

cate that in sodium vapour we have a medium which approaches more nearly to the ideal absorbing medium, with but a single natural period of vibration, than any substance heretofore investigated.

Of course I am speaking here only with reference to the natural vibration which appears to influence the dispersion. Strictly speaking, there are two natural periods, of course, which influence the velocity of the light in the medium, but when the medium is very dense the condition certainly approaches very nearly to that of a single period medium. As I have said before, the fluted absorption bands are without influence on the dispersion, at least their influence is too slight to be detected by the methods that have been employed thus far.

“On Skin Currents. Part II.—Observations on Cats.” By
AUGUSTUS D. WALLER, M.D., F.R.S. Received October 7,—
Read November 21, 1901.

In the first part of the present investigation* I have stated, as one of the principal conclusions with regard to the frog's skin, that the normal electrical response of the excited skin is of outgoing direction.

The chief object of the following observations was to ascertain whether or no similar effects of outgoing direction are manifested by the pad of the cat's foot, this having been, since the first observations of Hermann and of Luchsinger, the chosen object upon which to demonstrate the cutaneous (epithelial and glandular) currents aroused by nerve-stimulation.

I have examined the cutaneous currents, A indirectly aroused by nerve-stimulation, B directly aroused by electrical excitation of the skin itself in the manner described and figured in my previous communication (*loc. cit.*, p. 481).

A. INDIRECT EXCITATION.—The animals were decapitated, and used in the first instance for the observation of indirect effects and their possible modification in consequence of arrested circulation. In every case, without exception, the electrical effect of excitation of the sciatic nerve upon the pads proved to be an ingoing current, as described by Luchsinger and by Hermann.† The effect gradually declined with lapse of time, and disappeared within 1 hour after decapitation, without exhibiting any change of sign or other modification.

Although it was not my purpose to pay particular attention to this point, I may take the opportunity of stating that the experiment, as

* “On Skin Currents. Part I.—The Frog's Skin,” ‘Roy. Soc. Proc.,’ June 6, 1901, vol. 68, p. 480.

† Kendall and Luchsinger, “Zur Theorie der Secretionen,” ‘Pflüger's Archiv,’ vol. 13, 1876, p. 212; Hermann and Luchsinger, “Ueber die Secretionsströme der Haut bei der Katze,” ‘Pflüger's Archiv,’ vol. 17, 1878, p. 310.

made upon a freshly killed animal, affords a very convenient means of class-demonstration of the fundamental fact. The response is elicited by stimulation of the sciatic nerve after the latter has ceased to provoke muscular contraction, and can then be most conveniently demonstrated (and recorded) without resort to the curarisation and artificial respiration necessary in the case of the living animal. The method and its results will be made sufficiently apparent by the following experiments and figures :—

Experiment 1.—Electrical Response of the Skin to Indirect Excitation through the Sciatic Nerve.

Cat decapitated—Both sciatics exposed and cut—Large pad of each hind foot led off to galvanometer by unpolarisable electrodes—Tetanic excitation of peripheral end of one or other sciatic for 5 seconds at intervals of 5 minutes—Berne coil at 1000 units supplied by two Leclanchés.

Deflection + signifies that the skin of the right side is electro-positive, *i.e.*, that it is traversed by an ingoing current (directed from left side to right through the galvanometer).

Time after decapitation.	Deflection by excitation of left sciatic.	Deflection by excitation of right sciatic.	Remarks.
Mins.	Volt.		
15	-0·0100	—	Muscles contract.
20	-0·0150	—	Do.
25	-0·0110	—	Do.
30	—	+0·0050	Do. faintly.
35 and 36	-0·0100	+0·0160	No contraction.
40 and 41	-0·0060	+0·0100	Do.
45 and 46	-0·0010	+0·0060	Do.
50 and 51	Nil	+0·0010	Do.
55 and 56	Nil	Nil	Do.

The effect of excitation was thus in each instance an ingoing current of the skin of the excited side.

Experiment 2.—Similar Experiment. Excitation of Right Sciatic at Intervals of 10 minutes.

Time. mins.	Deflection.	Remarks.
20	+0·0050	—
30	+0·0045	Faint contraction.
40	+0·0035	No contraction.
50	+0·0020	Do.
60	+0·0005	Do.
70	Nil	Do.

Photographs of the effects 30 and 50 minutes after decapitation are given below. The first is taken on a slowly moving plate with tetanisation of the sciatic lasting for 30 seconds. The second is taken on a more rapidly moving plate with tetanisation lasting for 5 seconds, as shown by the signal line. The lost time in this (and in other) instances = 3 seconds. The effects are "ingoing."

FIG. 1. (4217.)

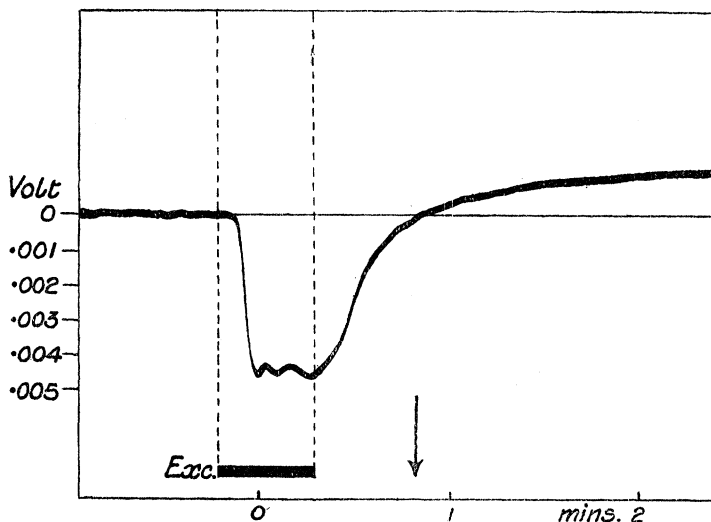
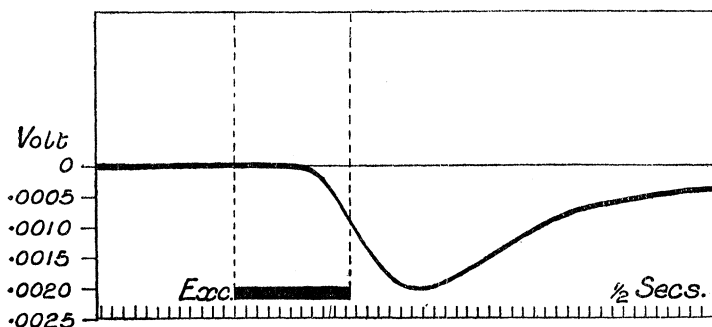


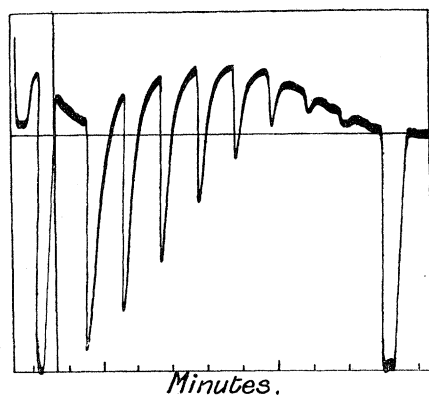
FIG. 2. (4218.)



Experiment 3.—Similar Experiment. Excitation of Right Sciatic at Intervals of only 1 minute. Rapid Exhaustion of the (ingoing) Response. No marked Alteration of Resistance. ? Increase by Drying.

Time after decapitation. Mins.	Voltage of response.	Resistance of pad (corrected for R. of electrodes).
25	—	100,000 ohms.
26	0·0050	
27	0·0085	
28	>0·0100	
29	—	100,000 „
30	Galvanometer shunted, photograph begins.	
31	—	100,000 ohms.
32	0·0100	
33	0·0093	
34	0·0080	
35	0·0060	
36	0·0040	
37	0·0020	
38	0·0005	
39	trace	
40	—	110,000 „

FIG. 3. (4220.)



B. DIRECT EXCITATION.—A pad of the cat's foot, cut off 1 to 48 hours after death, and set up between unpolarisable electrodes as previously described (*loc. cit.*, p. 481), generally manifests a small and gradually increasing ingoing normal current, not exceeding, as a rule, 0·0100 volt. With lapse of time this current gradually falls again. It is noteworthy that its direction (ingoing) is from the intact external surface towards the injured cut surface.

If after exact compensation of this normal current a single induction shock is sent through the pad, either in the ingoing or in the outgoing direction, the effect—or, properly speaking, the after-effect—is in nearly every instance outgoing, as in the case of the frog's skin. The few instances in which I have witnessed an ingoing response have been in the case of fresh skin, taken soon after decapitation, and tested by comparatively weak induction shocks. (I find in my laboratory notes only one instance of a late ingoing response—3 days after decapitation.) In such cases the ingoing response has been of comparatively low voltage, and has given place to an outgoing response at the end of a few hours. From review of a considerable number of observations I conclude that outgoing response is the rule, ingoing response the exception. I have kept the former under systematic observation up to 60 hours *post-mortem*, but have found under the conditions of observation that it may disappear at an earlier period from the skin of ill-nourished animals.

The physiological action of the skin is indicated : 1, by its invariable direction with both directions of excitation ; 2, by its complete abolition after immersion of the skin in hot water.

A series of responses provoked at short intervals exhibits summation. Tetanisation by alternating induction shocks in both pairs of directions, excites a larger response than that aroused by a single induction shock.

These several points will be made sufficiently clear by the following experiments and figures :—

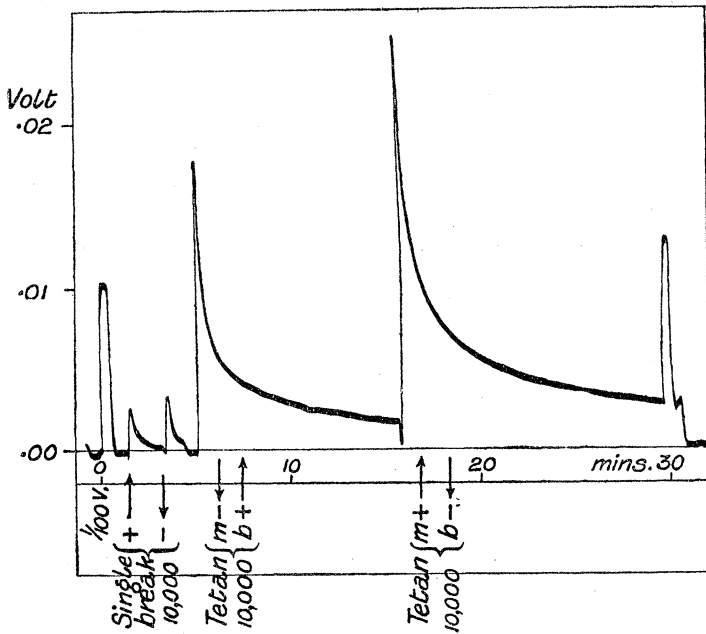
Experiment 4.—Direct Excitation. Same Cat as that of Experiment 2. Large pad cut off and set up between unpolar electrodes 9 hours after decapitation. Compensation. Direct Excitation in + (outgoing) and - (ingoing) directions. Berne Coil. 8 Leclanchés in primary circuit. 10,000 units.

Time.	Excitation.	Response.	After immersion in hot water.
9 hours	Tetan. $\left\{ \begin{array}{l} \text{m. -} \\ \text{br. +} \end{array} \right\}$	+ 0·0056 volt.	
	Do. $\left\{ \begin{array}{l} \text{m. +} \\ \text{br. -} \end{array} \right\}$	+ 0·0100 „	
24 hours	Single break +	+ 0·0025 „	- trace.
	-	+ 0·0032 „	+ trace.
	Tetan. $\left\{ \begin{array}{l} \text{m. -} \\ \text{br. +} \end{array} \right\}$	+ 0·0175 „	+ 0·0004
	Do. $\left\{ \begin{array}{l} \text{m. +} \\ \text{br. -} \end{array} \right\}$	+ 0·0242 „	- 0·0004

The response to both directions of excitation is outgoing; it is greater to tetanising currents than to single shocks; it is greater the day after death than on the day of death; it is abolished by immersion in hot water, the small residual deflections observed being such as would be caused by ordinary polarisation.

The 24-hour responses were recorded as under; they were throughout of outgoing direction, by both directions of single break currents, and by both pairs of directions of tetanisation.

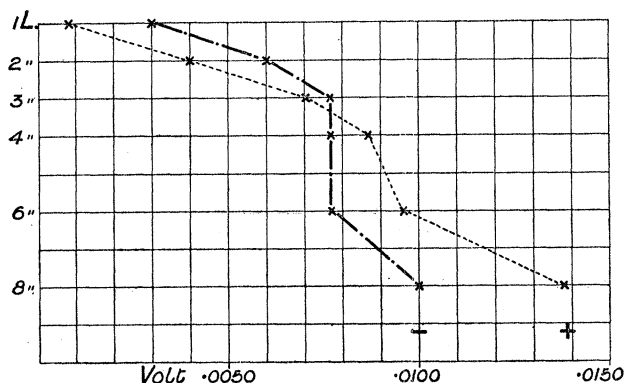
FIG. 4. (4219.)



Experiment 5.—Direct Excitation. Cat's Pad put up 8 hours after decapitation. Tetanisation for 5-sec. periods, by Berne Coil at 10,000 units with 1·2 8 Leclanché cells in primary circuit. Readings taken in scales of increasing and diminishing strengths of Excitation. (+ = outgoing.)

In primary circuit.	Direction of break.	Double series of readings.	Mean.	Mean voltage.
1 Leclanché	+	+10 — 2	+ 4	0·0008
1 "	—	+15 +15	+15	0·0030
2 "	+	+30 +10	+20	0·0040
2 "	—	+35 +25	+30	0·0060
3 "	+	+45 +25	+35	0·0070
3 "	—	+45 +33	+38	0·0076
4 "	+	+52 +36	+44	0·0088
4 "	—	+42 +34	+38	0·0076
6 "	+	+60 +36	+48	0·0096
6 "	—	+52 +24	+38	0·0076
8 "	+	+74 +64	+69	0·0138
8 "	—	+54 +50	+52	0·0104

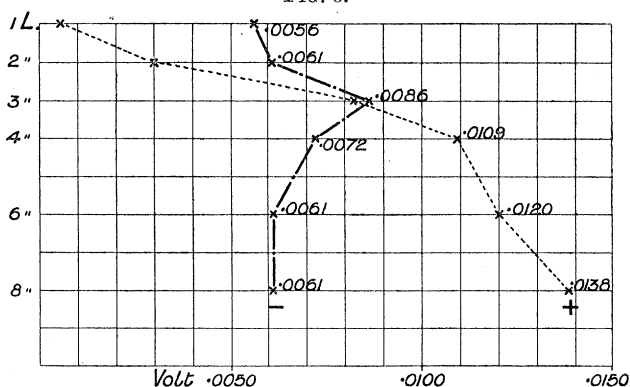
FIG. 5.



Experiment 6.—Direct Excitation. Fresh Pad of same Cat on the 3rd day after death. Excitation as in Experiment 5. Outgoing response throughout. Considerable Diminution of Resistance during Experiment.

In primary circuit.	Direction of break.	Readings on scale.	Mean readings.	Mean voltage.	Conductivity.
1 L.	+	— 2 + 3	+ 1	+ 0·0004	21
	—	+ 12 + 12	+ 12	+ 0·0057	
2 L.	+	+ 7 + 9	+ 8	+ 0·0030	26
	—	+ 18 + 15	+ 16	+ 0·0061	
3 L.	+	+ 30 + 18	+ 24	+ 0·0083	29
	—	+ 28 + 22	+ 25	+ 0·0086	
4 L.	+	+ 42 + 30	+ 36	+ 0·0109	33
	—	+ 25 + 23	+ 24	+ 0·0072	
6 L.	+	+ 45 + 50	+ 47	+ 0·0120	39
	—	+ 23 + 25	+ 24	+ 0·0061	
8 L.	+	+ 40 + 60	+ 50	+ 0·0138	36
	—	+ 23 + 22	+ 22	+ 0·00610	

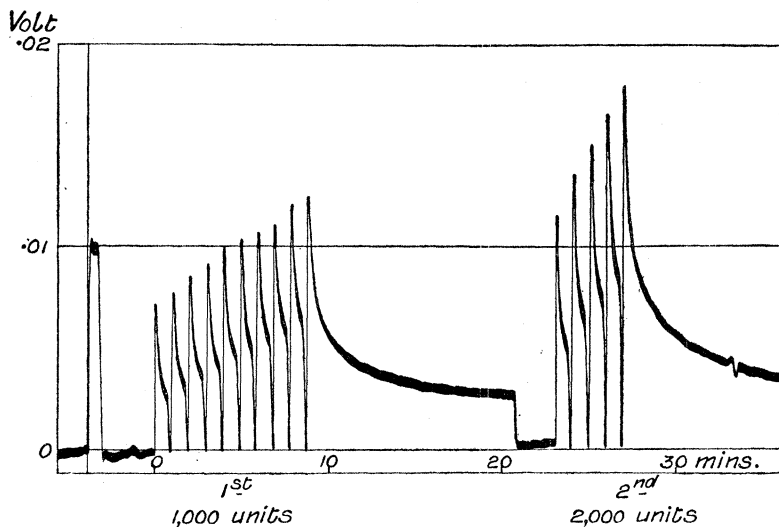
FIG. 6.



Experiment 7. Direct Excitation.—To illustrate summation of effects. Large pad of cat's foot set up 24 hours *post mortem*. Tetanisation for 5 seconds—at intervals of 1 minute. Break shock ingoing; response outgoing. Berne coil; 2 Leclanchés, at 1000 units in 1st group, at 2000 units in 2nd group. Compensation was adjusted at the commencement of each group, and left unaltered during the series; the galvanometer being short-circuited during each tetanisation, the spot then falls to the zero level.

	1st	5th	10th response.
1st series (1000)	+0·0070	+0·0100	+0·0125 volt.
2nd series (2000)	+0·0114	+0·0178	— „

FIG. 7. (4182.)



Experiment 8.—Direct Excitation. Response at first ingoing (—), subsequently outgoing (+). Berne Coil; 2 L. in primary circuit.

Time after decapitation.	Single-break currents.		Tetanising currents.		Tetanising currents.	
	10000 +	10000 —	1000 +	1000 —	10000 +	10000 —
$\frac{1}{4}$ hour	—0·0012	—0·0010	—0·0020	—0·0010	—0·0018	—0·0020
6 hours ...	+0·0005	+0·0010	+0·0006	+0·0006	+0·0092	+0·0068
24 hours ...	—	—	+ trace	+ trace	+0·0110	+0·0062

Experiment 9.—Direct Excitation. Similar Observation, more closely taken, with Photographic Records. Berne Coil; 2 L.; Tetanisation; + and - signify outgoing and ingoing.

Time after decapitation.	Excitation (+ and - denote) direction of break.	Response.
40 min.	1000 +	- 0·0020
	1000 -	- 0·0013
	10000 +	- 0·0019
	10000 -	- 0·0010
90 min. (same pad)	1000 +	+ trace.
	1000 -	+ trace.
	10000 +	+ 0·0020
	10000 -	+ 0·0020
135 min. (fresh pad)	1000 +	- 0·0020
	1000 -	- 0·0010
	10000 +	- 0·0010
	10000 -	+ 0·0004, - 0·0005
	10000 +	+ 0·0003, - 0·0004
	10000 -	+ 0·0008, - ?
	10000 +	+ 0·0010
4½ hours (same pad)	10000 +	+ 0·0016
	10000 -	+ 0·0022
24 hours (same pad)	1000 +	Nil.
	1000 -	Nil.
	10000 +	+ 0·0017
	10000 -	+ 0·0013

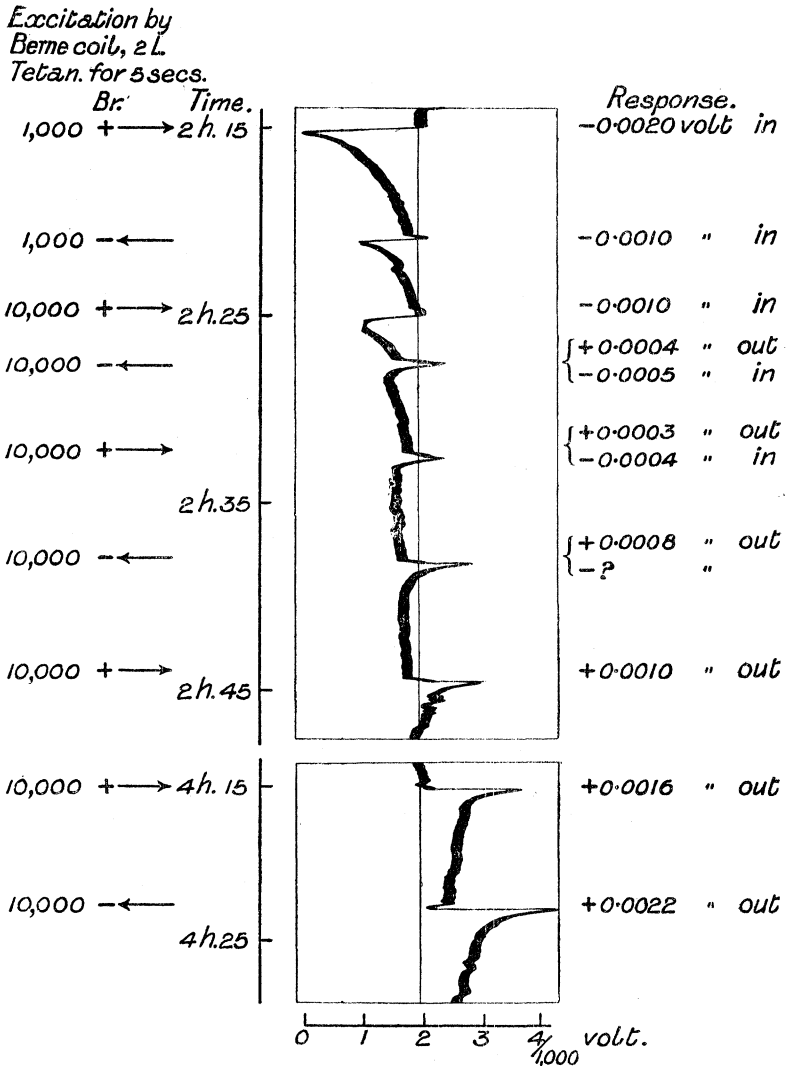
Similar results were observed in other observations of similar type (as well as in experiments according to the A, B, C plan, *vide infra*), weak excitation of the fresh pad giving ingoing, and strong excitation outgoing response. Weak subsequent to strong excitation gave no effect, while the latter gave regular outgoing effects.

Twenty-four hours *post mortem* weak excitation gave no effect; with strengthened excitation the first visible effect was outgoing, and with strong excitation the outgoing effect was generally larger than on the day of death.

In general the outgoing effect is the far more prominent and regular phenomenon; the conditions most favourable to manifestation of the less prominent and more evanescent ingoing effect being a fresh skin and not too strong excitation. With lapse of time, or as an immediate consequence of strong excitation, the ingoing effect of weak excitation is abolished.

Record of part of Experiment 9, showing transition from ingoing to outgoing effects, the former by "Weak" the latter by "Strong" Excitation.

FIG. 8. (4235.)



Response to Direct Excitation of the Intact Skin. A, B, C Method.

If two electrodes, A and B, are applied to the intact skin, *e.g.*, to the external surface of two separate pads, and tetanising currents are led in by these electrodes, the subsequent deflection is comparatively small

and of variable direction. Two outgoing currents are aroused at the points A and B, of opposed directions in the circuit, and the deflection under these conditions is only resultant of an inequality in the two forces aroused at A and at B.

In order to investigate separately the local reactions of A and of B consequent upon electrical excitation, of which these two points are poles, it is necessary to employ a third electrode, C, in the following manner :—

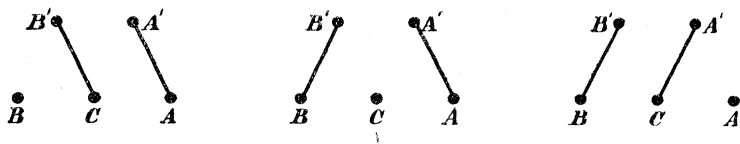
B and A are the exciting electrodes, C is an independent electrode through which no exciting current is passed, and which in conjunction with A or with B is to serve as leading-off electrode to the galvanometer.

If it be intended to examine the state at A after passage of an exciting current through A B, the procedure will be :—1. Compensation of the two points A and C. 2. Excitation through A B. 3. Connection of A and C with the galvanometer.

If it be intended to examine the state at B, the similar procedure will be :—1. Compensation of B and C. 2. Excitation through A B. 3. Connection of B and C with the galvanometer.

The necessary transposition from A to C or from B to C is most readily effected by means of a switch key of the following disposition :—

FIG. 3.



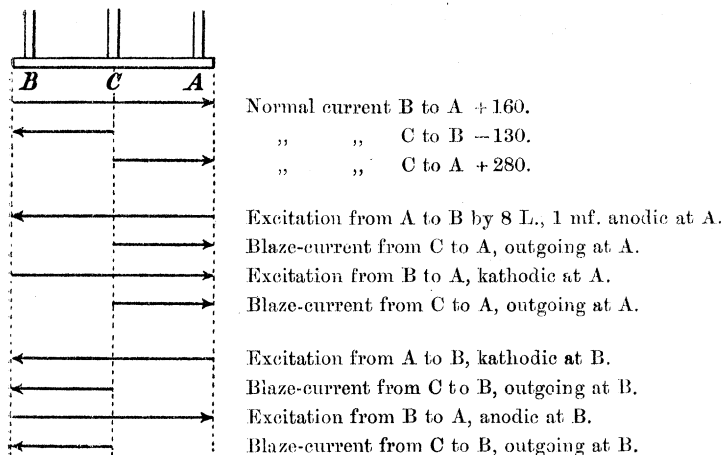
The three electrodes are connected with the terminals A, B, C. A is connected with A' and B with B' by revolving arms, either of which can be turned on to the middle terminal C.

This method is applicable to many cases other than that of the skin. I shall have occasion to refer to it as the "A, B, C Method," and for the sake of brevity shall call the above-described switch the "M switch."

The following protocol will best exhibit the results of a typical experiment and—which is a point of some practical importance—the system on which laboratory notes are taken so as to avoid confusion of direction during experiment.

Experiment 9. Frog's Skin, excited by Single Condenser Discharges.—Three electrodes, A, B, and C, applied to external surface. Excitation led in through A B. Response led off through A C, and B C, outgoing currents at A and at B.

FIG. 10.

*Experiment 10.—Cat's Paw ; 24 Hours Post-mortem.*

A, B, C as indicated below. Excitation by tetanising currents. Berne coil. Two Leclanchés. 10,000 units. The signs + and - refer to the direction of the break shock.

FIG. 11.

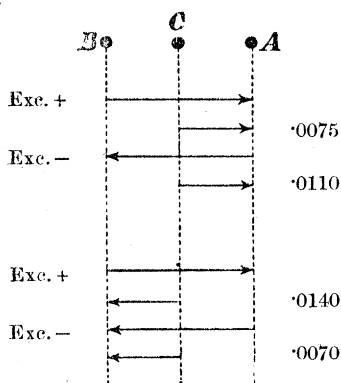
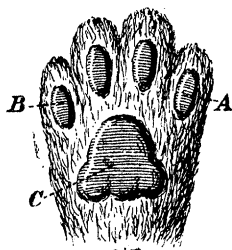


FIG. 12.

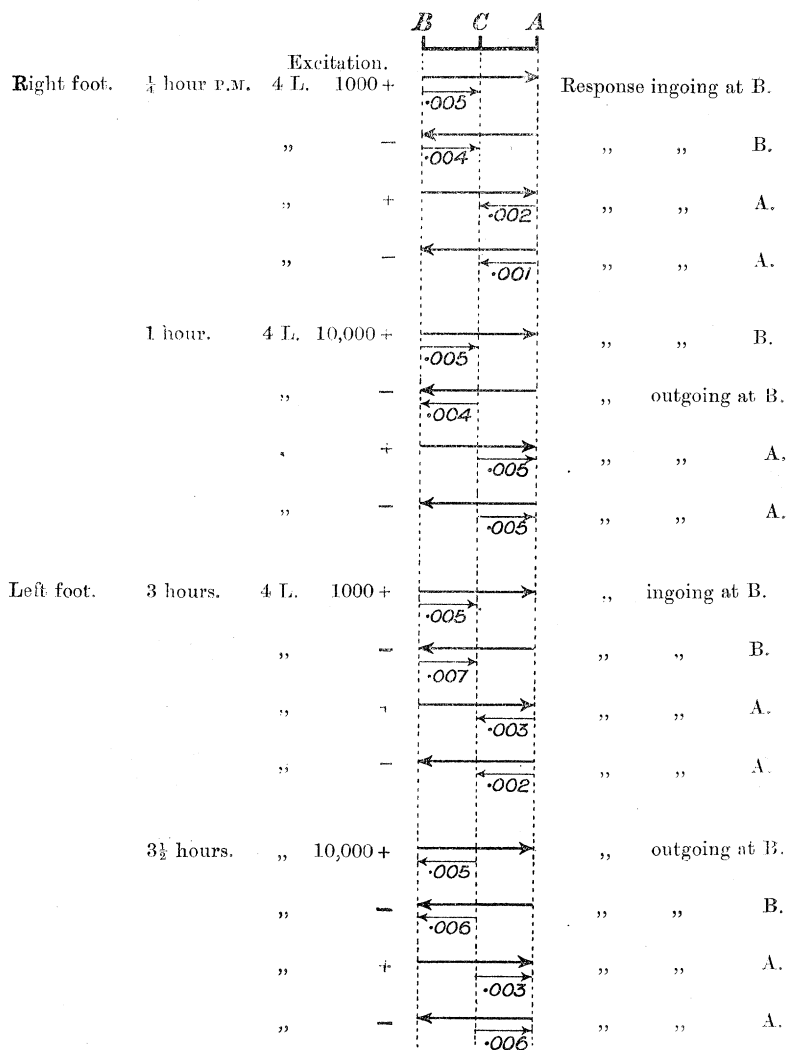


The response is always of the nature of an outgoing current at A, and at B for both directions of excitation.

Experiment 11. Cat's Paw.—Pads excited and led off as in previous experiment. Excitation "weak" and "strong" through electrodes A and B. Response through A and C and through B and C. Ingoing response after weak excitation; outgoing response after strong excitation. Berne coil. Four Leclanchés in primary circuit; tetanisation

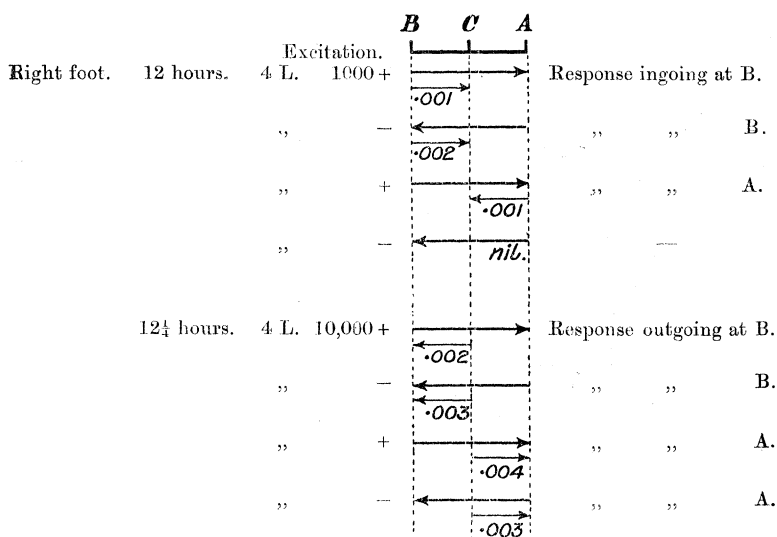
for 5 seconds; + and - signify outgoing and ingoing directions of break currents. Large arrow denotes excitation; small arrow denotes response; numbers below indicate voltage of response.

FIG. 13.



After this series of four trials at 10,000, a series of four trials at 1000 gave no effect. On transfer of an electrode to fresh pad ingoing response observed at 1000.

FIG. 14



After this series of four trials at 10,000, a series of four trials at 1000 gave no effect. On transfer of an electrode to fresh pad an ingoing response was observed after excitation at 1000.

Fallacy to be avoided.

The longest period at the end of which I have detected unmis-
takable physiological response of a surviving pad has been 7 days
post mortem. I have not, however, sought to follow out the reaction
to its last remaining trace so as to determine a maximum duration
of survival, because with declining voltage of reaction the disturbing
effects of polarisation counter-currents become more and more appa-
rent. At a comparatively early period the response to single shocks
disappears, and the galvanometer, if sensitive, manifests only polari-
sation effects contrary in direction to the test shocks. At this
period tetanisation by currents alternating in direction will still
bring out a true summated outgoing effect with both pairs of direc-
tions of currents; under these conditions the effect of polarisation is
relatively smaller. But at a later period, as the life of tissue is
coming to an end, and the response reaches a value to be measured in
ten thousandths of a volt, the disturbing influence of polarisation again
becomes apparent. In this case the deflection after tetanisation is
reversed with reversal of direction, and a resultant due to superior
polarisation by make is witnessed in the direction of break. The
shortest period after death at which I have observed this state has been

twenty-four hours, in the case of an ill-nourished cat. I regard this as indicating brief survival of tissue.

Fallacies due to anomalous polarisation require to be tested for and excluded. In my experience this kind of fallacy is liable to occur from a defectively amalgamated zinc, and is eliminated by reamalgamation.

I have not thought fit to use tetanising currents with tissue, secondary coil, and galvanometer in one circuit, but have always short-circuited the galvanometer during tetanisation (any current in circuit being of course neutralised by compensation), and non-short-circuited the galvanometer immediately after tetanisation. The time interval in this proceeding has been about 1 second, and upon occasion $\frac{1}{10}$ th second. I have not attempted to ascertain what the electrical state may have been during this transfer-time.

The following experiment is given to illustrate the fallacy of the electrodes and its correction ; the explanation offered of that fallacy is only tentative.

Preliminary Experiment to illustrate the Fallacy of the Electrodes and its Removal.

A pair of zinc rods, B A, in a U-tube, connected with a key-board coil, compensator, and galvanometer in the usual way.

(B to A is the + direction of current \longrightarrow
 (B from A is the - direction of current \longleftarrow)

		<i>Remarks.</i>
	<i>viz., anomalous or positive polarisation</i>	A electroneg. \longrightarrow B electroneg. \longleftarrow
	A e.neg. by break	> A e.neg. by make.
	A e.neg. by make	> A e.neg. by break.
1. Unamalgamated zinc in tap-water.		
Single break current + gives + after-deflection	m. -	
Tetanising currents	b. + } gives + after-deflection	
"	m. + } "	
"	b. - } "	
2. B amalgamated (A unamalgamated), in tap-water.		
Single break current + gives nil after-deflection	m. -	Ord. pol. at B e.neg. \longleftarrow — balanced by anom. pol. at A \longrightarrow
Tetanising currents	b. + } gives +	Ord. pol. at B e.pos. \longrightarrow > anom. pol. at A \longleftarrow
"	m. + } "	(Ord. pol. m. \longrightarrow > b. \longleftarrow) > anom. pol.
"	b. - } "	Anom. pol. > ord. pol.
3. B and A amalgamated, in tap-water.		
Single break current + gives - in tap-water	m. -	Ord. pol. at B \longleftarrow — and ord. pol. at A \longleftarrow
Tetanising currents	b. + } gives + after-deflection	" \longrightarrow — \longrightarrow
"	m. + } gives + after-deflection	Ord. pol. by make \longrightarrow > ord. pol. by break \longleftarrow
"	b. - } "	Ord. pol. by make \longleftarrow > ord. pol. by break \longrightarrow
4. B and A amalgamated, in sat. sol. ZnSO_4 .		
Single break current + gives nil	m. -	} No sensible polarisation.
Tetanising currents	b. + } gives nil	
"	m. + } "	
"	b. - } "	

The above experiment shows that the fallacy of the electrodes may be of complicated origin, and that care should be taken to ascertain, by separately testing the electrodes, that it has been eliminated. The interpretation of the fallacy that has been given above is purely tentative, and whether right or wrong does not form part of the principal argument, which is based upon experiments in which the fallacy has been eliminated. Nevertheless the fact that it might be present is important to bear in mind, especially in cases where reactions of low voltage (below 0.001 volt) are under examination. But, as previously stated, the fallacy, even if present, would not interfere with conclusions based on reactions of high voltage (above 0.01 volt).

The fallacy of the electrodes is easily recognised and easily avoided. To recognise the fallacy it is sufficient to bring the clay pads of the two electrodes into contact, exactly compensating any accidental current, and then pass testing currents through the circuit, just as when a test object is interpolated between the electrodes. There should be no movement of the galvanometer spot, or at most the slight movement due to defect of compensation or trace of polarisation, in either case less than the movement produced by 0.0001 volt thrown into circuit.

To remove the fallacy, if recognised, it is usually sufficient to carefully reamalgamate the zinc rods. From preliminary experiments with zinc rods, unamalgamated and amalgamated, in water and in saturated solution of ZnSO_4 , it appeared that fallacy of electrodes might be due to a defectively amalgamated cathodic zinc surface rendered electronegative by an exciting current.

Conclusion.

The regular electrical effect of indirect excitation is an ingoing current.

The usual and principal electrical effect of direct excitation is an outgoing current.

An ingoing current may be obtained by direct excitation immediately after death.

I think it probable that both ingoing and outgoing forces may co-exist in the excited skin at the same moment, and that the galvanometric deflection is an expression of this resultant.

This co-existence of two opposite forces is, however, less clearly evident in the case of the cat's skin than in those of the frog's skin and of the frog's eyeball.

FIG. 12.

