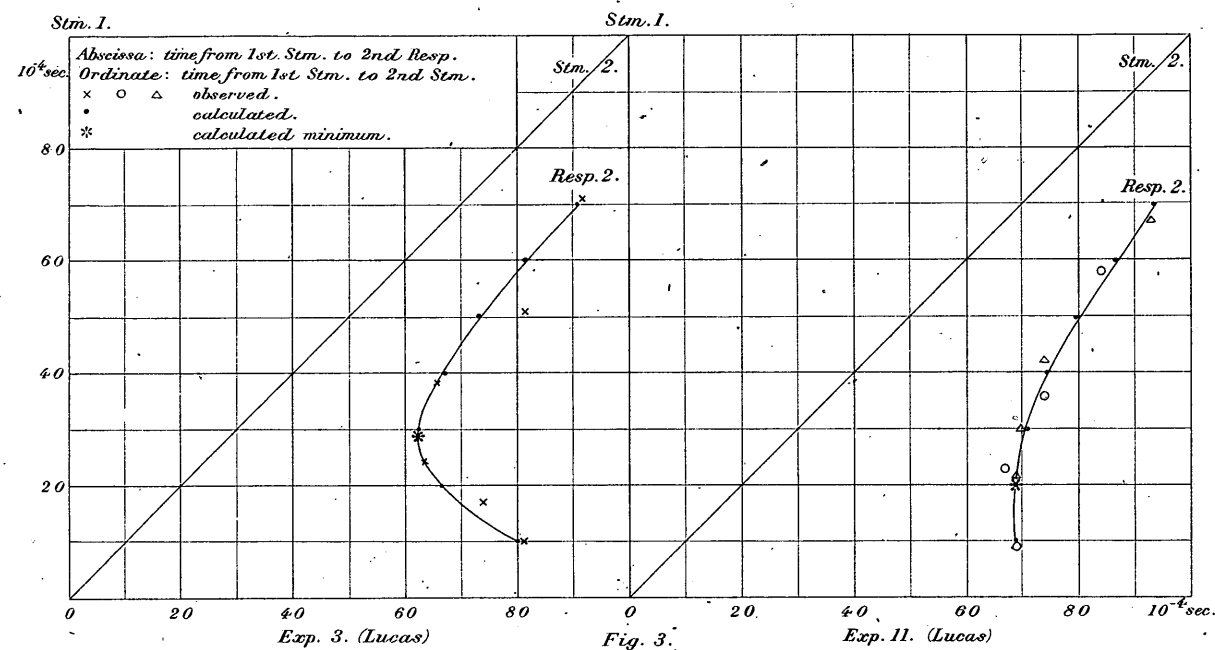
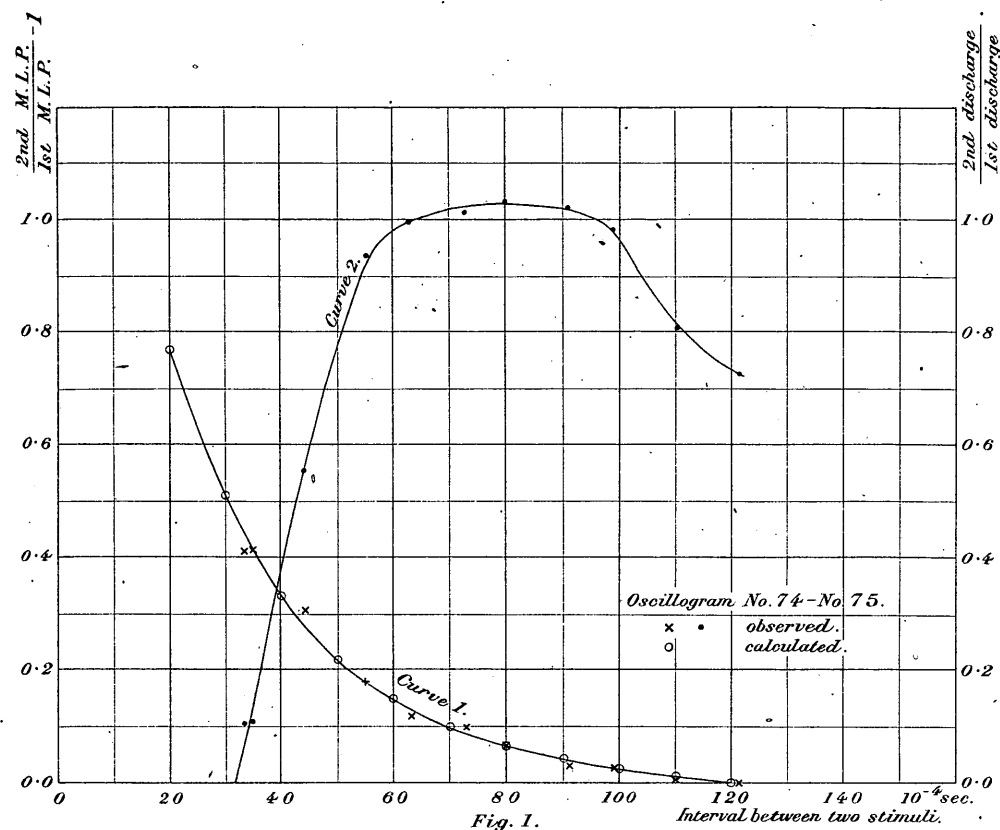




Fig. 1. Oscillogram No. 54,

Temperature of the organ :  $8.5^{\circ}-7.2^{\circ}$  C.

No. of exp. :	1	2	3	4	5	6	7	8	
E.T. :	3.07	3.13	3.08	3.06	3.13	3.24	3.33	7.14	in $10^{-4}$ sec.

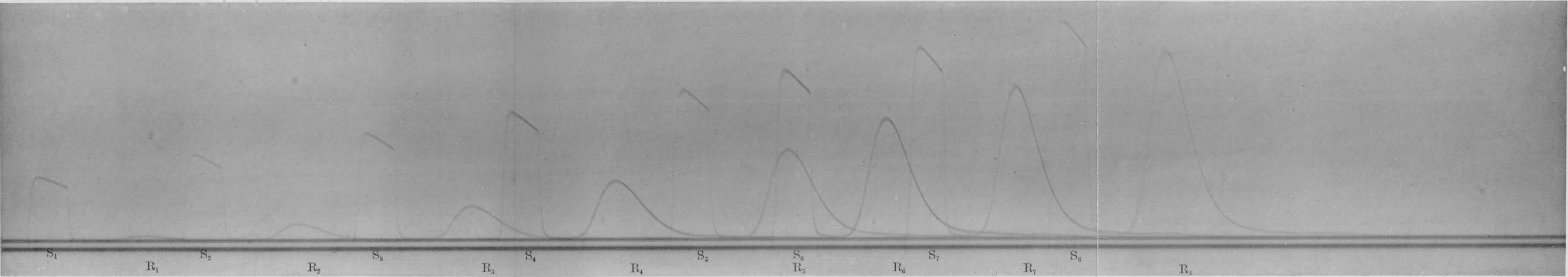


Fig. 2. Oscillogram No. 37.

Temperature of the organ :  $11.0^{\circ}$  C.

No. of exp. :	1	2	3	4	5	6	7	8	
E.T. :	3.03	3.03	2.95	2.88	2.75	2.75	2.61	2.58	in $10^{-4}$ sec.

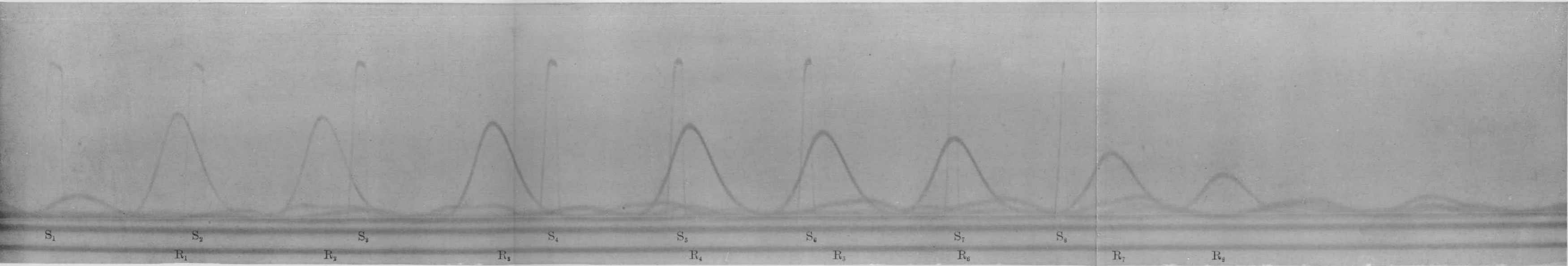
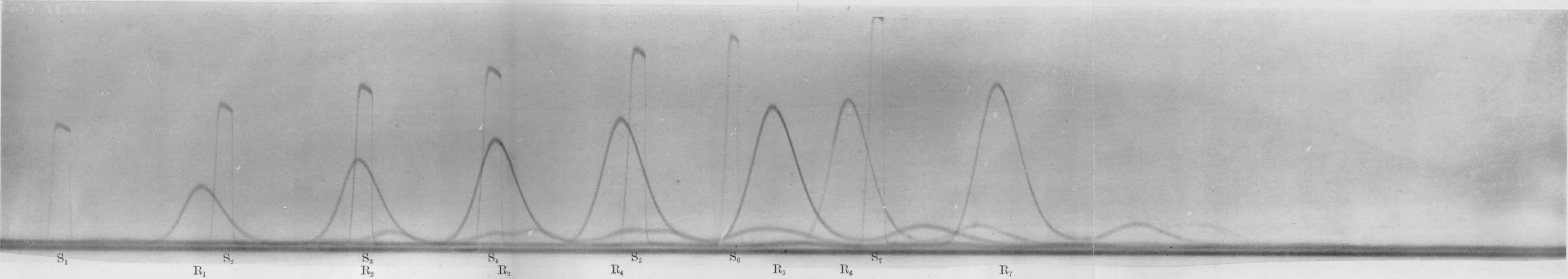


Fig. 1. Oscillogram No. 35. Temperature of the organ : 11.0° C.

No. of exp. :	1	2	3	4	5	6	7	
E.T. :	2.80	2.90	2.92	2.92	2.80	3.24	3.00	in 10 <sup>-4</sup> sec.



No. of exp. :	1	2	3	4	5	6	7	
E.T. :	2.90	2.61	2.60	2.70	2.69	2.58	2.76	in 10 <sup>-4</sup> sec.

Fig. 2. Oscillogram No. 36. Preparation same as No. 35. Order of stimuli reversed.

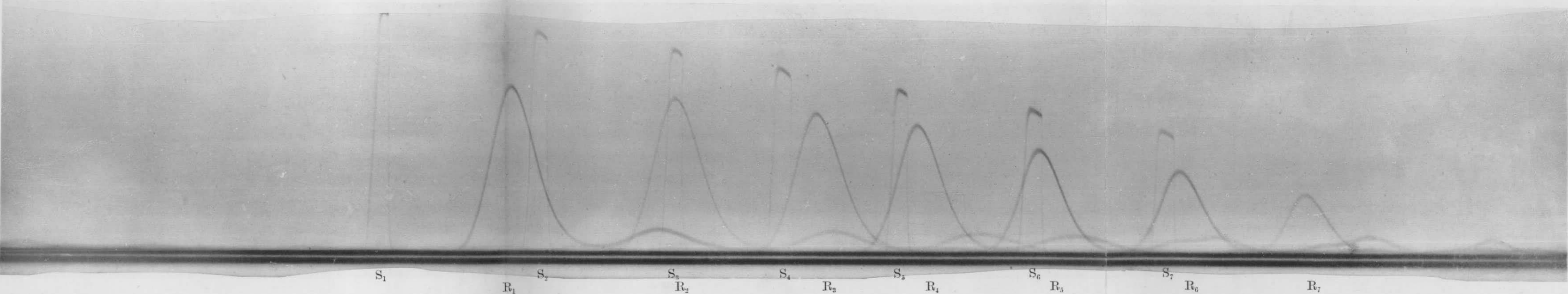




Fig. 1. Oscillogram No. 38.

Temperature of the organ: 11.5° C.

No. of exp.: 1 2 3 4 5 6  
E.T.: 2.86 2.78 3.26 3.14 2.96 2.84 in 10<sup>-4</sup>sec.

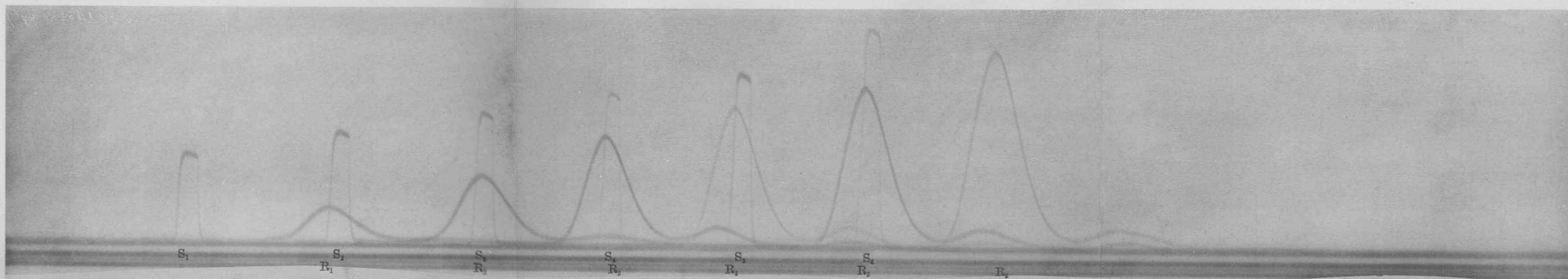


Fig. 2. Oscillogram No. 55.

Temperature of the organ: 10.4° C.

No. of exp.: 1 2 3 4 5 6 7 8  
E.T.: 3.06 3.22 3.19 3.13 3.34 3.01 3.34 3.34 in 10<sup>-4</sup>sec.

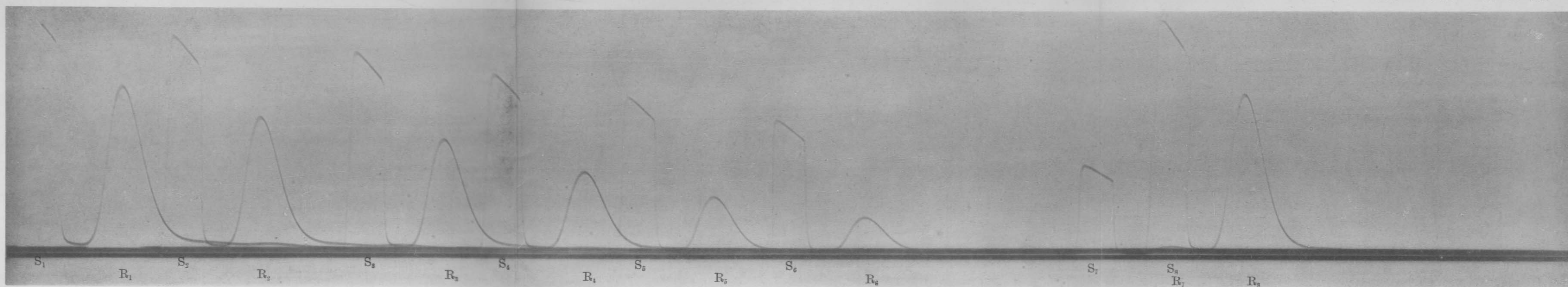


Fig. 3. Oscillogram No. 56. Preparation same as No. 55.

Order of stimuli reversed.

No. of exp.: 1 2 3 4 5 6 7 8  
E.T.: 3.38 3.48 3.67 3.66 3.64 3.47 3.72 3.47 in 10<sup>-4</sup>sec.

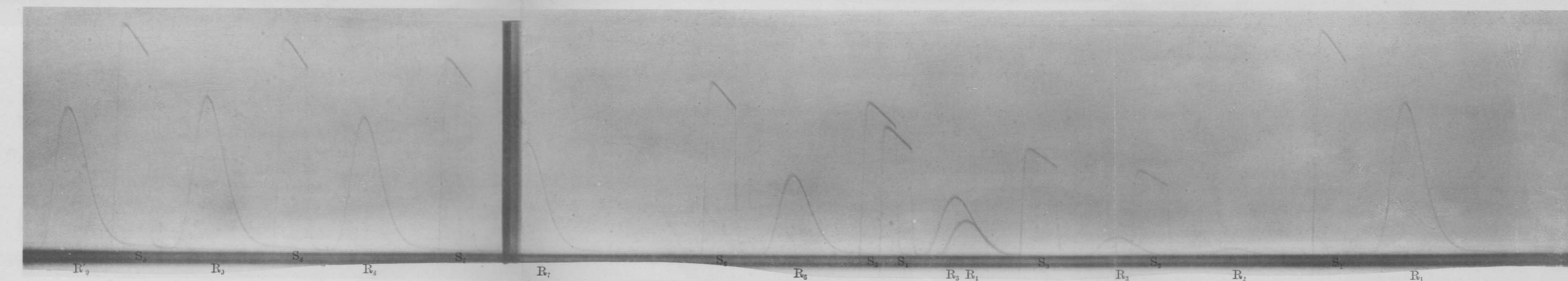




Fig. 1. Oscillogram No. 62.

Temperature of the organ: 13.5° C.

No. of exp.:	1	2	3	4	5	6	7	
E.T.:	3.10	2.76	2.88	2.86	2.87	2.78	2.73	in 10 <sup>-4</sup> sec.

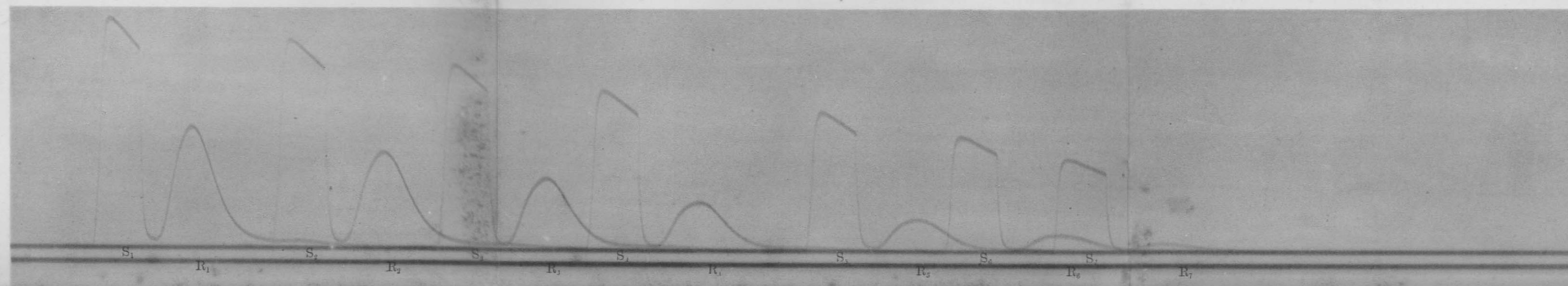


Fig. 2. Oscillogram No. 63.

Preparation same as No. 62.

No. of exp.:	1	2	3	4	5	6	7	8	
E.T.:	2.90	2.92	2.93	2.82	2.78	2.74	—	2.86	in 10 <sup>-4</sup> sec.

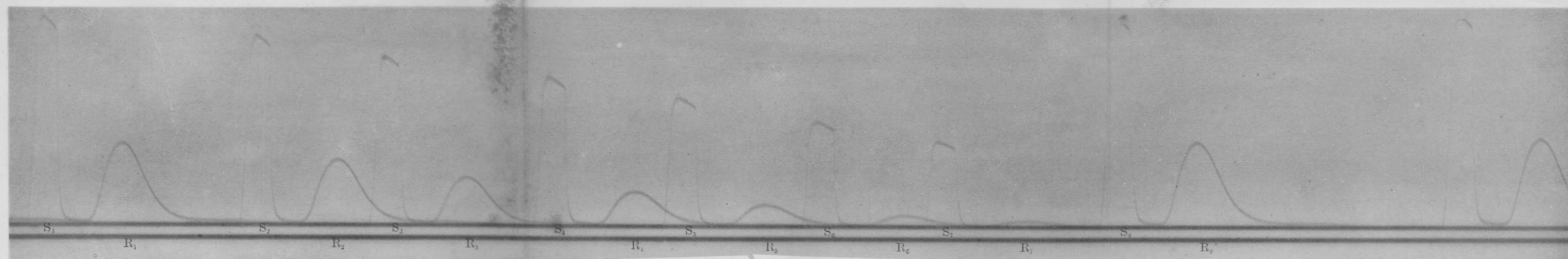
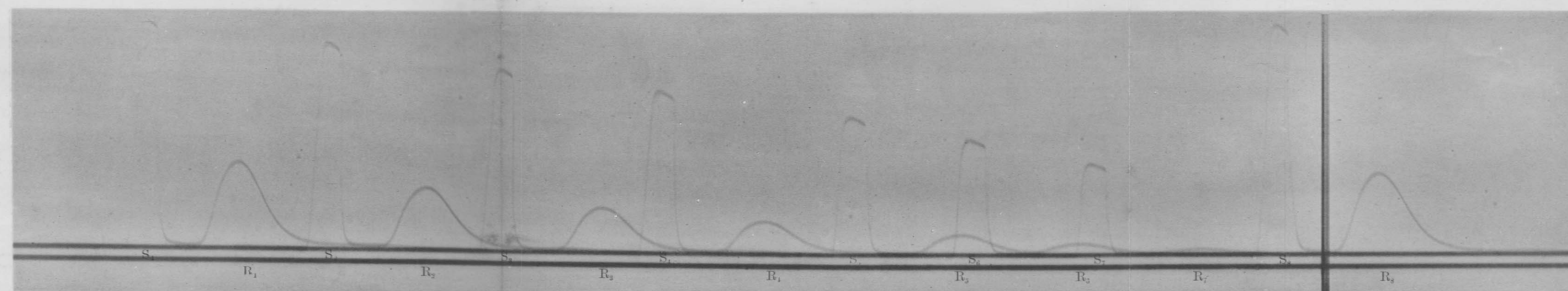


Fig. 3. Oscillogram No. 64.

Preparation same as No. 62.

No. of exp.:	1	2	3	4	5	6	7	8	
E.T.:	2.72	2.56	2.50	2.42	2.41	2.50	2.70	2.40	in 10 <sup>-4</sup> sec.



Oscillograms No. 62, No. 63 and No. 64 are of a set of experiments carried out with the same preparation.



Fig. 1. Oscillogram No. 40,

Temperature of the organ : 11.5° C.

No. of exp. :	0	1	2	3	4	5	6	7	
E.T. :	2.86	2.88	2.96	2.86	3.00	3.00	2.86	2.84	in 10 <sup>-4</sup> sec.

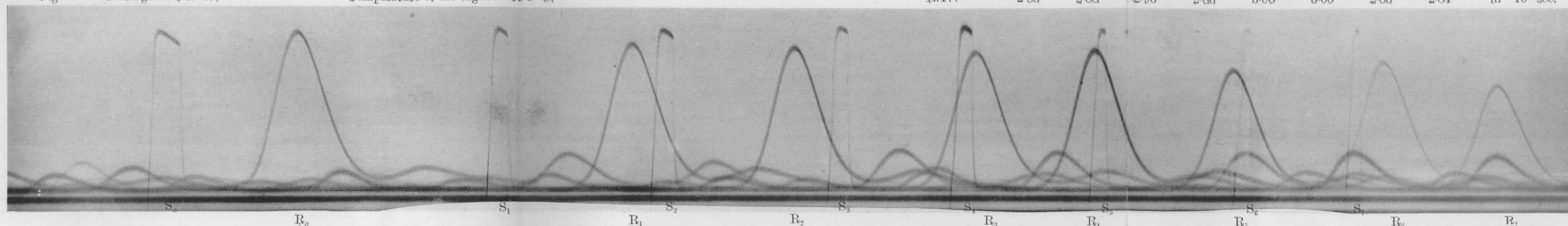


Fig. 2. Oscillogram No. 41.

Preparation same as No. 40.

Order of stimuli reversed.

No. of exp. :	0	1	2	3	4	5	6	7	
E.T. :	3.31	3.27	3.27	3.08	3.14	3.29	3.20	3.16	in 10 <sup>-4</sup> sec.

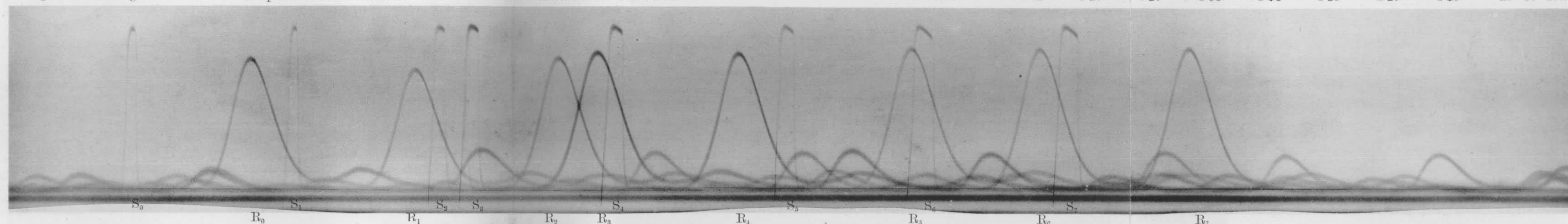


Fig. 3. Oscillogram No. 58.

Temperature of the organ : 13.3° C.

Resistance of the organ : 200 Ω.

No. of exp. :	1	2	3	4	6	7		
E.T. :	3.54	3.35	3.50	3.65	3.485	3.46	3.67	3.48 in 10 <sup>-4</sup> sec.

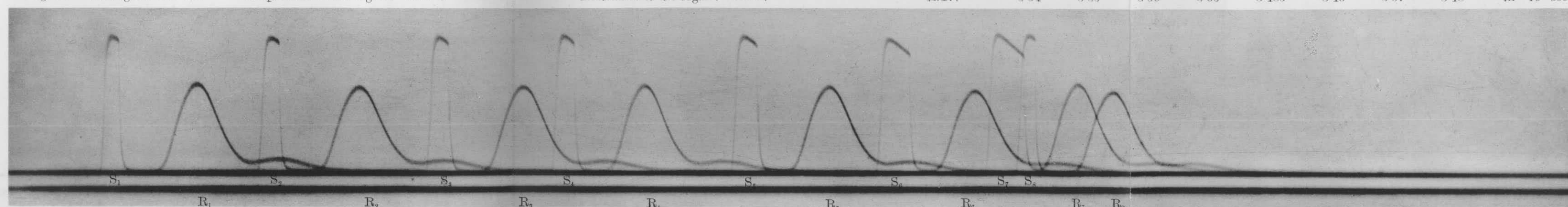


Fig. 1. Oscillogram No. 59.

Temperature of the organ: 13.5° C.

No. of exp.:	0	1	2	3	4	5	6	7	
E.T.:	3.33	3.18	3.66	3.51	3.41	3.46	3.53	3.34	in 10 <sup>-4</sup> sec.

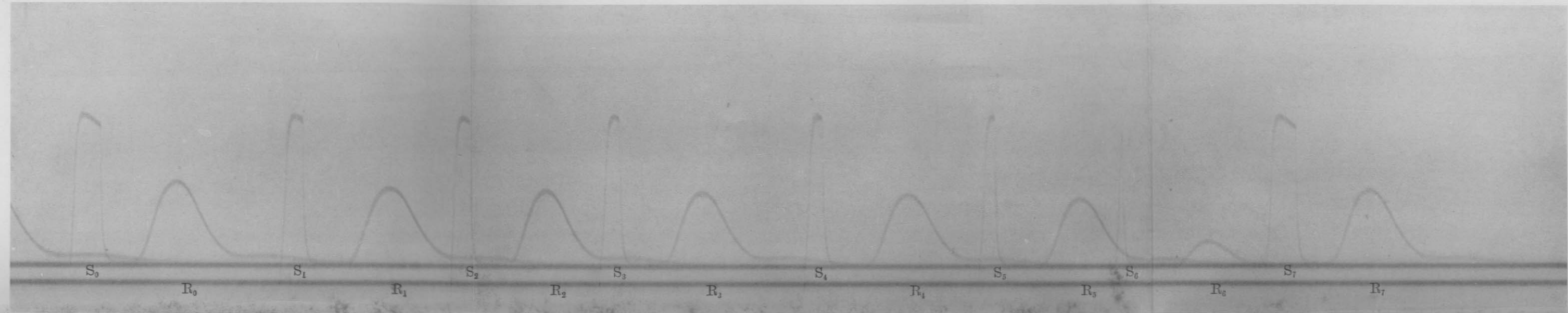


Fig. 2. Oscillogram No. 60.

Preparation same as No. 59.

No. of exp.:	0	1	2	3	4	5	6	7	
E.T.:	2.22	2.27	2.24	2.13	2.25	2.14	—	2.32	in 10 <sup>-4</sup> sec.

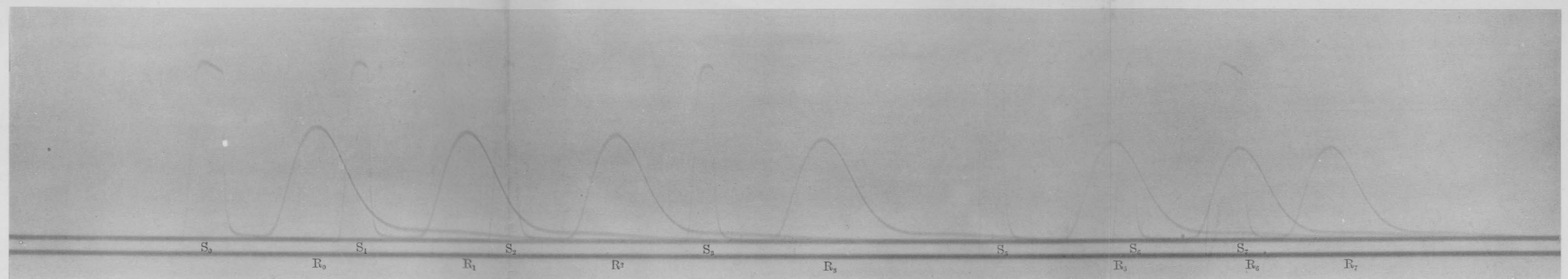
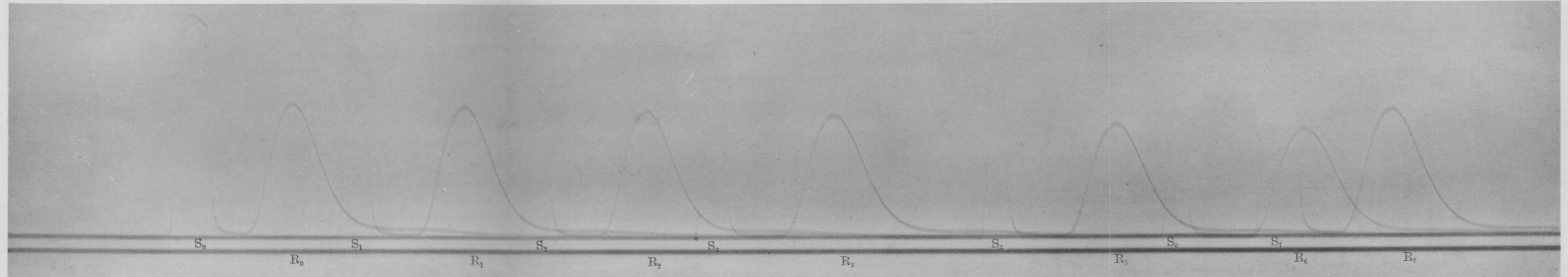


Fig. 3. Oscillogram No. 61.

Preparation same as No. 59.

No. of exp.:	0	1	2	3	4	5	6	7	
E.T.:	2.33	2.23	2.29	2.06	2.14	2.07	1.95	2.03	in 10 <sup>-4</sup> sec.



Oscillograms No. 59, No. 60 and No. 61 are of a set of experiments carried out with the same preparation.



Fig. 1. Oscillogram No. 74.

Temperature of the organ. 14.5° C.

No. of exp.:	1	2	3	4	5	6	7	8	
E.T.:	3.35	3.30	3.24	3.22	3.43	3.31	3.24	3.28	in 10 <sup>-4</sup> sec.

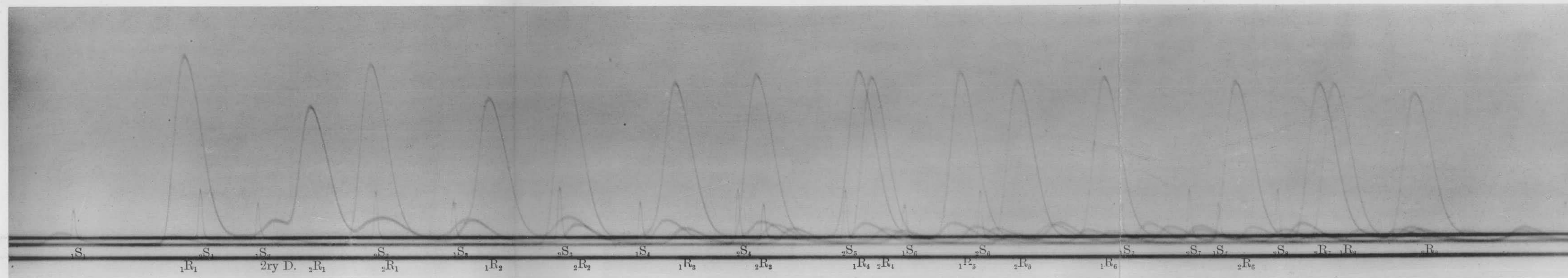


Fig. 2. Oscillogram No. 75.

Continued from No. 74.

No. of exp.:	9	10	11	12	13	14	15	16	
E.T.:	3.16	3.05	3.02	3.04	2.98	3.04	3.00	2.90	in 10 <sup>-4</sup> sec.

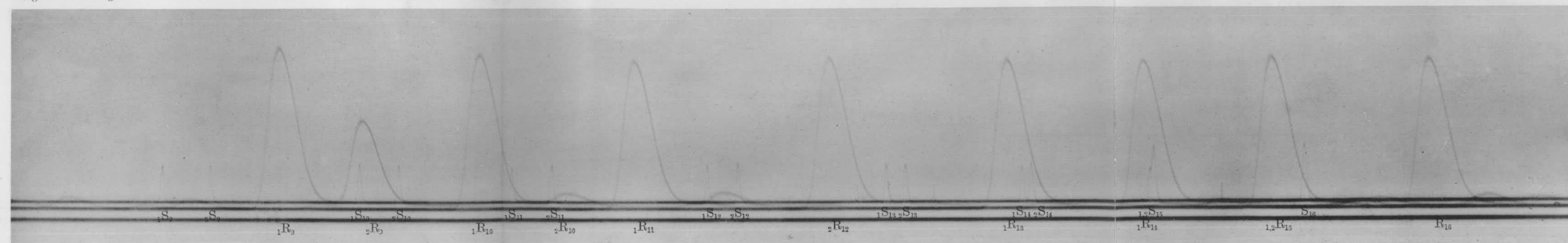


Fig. 1. Oscillogram No. 65.

Temperature of the organ: 13.5° C.

No. of exp.:	1	2	3	4	5	6	7	8	9	
E.T.:	3.16	3.04	3.05	3.22	3.19	3.14	3.09	3.06	3.06	in 10 <sup>-4</sup> sec.

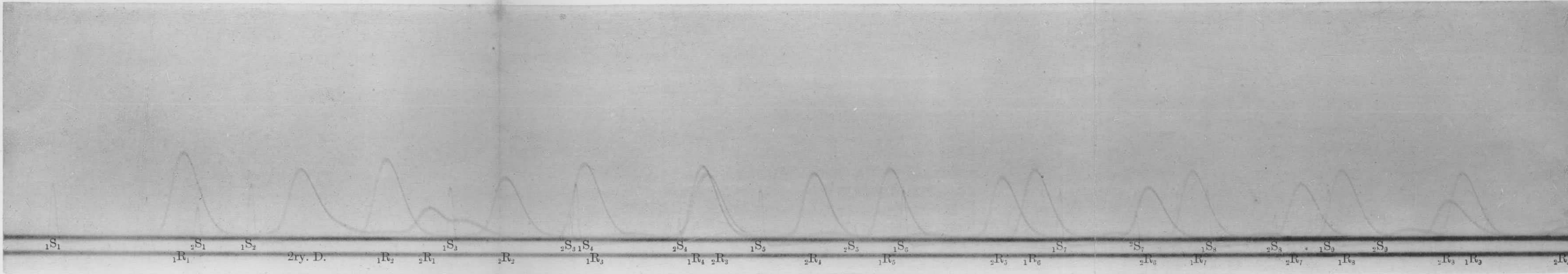


Fig. 2. Oscillogram No. 84.

No. of exp.:	1	2	3	4	5	6	7	8	9	
E.T.:	3.16	3.40	3.47	3.64	4.47	4.15	4.05	3.88	4.38	in 10 <sup>-4</sup> sec.

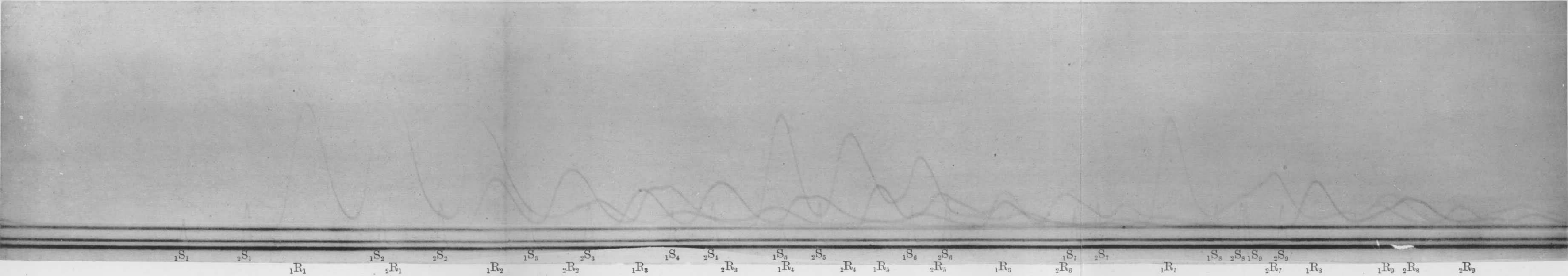




Fig. 1. Oscillogram No. 50. Temperature of the organ : 8.2° C. Inserted resistance : 200  $\Omega$ . No. of exp. : 1 2 3 4 5 6 7 in  $10^{-4}$  sec.  
E.T. : 2.50 2.50 2.50 2.60 2.60 2.74 2.74

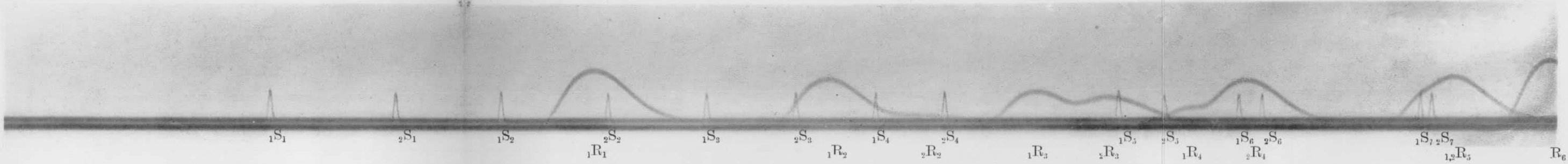


Fig. 2. Oscillogram No. 47. Temperature of the organ : 8.5° C. Inserted resistance : 300  $\Omega$ . No. of exp. : 1 2 3 4 5 6 7 8 in  $10^{-4}$  sec.  
E.T. : 2.64 2.67 2.53 2.50 2.35 2.41 2.36 —

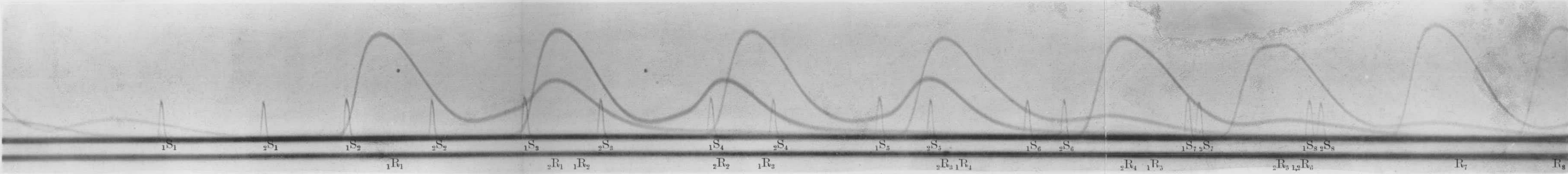


Fig. 3. Oscillogram No. 51. E.T. : Fail.

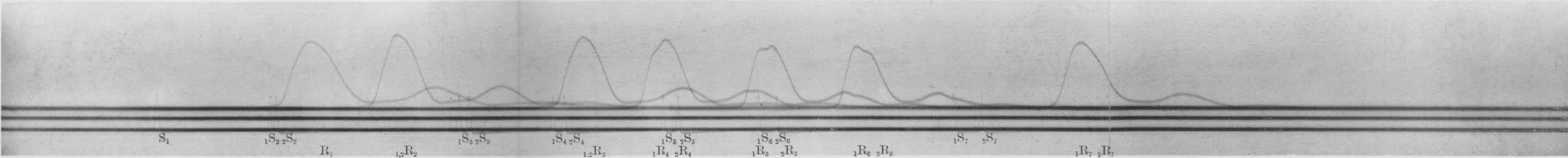


Fig. 1. Oscillogram No. 70, Superposition of the closing and the opening-discharge,

No. of exp. :	1	2	3	4	5	6	7	8	9	10	
E.T. :	3.45	3.39	3.38	3.29	3.31	3.32	3.62	3.67	3.79	3.67	in $10^{-4}$ sec.

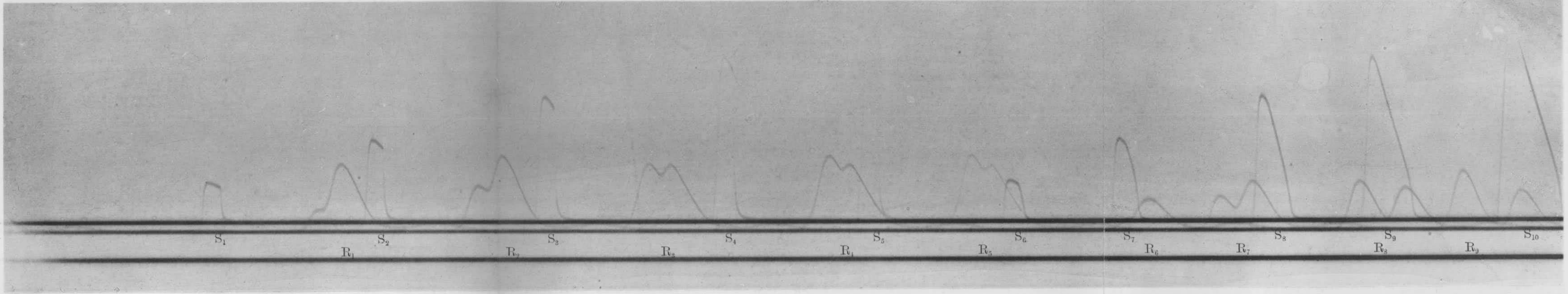


Fig. 2. Oscillogram No. 71, Stimulus: { 1.....5 : Descending.  
6.....8 : Ascending.  
9 : Descending.

No. of exp. :	1	2	3	4	5	6	7	8	9	
E.T. :	3.51	3.31	3.38	3.40	3.51	3.55	3.55	3.53	3.41	in $10^{-4}$ sec.

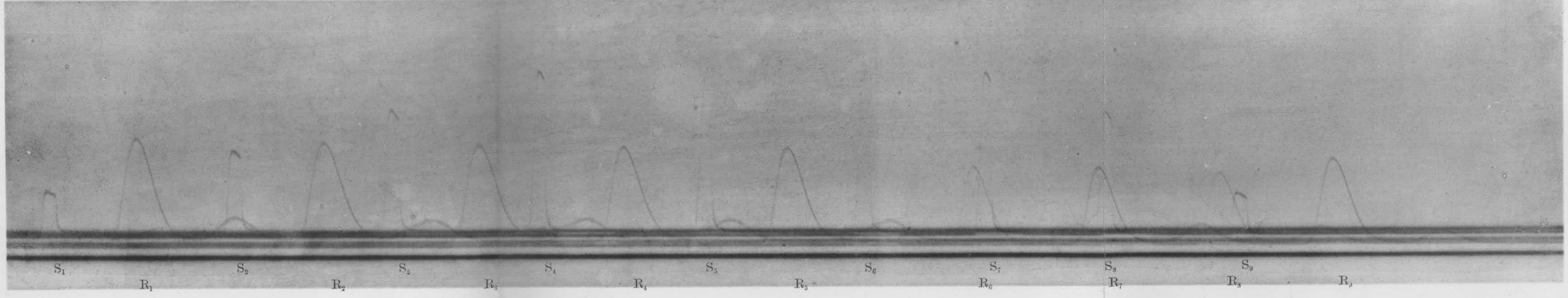




Fig. 1. Oscillogram No. 67.

Number of stimuli: 885 per sec.

E.T.:  $2.86 \times 10^{-4}$  sec.

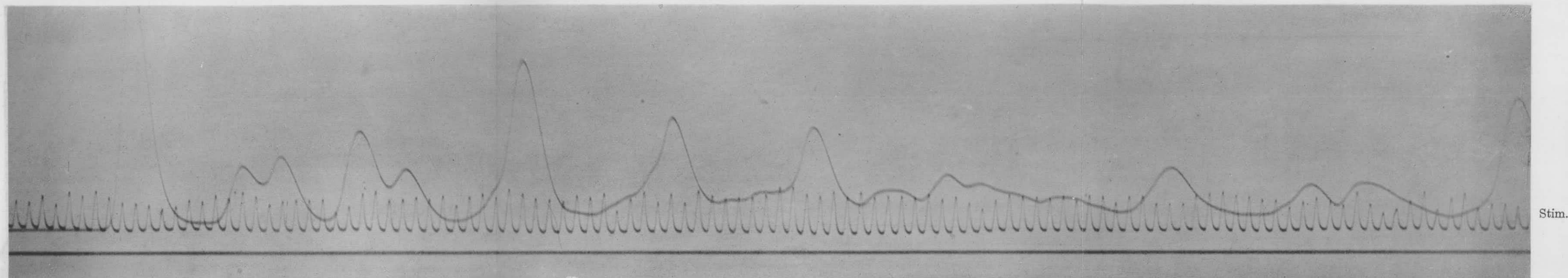


Fig. 2. Oscillogram No. 85.

Number of stimuli: 1412 per sec.

Temperature of the organ:  $15.5^{\circ}\text{C}$ .

E.T.:  $5.08 \times 10^{-4}$  sec.

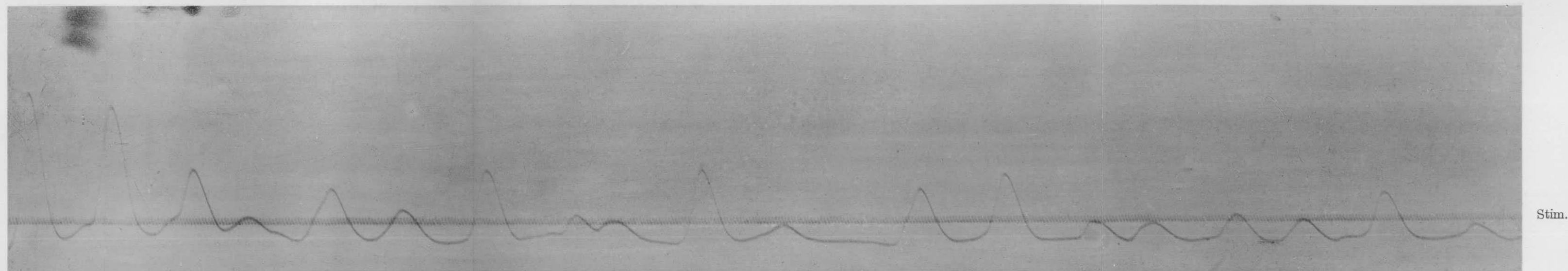
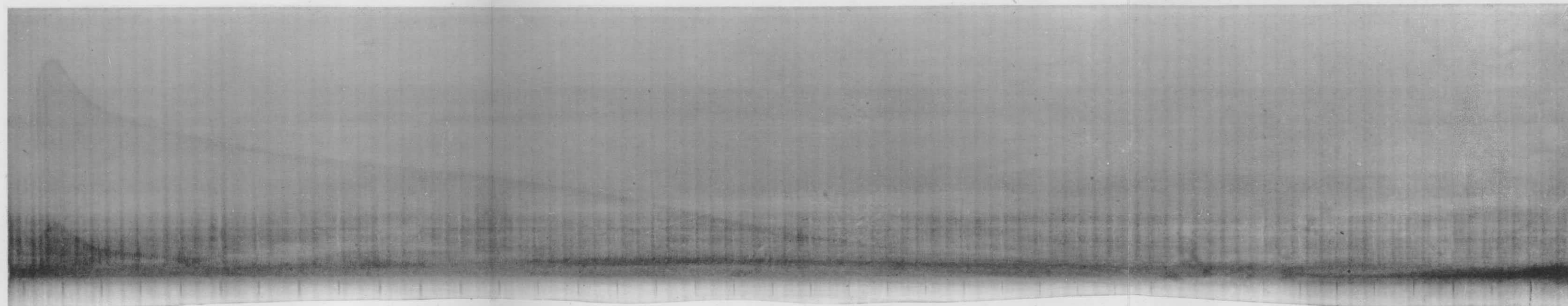


Fig. 1. Oscillogram. No. 1.

Typical form of fatigue curve.

Number of stimuli : About 27 per. sec.

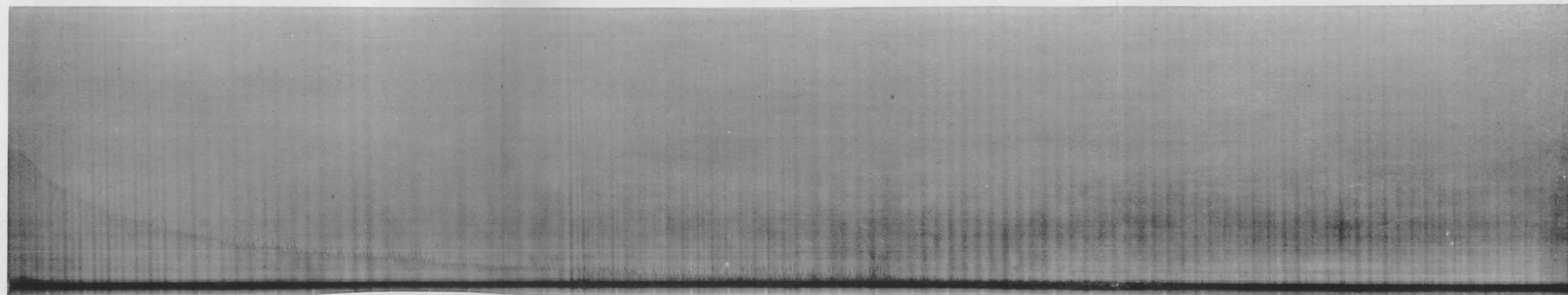


One mark  
per. sec.

Fig. Oscillogram No. 2.

Showing the irregularity of the discharge height in a tired state.

Number of stimuli : About. 28 per. sec.



One mark  
per. sec.



Fig. 1. Oscillogram No. 3. Number of stimuli: About 24 per sec.

2ry. D.

3ry. D.

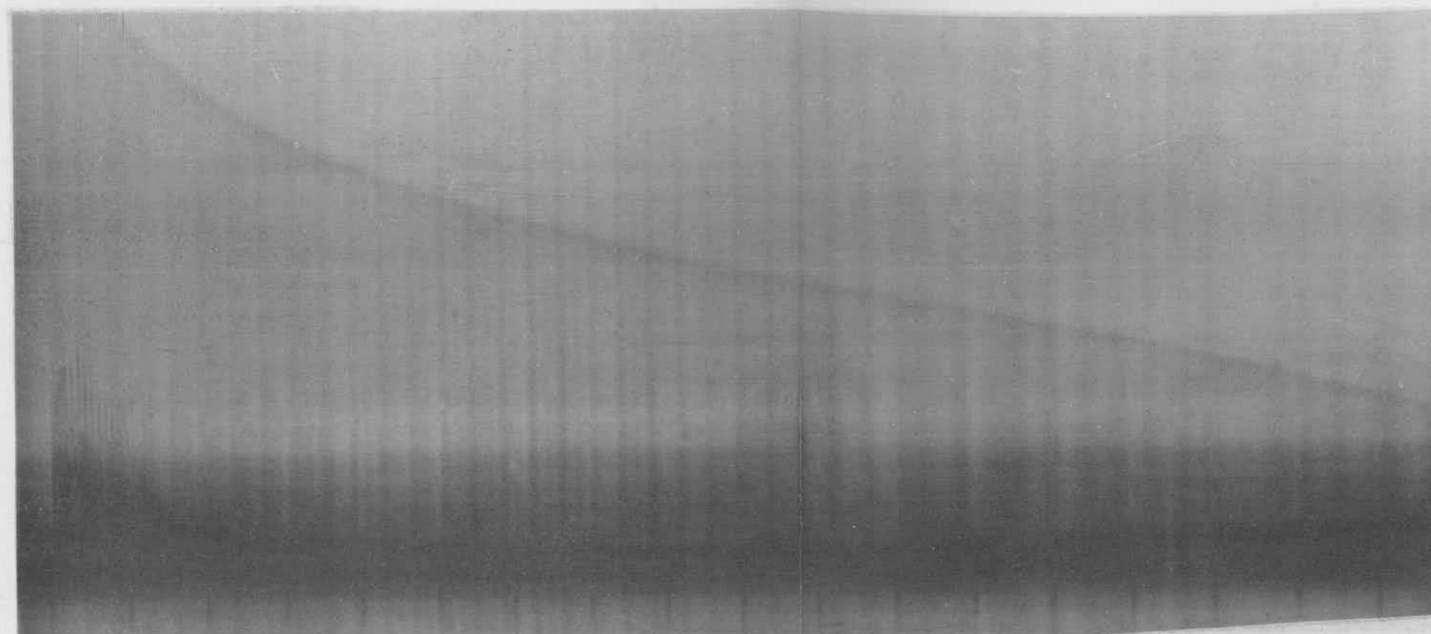
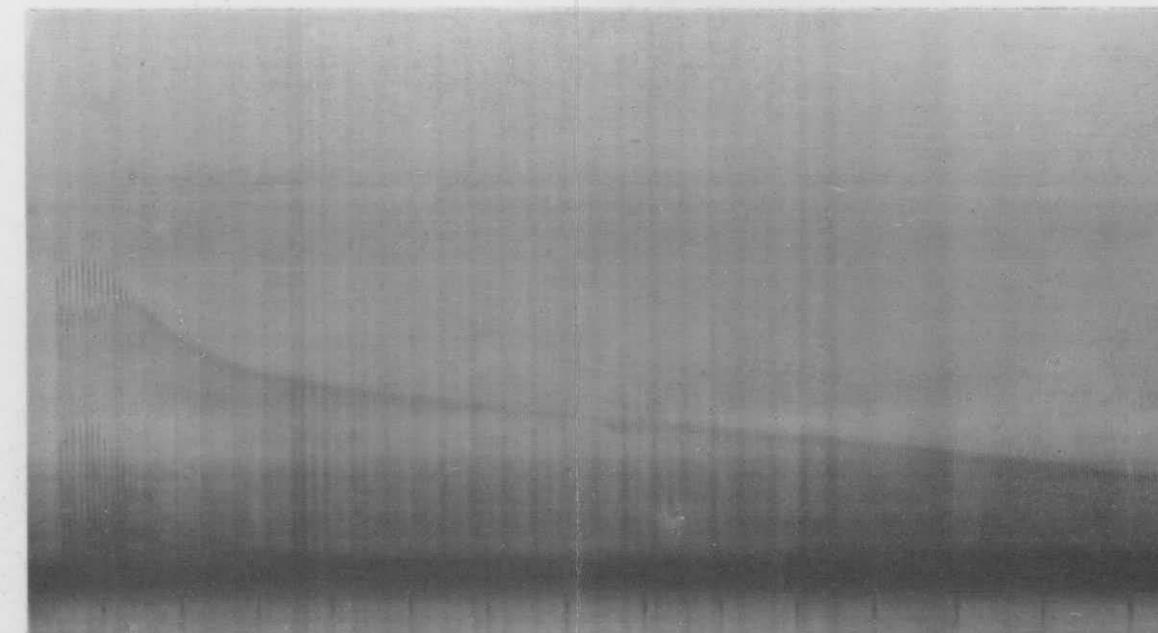
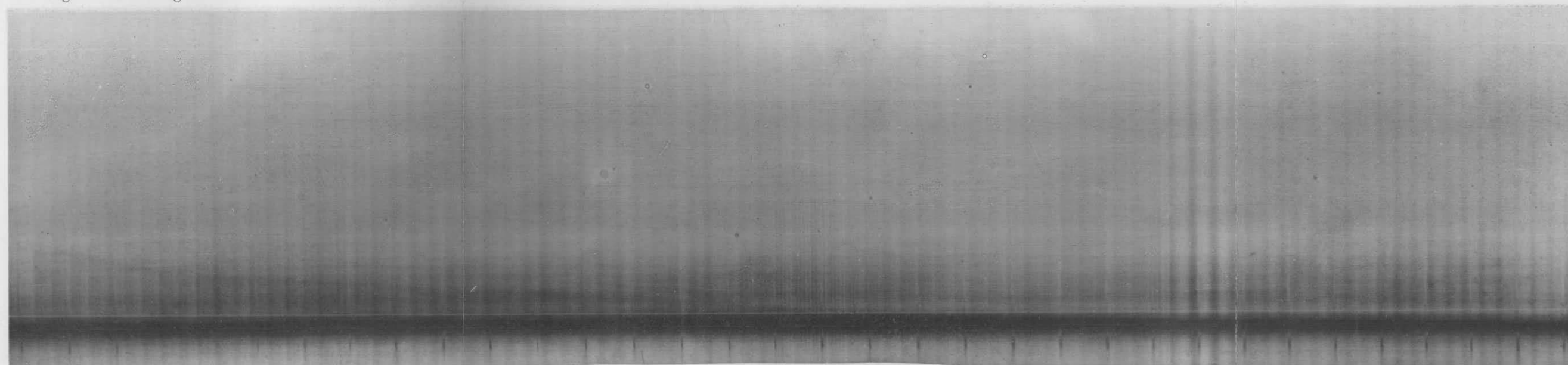


Fig. 2. Oscillogram No. 4. Taken at an interval of one hour after No. 3.



One mark  
per sec.

Fig. 3. Oscill<sup>o</sup>gram No. 5. Taken at an interval of 40 min. after No. 4.



Oscillograms No. 3, No. 4 and No. 5 are of a set of experiments carried out with the same preparation.

K. Fuji: Researches on the Electric Discharge of the Isolated Electric Organ of *Astrape* (Japanese Electric Ray) by Means of Oscillograph.

Fig. 1. Oscillogram No. 6. Fatigue by descending stimulating current.

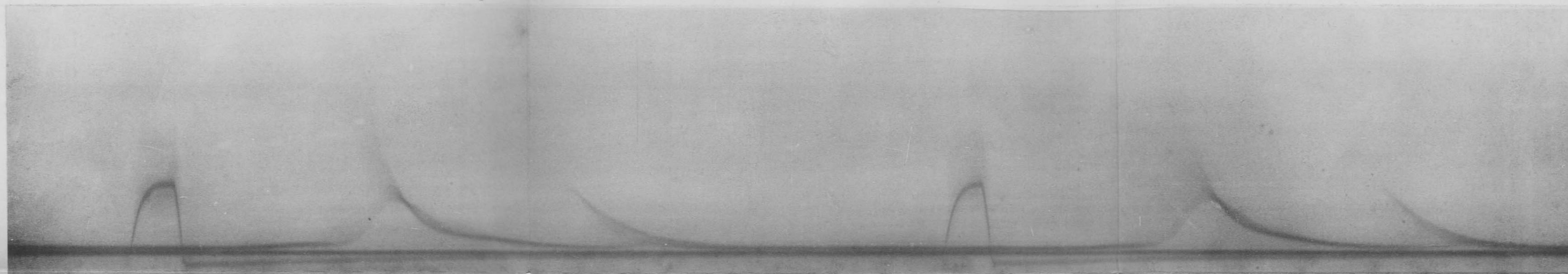


Fig. 2. Oscillogram No. 8. Fatigue by descending and ascending stimulating currents alternately given.

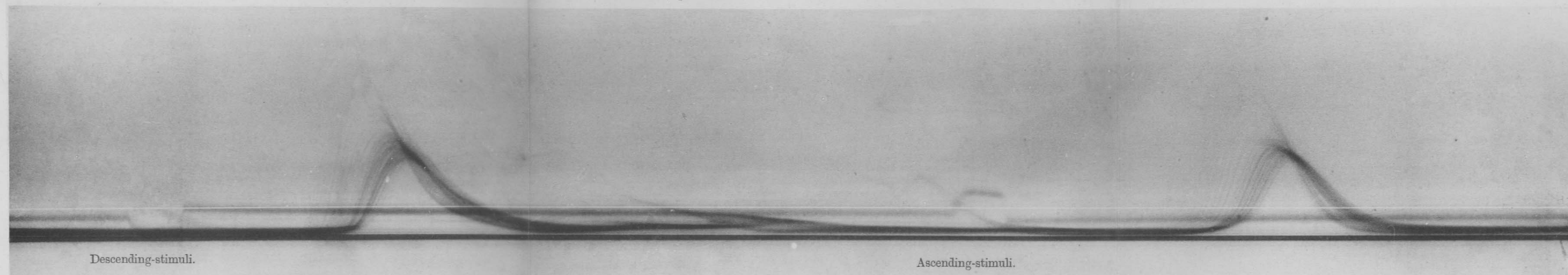


Fig. 3. Oscillogram No. 78. Descending-stimuli.

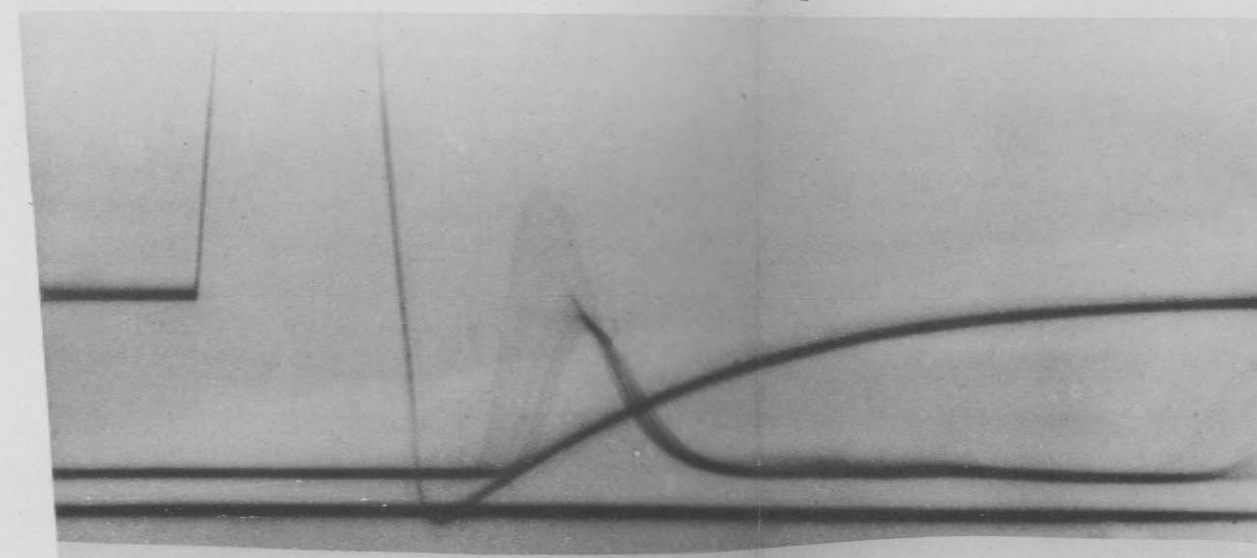


Fig. 4. Oscillogram No. 78'. Ascending-stimuli.

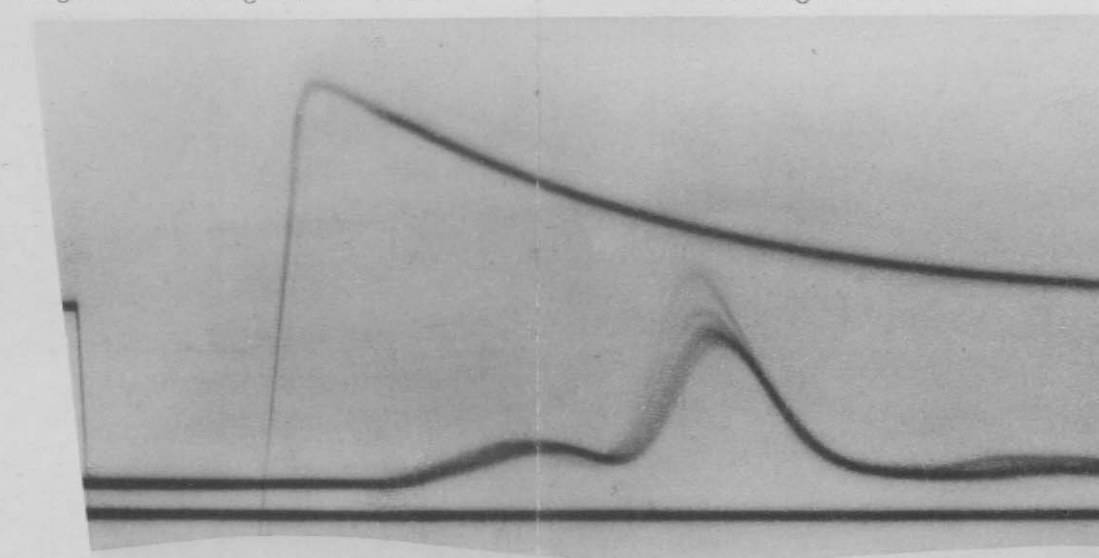




Fig. 1. Oscillogram No. 7.

Stimulating current : Ascending.

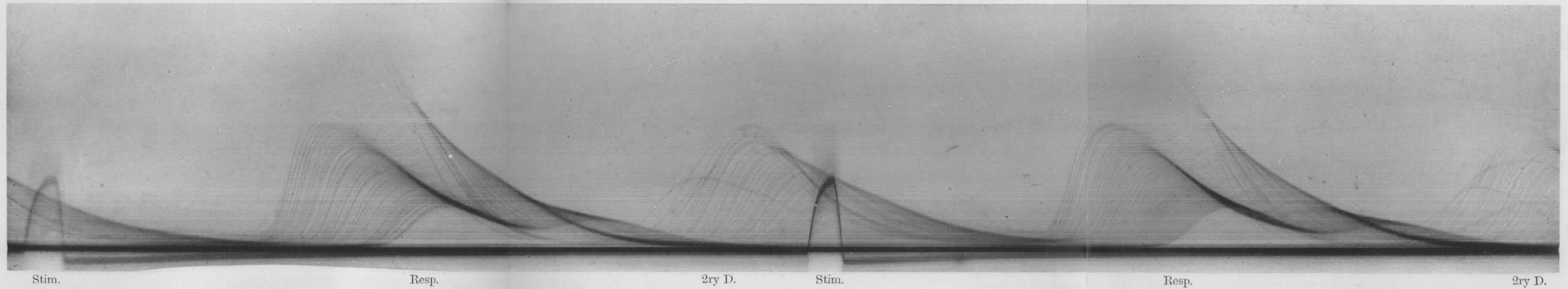


Fig. 2. Oscillogram No. 9.

Stimulating current : Direct.

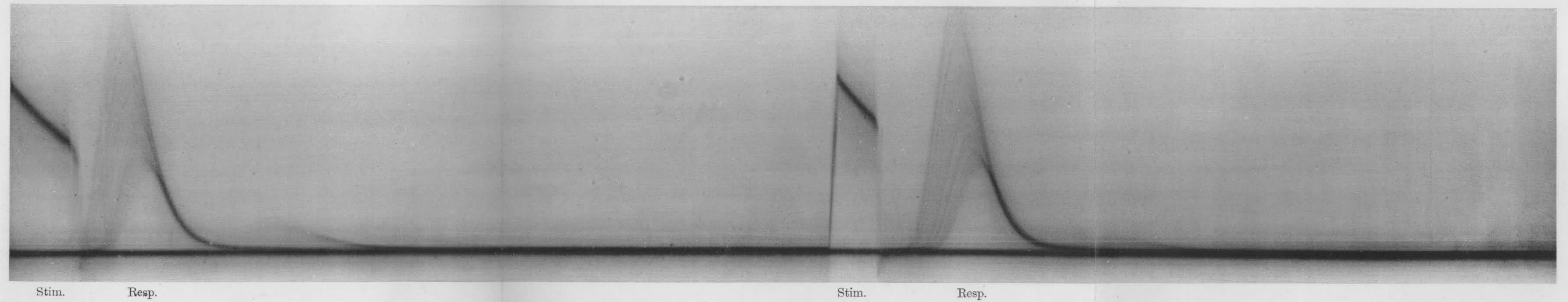


Fig. 1. Oscillogram No. C. 5. Temperature of the organ : 11.6° C. No additional resistance. No. of exp.: 1 2 3 4 5 6 7 in 10<sup>-4</sup> sec.  
E.T.: 1.515 1.533 1.565 1.520 1.508 1.650 1.710

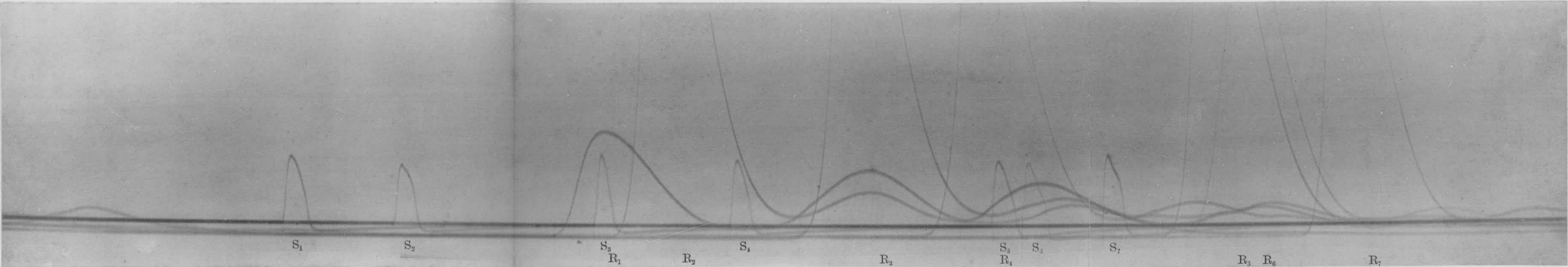


Fig. 2. Oscillogram No. 49. Temperature of the organ : 8.2° C. Inserted resistance : 200  $\Omega$ . No. of exp.: 1 2 3 4 5 6 7 8 in 10<sup>-4</sup> sec.  
E.T.: 3.64 3.58 3.58 3.64 4.00 3.58 3.61 3.64

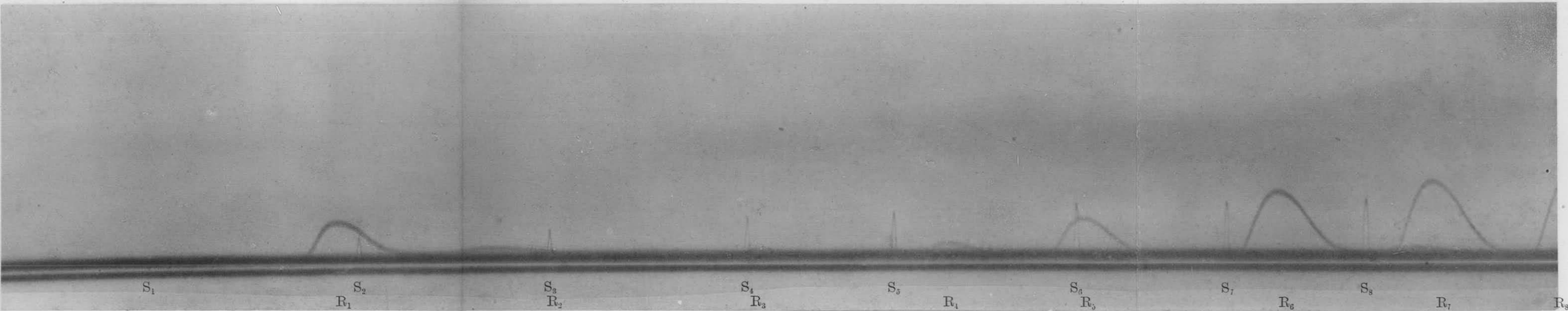




Fig. 1. Oscillogram No. 100. Spontaneous discharge. Inserted resistance : 100  $\Omega$ . Temperature : 23.0° C.

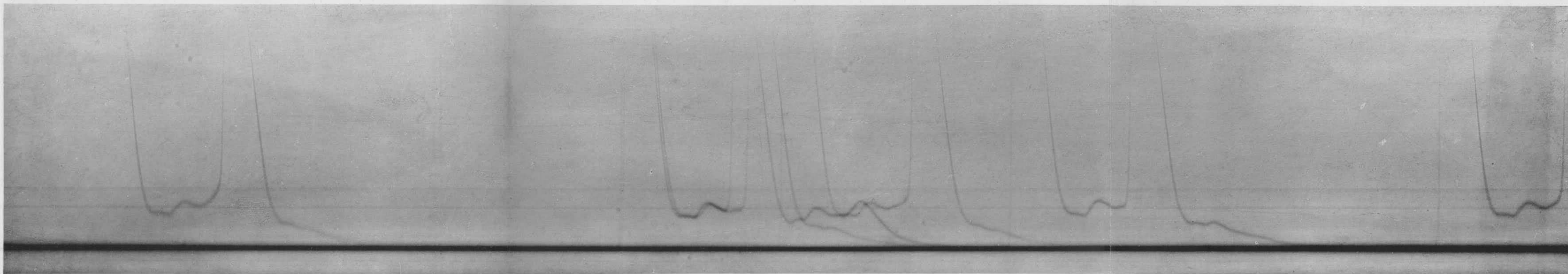


Fig. 2. Oscillogram No. 53. Spontaneous discharge. Inserted resistance : 200  $\Omega$ . Temperature : 13.5° C.

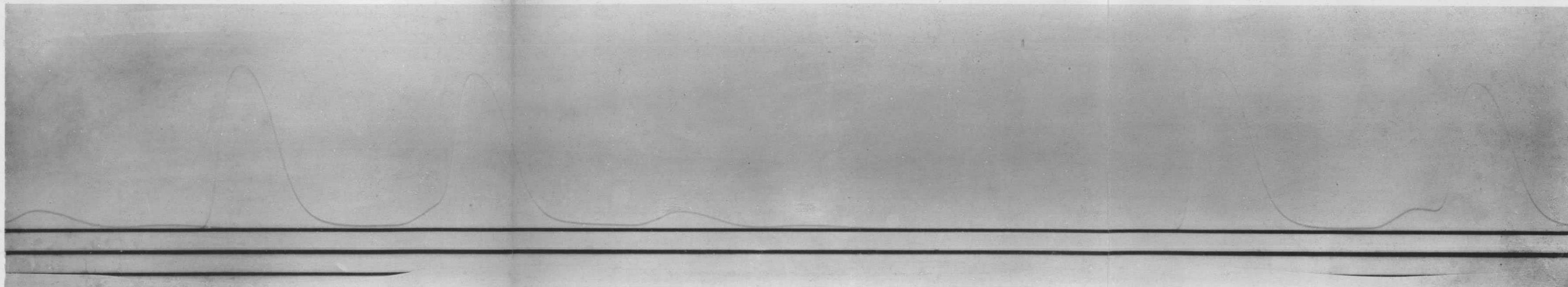


Fig. 1. Oscillogram No. 76.

Temperature of the organ: 14.5° C.

No. of exp.: 1 2 3 4  
E.T.: 2.30 2.20 2.23 2.36 in 10<sup>-4</sup> sec.

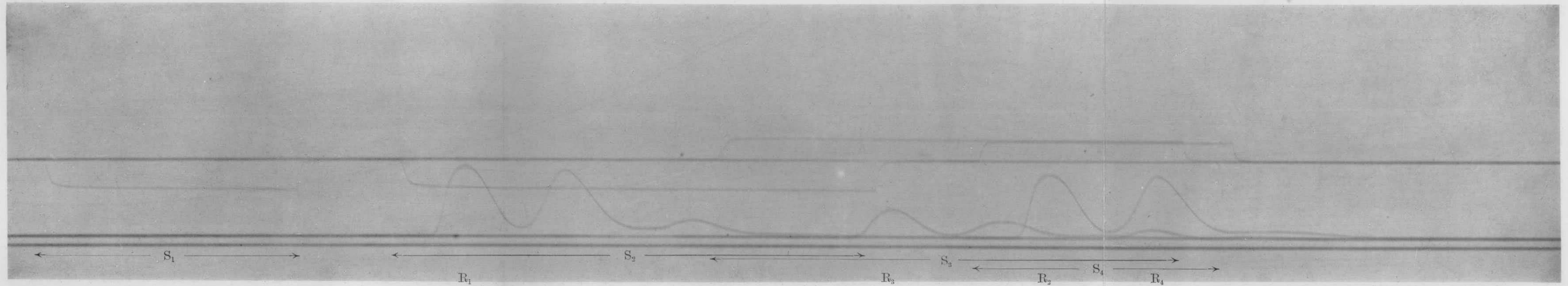
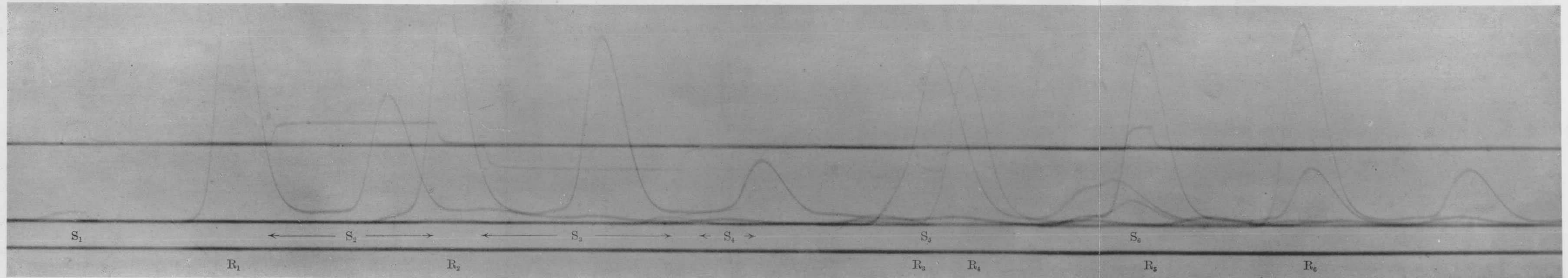


Fig. 2. Oscillogram No. 77.

Temperature of the organ: 14.5° C.

No. of exp.: 1 2 3 4 5 6  
E.T.: 2.50 2.53 2.87 2.43 2.40 2.49 in 10<sup>-4</sup> sec.



## CORRIGENDA.

Page 26, foot note, for "Plüger" replace "Pflüger."

Page 45, last two lines, for "to an instant *corresponding to a point on the ascending branch of the first discharge*" replace "to an instant *a little earlier than the commencement of the first discharge.*"

Page 86, TABLE II., forth line in the last column, for 3.88 read 2.88.

Plate XI., as a whole, red points were printed somewhat lower than their true places. For their correct places, see TABLES XIV. and XV. in pp. 37-40.