PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

On the Electromotive Properties of the Leaf of Dionaea in the Excited and Unexcited States. Second Paper

J. Burdon Sanderson

Phil. Trans. R. Soc. Lond. B 1888 **179**, 417-449
doi: 10.1098/rstb.1888.0016

XVI. *On the Electromotive Properties of the Leaf of* Dionæa *in the Excited and Unexcited States.*—Second Paper.

By J. BURDON SANDERSON, *M.A., M.D., F.R.S., Professor of Physiology in the University of Oxford.*

Received April 17,—Read May 17, 1888.

[PLATES 69, 70.]

IN the paper which I communicated to the Royal Society in 1881, I presented the results of experiments made at various periods during the preceding five years, and the conclusions which I was then able to found upon them. These conclusions, which are set forth in full in the closing pages of my paper ('Phil. Trans.,' 1882, Part 1, p. 1) may be shortly stated as follows :—If by proper means the electrical relation between opposite points of the upper and under surfaces of the leaf of *Dionæa* is investigated while the leaf is "excited," either by touching one of its sensitive filaments or by passing an induction current through the opposite lobe, it is found that the excitation is followed after a few hundredths of a second by a sudden electrical disturbance of less than half a second duration, in which the under surface becomes negative to the upper; and that this is succeeded towards the end of the first second after the excitation by a change of less intensity, but of longer duration and *opposite sign*.

From the character and relative durations (time relations) of these changes, which together, constitute what may be conveniently termed the "excitatory disturbance" or "response," it was concluded that the first was of the same nature with the "excitatory variation" or "action current" of animal physiology, and must be regarded as the expression of a molecular change similar to that which occurs in nerve, muscle, or the electrical organ under analogous conditions. As regards the second, which was designated the "after effect," it was observed first that it was present only when the leaf was "fresh," that is, had not been excited immediately before; and, secondly, that it was associated with the previous and subsequent electrical state of the two "led off" surfaces in such a way that each excitation appeared to leave behind it what might be described as a lasting remainder of the after effect, that is, a permanent and homonymous difference of potential: in other words, that each excitation tended to make the under surface relatively *more* positive if it were before positive, *less* negative if it were before negative; and that, if the leaf were subjected to repeated excitations, it generally happened that the lasting electrical relation between opposite points of its upper and under surfaces underwent a gradual change, that is, the under surface became more positive the longer the observation was continued. It was further observed that in any leaf a similar modification could be brought about much more rapidly by leading through the explored part a very weak voltaic current in the direction of the after effect, that is, from the upper to the under surface.

These facts clearly indicated that what, in the language of DU BOIS-REYMOND, would be called the leaf current, that is, the lasting difference of potential between the two surfaces, has a physiological relation with the phenomena above referred to as constituting the excitatory disturbance. As regards the nature of that relation, it seemed to be indicated that it was in accordance with what, in animal physiology, is called the "pre-existence theory" of the same physiologist; that is, that the "excitatory variation" (see above) is not to be regarded as the setting up of a new electromotive action (action current of HERMANN), but as the result of a sudden diminution of a previously existing electromotive force (in the language of DU BOIS-REYMOND, a negative variation of the leaf current).

On this question, much light has been thrown since the publication of my last paper by the progress of experimental investigation in animal physiology, and particularly by the investigation of the electromotive properties of the ventricle of the heart of the Frog. It was first demonstrated by DONDERS, that the muscular surface of the ventricle when at rest is equipotential, and that electrical inequalities between different parts only manifest themselves either when one or both parts are in a state of excitation, or, in the absence of this condition, when the two parts are in different states of physiological activity. In 1883, I investigated these phenomena with reference to their time relations, and subsequently succeeded in recording them photographically. With reference to the surface of the ventricle, I was able to show (1) that all the facts are comprised in the statement that relative *positivity* of any point of that surface is the concomitant or sign of the physiological endowment of susceptibility of excitation, and (2) that the effect of excitation or injury is to diminish that condition, the degree of diminution increasing with the degree of pre-existing *positivity;* or, more briefly, that the excitable tissue enjoys the faculty of undergoing a change *towards relative negativity* whenever it is interfered with in such a way as either to excite or injure it. Beyond such a statement as this, which involves no physical theory whatever of the nature of the observed relation, it is not, in my judgment, possible to proceed at present. In so far as the so-called theory of pre-existence can be brought within such a definition, I accept it, in preference to the other way of putting it (the "alteration theory"), according to which, devitalised or injured parts are negative, because they are not alive enough, and excited parts negative, because they are too alive.

In comparing the electromotive properties of the ventricle with those of the leaf we encounter on the threshold a difference which requires to be taken into account before proceeding further. This is the absence of localisation in the ventricle, its presence in the leaf. In the former, the excitatory change may take its start from any point excited, and may be propagated in any direction. In the leaf, the change, even when, as in the "fundamental experiment," the impulse is received from the opposite lobe, probably has its chief seat in the sensitive hairs and in the subjacent tissue in their immediate neighbourhood. In my former paper I gave reasons for concluding that in plant tissues the electromotive surfaces are those of *contact between cells in different states of physiological activity*, that is, that when one of the layers of cells is excited, the other remaining quiescent, this gives rise to a difference of potential between them. Irrespectively, therefore, of the sign of this difference, it may be assumed that the primary effect of excitation, that is, the first phase of the excitatory variation as described above, is the expression of a sudden difference of activity between the superficial and deeper cells near the upper surface.

If the law above enunciated, namely, that change from the less active to the more active state is accompanied by an electrical change in the direction of relative negativity, holds good in the plant, as in the animal, we should expect that so long as the leaf retains its state of integrity, the upper surface, being the seat of greatest activity, would be positive to the under, and that the response to excitation would consist in a diminution of its positivity. We should also expect that those more gradual changes which in the plant are manifested by the loss of turgor, and which we may compare with the effects of injury in animal tissues, would have their electrical counterparts in equally gradual changes towards negativity of the affected part. And, inasmuch as by our mechanical experiments we know that the loss of turgor, in common with other physiological changes, is localised in the superficial layer of cells of the upper surface, we should expect that complete freshness of the leaf would be indicated by relative positivity (leaf current ascending), diminished turgor by diminishing positivity or equipotentiality, and complete limpness by relative negativity (leaf current descending); and, further, that in the first condition, the sign of the primary excitatory response being in each state opposed to that of the difference of potential, it would in the first state be descending, but as the cells of the upper surface gradually lost their predominance of activity it would be diminished, and finally become ascending.

When I resumed my investigation of the leaf of *Dionæa* in 1885, the fact which served as the starting point was the change in the electrical relation of the upper to the under surface which is produced by leading through it a weak descending voltaic current. The investigation of this change soon led to the discovery that the condition of the leaf which I had called normal, in which the upper surface is negative to the lower, is not that of its prime, but one of transition towards a state of diminished activity. Then it was learned that, although the excitatory electrical effects which I had described as belonging to this state are of greater intensity than those which are witnessed when the leaf is in its prime, their right to be called normal is equally questionable; in short, that in vigorous leaves which have been successfully prepared, the state which was before called normal is preceded by a primary state in which the "leaf current" is descending, the excitatory response ascending. My excuse for making this error in 1882 is that the primary state passes rapidly into the secondary, and that the phenomena of the latter, being of greater intensity and more permanent, are much easier to observe. I have only to add that in my new investigations I have had occasion to repeat all my former experiments; and that, although I have learned to understand them better, I have no corrections to make in my experimental results. What was stated was the truth, but not the whole truth.

Section 1.—*Preliminary Study of the Influence of Voltaic Currents led through the Leaf from the Upper to the Under Surface, or in the opposite direction. Discovery of the Process of "Modification."*

Method.—As the phenomena which it was my purpose to observe in the leaf of *Dionæa* correspond as regards their mode of origin to the localised "secondary electromotive" effects which have been during the last few years described and investigated in muscle and nerve by DU BOIS-REYMOND, HERING, and HERMANN.* I had recourse to methods similar to those employed by these physiologists. My object was to lead a current, of which the electromotive force was known, through the lamina for a measured short period (designated the period of closure of the external current), and then, after a certain interval (corresponding to the "Uebertragungszeit" of DU BOIS-REYMOND's experiments), to close the galvanometer circuit through the same electrodes. The arrangements by which this was accomplished were as follows:—

As in the experiments of 1881, the "leading off" or galvanometer electrodes were applied to opposite points on the upper and under surfaces of the lamina, and the difference of potential compensated. Professor DU BOIS-REYMOND's round compensator was used instead of my own.

By a second circuit the leading off electrodes were connected with the poles of a Daniell battery of one or more cells, but in such a way that the current was led through the leaf for a very brief period, which preceded the first closure of the galvanometer circuit and was separated from it by an interval of one-seventh of a second. This was effected by a rheotome specially designed for experiments on secondary electromotive phenomena in muscle and nerve, the construction of which will be readily understood from Diagram 1.

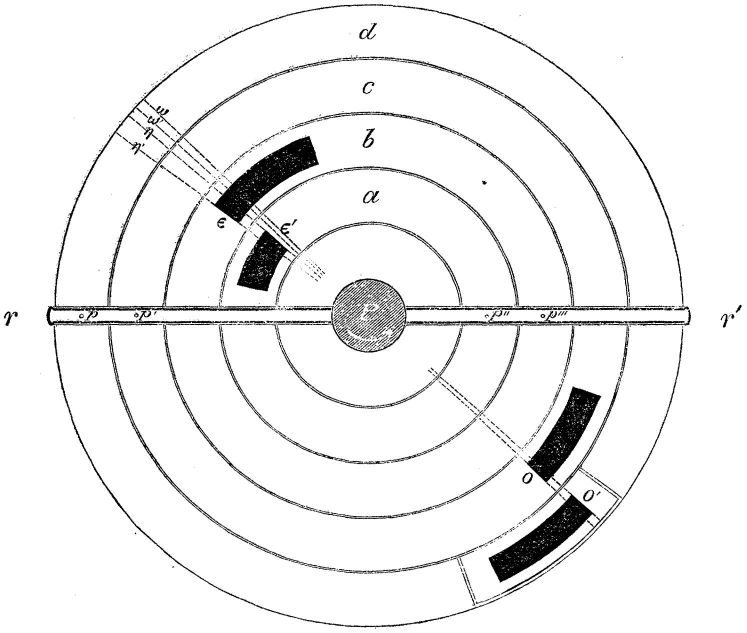
The central circular space p, represents a pulley by which the horizontal bar $r\ r'$ is made to revolve, say three times per minute. The bar is of sealing wax, with a core of brass rod. At p, p' and p'', p''' there are platinum wires which pass vertically downwards to such distance as to dip into the pools of mercury ϵ, ϵ', o, o'. a is a

---

* Translations of the most important papers relating to this subject will be found in the first volume of the 'Oxford Biological Memoirs,' Part 2, pp. 163–330.

fixed trough of brass, which is filled with solid paraffin. Around this a similar trough of the same material, *b*, also filled with paraffin, revolves, so that it can be placed in any desired position with reference to *a*; *c*, is another trough of the same construction as *b*; a short trough, *d*, which travels in an annular groove, so that it can be placed in any required relation to *c*, contains the pool o'; o, o' and ϵ, ϵ' are severally connected with binding screws correspondingly marked out but not shown in the diagram, of which o, o' are in the battery circuit, and ϵ, ϵ' in the circuit of the galvanometer. It will be readily seen that when the bar revolves in the direction of the arrow, o, o' will be first closed, then ϵ, ϵ'; but, inasmuch as the battery and galvanometer circuits are never closed at the same time, and both include the electrodes which are applied to the opposite sides of the leaf, the battery current is led into the leaf during the parts of the revolution limited by the radial dotted lines ω, ω', and the leaf difference led off through the galvanometer during the part limited by the lines η, η'. Before each experiment the instrument is adjusted, and the duration of the contacts, as well as the interval between them, is measured by connecting both contacts with a DESPREZ's time-marker, which inscribes them on a smoked surface.

Diagram 1.



The purpose of this arrangement is to determine not only the immediate effect produced on the leaf by leading through a battery current for a very short period, but also to ascertain the duration and time relations of the effect by measurements made at periods following each other at regular intervals. The method of observation is as follows :—

The revolving bar of the rheotome is placed in such a position that the galvanometer circuit is permanently closed. The difference of potential between the upper an-under surface is then compensated, and the bar allowed to revolve. The completeness of the compensation is indicated by the absence of any effect when the wires p'', p''' enter and leave the pools. The battery circuit, which up to this time has been broken, is now momentarily closed by the hand in such a way as to allow the battery current to pass through the electrodes and the leaf *once* during the period ω, ω'. The immediately following effect, and the successive effects which occur at each revolution of the bar (that is, at intervals of 20 seconds) are observed and noted. As the falling time of the galvanometer used is considerably less than 20 seconds, this could be accurately done, so that a series of readings is obtained which, excepting in so far as they may be affected by change of resistance, truly represents the electrical state of the leaf during the period of observation.

The first experiment (July 3) gave the following results:—

The cross difference, *i.e.*, the difference of potential between the two opposite surfaces (which in this, as in my former paper, I propose to indicate by the mode of printing the word) was such that the under surface was positive to the upper. Its direction as regards the leaf was consequently descending ↓. It was balanced by 90 divisions of compensator wire, the battery used being a Raoult, that is, a Daniell with half-saturated zinc sulphate solution instead of dilute acid.[*] A battery current of two Daniells was led in in the direction of the difference for four-tenths of a second. The succeeding closure of the galvanometer circuit was of the same duration, *i.e.*, four-tenths of a second, and the interval between the two closures was $0''\cdot14$. The successive effects (with one-tenth of the current led through the galvanometer) were very large, the needle being deflected beyond the scale each time; and it was not until a minute after the passing of the external current that the difference became small enough to be measured. Half-an-hour later the difference, which was increased as the result of the first experiment, had subsided to ↓80 divisions of wire, and the results with the rheotome (deflections) were (all other conditions being the same) ↓400, ↓70, ↓28, ↓10, and still later ↓100, ↓20, 0, showing that the relative positivity of the under surface is much increased by sending a current in the direction of the difference.

On repeating the experiment on the following day the difference had increased to ↓197 divs.,[†] and the series of deflections observed at intervals of 20 seconds were ↓∞,[‡] ↓∞, ↓∞, ↓600, ↓500, ↓450, ↓370, ↓320, ↓290, ↓270, ↓240, ↓220, ↓180, ↓170. The difference having, as the effect of the passage of the current, increased to ↓280 divs., the current of one Daniell was five minutes later led through in the opposite direction, viz., ↑. The deflections were ↓120, ↓20, ↓10. Then, on again passing the

---

[*] With one Raoult element in circuit the value of the whole length of the wire of the "round compensator" is about 0·037 volt. 100 divisions means, therefore, 0·00037 volt.

[†] Here "divs." stands for "divisions of the compensator wire."

[‡] Here the sign ∞ is used, in accordance with custom, to signify that the deflection extended beyond the scale of the galvanometer.

↓ current (the difference having in the meantime sunk to ↓185) we had ↓∞, ↓∞, ↓400, ↓275, ↓210, ↓180, ↓170, ↓160, ↓155, ↓145, ↓120, ↓120, &c., at $\frac{1}{3}'$ intervals. Finally, repeating with the ↑ current, as before, the deflections were ↓120, ↓25, ↓18, ↓15, &c. This experiment showed that, although the effect of the ↓ current was about twenty times as great as that of the ↑, both acted similarly.

In confirmation of this, it was found that when the current of two Daniells was led through in the ↑ direction, the deflections were ↓∞, ↓240, ↓130, ↓90, ↓70, &c. Subsequent observations of the same kind with still stronger currents showed that, *e.g.*, with a ↑ current of six Daniells of the same duration as before, the difference having gradually increased to ↓640 divs., the deflections at 20″ intervals were ↓∞, ↓∞, ↓∞, ↓350, ↓300, ↓260, ↓240, ↓205, ↓190, ↓170, ↓67, &c. A few minutes before, a current of one Daniell in the favourable direction (↓) had given ↓∞, ↓∞, ↓420, ↓340, ↓310, ↓280, ↓260, &c., a series entirely comparable with the second of the two examples given above, so that the after effect of the current of one cell descending appeared to be scarcely less than that of six cells ascending.

It was thus evident that the effect of repeated "galvanisation" of the leaf for very short periods is to increase the difference. It was suspected that the resistance of the preparation was diminished, but no measurement was made.

The next step in the investigation seemed to be to ascertain whether the effect of an external current had any relation to the excitatory disturbance, a question which could be answered by determining whether it is associated with any change which is propagated from the part directly acted on to distant parts, and whether it identifies itself as regards the time of its occurrence with the positive (↓) after effect of excitation described in my previous paper. This, it was found, could be decided without any difficulty, as follows:—

The arrangement (July 15) was the same, excepting that, instead of leading through the whole current of one or more Daniells, I used a derivation current led off from a rheochord of which the end-blocks were connected by thick wires with the terminals of the cell, the rheochord wire being divided into 100 equal parts. The object was, of course, to increase the external current gradually from a strength at which it was inadequate to produce any effect, to exciting strength, *i.e.*, to such a strength as would be sufficient to produce a true excitatory response—one which was propagated to the opposite lobe. It was found that when currents of gradually increasing potential were led through the lobe, beginning with 75 divisions and increasing the length of wire by one division after each observation, the transmission to the opposite lobe took place for the first time at 88 divisions, and that until that happened the electrical state of the lobe remained perfectly unaltered. On then observing the condition of the lobe through which the external current was led, with the aid of the slow rheotome, by the method described in the preceding paragraph, we had, after passing a current of a strength just over that necessary to give rise to a propagated effect at 20″ intervals,* deflections of ↓225, ↓15, ↓5; but when the current was increased by substituting two Daniells in series for one, the effect was biphasic, consisting of a ↓ swing followed by a ↑ one off the scale. Comparing these two with the transmitted effects observed under the same conditions when the opposite lobe was connected with the galvanometer, it was seen that, although the ↑ *local* effect of the stronger current was many times as strong, there was no sensible difference in the propagated excitation, which in both cases was characteristic. The conclusion to be derived from this observation is, it need scarcely be said, that the greater part of the local effect is not transmissible, or, putting it otherwise, that it is the sum of two effects, one of which is transmissible, the other limited to the part of the lamina through which the current has passed, and that of the two the latter is much the longest.

In the experiments with the stronger current the existence of an excitatory change was indicated by a preliminary ↑ jerk of the needle; with the weaker current this was not of sufficient duration to overlast the interval.

The observations were now discontinued for a time, in order that arrangements might be made for measuring galvanometrically the strength of the external current used in each experiment. With this view, a second galvanometer was introduced into the battery circuit (July 31). The first observation was a repetition of the comparison made on July 15 of the local with the propagated effect. The results confirmed those previously obtained; they are given below:—

EXPERIMENT I.—Propagated Effect.

Observation.	Direction of external current.	Strength of external current.	Effect as led off from opposite lobe.	Difference in divisions of DU BOIS-REYMOND'S round compensator.
1	↓	120	↑250, ↓200, ↓50, &c.	↓100
2	↑	100	None	↓140
3	↓	120	↑310, ↓130, ↓30, ↓30	↓165

EXPERIMENT II.—Local Effect.

Observation.	Direction of external current.	Strength of external current.	Effect as led off from the lobe through which the current has just passed.	Difference.
4	↑	140	↓50, ↓5	↓300
5	↓	150	↑220, ↓∞, ↓100, &c.	↓290
6	↓	145	↑440, ↓∞, ↓100, &c.	↓300

---

* The reader is requested to notice that, as here, so in the following paragraphs, the series of numbers with ↑ or ↓ signs before them represent deflections observed at 20 seconds intervals.

These two experiments show, as before, that the local after effect much exceeds the transmitted one; that even strong currents when ↑ fail to excite (see previous paper, p. 42); and, further, that, as will be better seen from other modes of observation, when two excitations of the same kind follow each other, the initial galvanometrical effect is stronger in the second than in the first.

The observations of the next few days were directed to a comparison of the local effects of ↑ and ↓ currents, their purpose being to ascertain to what extent the direction is influential. The method was the same, but the period of closure was shortened to one-tenth of a second, and the interval to one-twentieth. The same leaf was observed during two days, the right lobe on August 4, the left on August 5.

In the right lobe the difference was at first ↑500 divs., and in an hour it sank to 370. At this time the current of one Daniell gave when descending ↓∞, ↓110, ↓80, ↓65, when ascending ↑300, ↑220, ↑130, ↑100. The galvanometer in the battery circuit showed the current strength to be the same in the two cases; and it was further found that, whereas the effect of the ↓ current was to diminish the difference, that of the ↑ was to increase it. But on increasing the strength of the external current, by substituting two Daniells for one Daniell, the opposite effects were produced. The experiment when repeated in a slightly different way, namely, by leading off derived currents of which the strengths were regulated by a rheochord, gave corresponding results, viz., that up to a certain strength (*e.g.*, 75 lengths of the rheochord wire) the effect was exclusively ↑, that is, in the same direction as the current which caused it; but immediately above this it changed its sign (3.45 p.m.), being ↑5, ↓25, ↓25, ↓25, &c.; and, subsequently, with a current strength of 150 scale of the control galvanometer, ↓105, ↓40, ↓30, ↓10; still later (4.9 p.m.) with 190 scale, the deflections were ↓220, ↓95, ↓55, ↓35. And it was specially observed that *pari passu* with the change in the immediate after effect, the difference, which was ↑80 divs. at 3.45 p.m., changed its sign, and was at 4.11 p.m. ↓55. A further increase of the current strength to 380 scale brought the difference to ↓160, and the local effect to ↑20, ↓∞, ↓∞, ↓370, ↓350, ↓270. In all of these observations one-tenth only of the current was led through the galvanometer.

On the following day (August 5) a similar series of observations were made on the opposite lobe, of which the difference was at first from ↑285 to ↑300 divs. At 12.52, with a current strength ascending of 89 scale, we had ↑180, ↑105, ↑100, ↑90; with 150 scale ↑45, ↑35, ↑35; with 180 scale ↓53, ↓35, ↓25; and at 1.10 p.m., with 260 scale ↓180, ↓160, ↓100, &c.; then finally, at 1.33 p.m., with 520 scale ↑40, ↓∞, ↓250, ↓230, &c. In this case, as before, the change of sign of the local after effect preceded the change of sign of the difference, the upper surface remaining positive until 1.20 p.m., whereas the after effect became ↓ instead of ↑ at 1.1 p.m. During the course of the experiment, and for some time before and after it, the observations were made regularly every three minutes.

This subject was further investigated (August 6), with, however, this difference, that intercurrently with the observations on the local effect in the right lobe, others were made on the propagated one in the left. As regards the local effect, the results confirmed those of the preceding day. At 12.54 p.m. we had, with an ascending current strength of 90 scale through the right lobe, ↓10, ↑30, ↑∞. ↑∞ ; 80 scale gave at 1.20 ↓175, ↓65, ↓50, &c., the difference being still ↑. At 3.22 p.m., with a current strength of 240 scale, it was ↑ jerk ↓∞, ↓190, ↓140. At 3.41 p.m., with 310 scale, ↑30, ↓ ∞, ↓220, ↓140, ↓100, ↓80. Between the two last-mentioned periods the difference had changed sign being ↑55 divs. at 3.22 p.m., but ↓110 divs. at 3.41 p.m. In this case the change of sign in the difference was about two hours later than that of the after effect, but during the whole of this period it was diminishing. In this experiment, as in the preceding one, the observations were made at 3 minutes intervals. In each case there was a propagated excitation. Later on the same day we made a similar set of experiments on the right lobe. They were of interest as showing a remarkable point of difference between the local effects of ascending and descending currents.

The observations were begun at 4.20 p.m. A series of current strengths from 2 scale to 26 scale gave no effect. Above this a small ↑ effect appeared, which increased with the current strength, until at 4.50 p.m. we had, with 52 scale, ↑230, ↑260, ↑210, ↑190, ↑130, ↑105, ↑80, and later ↓ deflections, the difference having diminished from ↑ 155 to zero.

During the next 40 minutes the current strength was gradually increased from 65 scale to 380 scale, with the effect of changing the sign, first of the difference, then of the after effect. I give the last five observations tabularly.

Time of observation.	Difference.	Current strength.	Local galvanometer effect with rheotome.
P.M. 5.12	↑5	↓90	↑160, ↑220, ↑190, &c.
5.18	↓20	↓130	↑200, ↑250, ↑230, &c.
5.23	↓60	↓180	↑50, ↑160, ↑100, &c.
5.28	↓140	↓260	↑40 followed by ↓50, ↑25, 0
5.35	↓180	↓380	↑55 followed by ↓190, ↓170, ↓140

The next experiments were made for the purpose of determining more precisely the effects of ascending currents of different strengths. It had already been ascertained that a very weak current of the duration of four-tenths of a second produces no after-effect whatever in the same direction, but is followed by a small after effect in the opposite direction resembling the ordinary physical polarisation of PELTIER, and that as soon as the difference of potential at the leading in contacts amounted to something like 0·4 volt the descending effect became much stronger, the actual results being as follows :—

Length of rheochord wire in inches (one inch = 0·006 volt.)	Local galvanometer effect with slow rheotome.
40	↓30, 0, 0, &c.
50	↑8, ↓50, ↓20, &c.
60	↓450, ↓70, ↓30, &c.

On August 7 a number of experiments were made with a shorter closing time and interval than had before been used, each being 0″·07. The leaf was in a perfect state, and its difference was very high (↑918 divs.). The external current was derived, as before, from a rheochord wire divided into 100 divisions, of which the difference of potential at the ends was about 0·6 volt. The current strengths were measured by a galvanometer introduced into the derived circuit. The relation between the length of wire and the current strength depended, of course, on the resistance of the preparation, which, as will be shown later, tends to diminish, but in the present instance was fairly constant. With very feeble ↓ currents it was observed that the effect of the first closure was to render the upper surface of the leaf more positive, the difference gradually increasing from ↑400 to ↑918. A second closure of which the current strength was 9 divs. gave a very small ↓ deflection, preceded by an ↑ jerk, then ↓22, ↓26. Subsequently a current strength of 18 scale gave ↓∞, ↓50, ↓30, ↓10; 35 scale gave ↓∞, ↓190, ↓50, &c. Up to this point it was ascertained by leading off from the lobe to the galvanometer *that there was no propagated effect.* The strength of the external current was then increased to 78 scale, which gave ↓380, ↓200, ↓150, &c., and it was found that each excitation was followed by a permanent diminution of the difference, and that an excitatory effect was propagated to the opposite lobe.

An hour-and-a-half had now passed, during which the external current had been led through the leaf 25 times, that is, for an aggregate duration of a second-and-three-quarters. Its upper surface was still positive, but its positivity was evidently diminishing. At 5.30 p.m. the difference was still ↑147, at 5.52 p.m. it was ↑95, at 6.12 p.m. ↑50, at 6.43 p.m. ↓125. In all, eight currents had been previously sent through it of above exciting strength, but during the period between 5.30 and 6.50 p.m. the lobe remained untouched. It thus appears that the gradual change of modification in the electromotive relations to each other of the upper and under surfaces of the laminæ, when once started by external currents, continues without external interference.

Section 2.—*Further Study of the Process of "Modification."*

By the observations related in the previous paragraph, it had been learned that the effect of leading weak currents through the leaf of *Dionæa*, especially if they enter by the under surface, is to produce a permanent and progressive change in its electrical condition. I have now to add some observations made for the purpose of studying the nature of this modification.

On August 12 experiments were made in which a leaf, of which the left lobe was connected with the galvanometer, was excited mechanically on the right side, as in the fundamental experiment, by touching the hairs with a camel-hair pencil. The excitations occurred at intervals of three minutes during half-an-hour. The difference was descending, and remained so. It was balanced by from 130 to 141 divs., and produced when one-hundredth of the current was led through the galvanometer a deflection of 25 scale. At the end of the period mentioned, a current of a single Daniell was led through the leaf twenty times at intervals of 20 seconds, the current being each time three-hundredths of a second. The immediate local effect of each external current was led off to the galvanometer during the interval which followed each leading in. There occurred therefore, as before, a series of excursions at 20 seconds intervals, by which the progress of "modification" was indicated. These were (one-hundredth of the current passing through the galvanometer) ↑22, ↑20, ↑18, ↑0 0, ↓15, ↓26, ↓35, ↓40, ↓52, ↓57, ↓67, ↓71, ↓75, ↓76, ↓80, ↓85. On connecting the surfaces of contact with the galvanometer without the rheotome, there was a deflection of ↓200 scale, which was balanced by 320 divs., but rapidly subsided to ↓150.

The leaf having been thus completely modified, it was subjected to a second series of mechanical excitations as before, lasting for an hour. The rough galvanometric results of these excitations are compared below with those before modification.

Before .	3.20 to 3.50 p.m.	↑20 ↓270	↑25 ↓225	↑20 ↓220	↑15 ↓225	↑20 ↓260
After . .	4.20 to 4.50 p.m.	↑400 ↓300	↑370 ↓400	↑350 ↓400	↑260 ∞	↑330 ↓700

The difference had diminished from ↓200 to ↑25.

At five o'clock the external current was again led through the same way as before, but only ten times instead of twenty. Each passage of the current was followed by an increase of the relative negativity of the upper surface of the leaf, the effect of which showed itself, when the galvanometer circuit was closed at the end of the period during which the leaf was acted upon, by a difference corresponding to 500 divs., which declined as before, so that three minutes later it was balanced by 380 millims. Taking the mean of five galvanometrical observations, the effects of excitation at intervals of three minutes now gave (with one-tenth of the current through the galvanometer) ↑105·0 ↓14·5; so that we have, as the general result, the excitatory effects observed in successive stages of modification:—

Before	↑2 ↓24
After modification	↑34 ↓45
After further modification	↑105 ↓14

All of these are given in round numbers as they would have been observed had one-tenth of the current been led through the galvanometer.

On August 13 a leaf was prepared and observed, as in the fundamental experiment, with leading off contacts on the left lobe. The difference was compensated by 920 divisions of wire, and gave (with one-hundredth of the current through the galvanometer) a deflection of ↑330 scale. The transmitted effect of mechanical excitation of the right lobe was ↓10 ↑70, and that of electrical was similar (mean of three observations with one-tenth of the current through galvanometer, ↓5 ↑31). Without shunting, it was seen that the ↑ phase was preceded by a jerk of the needle in the opposite direction. After an hour, during which the difference was little altered, the leaf was modified by passing feeble external currents through the leading off electrodes of one-twentieth of a second duration at 20″ intervals, but no further observations were made till next morning.

At 11.30 next day the difference was found to have changed sign (↓48 divs.). During the next hour-and-a-half the transmitted effects of the electrical excitation of the opposite lobe were observed. The difference gradually increased from 48 divs. to 120 divs. In order to obtain a notion of the character of the transmitted effect, curves were sketched after each observation, which, however, are valueless as records, as not truly representing the time relations of the electrical changes which produced them; for, as will be seen afterwards, the excitatory effect lasts little more than a second, whereas the swing of the needle to which it gives rise lasts the greater part of a minute. The final effect of each excitation was to increase the difference, so that the length of wire required for compensation increased after each excitation, the numbers (divs. of compensator) being 48, 48, 50, 65, 75, 83, 95, 102, 108, 120. On now leading weaker ascending currents through the electrodes of one-twentieth of a second duration ten times at 20″ intervals, and closing the galvanometer for the same time after each excitation, we had, as the immediate local result of each current, ↑15, ↑15, ↑10, ↑5, ↓3, ↓15, ↓22, ↓25, ↓28, ↓33, and at the end of the process, instead of 120, 600 divs. of wire were required to compensate the difference. The excitatory effect had undergone a corresponding change, giving now as large deflections when one-tenth of the current passed through the galvanometer as it had previously done with the whole.

On the following day (Aug. 14) a similar observation was made, of which the results were still more striking. The leaf was prepared at 3 P.M. The lobe, of which the surface was connected with the galvanometer, showed at that time an ascending difference which was balanced by 480 divisions of compensator wire, subsequently by 550, 576, 560 divs. The transmitted excitation effect was ↑3 ↓48 as observed with one-tenth of the current through the galvanometer, but when it was observed without shunting it could be seen that the ↓ effect was preceded by a jerk of the opposite sign. At 3.35 P.M. a ↓ external current was led through the leaf of 0″·03 duration, and repeated at intervals of 20″, as before, for five times. Each was followed by a change in the condition of the leaf, the immediate after effect being ↓10, ↓25, ↓53, ↓65, ↓105; and at the end the difference, which just before had been ↑487, was found to have altered its sign, being at first ↓815, then gradually increasing to about 900 (these numbers, of course, indicating the length of wire required for compensation). The excitatory effect was represented by ↑265, ↓183·3, these numbers being the means of six successive observations made between 3.45 P.M. and 4 P.M., one-tenth of the current passing through the galvanometer. Once more the same process was repeated, that is, a current of the same strength was led through at 20″ intervals, with the effect of bringing up the difference to 975 divs., the mean of six observations being ↓308 ↑50. Thus, we have the following striking contrast:—

	Difference.	Excitatory effect.
3.30 P.M.—Before modification	↑576	↑3 ↓48
3.45 P.M.—After modification	↓900	↓265 ↑183
4.0 P.M.—After further modification . . .	↓975	↓308 ↑50

This observation made it clear that the condition of the leaf which in 1881 I had regarded as normal, is preceded in vigorous leaves by another in which the galvanometrical effects are much smaller, the "leaf current" is in the opposite direction, that is, ascending, and the first phase of the excitatory effect descending. It was also apparent that the small galvanometric effect of the variation in the unmodified state was in part due to the very high resistance which then prevailed; for, whereas after modification one hundred divisions of compensator wire gave a current of 280 scale, the same length of wire before modification gave only 123.

Section 3.—*Observations as to the influence of conditions other than the passage of External Currents in producing "Modification." Proof that the Effect of the Current does not depend on its evoking an Excitatory Response.*

The first of these series is important, as showing that, although "modification" is immediately and with certainty effected by the passage of an external current, the antecedent state may last for some time even when the leaf is repeatedly excited, and (as had often been observed before) that the two lobes may be in very different stages, notwithstanding the complete identity of the conditions under which they have been placed.

The contacts were arranged for leading off from either lobe as required. The right lobe showed the antecedent state, the other was in a transitional one—the difference being on the right side ↑1050 millims.,* on the left ↑29. During a period of 40 minutes the leaf was excited mechanically at intervals of 3 minutes, each lobe receiving six excitations, of which the first five were led off from the opposite lobe, and those of the last of each series from the same lobe.

The characters of the five propagated effects were as follows:—On the right side (small difference) the first phase was negative from the first, and gradually increased from 6 to 30 scale (with one-tenth of the current), and was followed by a deflection of more than four times the extent in the opposite direction. On the left side, when the whole current was allowed to pass through the galvanometer, the same phenomenon as before described was witnessed, namely, that the swing of the needle in the ↑ direction was at once caught by a movement to the opposite side, and this was followed by a ↑ swing of much greater extent (over 400 scale).

The two observations in which the effect was led off from the excited lobe showed substantially the same phenomena (with one-tenth of the current).

Right lobe	↑jerk, ↓jerk, ↑48.
Left lobe	↑35, ↓150.

A ↑ current of 4 Daniells was now passed for three-twentieths of a second through the left lobe, and four times repeated at intervals of 20 seconds. It was found that the right (opposite) lobe was unaltered, that is, still remained in the antecedent state (diff., ↑920; exc. effect, ↓18 ↑73). In the left lobe the difference had changed sign, being now ↓1100, instead of ↑340, and the excitatory effect (with one-tenth of the current through the galvanometer), ↑270 ↓ off the scale, that is, over 300; this observation having been confirmed by repetition, five ↑ currents of the same strength and duration as before were led through the right lobe. Immediately after the difference had changed sign, and was now ↓858 instead of ↑920, and the excitatory effect, ↑230 ↓270. In other words, the two lobes, which were in the first instance in such different stages of modification, were when subjected to the same modifying process brought into perfect conformity with each other.

The preceding experiment shows that the influence of mechanical excitation in producing modification cannot be compared with that of a current, for both lobes were repeatedly excited mechanically without any material change in their electrical state, and it was further observed that the modification of one lobe had no effect on the other, as would have been the case had the result been producible by propagated excitations. It could, therefore, scarcely be supposed that the modifying influence of the current is at all dependent on its evoking an excitatory reaction; but to make this clear it appeared desirable to repeat the preceding experiment, taking especial care that the currents used should be below exciting strength.

On October 5 a leaf was prepared with leading off contacts on the right lobe.

---

* In these experiments a compensator, of which the wire is divided into 1200 millims., was used. 100 millims. of wire corresponded to about 0·0074 volt.

The difference was ↑810, and the excitatory effect of mechanical excitation of the opposite lobe was (with one-tenth current) ↓10, ↑20. With the whole current through the galvanometer, it was seen that the initial ↓ phase was preceded by a ↑ jerk of the needle. Five series of very feeble ↑ currents, each of 0″·22 duration, were passed through the lobe by means of the slow rheotome, which, as in the previous observations, was so arranged as to close the leading off circuit for a period of half a second after each excitation, so as to afford an indication of whatever change might occur in the electrical state of the surfaces led off from. There were in all 40 closures. Up to 20 closures the deflections were still ↑, but between 20 and 30 they gradually became ↓, increasing at the same time in amplitude. The after effects had therefore changed sign, but even after 40 closures the difference was found to be still ↑. The leaf was then subjected during the next quarter-of-an-hour to a series of excitations at one minute intervals, in the course of which the difference, which was at first balanced by 240 divs., gradually diminished to 0, and then changed sign, so that at the end of the observation it was ↓40. The second phase of the excitatory effect gradually diminished in extent until it disappeared (at first ↑50 ↓105, eventually ↑65 ↓0). The leaf was left in the moist chamber until the next day (19 hours). Its upper surface was now strongly negative, the difference being ↓510, and the excitatory variation (with one-tenth current) ↑70 ↓280. These results confirm the evidence previously given, that the process of modification once started in the leaf is a progressive one, for the change which was observed immediately after the passage of the current not only went on rapidly during the next half-hour, in the course of which it was excited mechanically, but continued during the night, notwithstanding that the leaf was not interfered with.

Our next endeavour was to ascertain whether, by methods other than electrical, it was possible to initiate a similar series of changes. For, inasmuch as it so often happens that leaves which have certainly not been subjected to the action of any external current exhibit the condition which in others results from modification, it seems clear that the current acts merely as a stimulus by which a physiological process, for which the essential conditions are internal, is called into activity. With this view, various observations were made during the first week of October, 1885, on leaves of which the under surface was negative to the upper, and the initial phase of the excitatory disturbance was ↓, for the purpose of ascertaining whether, either by mechanical excitation or by the application of heat to the surface (by bringing near it a small platinum coil through which a current was flowing), the process which has been described could be initiated. It was found that in some leaves the change began as soon as the leaf was prepared, that is, that when first observed it was in a state of change, which was sometimes so rapid that the length of wire required to balance it was reduced to a half or a third in a few minutes. In such leaves it was always found that the change was promoted either by warming or by touching the sensitive filaments of the opposite lobe, but we were not able to find that either of these expedients produced effects comparable to that of leading through an external current.

Section 4.—*Observations relating to the Influence of "Modification" on the Electrical Resistance of the Lamina.*

In the course of the preceding observations it had been learned that, in general, the extent of the galvanometric effects was much larger in the modified than in the antecedent state; and it was surmised that this was partly due to diminished resistance. To determine this, a simple but sufficient method was adopted—that of passing through the leaf by the electrodes used ordinarily for leading off, before and after modification, a current derived from the same length of compensator wire. The ratio of the two galvanometer readings thus obtained, for a reason to be immediately referred to, affords a sufficiently exact indication of the difference of resistance. Thus, in a leaf examined on October 2 it was found that 100 divs. gave through the right lobe, which had not been modified, a deflection of 38 scale, through the left, partly modified, 150 scale; but after both had been completely modified by the passage of a current through them, the same length of wire gave a deflection of 360 in the right and of 340 in the other. It was thus evident that in the modified state both were, as regards resistance, in the same condition. In another leaf, which was the subject of observation on October 9, the same difference of potential which gave a current of 38 scale before modification gave 110 when it had just changed sign, that is, immediately after passing the modifying current.

To elucidate the effect, the following more exact, but more circuitous, method was adopted :—

Two Daniell cells were connected with the end-blocks of the compensator, in the circuit of which a variable resistance was interposed, so that the difference of potential between its ends could, within certain limits, be varied at will. One of the end-blocks was connected through a fixed resistance (30,000 ohms) to the shunt of a galvanometer, the wire from the other terminal being led to the slider of the compensator. The resistance in the compensator circuit was then adjusted so that 100 millims. of wire gave a deflection of 300 scale in either direction.

This having been done, the leading off electrodes were applied to the opposite surfaces of the leaf, and the leaf, with its electrodes, so introduced into the galvanometer circuit as to take the place of the fixed resistance. The ↑ difference was balanced by 210 millims. of wire (the value of which in actual difference of potential was now about twice as great as in the previous experiments), and 10 millims. gave through the leaf a deflection of 355 scale (one-tenth of the current). The propagated effect was (mean of five successive observations) when observed with the whole current through the galvanometer ↓29, and was preceded by a small preliminary jerk of the needle in the ↑ direction, followed by ↑ after effect. The lobe was therefore completely unmodified. The current of two Daniells was now led through in the ↓ direction for 30 seconds. The difference had changed sign, and was now ↓640, instead of ↑200, the first phase of the propagated excitatory effect being ↑160, instead of ↓3. The resistance had undergone an equally remarkable change, for the same difference of potential, which a few minutes before gave a deflection of 35·5 scale, now gave (mean of seven observations) 335 scale.

As the resistance of the galvanometer and electrodes together was about 7000 ohms in both of the experiments on the leaf, whereas in the preliminary experiment the total resistance in the circuit was about 32,000 ohms, we have, designating by R the resistance of the lobe before modification, and by R′ the resistance after modification, the following relation. The difference of potential corresponding to 100 millims. of wire gave, with the resistance 30,000 ohms, a deflection of 300 scale. In the second experiment, with the resistance R in the leaf, in addition to 7000 ohms in the circuit, the same difference gave 35·5 scale. In the third experiment, after modification, with the resistance R′ in the leaf, in addition to 7000 ohms in the circuit, the deflection was 246 scale.

Consequently,

$$R = \frac{300 \times 32,000 = 9,600,000}{35\cdot5} - 7000 = 263,422 \text{ ohms,}$$

and

$$R' = \frac{300 \times 32,000 = 9,600,000}{246} - 7000 = 32,024 \text{ ohms.}$$

In a similar experiment with another leaf, we had with the invariable resistance 330 scale, with the unmodified leaf 155 scale, and after modification 375 scale.

Consequently,

$$R = \frac{330 \times 32,000 = 10,560,000}{155} - 7000 = 61,120 \text{ ohms,}$$

$$R' = \frac{330 \times 32,000 = 10,560,000}{375} - 7000 = 21,160 \text{ ohms.}$$

Hence, in the first experiment the ratio of the resistance in the modified leaf to that in the unmodified was 1 : 8, in the second 1 : 2·9.

Had we considered the deflections without taking into account the difference of resistance in the circuit, we should have had in the first experiment 1 : 6·95, in the second 1 : 2·40. The resistance of the leaf is so enormous, as compared with that of the circuit, that for the purpose we have in view the latter may be neglected.

In the other examples given, the ratios were 1 : 9·5, 1 : 2·3, and 1 : 2·8. The great difference between them is readily explained by the circumstance that, although apparently every leaf can be brought into the modified state, the process of modification has in many instances already made some progress before the resistance can be measured.

Section 5.—*Investigation with the aid of the Pendulum Rheotome of the Time Relations of the excitatory Variation in the Modified and Unmodified states of the Leaf.*

I have now to give an account of two series of observations, made respectively in August and October, 1887, which were undertaken for the purpose of confirming and correcting the knowledge which had been gained in 1885, with respect to the nature of the change which, in the preceding section, has been termed "modification." In the first series my object was to determine the time relations of the excitatory process in the unmodified and unmodifiable states respectively, with the aid of the rheotome; in the second to obtain photographic records of the characteristic electrical phenomena.

Observations with the Rheotome.

The pendulum used for the purpose was one which has been recently constructed in the Oxford Laboratory. Its period of oscillation is 1″·4.

The arrangement of its keys is the same as in an instrument I employed in 1881, but for the present purpose it has the advantage that, in consequence of its much greater length, a much longer period can be investigated. The leaves were prepared in the way described in my previous paper, and were placed in a moist chamber at the ordinary temperature of the room in August. The temperature varied during the experimental days from 60° to 67° Fahr. Each leaf was, of course, provided with two pairs of non-polarisable electrodes, which were applied, one to the upper surface between the three hairs, the other to the under surface exactly opposite. The direction of the break induction shock produced by the zero key of the rheotome was, of course, always (↓) descending; and in all the experiments the period of closure (the interval of time between the opening of the short circuiting key (K_2) and the opening of K_3) was the same, namely, one-tenth of a second.*

The observations were made on Aug. 13, 15, 16, 17, 18, 1887, and are numbered 1, 2, 3, 4, 5. It was found convenient to use as a compensator a German silver wire 300 inches long, divided into 100 equal parts. The value in volts of each division was determined subsequently. It was 0·014 volt.

In four of the observations the method was exactly the same. Two series of rheotome observations were made, the first series with the leaf in the condition in which it presented itself when first prepared, the second after it had been modified. The modification was in each case effected by passing the current of two Callaud's cells six times through the leaf for ten seconds each time, reversing the direction each time, so that three currents were descending and three ascending. The diagrams give the result. The intervals between successive excitations were about one minute each; sufficient time was thus given to allow of the difference being satisfactorily compensated. The amount of the difference was of course recorded in each case.

In each of the diagrams the dots connected by faint unbroken lines indicate the rheotome observations of the excitatory reaction in the unmodified leaf, made during the first eight-tenths of a second, the numbers being the deflections observed when the time of closure (the duration of which, as above stated, was always 0″·1) ended 0″·1, 0″·2, 0″·3, 0″·4, 0″·5, 0″·6, 0″·7, or 0″·8 after excitation. The dots connected by broken

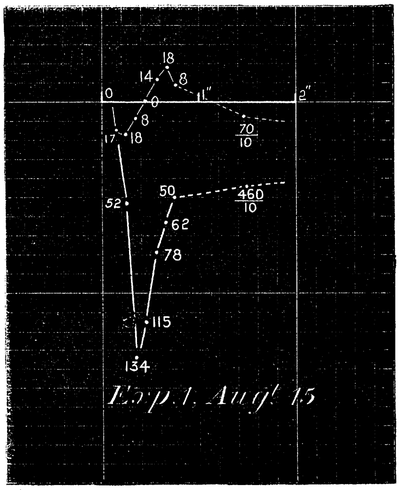
---

* See 'Phil. Trans.,' 1882, p. 18, and fig. 8.

lines relate to observations of the deflections observed when the galvanometer circuit was closed during the whole of the second or third second respectively by the hand guided by the metronome. The dots connected by *stronger* unbroken lines, and the numbers, have the same meaning with reference to the excitatory variation in the modified state.

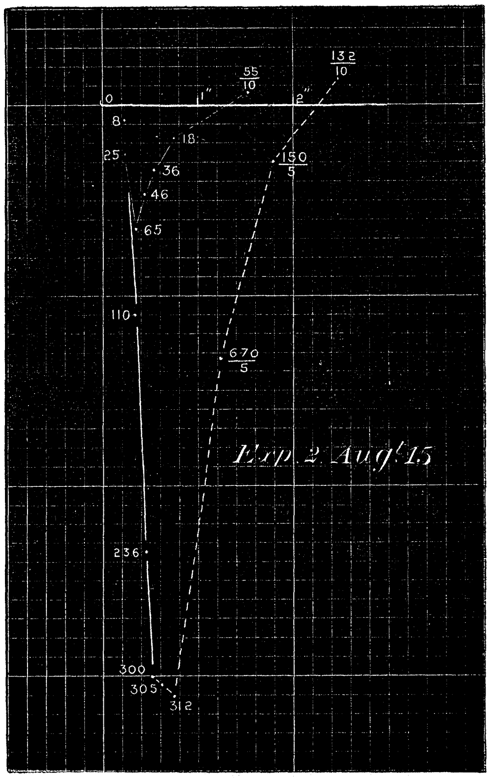
Experiment I. (diagram 2).—In this experiment the difference when the leaf was prepared was high (↑16·3). At the beginning of the rheotome observation it was ↑15, and fell during its course to ↑13. The excitatory effect, as observed with the galvanometer, was ↑10, ↓15, ↑250, that is, it was a long ascending swing preceded by an oscillation. The rheotome showed that the oscillation, though its galvanometric effect occupied several seconds, was over before the end of the first second. Immediately afterwards modification was effected (this time by passing the current of one Callaud ↓ for 20 seconds). The difference was now ↓2·1, and in the excitatory effect no preliminary oscillation was visible, only a negative swing followed by a prolonged after effect in the opposite direction. The resistance was much diminished, so that the same length of wire which gave a deflection of 9·2 before now gave 69.

Diagram 2.



In *Experiment II.* (diagram 3) the difference, which was at first 8·5 wire, increased during the observation to 12·5. As the alternate short currents did not produce the desired effect, the current was closed in the ascending direction for a minute, after which the difference changed sign. It was at first ↓7, but subsided during the rheotome observation to ↑4·5. The diminution of resistance was such that with the same length of wire the deflection representing the difference, which before modification was 370 scale, increased after modification to 115 × 10, that is, 115 scale, with one-tenth of the current through the galvanometer. It will be noticed that in this leaf the resistance both before and after the passage of the external current was much less than in Experiment I. When the first rheotome observation was made, the excitatory variation was (with the galvanometer) ↑120, ↓220. It showed already, therefore, the characters of the "modified state," although the difference was still ↑. But from the rheotome readings it appeared that the first phase was of relatively short duration, for during the second half of the first second the relative negativity of the under surface was very rapidly diminishing, and during the second second it was reversed. The comparison of the two records shows that the change of sign did

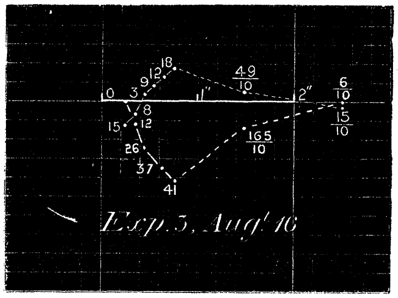
Diagram 3.



not occur until a second later, the operation in the less modified state of what may be designated the ↑ element in the excitatory effect of the external current being to annul this action, or so far to diminish it as to give complete predominance to its opposite. Here again it must be noted that the great amplitude of the deflections in the second rheotome observation was due to diminution of resistance.

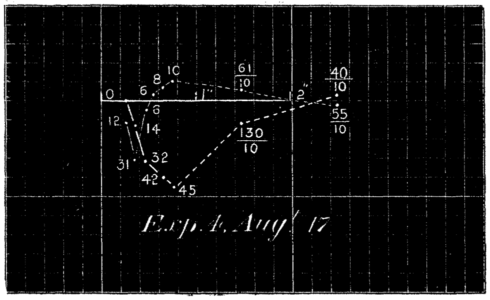
Experiment III. (diagram 4).—In this preparation the difference remained constant, namely, between 14 and 15, during the whole observation. The excitatory effect was observed with the electrometer, and had the character shown in photograph 13 (Plate 70). The rheotome observation showed that the oscillation was, as in Experiment I., completed during the first second. After modification, which was promptly effected in the usual way, the difference changed sign from ↑7 to 0, or ↓0·5, and the prevailing direction of the excitatory effect became ↑; so that in every respect but one, the curves are seen to be counterparts of each other. Both effects began in the same direction, but in the modified preparation the initial negative phase, which before modification is interrupted or cut short by an effect in the opposite direction, rose to its highest point at about the same time after excitation as the positive phase had culminated before. In both conditions there was an after effect, but the two after effects had opposite signs. In the unmodified state the under surface became more negative as a consequence of each excitation; after modification it became more positive. The diminutionof resistance was as great as in the other cases. With equal lengths of wire the deflection before modification was 160; after, 110 × 10.

Diagram 4.



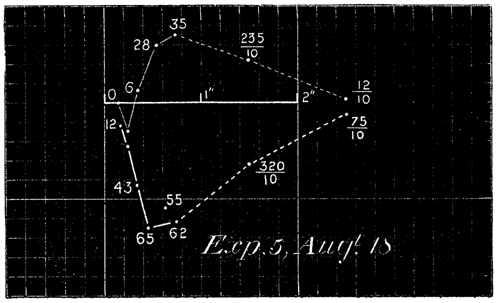
Experiment IV., *Aug.* 17 (diagram 5).—In preparation IV. the difference was 61, but, as in Experiments I. and II., diminished considerably before the rheotome observation could be taken. For the purpose of bringing about modification, the current of two Callaud cells was passed through the right lobe for one minute, changing the direction every ten seconds. One such operation failed to produce the desired result, the difference remaining in the old direction; but after a second minute it had changed from ↑2·5 to ↓3·0, and there was a corresponding change in the excitatory variation as observed by the electrometer. Before modification the excitatory effect consisted of an excursion in the ↓ direction, which was preceded by a sharp jerk in the ↑, and followed by a prolonged ↑ after effect. After modification a preliminary ↓ effect was followed by a prolonged ↑ after effect. With the same difference of potential, the galvanometric deflection was 68 after modification, 26 before.

Diagram 5.



Experiment V., Aug. 18 (diagram 6).—Here the difference was ↑10·6, but diminished to 9·3 during the first rheotome observation. The character of the excitatory effect resembled that observed in Experiment III., but the ↓ phase lasted longer. The after effect, as in Experiment III., was ↓.

Diagram 6.



A second observation was made an hour after the first, in which the preparation was found to be changing in the direction of modification, though no extraneous current had been led through it, for the ↓ phase was both weaker and of much shorter duration, as evidenced by the fact that during the second second the under surface was feebly negative, instead of strongly positive. Modification was promptly effected in the usual way. The difference, which had diminished to ↑5·6, changed sign and became ↓3·5, and the resistance had so diminished that with the same length of wire the deflection, which had before been 280, became 75 × 10. In this case the electrometer displayed the change which had occurred in the electrical response very strikingly. Before modification it resembled photograph 12; after, photograph 1.

Section 6.—*Photographic Records.*

I have now to submit to the reader, in further illustration of the nature of the excitatory effect, as observed before and after modification, a series of photographic records (Plates 69, 70) obtained by a method which I used in observations made some years ago on the Electromotive Changes in the Heart, and published in the 'Journal of Physiology,' vol. 4, p. 327.

This method consists in connecting the leading off contacts of the leaf to the capillary electrometer, instead of the galvanometer, and photographing the movements of the mercurial column. For this purpose the capillary is projected by means of a half-inch objective on a slit at a distance of about two feet. Immediately behind the slit a photographic plate moves horizontally, with a velocity of about 1 centim. per second.* The photographic curve thus obtained expresses the movement of the

---

* This method is here described as used for my observations on *Dionæa*. It has since been considerably improved, and will be described in a future communication.

column during the period of observation, viz., about 25 seconds. In most of the experiments time was marked on the plate photographically by a vibrating shutter, which covered one end of the slit, and was opened by an electro-magnet in circuit with a tuning-fork, either ten times or twenty times a second, producing a dark bar on the plate each time it was opened.

Photographs 1, 2, 3, and 4 represent experiments made in 1883, the mode of observation being precisely that described in my former paper as used in the "fundamental experiment." Photograph 1 may be considered as a typical record of the excitatory variation in a modified leaf when subjected to repeated excitation by passing a weak induction shock through the opposite lobes and in the ↓ direction every five seconds. The four photographs differ chiefly as regards the duration of the primary effect, or ↑ phase (descending in the photograph). In all, it is seen that the first phase begins about one-fifth of a second after the moment at which the current in the primary coil of the induction apparatus is opened (in accordance with the rheotome observations), and that the primary effect of the first excitation is followed by an after effect in the same direction, and that this after effect is neither increased nor diminished by the succeeding excitations, but subsides gradually during the whole period of observation. In photograph 6 it is seen that when the interval between succeeding excitations is longer, so that the after effect has time to subside, the second effect resembles the first, though the second phase is of less amplitude. Photograph 5 is the record given by the same leaf as photograph 2, when "exhausted" by repeated excitation. The difference is greater, and the resistance less; the first excursion of the electrometer exceeds the rest in amplitude, but *is followed by no after effect* (see 'Phil. Trans.,' 1882, Part 1, p. 31). In the observation recorded in photograph 7 the opposite lobe was excited, not electrically, as in all the preceding instances, but mechanically, by touching the tips of the sensitive filaments with a camel-hair pencil, which was so used as at first to touch a single filament and afterwards accidentally two filaments. It is seen that, although in each of the double excitations the interval between the two immediately following effects was about three-quarters of a second, there was little difference between them in amplitude.

Photographs 8 and 9 are records of an experiment in which the leading off contacts were on opposite and corresponding spots on the middle of the under surface of the two lobes, as shown in my former paper ('Phil. Trans.,' *loc. cit.*, p. 36, fig. 13). The right lobe was connected with the sulphuric acid, and the left with the mercury, that is, with the capillary. In the first observation the right lobe was excited by touching one of the sensitive filaments with a camel-hair pencil in the neighbourhood of the leading off contact; in the second, the excitations took place alternately on opposite lobes, that is, in the neighbourhood of the two opposite leading off contacts. It is seen that in the first case (photograph 8) the under surface of the right lobe becomes first relatively positive, then that of the left; and in the other that the same diphasic effect is witnessed as the result of the first and third excitations, but that the effect of the second and fourth are counterparts of the others, the explanation being, of course, that in the first and third excitations the right lobe was first excited, in the second and fourth the left, and that in either case the effect showed itself first in the excited lobe, later in the opposite one. Photograph 10 represents an observation in which the sensitive hairs on the left lobe in the neighbourhood of the leading off contact were successively touched, in the same way that those of the right lobe had been in the preceding observation. It is complementary to 8.*

It will be understood that all of the preceding photographic records relate to the unmodifiable state, and that in every instance the upper surface was positive to the under. Figs. 11 and 13 (Plate 70) relate to the previous condition. They are records of the excitatory effects in leaves in which the " leaf current " is descending, that is, in which the upper surface is still positive to the lower.

Photograph 11 represents the usual form of such a tracing. It is seen that the electrometer effect consists of (1) a momentary ↑ effect, in which the mercury receded for a period not exceeding one-tenth of a second; (2) a longer excursion in the opposite direction, which lasted about four-tenths of a second; and that the after effect, in which the negativity of the under surface of the leaf was much increased, attained its maximum about a second after excitation, and gradually declined subsequently. It is also seen that, as in the permanent state, the after effect is neither increased nor diminished by the subsequent excitation. At the time the photograph was taken the relative negativity of the under surface (difference) was about 0·11 volt. This was increased to about 0·14 as the after effect of the excitation.

Photograph 12 is introduced to show the reversal which the excitatory effect undergoes in consequence of modification. In both, as has already been shown by the rheotome observations, the first effect is negative, but in every other respect the two tracings are counterparts, the period of negativity in either surface in the one corresponding to that of positivity in the other. When the second photograph was taken the relative positivity of the under surface was about 0·005 volt, but subsequently increased to about 0·03 volt.

The large after effect seen in photograph 9 is only observed when the leaf has not before been excited, or has been excited only once or twice. It expresses, therefore, a state of things which is very transitory. A more easily observed condition is that in which there is no after effect, and the variation consists simply of the primary ↓ excursion with its ↑ precursor, as in photograph 13.

---

* These tracings may be compared with the photographic records similarly obtained of the diphasic excitatory effect in the ventricle of the heart of the Frog or Tortoise (see 'Journal of Physiology,' *loc. cit.*, Plates 1 and 3). The conditions of the observation correspond, and the effects are in harmony with each other.

ADDENDUM.

The following experiment was made for the purpose of obtaining experimental proof that, in the process of modification, the change has its seat at or near the upper surface of the lamina, and does not affect the under surface. It was anticipated that if one lobe were modified, leaving the other in its original state, the comparison of the electrical relations between symmetrical points of the upper and under surfaces respectively would afford the required demonstration.

Diagram 7.

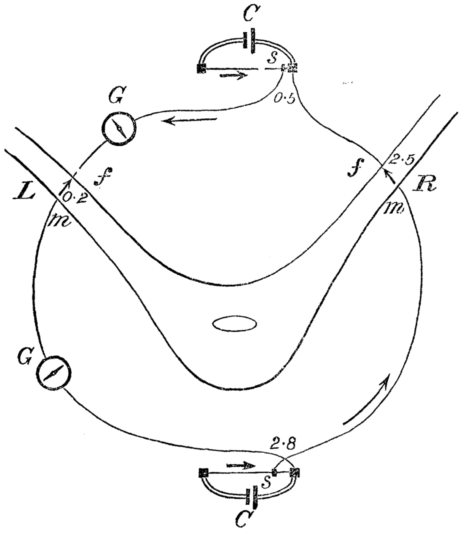
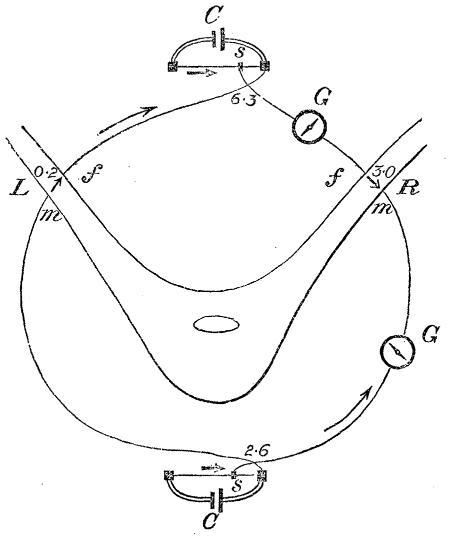


Diagram 8.



The observation was so arranged that the opposite surfaces of either lobe could be connected with the galvanometer. As usual, these were found in very different conditions, but in both the direction of the difference was ↓, and in both the excitatory responses were those seen in unmodified leaves. The galvanometer circuit was so arranged that it could be connected symmetrically either (1) with the two under surfaces or (2) with the two upper ones, that is, with the two spaces between the hairs on opposite sides. The condition of the leaf was carefully observed, and it was found that the state of things was, an hour or two after the leaf had been prepared, as represented by diagram 7. The upper surface of each lobe was positive to the under, but the difference was much greater on the right side than on the left, and the right under surface was positive to the left under surface. The current of a single Daniell's cell was now led for 10 seconds through the right lobe from *m* to *f*, and the process repeated six times in alternately opposite directions, with the usual result. On again investigating the condition of the leaf, it was found that, while the electrical relation between the under surfaces remained the same, that between the upper surfaces was reversed, the right having now become strongly positive to the left. On comparing the upper surface of the right lobe with the under surface, it was found about as much positive as it had before been negative. The result will be best understood from the diagrams, in each of which the contour of a section of the lamina is indicated by the curved lines *f f* and *m m*.

C, C, C, C represent compensators, each of which is so arranged that by placing the slider, *s*, at the proper distance from the end block to which it is nearest, whatever current flows through the galvanometer in connection with it may be balanced so that the needle is at zero. The number written near each compensator in diagram 7 expresses the length of wire which was required to balance the existing currents between the two under and the two upper surfaces respectively in the unmodified state, and the corresponding numbers in diagram 8 express the corresponding lengths after modification of the right lobe. Similarly, the numbers between *f* and *m* indicate the differences of potential between the upper and under surfaces respectively of the right and left lobe (*L* and *R*); in diagram 7 in the unmodified leaf, in diagram 8 after modification of the right lobe. The short arrows (at *L* and *R*) indicate the directions of the currents to be balanced, and the long ones those derived from the compensator wires. In diagram 7 the two upper surfaces are represented as nearly equipotential. In diagram 8 the upper surface of the right lobe, which has been modified, is strongly positive to the left. The relation between the under surfaces, *Lm*, *Lr*, remains practically unaltered. *Lm* is as much positive to *Rm* as it was before.

Conclusions and Summary of Results.

In the conclusions which were appended to my former paper I did not advance any theory of the relation which exists between the electromotive phenomena described and the property of responding by movement to mechanical or electrical stimulation which distinguishes the leaf of *Dionæa* from other leaves. As, however, it is possible that I may not have the opportunity of resuming my investigations, it is perhaps desirable that I should no longer content myself with bringing together the bare results of my labours, but state as clearly as I can what their bearing appears to be on one of the most fundamental questions in physiology—that of the way in which the excitable protoplasm of plant or animal reacts when stimulated or injured.

With this view it seems to me necessary to place before the reader the notions which were until recently, if they are not now, entertained by botanical authorities on this subject; and I cannot do so better than by referring to the very full discussion of it contained in the 34th of Professor Sachs' Lectures on the Physiology of Plants, which were published a year after my last communication.*

Professor Sachs defines excitability as the property by virtue of which living

---

* An English translation has recently been issued by the Clarendon Press, entitled 'Lectures on the Physiology of Plants,' by Julius von Sachs; translated by H. Marshall Ward, M.A., F.L.S. Oxford, 1887.

organisms react to stimuli. This reaction, he says, is "physiological," not "physical," and belongs to "protoplasm"; and he emphasises the statement that the "phenomena of the effect need have no similarity or proportionality to the stimulus." "Excitable structures" he distinguishes as being "in a state of unstable equilibrium, of which every disturbance will sooner or later be compensated." The state of disturbance he characterises as a "new condition, that of excitatory action in which excitation can no longer be effective." Finally, he observes that in plants "the effects of excitation make their appearance slowly." . . . "Several seconds, minutes, or even hours pass before the local excitation has traversed a path of 10, 20, or even 30 centims."

As regards the leaf of *Dionæa* the definition with which Professor SACHS sets out holds good. There can be no question that the response of the leaf to stimulation is physiological, not physical, and that the effect is "disproportional" to the cause. But here correspondence ceases, and it becomes evident, from the subsequent passages in which he discusses the nature of the effect and its propagation, that he confounds with the physiological reaction the mechanical effects which the reaction eventually brings about long after it has itself ceased to exist. The only effect of stimulation which Professor SACHS recognises is change of form—the only reaction, that of which change of form is the visible sign. What *we* mean by reaction or response to stimulation is a *molecular change*, which begins *immediately after its cause, and is propagated wherever there are continuous paths of excitable protoplasm*; and we recognise its existence, measure its duration, and determine the velocity with which it is propagated, not by the visible motions of organs which follow the reaction after long intervals of time, *but by the electrical disturbances which are their immediate concomitants.* The evidence that Professor SACHS, when speaking of propagation, means propagation of visible effects only, is to be found in such words as I have quoted as to the rate of propagation and the ineffectiveness of second stimulation. The highest rate of propagation which he recognises in plants is 10 centims. in several seconds. If by "several" we understand two or three, this would mean four centims. in a second. In *Dionæa* the rate is, at ordinary temperature, 20 centims. per second; that is, the local response takes place at a distance of 1 centim. from the stimulated point $0''\cdot05$ after the stimulus. Similarly, when Professor SACHS says that after a first stimulation a second is ineffectual, what he means is that, after the leaf of *Dionæa* has closed, after the leaf of *Mimosa* has drooped, or the filaments of *Cnicus* or *Centaurea* have straightened, they cannot undergo these several changes again until they have had time to resume their original form. But is it possible that Professor SACHS does not recognise that the reason why this is the case has nothing to do with protoplasm or its physiological reaction to stimulation? These movements cannot be repeated, not because the organ has thereby lost its excitability, but simply because for purely mechanical reasons repetition is impossible. It depends on the discharge of water from the constituent cells, and consequent loss of turgor, which cannot be reinstated until the cells have had time gradually to fill themselves again.

The purpose of Professor SACHS' remarks is to make it appear (1) that plants do not contain nerves, and (2) that there is nothing in them of the nature of nerves. As certainly as the first of these propositions is true, the second is mistaken. The "nature" of a nerve is that it is excitable, that the effect of excitation is propagated, and that the excitation can be repeated immediately after with the same effect as the first time. So far as is known, the sole characteristic of this effect is that it is accompanied by electrical change, and its sole essential condition is that which was clearly indicated by NEWTON—continuity of substance in the channels of conduction.* In all these respects there is complete correspondence between the excitatory reaction in the protoplasm of the cells of the leaf and the excitatory reaction in nerve—the only difference being in the rate of propagation, and in the form and distribution of its paths. The difference of rate may be shown to be unessential by comparison with other examples derived from animal physiology. In nerve the electrical change travels 100 times (30 metres) as fast as in the leaf (in which at high temperatures the rate of propagation is not less than 30 centims.), in ordinary striped muscle about 10 times (3 metres) as fast; but in the muscular tissue of the ventricle of the heart of the Frog, at about half the rate (15 centims.). As no one doubts that in these three instances the process is essentially the same, the relatively slow propagation in *Dionæa* (enormously rapid as it appears as compared with Professor SACHS' standard) is unessential.

Having thus come to an understanding of Professor SACHS' theory (if it may be rightly so termed) of "irritability," all that remains is to inquire what his attitude is as regards the phenomena themselves. Does he deny them, or simply decline to recognise their bearing? The answer will be found in Lecture 37, in which, in commenting on my observations as to the electrical concomitant of the reaction, he sets forth his theory of its nature. Irritation produces migration of water—migration of water, electrical disturbance. He admits, therefore, the existence of an electrical disturbance consequent on excitation, but in accounting for it strangely disregards its time relations, forgetting that it has time to accomplish itself twice at least before its supposed cause comes into existence, and that its intensity is out of all proportion greater than that of the osmotic currents with which he identifies it. Happily, although some facts relating to the subject are perplexing, it is very easy for any one who has at his command the common appliances of a physiological laboratory, if he is not satisfied with my experiments, to observe himself all that is necessary to prove the impossibility of Professor SACHS' position.

It being once admitted that the excitatory process in the leaf is of the same nature as that which follows stimulation in animal structures, and more particularly in nerve, and organs belonging to the nervous system, there is reason for hoping that, just as the study of the excitatory process in animals affords a secure basis for its investiga-

---

* See query 24 at the end of Book III. of the "Optics," HORSLEY'S Edition of 'NEWTON'S Works,' vol. 4, p. 226.

tion in plants, so the relations we may be able to establish between observed phenomena in plants may guide us to the better understanding of corresponding relations in animals. As was shown in the introduction, the question in animal physiology at present lies between those who regard the action of a stimulus as a mere interference with a previously existing state of electrical activity, and those who think that the electrical concomitant of excitatory reaction has no necessary connection with any such state. According to the former view, it is held that when a muscle is excited the excitatory variation comes into existence *d'emblée*; according to the latter, the constant operation of one or more such forces is presupposed, as well as their liability to be disturbed by external influences. In the leaf, observed facts show most conclusively that the two sets of phenomena—those of the excited and those of the unexcited state—are linked together by indissoluble bands; that every change in the state of the leaf when at rest conditionates a corresponding change in the way in which it responds to stimulation, the correspondence consisting in this, that the sign, that is the direction, of the response is *opposed* to that of the previous state, so that as the latter changes sign in the direction from ↑ to ↓ the former changes from ↓ to ↑.

This remarkable relation, the discovery and experimental demonstration of which has been the most important fruit of my more recent work, can only be understood to mean that the constantly operative electromotive forces which find their expression in the persistent difference of potential between the opposite surfaces, and those more transitory ones which are called into existence by stimulation, have the same seat—the opposition between them being in accordance with the general principle that, whereas the property which renders a structure capable of undergoing the excitatory change is expressed by relative *positivity*, the condition of discharge is expressed by relative *negativity*.

Much light is thrown on the relation between the excitatory reaction (action current) and the previous difference (leaf current) by the observation of the influence exercised on both by external voltaic currents. We have seen that when such a current is led through a leaf for a very short period it produces a lasting effect, which is always in the same direction, that of the excitatory reaction, whatever may be the direction of the external current. But this influence is exercised more effectually when the direction of the external current is descending (that is, when it coincides with that of the effect to be produced) than when it is ascending. In animal structures analogous to the leaf, and particularly in the electrical organ of the Skate or Torpedo, we find the direction of the lasting effect of a current led across the disks or plates to be always normal, whatever may be that of the current itself—*i.e.*, that of the natural discharge of the organ; but a homonymous current is much more effectual than one in the opposite direction. In the application by DU BOIS-REYMOND of the term "positive polarisation" to the after effects of voltaic currents led through muscles and nerves, a similar relation is suggested, which, however, is complicated by other conditions which cannot be here discussed. But in the leaf, as in the electrical organ, the relation admits of being very simply stated, and in the same terms for both. The sub-excitation which the external current leaves behind it operates always in the same direction, its intensity, not its sign, being dependent on the direction of the current which has produced it.

As regards the localisation of the electromotive changes which are associated with "modification" and "excitation," we have given experimental evidence that they have their seat at or near the upper surface of the lamina. Accepting the principle already formulated, that all such action depends on difference of physiological activity between adjacent cells or strata of cells, provided that their protoplasms are in continuity, we may account for the phenomena observed, by supposing that in the unmodified state the most superficial strata are positive to those subjacent to them; and that the effect of sub-excitation, as well as of the excitatory explosion, is to diminish, annul, or reverse this difference, so that eventually the excited superficial cells become less susceptible of excitatory change—the result being that the excitatory variation, which in the unmodified state may be compared to a contest between opposing electromotive forces, assumes the decisive character which belongs to modification. Without venturing to say that this is precisely the way in which the result is brought about, it seems clear that the process of modification may be rightly compared to a contest between two electromotive actions, of which the one represented by the ascending arrow (↑), at first predominant, eventually yields to the other (↓).

By way of conclusion, I propose to state in the shortest language the experimental facts which have been established.

1. In the leaf of *Dionæa*, in its prime, the upper surface is positive to the under. On excitation it becomes suddenly negative. This change, constituting the first phase of the excitatory variation, occupies for the most part the first second after excitation. It is often preceded by a momentary change in the opposite direction.

2. Subsequently it undergoes a gradual change, which is designated in the experimental part of the paper by the term "modification." This consists in diminution of the negativity of the upper surface, and its eventual replacement by relative positivity. The change is accompanied by (*a*) reversal of the sign of the excitatory variation; (*b*) (later) by diminution of the electrical resistance of the leaf.

3. The first phase of the excitatory variation is followed both in the modified and unmodified state of the leaf, provided that it has not been excited immediately before, by an after effect which has always the opposite sign. If the leaf has been excited immediately before, the second phase is absent.

4. Modification may be produced at will by passing a voltaic current for a very short period through the leaf in either direction, even though the current be so weak that its closure is not followed by an excitatory variation. It is a local effect which is not propagated. One lobe may be modified without the other, and even one part of a lobe without the surrounding parts.

5. The propagated excitation reaching a part of the leaf which has undergone

modification evokes a modified response of which the direction of the first phase is ascending, and a response of the opposite sign in the unmodified region.

Two questions, among others, may be mentioned as requiring further investigation. One relates to the cause of the diminution of electrical resistance which accompanies the process of modification, particularly its relation to the disappearance of turgor. The other concerns the process by which the modified part regains its pristine state, and the time required for its accomplishment. To these I shall give attention, if opportunity offers.

My thanks are due to Mr. F. GOTCH for his able assistance in the experiments recorded in this Paper, and to Messrs. F. J. M. PAGE and G. BURCH for their aid in the photographic observations.

EXPLANATION OF PLATES.

PLATE 69.

Figs. 1 to 4. Photographic records of the "Fundamental Experiment" in different leaves. (See 'Phil. Trans.,' 1882, p. 25.) The leaf is excited at intervals of about 5″ by a single induction shock led through the opposite lobe at the moment indicated in the photograph by the break in the bright line. As the make induction shock was cut off, the moment of excitation corresponds to the right-hand edge of the interruption. Figs. 1, 3, 4 are at ordinary temperature, fig. 2 at a high temperature (25° C.).

Fig. 5. Same experiment as fig. 3. Leaf exhausted.

Fig. 6. The same experiment. Interval between the excitations prolonged; hence the second phase of the response, which is usually only observed after the first excitation, here occurred after the second.

Fig. 7. The same experiment. Mechanical, instead of electrical, excitation. Double effect, due to accidental touching of two sensitive filaments one after the other.

PLATE 70.

Fig. 8. Experiment described in 'Phil. Trans.,' 1882, pp. 32–38; the leaf was led off by corresponding points on the under surface of opposite lobe. The tracing shows the combined result of opposite electromotive changes taking place in the two lobes. Leaf excited mechanically on right side.

Fig. 9. The same leaf excited alternately on right and left sides.

Fig. 10. Leaf excited on left side.

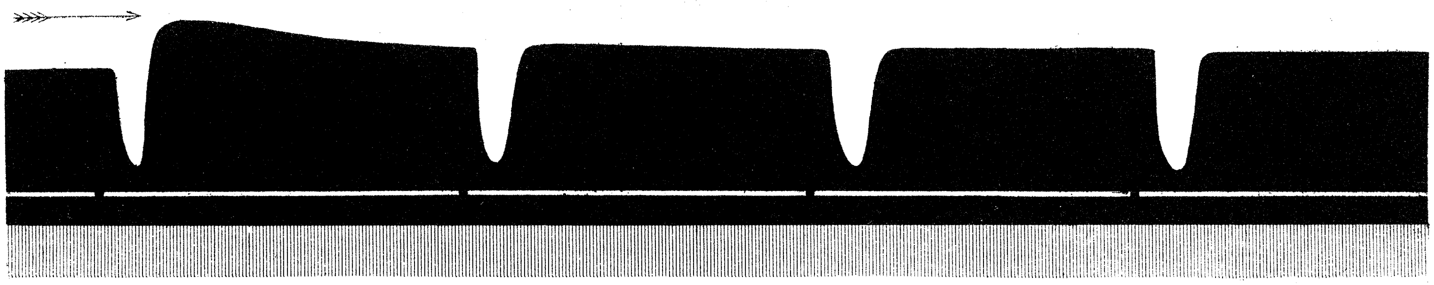


Fig. 1.

20 per sec.

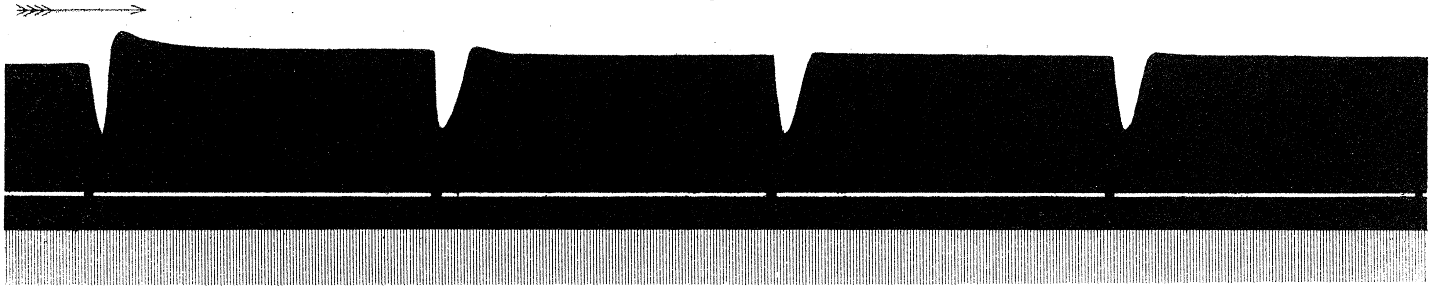


Fig. 2.

20 per sec.

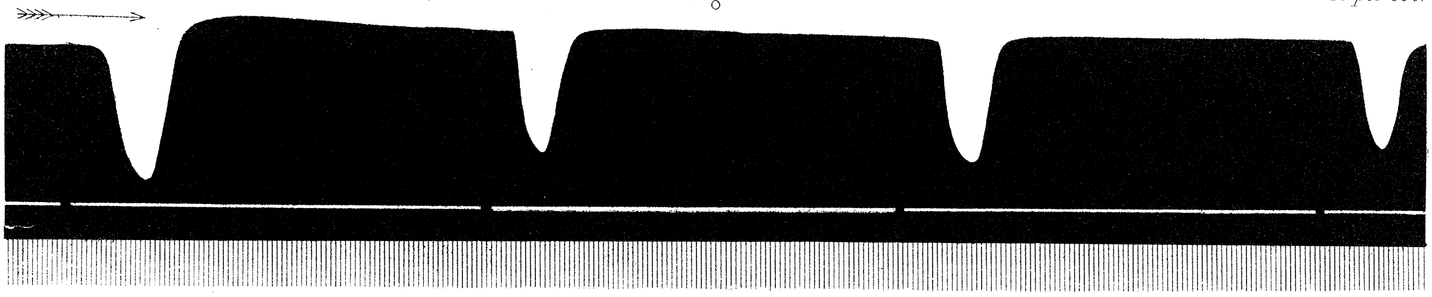


Fig. 3.

20 per sec.

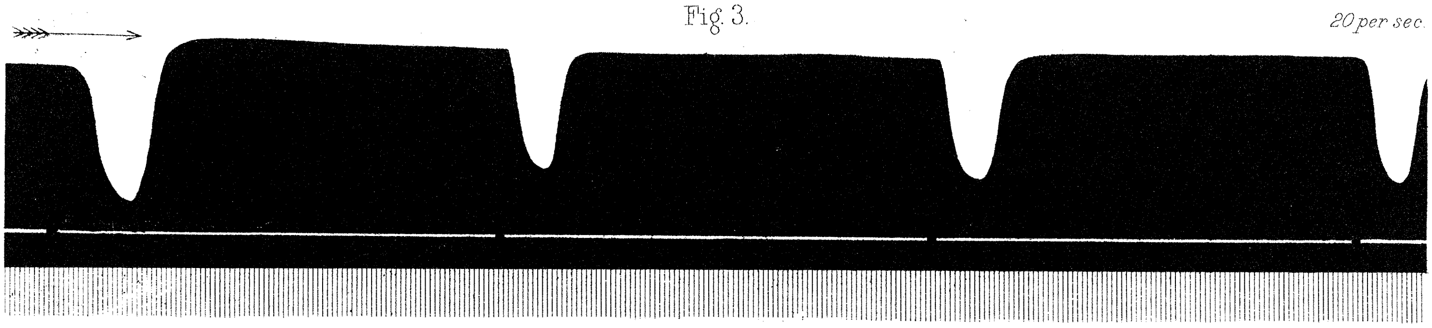


Fig. 4.

20 per sec.

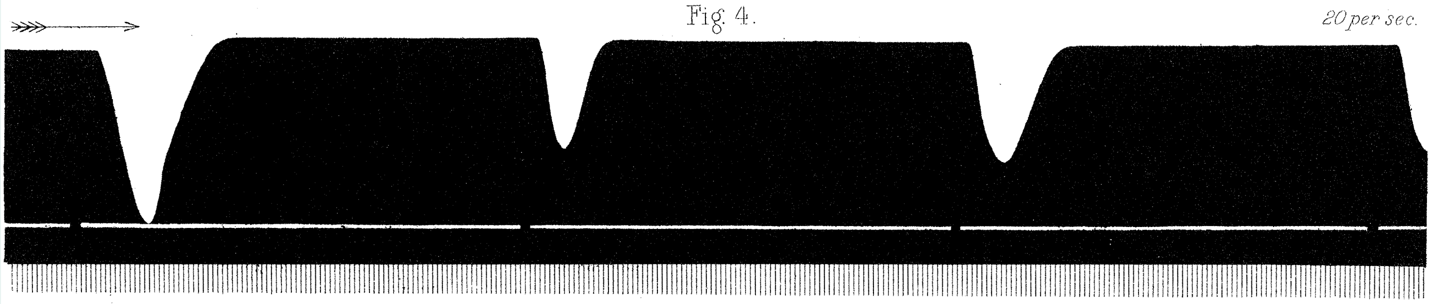
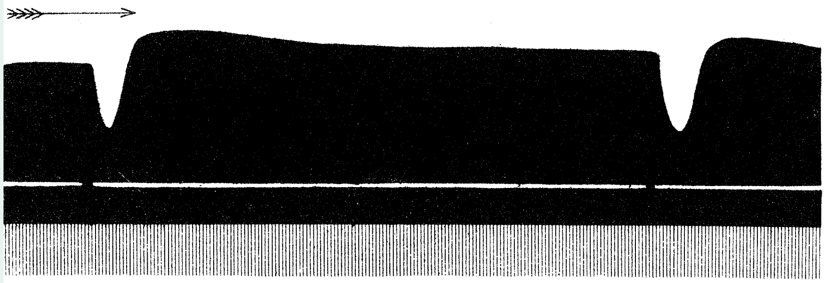


Fig. 5.

20 per sec.



20 per sec.

Fig. 6.

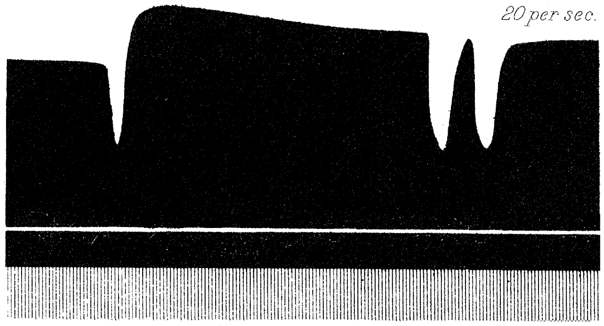


Fig. 7.

20 per sec.

Lith. & Imp. Camb. Sci. Inst. Co.

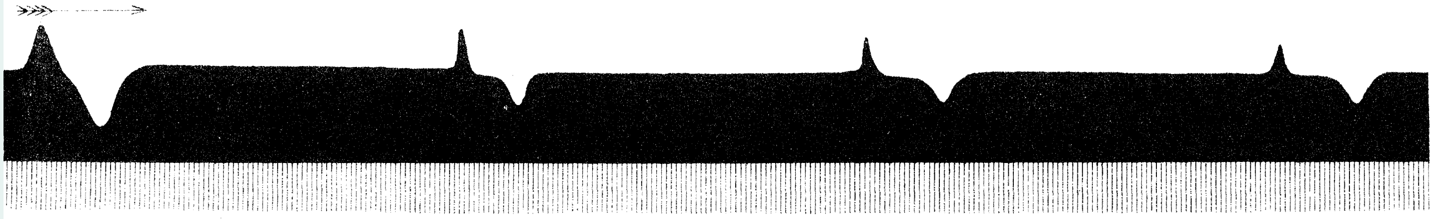


Fig. 8.

20 per sec.

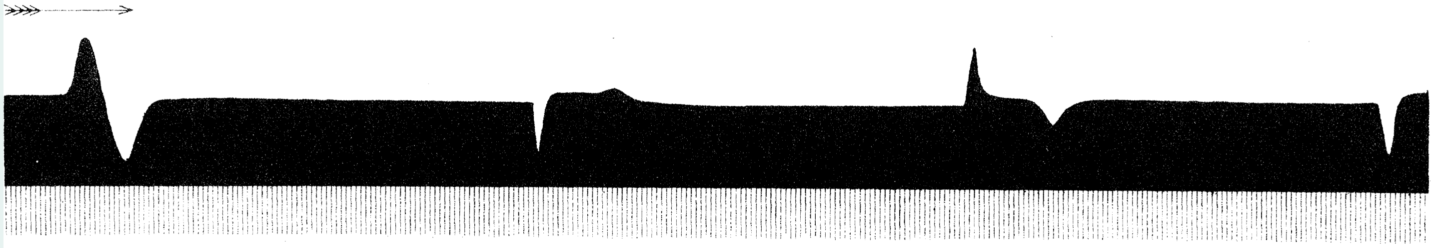


Fig. 9.

20 per sec.

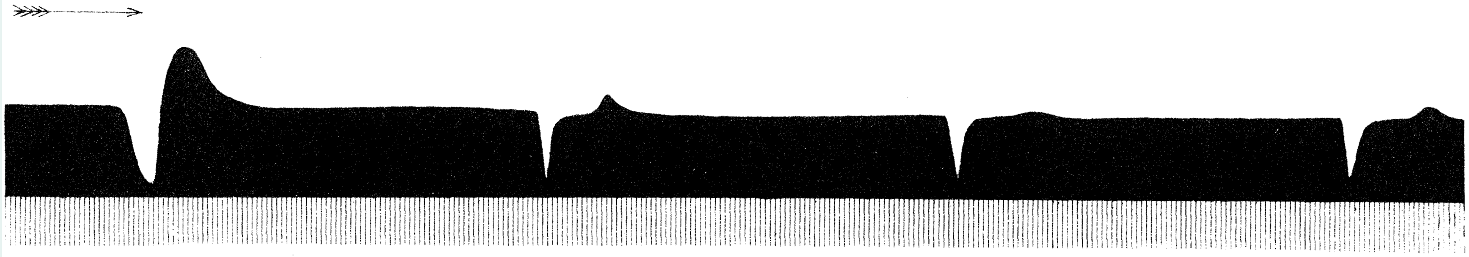


Fig. 10

20 per sec.

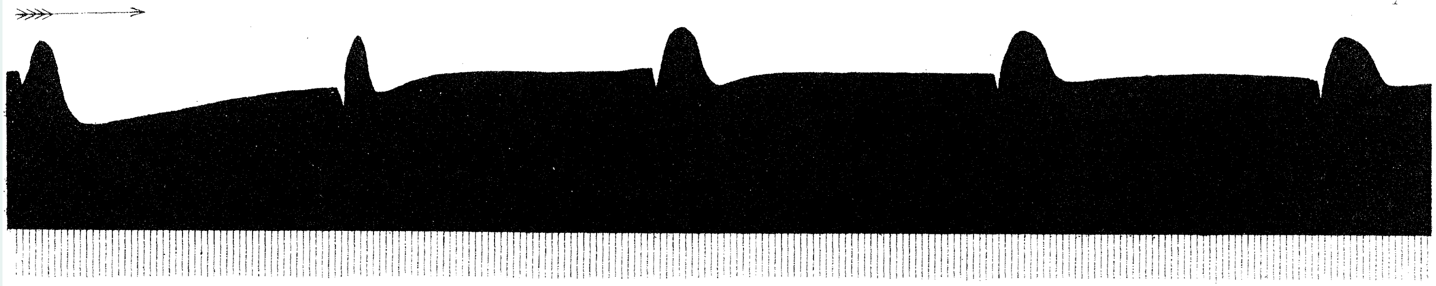


Fig. 11

10 per sec.

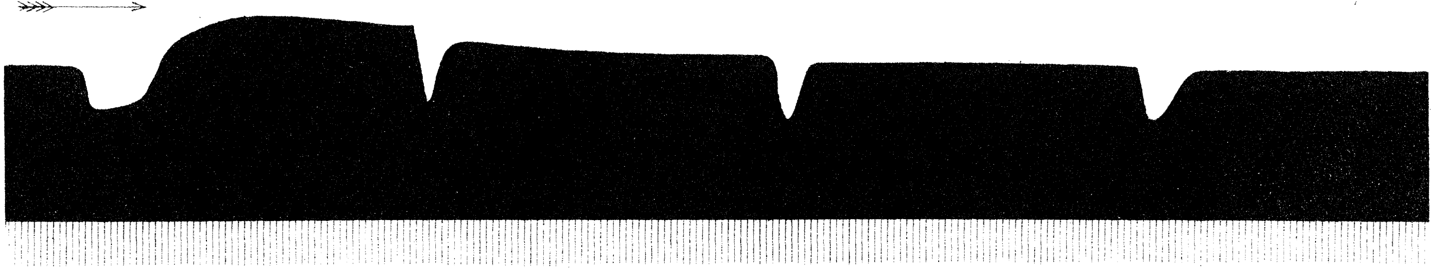


Fig. 12

10 per sec.

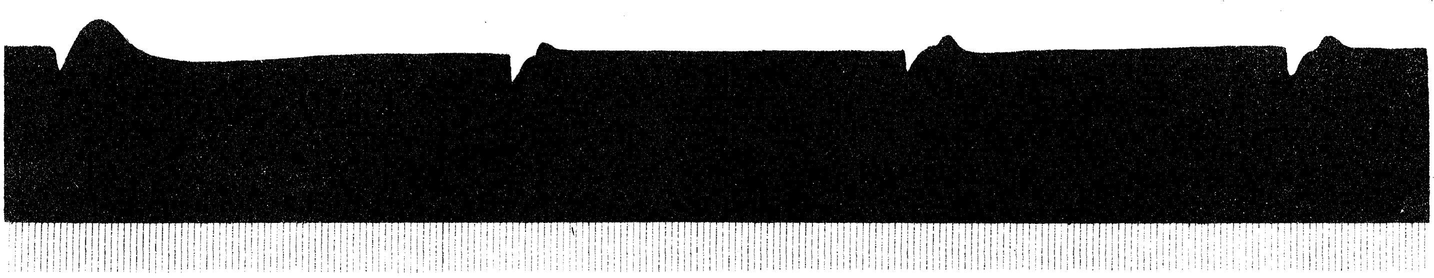


Fig. 13.

10 per sec.

Lith. & Imp. Camb. Sci. Inst. Co.

Fig. 11. Photographic record of the "fundamental experiment" in a perfectly "unmodified" leaf.

Fig. 12. Effect as led off from the same contacts in the same leaf after "modification."
[The photograph shows an imperfection, due to a temporary defect in the electrometer. The first of the four notches ought to have been deeper.]

Fig. 13. Effect often observed in leaves just prepared. It corresponds to a state intermediate between figs. 10 and 11.

N.B.—In all cases the difference was compensated just before the observation was made.

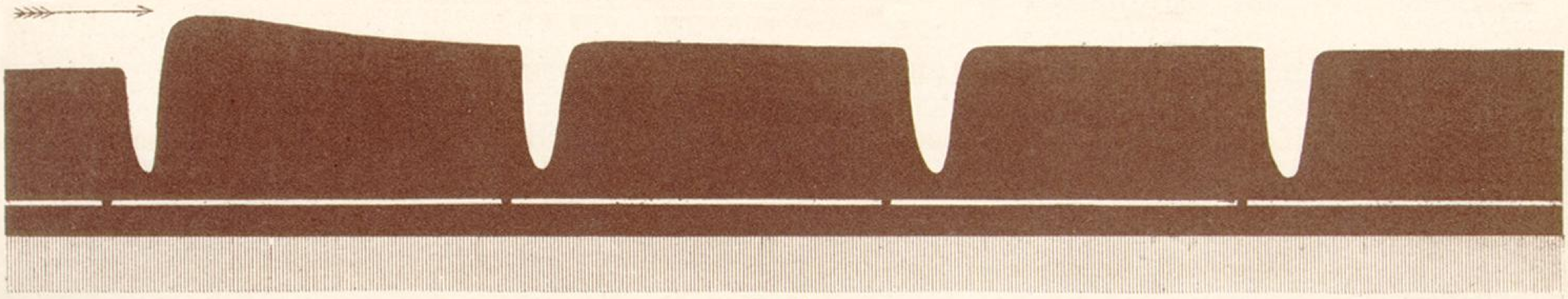


Fig. 1.

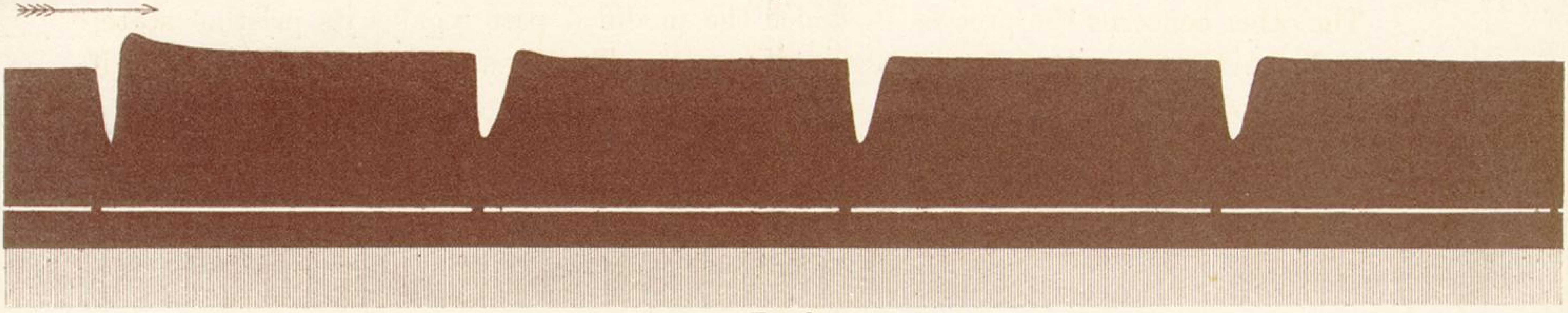


Fig. 2

Fig. 3.

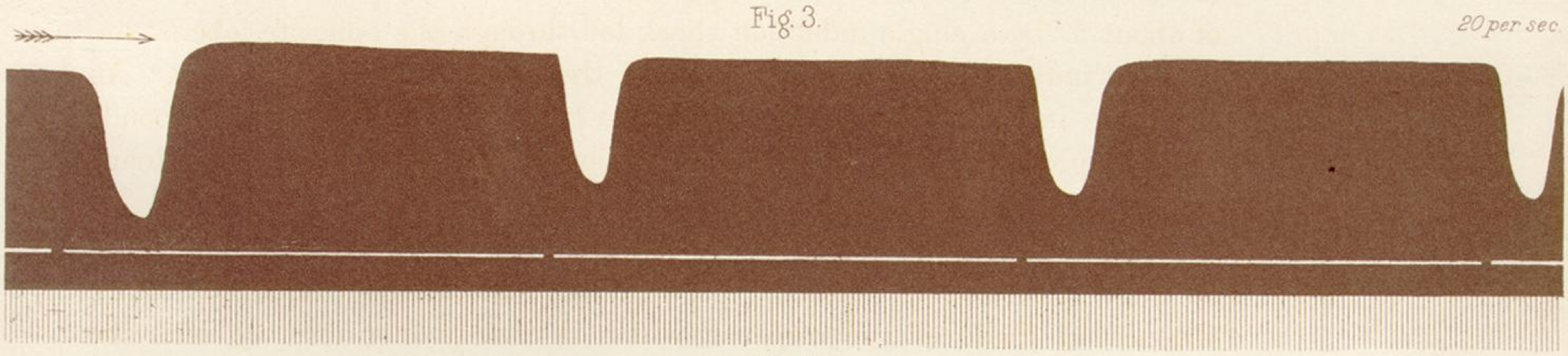


Fig. 4.

Fig. 5.

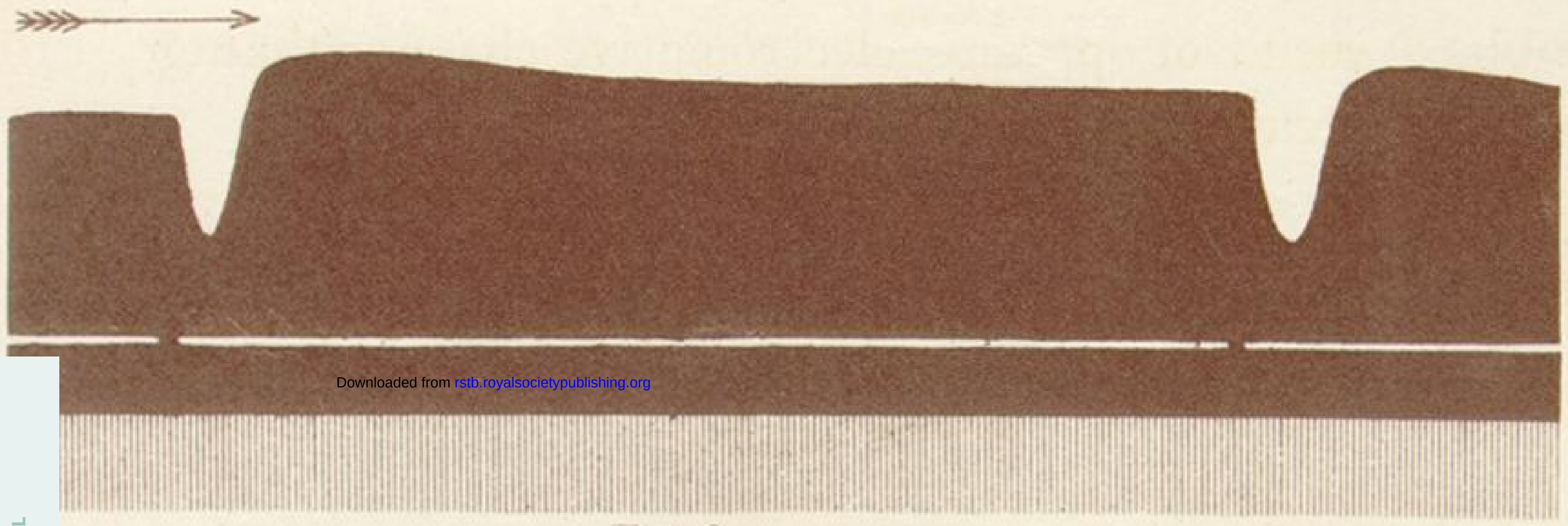


Fig. 6

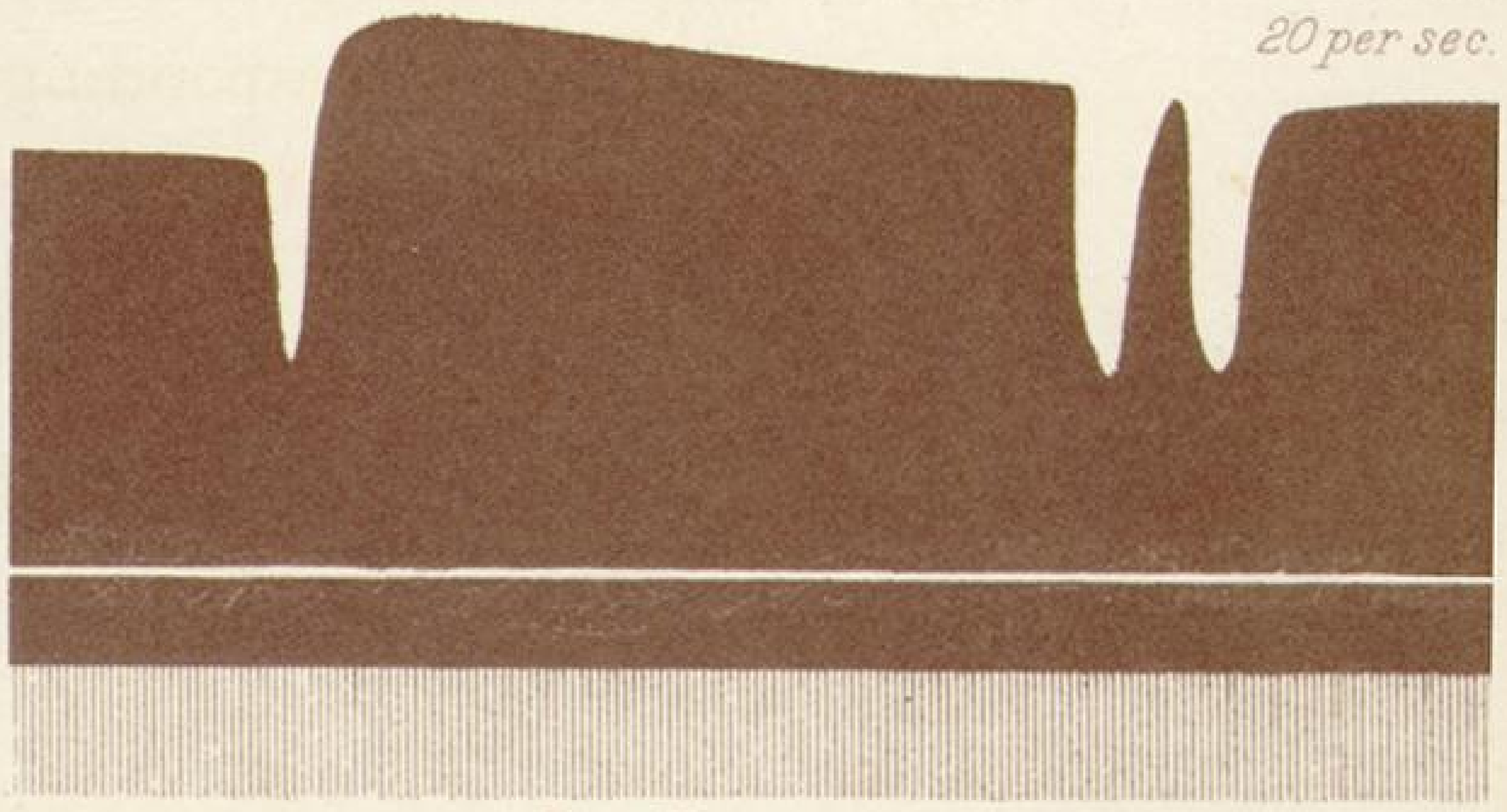


Fig. 7.

PLATE 69.

Figs. 1 to 4. Photographic records of the "Fundamental Experiment" in different leaves. (See 'Phil. Trans.,' 1882, p. 25.) The leaf is excited at intervals of about 5″ by a single induction shock led through the opposite lobe at the moment indicated in the photograph by the break in the bright line. As the make induction shock was cut off, the moment of excitation corresponds to the right-hand edge of the interruption. Figs. 1, 3, 4 are at ordinary temperature, fig. 2 at a high temperature (25° C.).

Fig. 5. Same experiment as fig. 3. Leaf exhausted.

Fig. 6. The same experiment. Interval between the excitations prolonged; hence the second phase of the response, which is usually only observed after the first excitation, here occurred after the second.

Fig. 7. The same experiment. Mechanical, instead of electrical, excitation. Double effect, due to accidental touching of two sensitive filaments one after the other.

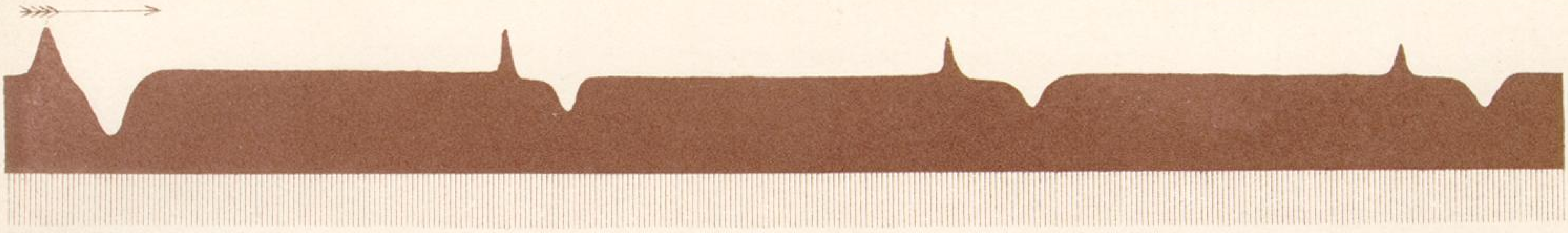


Fig. 8.

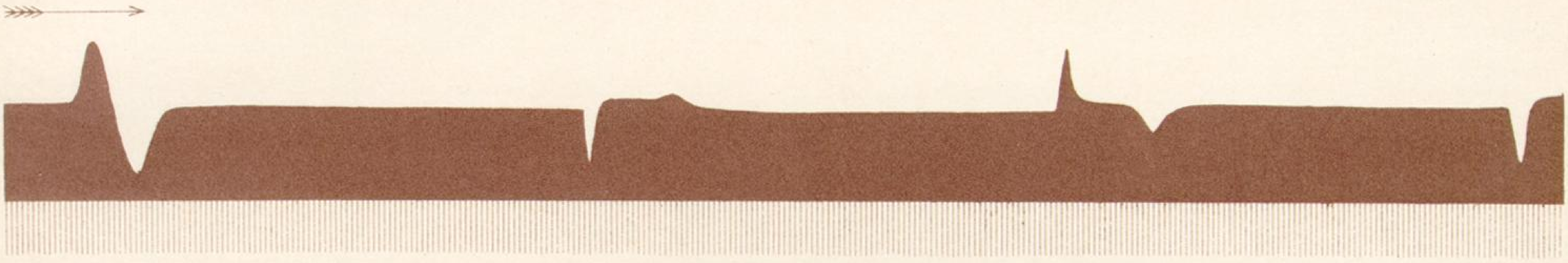


Fig. 9.

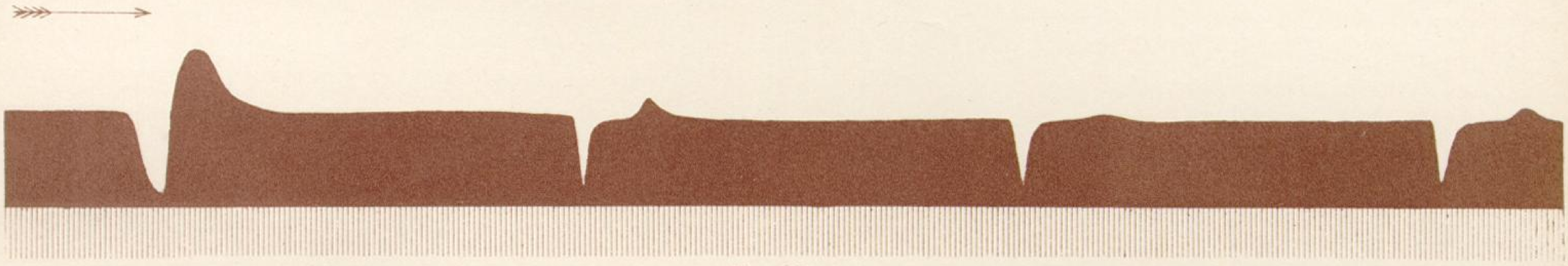


Fig. 10

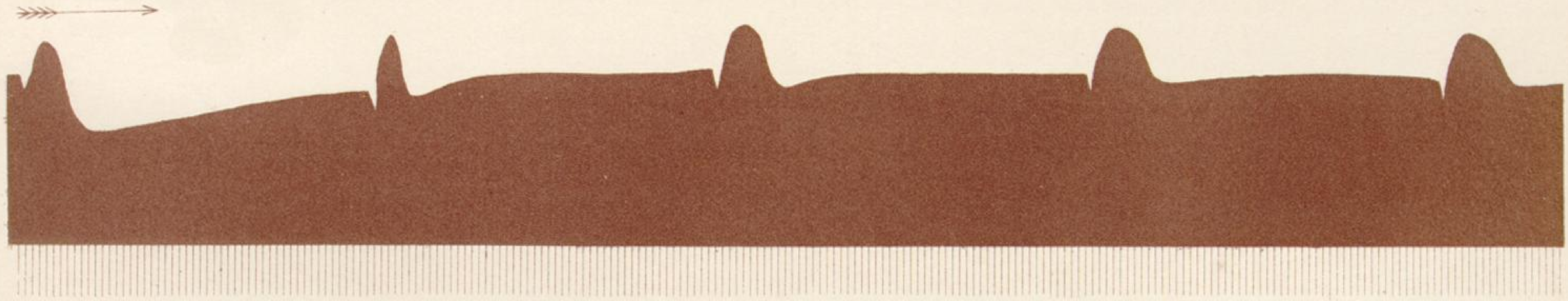


Fig. 11

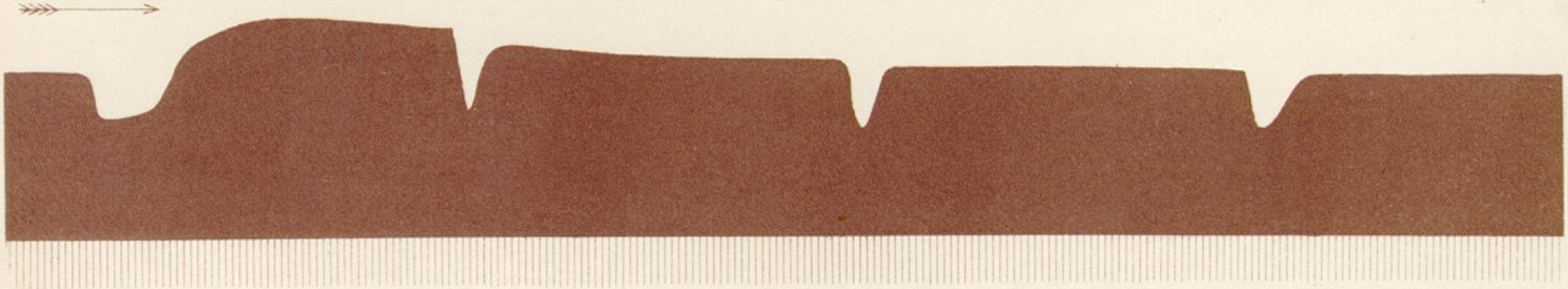


Fig. 12


Fig. 13.

PLATE 70.

Fig. 8. Experiment described in 'Phil. Trans.,' 1882, pp. 32–38; the leaf was led off by corresponding points on the under surface of opposite lobe. The tracing shows the combined result of opposite electromotive changes taking place in the two lobes. Leaf excited mechanically on right side.

Fig. 9. The same leaf excited alternately on right and left sides.

Fig. 10. Leaf excited on left side.

Fig. 11. Photographic record of the "fundamental experiment" in a perfectly "unmodified" leaf.

Fig. 12. Effect as led off from the same contacts in the same leaf after "modification." [The photograph shows an imperfection, due to a temporary defect in the electrometer. The first of the four notches ought to have been deeper.]

Fig. 13. Effect often observed in leaves just prepared. It corresponds to a state intermediate between figs. 10 and 11.