I

Stewart (G.N.)

Electrotonus

REPRINTED FROM THE

PROCEEDINGS OF THE ROYAL SOCIETY OF EDINBURGH.

The Electrotonic Variation with Strong Polarising Currents. By George N. Stewart, D.Sc., *Owens College, Manchester.*

(Read January 21, 1889.)

Let AB (fig. 1) be a piece of nerve interposed in the galvanometer circuit, and C D in the battery circuit. Then, as has long been known, on closing the battery circuit, one obtains a current in the galvanometer circuit, the direction of which in the nerve is the same as that of the polarising current. If, now, stimulation be made, say at I, this current undergoes a negative variation. Hermann, who investigated the subject, after Bernstein, was at first inclined to explain the negative variation by his law of "polarisation increment." He assumed that the excitation in passing along a polarised nerve undergoes changes in its intensity, increasing as it passes through regions under the influence of the anode, decreasing as it passes through parts dominated by the cathode.

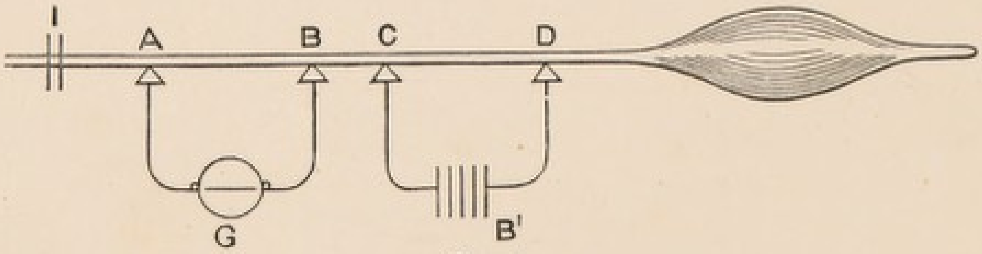

Fig. 1.

Now, if the current be ascending in the nerve (fig. 1), the electrotonic current in AB is also ascending. As B is nearer the cathode than A, the excitation will pass B in less intensity than A. Accordingly, during tetanus, B may be considered as less negative than A. In other words, B will be positive to A, and a current of action will pass through the galvanometer from B to A.* This will have the opposite direction to the electrotonic current, and will therefore look like a diminution or negative variation of that current. Similarly, if C be the anode, and the current be descending, the excitation will pass over B in greater intensity than over A, and again there will be a negative variation of the electrotonic current. Hermann, as already stated, seemed at one time to suppose that this was a complete explanation of the phenomena. But he was afterwards led by rheotome researches to modify his view, and, while retaining the law of "polarisation increment" as an essential factor in the explanation, to postulate besides, as Bernstein had previously done in a somewhat different form, an actual diminution in the polarisation, a negative variation, so to say, in the capability of the nerve to take on polarisation between core and sheath. ("Untersuchungen über die Actionsströme der nerven," *Pflüger's Archiv*, Bd. xlii. s. 246, &c.).

According to Hermann, the electrotonic currents are branches of the polarising stream which spread beyond the electrodes, owing to the transverse resistance caused by polarisation between this hypothetical core and sheath. The greater the polarisation coefficient is, the more widely do these branches spread, the stronger are the electrotonic currents. If stimulation diminishes this polarisation coefficient it will, in general, diminish the electrotonic currents. If the excitation be confined to special parts of the nerve, then it will depend upon the ratio of the transition resistance between core and sheath to the longitudinal resistance of the nerve, and upon the magnitude and position of the unexcited or relatively unexcited parts, whether the electrotonic variation (as we may for shortness call the variation of the electrotonic currents produced by stimulation) will be negative or positive. All this he deduces from his theory, and supports by experiments with the "Kernleiter Modell." He looked, in vain, however, for a positive phase in his rheotome work on nerve, the experimental difficulties being very great.

It was not from Hermann's theoretical standpoint that I entered

* Strictly speaking, if $E_{(A)}$, $E_{(B)}$, represent the intensity of excitation at A and B, $\int E_{(A)}dt$ is $> \int E_{(B)}dt$ for corresponding limits. Considering time-integrals, B may, therefore, be looked on as positive to A during the tetanus. The galvanometer deflection produced by stimulation will be a measure of the difference of these integrals.

upon the work of which this paper is an account. But from certain experiments on the effect of stimulation on the intrapolar current during the flow, and on both extra and intrapolar currents after the opening of the polarising stream, I suspected that, if one of the galvanometer electrodes were placed very near the polarising circuit, and the strength of the current increased sufficiently, a positive electrotonic variation ought to appear on the side of the anode, but not on that of the cathode. For the explanation of those experiments it was assumed, and the assumption was supported by direct experiments on muscular contraction, that during the flow of the polarising current the conductivity of the nerve for the excitatory change is less around the cathode than around the anode, and that, with increasing strength of current, complete block occurs sooner at the former than at the latter, although eventually it prevails at both. Whether, when this last stage is reached, the whole intrapolar area has lost its conductivity, was left an open question, and need not be considered here.

Going back now to fig. 1, let us inquire what the effect would be on the side of the anode, *i.e.*, with descending current, at a time when complete block was established there, and at the same time let us suppose that the galvanometer circuit is brought quite close to the anode, so that the lower galvanometer electrode is within the non-conducting region. If stimulation be now made at I, the excitation will pass A with a certain intensity, but will altogether fail before reaching B. B will, therefore, be strongly positive to A. We leave out of account for the moment any possible effect of the excitation on the electrotonic currents as such. There will be a current of action developed in the descending direction through the nerve—that is, in the same direction as the anodic electrotonic current. If this true action current be not masked by an overwhelming negative electrotonic variation, it will appear as a positive variation of the electrotonic current.

Now let us take the case of the ascending current in fig. 1. Here the lower galvanometer electrode is in the cathodic region, and we know that even with comparatively weak currents the cathodic block appears. B will therefore, above a low limit of current density, be positive to A when the nerve is excited, and the true action stream will be descending. The cathodic electrotonic current, however, is ascending, and the action stream will appear as a negative variation of it.

These are the considerations which led me to expect that a positive variation, if it existed, would be found with strong currents upon the anodic side, but not upon the side of the cathode. It was not overlooked that the ordinary electrotonic negative variation might be so large as to reverse the action current. Still it was hoped that, even in this case, indications might be found in the curve of the stimulation effect to show that the expected true action current was really in play.

Method of the Investigation.

The first one or two observations were made without compensating the electrotonic currents. They, indeed, give the same general results as when compensation was used. But it was obvious that it would not do to accept a positive variation on the evidence of an uncompensated anodic current. For it would be necessary to show

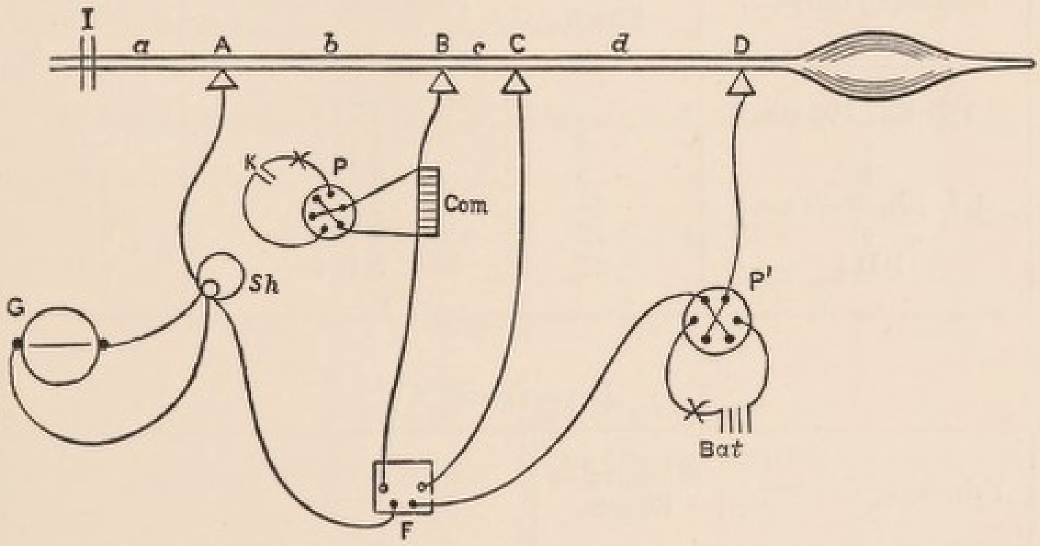

Fig. 2.—A, B, C, D are electrodes; I, stimulating electrodes; G, galvanometer; P, P′, Pohl's commutators; Com., compensator; Bat., polarising battery; K, cell connected with commutator; F, is a paraffin double key by which the polarising and galvanometer circuits were closed at the same time.

that the apparent positive variation was not analogous to that which the intrapolar current undergoes when the nerve is stimulated, the so-called "charge of resistance effect." It was found that after compensation the positive variation continued in undiminished or scarcely diminished amount. Nay more, over-compensation did not abolish, nor begin to abolish it. Fig. 2 shows the arrangement which was at first used; *a*, *b*, *c*, *d*, represent the lengths of nerve IA, AB, BC, and CD, respectively.

Experiments 1 and 2 are examples of the first method without compensation; Experiments 3 and 4, with compensation. It will be seen that on the cathodic side, *i.e.*, with ascending current, the stimulation effect has the negative sign with reference to the direction of the polarising stream. On the side of the anode the same is true up to an electromotive force of about 3 Daniells working through 9 mm. of nerve. Above this the effect becomes positive. This is so only when the distance C is small. In Experiment 4 it is seen that, with C = 6½ mm., the positive effect does not appear with 7 Daniells, nor even when C = 3½ mm. When C is reduced to 1 mm., it comes in even with 3 Daniells.

Experiment 1.

Distances—*a*, 9 mm.; *b*, 10 mm.; *c*, 2 mm.; *d*, 9 mm.

Polarising Current.	Stimulation Effect.	Polarising Current.	Stimulation Effect.
1 D Rh. 100 cm.*		1 D ↑	−12
↓	− 3	1 D ↓	−15
↑	− 3	3 D ↑	−55
1 D Rh. 2000 cm. ↓	−25	3 D ↓	+50
↑	−20	5 D ↑	−42
1 D ↓	−20	5 D ↓	+53

Experiment 2.

Polarising Current.	Stimulation Effect.	
1 D ↑	−14	Galv. shunt 10.
1 D ↓	−16	
3 D ↓	+45	
4 D ↓	+29	

No compensation in Experiments 1 and 2.

Experiment 3.—Here two sets of observations were taken on the same nerve, the distance between electrodes B and C being altered.

* The total resistance of the Rheochord was 2000 centimetre units.

1st set.—Distances—*a*, 7½ mm.; *b*, 9 mm.; *c*, 1½ mm.; *d*, 9 mm.

Polarising Current.	Stimulation Effect.	
5 D ↓	+ 45	Shunt 10.
1 D ↓	− 6	
5 D ↓	+ 27	Not compensated.
5 D ↓	+129	Compensated. No shunt.
5 D ↑	− 51	,, ,,

2nd set.—Distance—*c*, 7½ mm. Other distances the same as before.

Polarising Current.	Stimulation Effect.	
5 D ↓	−22	Compensated. No shunt.
5 D ↓	−10	,, ,,

Experiment 4.

Distances—*a*, 7½ mm.; *b*, 9 mm.; *c*, 6½ mm.; *d*, 9 mm.

Polarising Current.	Stimulation Effect.
1 D ↓	* { −47, −42 }
2 D ↓	−41 (?)
3 D ↓	{ −68, −69 }
2 D ↓	{ −65, −82 }
1 D ↓	{ −28, −32 }
5 D ↓	{ −45, −50 }
7 D ↓	−28

Same nerve; distance *c* made 3½ mm.

Polarising Current.	Stimulation Effect.
7 D ↓	−37
1 D ↓	− 5

Same nerve; distance *c* made 1 mm.

Polarising Current.	Stimulation Effect.
1 D ↓	−22
3 D ↓	+34
5 D ↓	+26

* The bracketed numbers represent double readings.

In Experiment 4 only half of the galvanometer was in circuit. The deflections given must be doubled in order to compare with the preceding experiments.

These results suggested that it might be still better to put electrodes B and C in contact, so as practically to make them one electrode. Of course it was here necessary to attend to compensation even more strictly than before; for the danger of a direct escape of current was greater than before; but so long as the galvanometer circuit was fully compensated, even such an escape would introduce no error.

Experiment 5 gives an example of this method.

Experiment 5.

Polarising Current.	Stimulation Effect.	
1 D Rh. 1000 cm. ↑	− 80	
1 D Rh. 100 ↑	+ 6	After 30″ closure.
	− 18	,, 1′ ,,
	− 22	,, 2′ ,,
	− 28	,, 3′ ,,
	− 35	,, 4′ ,,
	− 38	,, 5′ ,,
	− 43	15″ after opening polarising current.
2 D ↑	−110	
	−133	30″ after opening.
3 D ↑	?	Owing to unsteadiness, difficult to read amount, but certainly less than −100.
	−117	20″ after opening.
3 D ↓	+255	
	−215	Another reading. Current kept closed for 5′ before readings taken.
	+ 48	30″ after opening.

With 1 D Rh. 100 ↑ a small positive deflection was got. I have a good many times observed that when the nerve is perfectly fresh, the polarising current very weak, and the reading taken very soon after closure, a positive stimulation effect is got on the side of the cathode. This would suggest that the conductivity around the cathode is not reduced immediately on closing such a current, but may even be increased. This agrees with what I saw occasionally when stimulating in the middle of the intrapolar area, with the muscle attached. Sometimes with weak currents the descending was more favourable than the ascending for getting contraction. This never happened when the currents were fairly strong.

Werigo also, in his experiments on intrapolar stimulation, quite different in purpose from mine and essentially different in method, found that the cathodic block took time for its establishment, and that, when it appeared, it appeared suddenly.

In the example given in Experiment 5 the initial positive effect is seen to change in 30″ into a negative effect thrice as great, and this negative effect then gradually increases with still longer time of closure.

In order to diminish, as far as possible, the irregularities in the deflection, which are always a source of trouble with strong electrotonic currents, especially on the anodic side, I thought of using the currents led off to the galvanometer from two separate nerves of the same frog to compensate one another, a method resembling somewhat in principle that which Hermann has used in some of his polarisation work. Then, on exciting one of the nerves, one ought to get the stimulation effect, weakened, of course, by the extra resistance of the second nerve. The same battery was connected with both nerves, so that irregularities in the battery itself might be eliminated. The result was very satisfactory.

Figs. 3 and 4 show the arrangement.

In the arrangement of fig. 4 two nerves were placed on two separate sets of electrodes A, B, D; A′, B′, D′, a compensator (Com.) being introduced into the galvanometer circuit.

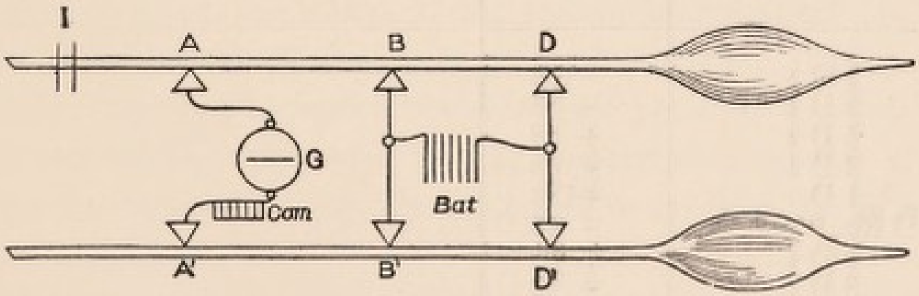

Fig. 3.—G is the galvanometer; Bat., the battery; I, the stimulating electrodes.

The pieces of nerve BD, B′D′ were made as nearly as possible equal in length, and therefore the current would have nearly the same density in each. The electrotonic currents in AB, A′B′ would be nearly equal, and they would pass through the galvanometer in opposite directions. The balance was completed by means of the compensator.

In the arrangement of fig. 4 the polarising current passed to both nerves through the same electrodes C,D, and the density would therefore be more nearly equal in the two than with the arrangement of fig. 3. As before, a compensator was put in the galvanometer circuit. B was not an electrode, but only a movable

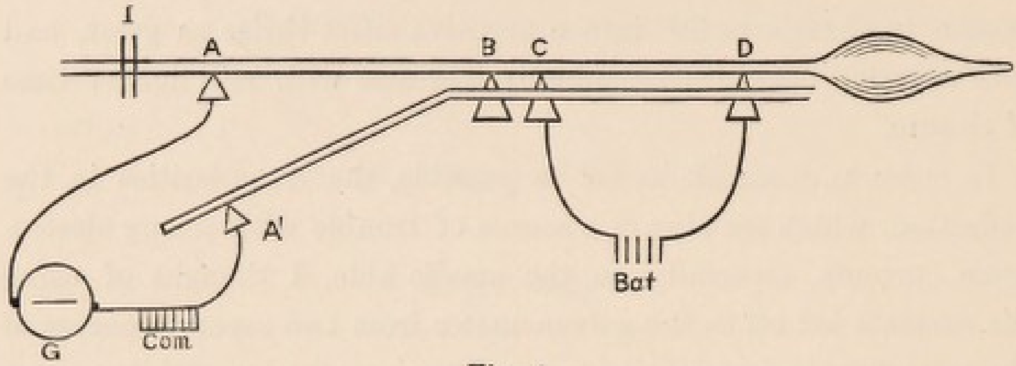

Fig. 4.

bridge of clay. If we stimulate at I, it will depend upon the distance of B from C whether the anodic effect will be positive or negative.

Experiments 6 and 7 are samples of the results got by this method.

Experiment 6.

Distances—*a*, 10 mm.; *b*, 10 mm.; *c*, 2 mm.; *d*, 13 mm.

Polarising Current.	Stimulation Effect.	
1 D ↓	−184	
3 D ↓	− 38	
5 D ↓	+ 58	
8 D ↓	+ 68	
1 D	+138	
1 D Rh. 90 cm. ↓	− 53	
5 D ↓	+ 30	
8 D ↓	+ 63	
1 D ↓	− 79	
2 D ↓	− 76	

Experiment 7 shows the change of sign on the anodic side even with 2 D. The negative effect on the side of the cathode seems here to diminish with increase of current, and this might suggest that with still stronger currents a positive phase might be found. I cannot say that I have found any trace of such an effect, and it is only in exceptional cases that the diminution in the negative effect appears.

Experiment 7.

Distances—*a*, 7½ mm.; *b*, 7½ mm.; *d*, 10 mm.

Polarising Current.	Stimulation Effect.	
2 D ↑	− 40	B and C in contact.
1 D Rh. 90 cm. ↑	− 8	
3 D ↑	− 28	
5 D ↑	{ − 24 − 22	
1 D ↑	− 9	
2 D ↑	− 14	
5 D ↑	− 3	
1 D ↓	{ −127 −114	
2 D ↓	{ + 28 + 22	
5 D ↓	{ +126 +119	
1 D ↓	{ − 46 − 49	

It was now desirable to compare the amount of the intra- and extrapolar stimulation effects; and in order to avoid the uncertainty which must always exist when one tries to get quantitative comparisons from experiments made on different days with different nerves, I determined to control the other observations by means of a set in which the intrapolar and extrapolar regions of the same nerve were led off alternately to the galvanometer. It was particularly important to notice how the *ratio* between the amount of the two effects varied with varying density of polarising current when the latter was nearly strong enough to suppress the intrapolar effect altogether.

The arrangement is shown in fig. 5 for the case where the two extrapolar regions compensate each other, and the two intrapolar regions are placed one in each coil of a differential galvanometer.

A, B, C, D are, as before, the electrodes of one of the nerves; A′, B′, C′, D′ those of the other. G, G′ are the two coils of the differential galvanometer; P is a Pohl's commutator without cross wires, by means of which either AB or CD may be joined on to G; P′ is a Pohl with cross wires, to alter the direction of the polarising current; Com. is a compensator to complete the compensation when the extrapolar areas are led off; R is a rheostat to equalise the intrapolar currents. By an arrangement not shown it could be thrown either into CD or into C′D′.

The balancing arrangement was used for the intrapolar currents in order to diminish the irregularity in the deflection, which is much more troublesome than even in extrapolar experiments. Of course, only one nerve was stimulated.

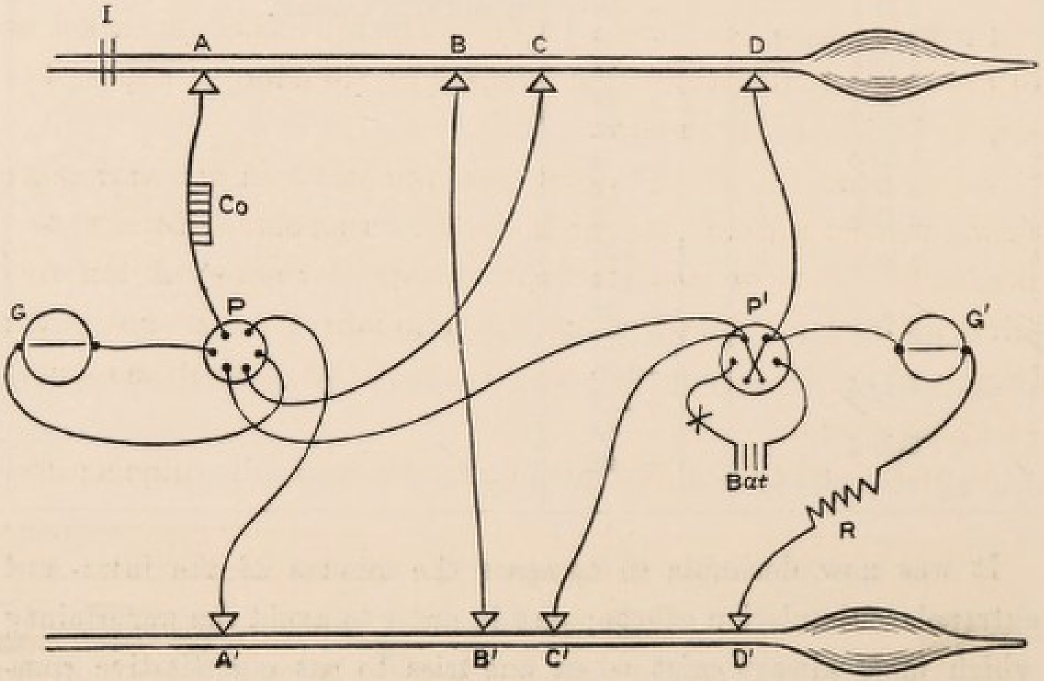

Fig. 5.

The circuit of G′ was broken by a simple key, whenever the extrapolar regions were to be connected with G. The current was then passed through CD, compensation completed in the galvanometer circuit, and the stimulation effect read off. After the nerves had recovered, the two intrapolar regions were thrown on to G and G′, the extrapolar being off. The same current was now passed again in the same direction, for the same length of time, and the stimulation effect again taken. A given number of cells would give practically the same current density in CD, whether the alternative circuit C′D′ was open or closed, since the internal resistance of the battery is very small compared with the resistance of the nerves.

Experiments 8, 9, and 10 (pp. 246, 247) are examples of this method as applied to currents near the limiting intensity. An electromotive force of about 5 Daniells working through 9 mm. of nerve gives the density corresponding to the disappearance of the intrapolar effect. This limiting electromotive force will be inversely as the length of nerve included in the circuit, if we assume that the specific resistance of nerve in the longitudinal direction is a constant. Of course it will vary slightly even for the two nerves of the same frog, as it will depend mainly at least upon the amount and kind of the dissolved crystalloids. In my former results on the intrapolar effect I found that the limiting electromotive force varied from 8 to 9 Daniells, when the length of nerve was from 12 to 14 mm. The two sets of experiments therefore agree as well as one is entitled to expect in observations of this sort. The strength of stimulus, of course, has also to be taken into account.

Experiments 12 and 13 show how the effect in the extrapolar region reaches a maximum, while in the intrapolar it declines to a minimum. This of itself is quite enough to dispose of the possibility that the suppression of the intrapolar effect is due to the decline of excitability at the point of stimulation through the spread of anelectrotonus.

Experiment 14 is an example of stimulation on the cathodic side.

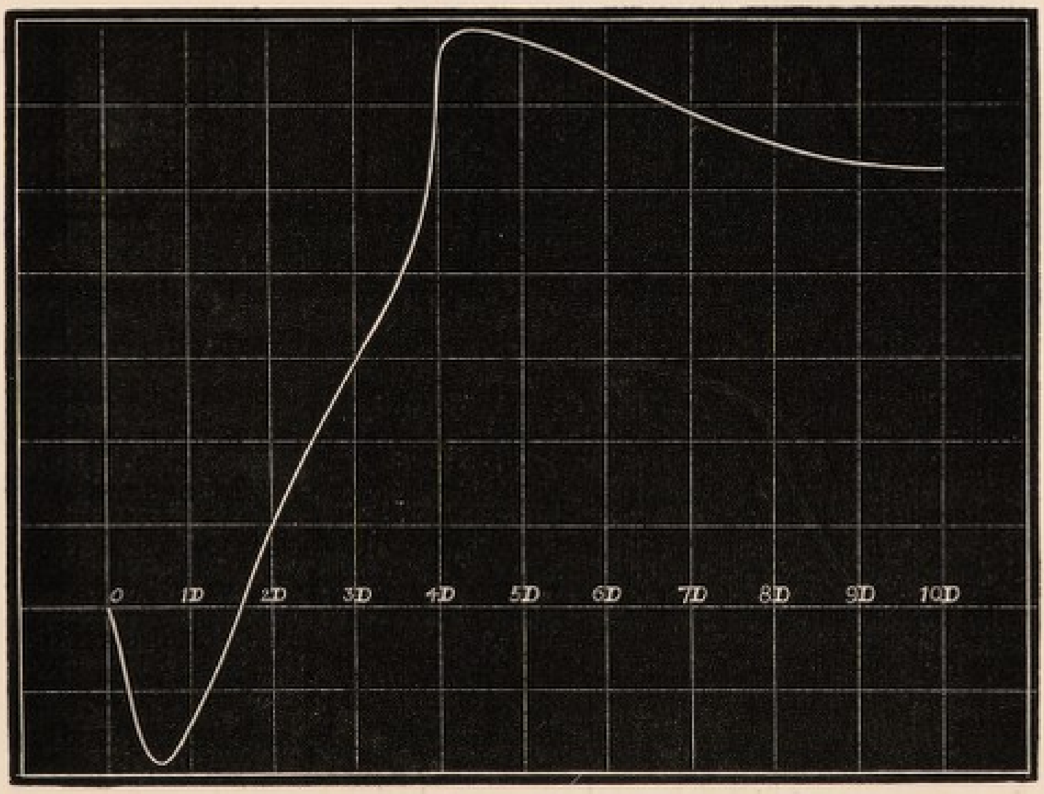

Fig. 6.

Fig. 6 shows the curve of the effect in Experiment 12 plotted to scale.

The number of points are too few to determine the details. Almost the whole of the ascent lies very nearly in a straight line.

Summary of Results.

1. With weak currents there is the ordinary negative variation both on anodic and cathodic side, however close the galvanometer and polarising circuits may be brought to each other.

2. As the strength of the polarising current is increased, the negative variation on the anodic side passes into a positive variation, which increases and apparently reaches a maximum.

3. The maximum of the positive anodic variation corresponds to a density of current which is not far from that for which the intrapolar variation is at its minimum (zero).

4. On the cathodic side the variation is always negative with currents above the very weakest. (With very weak currents, fresh nerves, and short period of flow, sometimes a small positive variation seems to be got.)

5. The greater the distance between the polarising and galvanometer circuits, the stronger must the polarising current be for which the positive anodic variation first appears.

All these results hold when the electrotonic currents are compensated.

Experiment 8.

Distances—*a*, 9 mm.; *b*, 7½ mm.; *c*, 1 mm.; *d*, 9 mm.

Polarising Current.	Extrapolar Stimulation Effect.	Intrapolar Stimulation Effect.	
4 D ↓	38	0	
4 D ↓	57	5	
4 D ↓	39		

Experiment 9.

Distances—*a*, 9 mm.; *b*, 7½ mm.; *c*, 1 mm.; *d*, 9 mm.

Polarising Current.	Extrapolar Stimulation Effect.	Intrapolar Stimulation Effect.	
4 D ↓	+214	+50	Here before passing current there was a stimulation effect of 38 in same direction as intrapolar effect.
4 D ↓	+ 81	+55	Here there was a stimulation effect of 87 in same direction before passing current.
4 D ↓	+230		
4 D ↓	+170		

Experiment 10.

Polarising Current.	Extrapolar Stimulation Effect.	Intrapolar Stimulation Effect.	
5 D ↓	+180	0	

Experiment 11.

Distance—*d*, 12 mm.

Polarising Current.		Intrapolar Stimulation Effect.	
1 D ↑ Rh. 2000	...	+66	Stimulus 85.
5 D ↑ 2000	...	0	Even with strongest stimulation.
5 D ↓ 2000	...	+55	Coils close up.
1 D ↓ 2000	...	+87	,,
5 D ↓	...	+30	,,
7 D ↓	...	+14	,,
1 D Rh. 2000	...	{ +85, +90 }	,,

Experiment 12.

Distances in Experiments 12 and 13—*a*, 9 mm.; *b*, 9 mm.; *c*, 1½ mm.; *d*, 9 mm.

Polarising Current.	Extrapolar Stimulation Effect.	Polarising Current.	Extrapolar Stimulation Effect.
1 D ↓	−26	7 D ↓	+126
2 D ↓	+25	10 D ↓	+106
3 D ↓	+62	4 D ↓	+115
4 D ↓	+135	4 D ↓	+75
5 D ↓	+138		

Experiment 13.

Polarising Current.	Intrapolar Stimulation Effect.	
1 D Rh. 50 ↓	+22	Same strength of stimulus.
1 D Rh. 2000 ↓	+41	
2 D ↓	+28	
3 D ↓	+17	
4 D ↓	+24	
5 D ↓	0	
1 D Rh. 2000	+36	

Experiment 14.

Polarising Current.	Cathodic Extrapolar Effect.
1 D ↑	−27
2 D ↑	−29
3 D ↑	−31
5 D ↑	−43 ?
10 D ↑	−44

I do not propose to discuss here, further than I have done, the real significance of the results stated, as I hope soon to have an opportunity of doing so in connection with a more extended research, embracing the effect of stimulation on the whole of the polarisation phenomena of nerve and muscle. I should just like to say, that it is by no means impossible that a real positive electrotonic variation may be mixed up with a true action current in the positive direction.

The work was done partly in the Owens College, and partly at Edinburgh in the Laboratory of Professor Rutherford, whose great kindness I take this opportunity of acknowledging.