PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

On the "Blaze Currents" of the Frog's Eyeball

Augustus D. Waller

Phil. Trans. R. Soc. Lond. B 1901 **194**, 183-233
doi: 10.1098/rstb.1901.0005

V. *On the "Blaze Currents" of the Frog's Eyeball.*

By Augustus D. Waller, *M.D., F.R.S.*

Received December 6,—Read December 6, 1900.

Contents.

In a recent communication to the Society* I have stated that the normal electrical response of the eye to light consists in a current traversing the eyeball in a positive direction, *i.e.*, from fundus to cornea, and that a similar positive response is aroused

* A. D. W., "On the Retinal Currents of the Frog's Eye, excited by Light and excited Electrically," 'Phil. Trans.,' B, vol. 193, p. 123, §§ 13 and 14.

18.7.1901

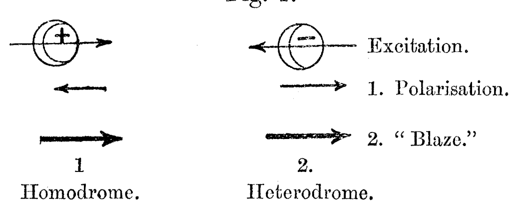
by mechanical and by electrical stimuli, whatever be the direction of the latter. I have designated this positive response to non-luminous stimuli as the retinal discharge or blaze.

With reference to electrical stimulation, its most characteristic form is when it occurs in the same direction as the current by which it is excited, *i.e.*, when it cannot be a polarisation counter-current. It is in such case analogous with the discharge of an electrical organ excited by an electrical current in the direction of normal discharge, and, indeed, it may be of such magnitude as to lead an observer to regard the retina in the light of an electrical organ.

Its less obvious form is when it occurs in an opposite direction to that of an exciting current, and might, therefore, be considered as being nothing more than an ordinary polarisation current. Nevertheless, its magnitude and time relations, as compared with those of polarisation effects manifested after death, are such as to compel us to the conclusion that in this case also we have to do with a physiological effect—a true retinal action current—analogous with the discharge of an electrical organ excited by an electrical current in the homonymous direction.

With regard to the nature and seat of origin of this retinal blaze current, I may say at once that it appears to be a phenomenon of the same order as the secondary (positive) electromotive effects discovered and minutely studied by DU BOIS-REYMOND* in the three cases of muscle, nerve, and electrical organ, and designated by him as "positive polarisation." Accepting further the subsequent amendment almost simultaneously presented by HERMANN and by HERING, to the effect that such positive polarisation currents are, in reality, post-anodic action currents, it follows that retinal blaze in its most characteristic form is an action current, of which the electromotive origin is situated in the deeper layers of the retina, and consists in an electro-positive state (galvanometrically negative) of previously anodic elements. Finally, if we admit that the heterodrome reaction is of physiological character, we are constrained to admit that an action current may originate from previously kathodic as well as previously anodic regions of living matter. These two points may most easily be followed by reference to this diagram, which is taken from my previous paper:—

Fig. 1.



On first witnessing the phenomenon, I considered it as being of retinal origin. I

* DU BOIS-REYMOND, 'Ueber secundär-elektromotorische Erscheinungen an Muskeln, Nerven und elektrischen Organen.' Sitzungsberichte, Berlin, 1883.

then sought to learn whether it were exclusively retinal, by means similar to those by which I had previously satisfied myself of the exclusively retinal origin of the electrical response to light. I compared, namely, the effects of electrical excitation of the two halves, anterior and posterior, of the eyeball, but at once was met with the difficulty that the injury and compression incidental to the division of the eyeball into two halves greatly modified the phenomenon. And whereas in the case of light the contrast between effects of light upon the two halves was generally sufficiently well marked by reason of there being no distinct effect at all on the anterior half, the similar contrast between the effects of electrical stimulation of the two halves was far less absolute; I generally obtained a comparatively small effect upon the anterior half of the eyeball, and, but by no means in every case, a comparatively large effect upon the posterior half; but in at least two instances I find noted that the anterior gave a larger effect than the posterior half. I therefore concluded that whereas in the electrical response to light the retina is the principal, if not solely, effective factor, tissues of the eyeball other than retinal are coeffective in the electrical response to strong electrical stimulation; and I recognised in this fact an indication that blaze currents might be expected to occur in other living tissues. The consequent investigation* to which this gave rise will be reported on in due course; my present paper deals exclusively with the phenomena as witnessed upon the eyeball.

At a later period of the investigation I made careful comparison between alterations of response to light and of response to electrical stimulation (*vide infra*).

The conclusion I arrived at from such comparisons may be expressed in the following apparently contradictory propositions to the effect that: (1) There is a degree of parallelism between response to light and response to electrical stimulation, indicating that the retina is concerned in both kinds of response; (2) There is a defect of parallelism between response to light and response to electrical stimulation, indicating that tissues of the eyeball other than retinal (*e.g.*, the corneal epithelium) are coeffective in response to electrical stimulation. I prefer, therefore, to designate the effects under investigation as eyeball currents rather than as retinal currents, although, no doubt, the retina is a principal factor in the effects.

The typical response to light is positive, but with lapse of time or by injury (pressure more especially), a negative component becomes manifest, until finally the response is purely negative.

The typical response to an electrical stimulus, whether homodrome or heterodrome, is positive, but, as indicated in my previous paper (p. 32), the effects become variable at later stages.

The first object of the experiments reported on in the present communication was to obtain a clearer general view of such variations, and of the parallel effects of electrical and luminous stimuli in various states of retina.

* Preliminary note in the 'Comptes Rendus de l'Académie des Sciences,' 3rd September, 1900.

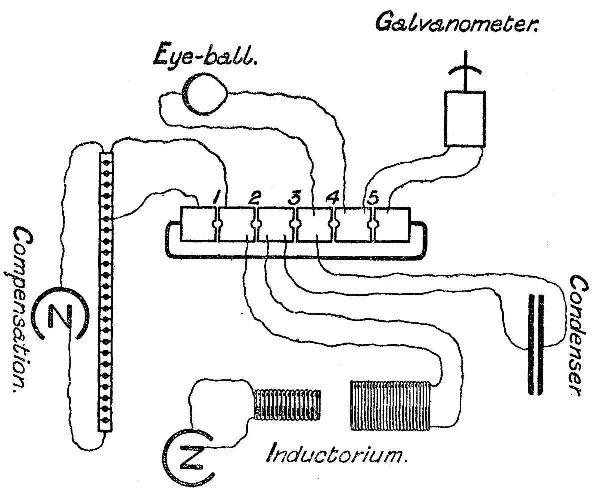
Towards the conclusion of my first series of experiments I had found means of experimentally controlling the retinal response to light, of converting, *e.g.*, the normal positive response of the first stage into the abnormal negative response of the third stage. I have since found (1) that the changed response to light can be gradually effected by gradually increased pressure; (2) that by similar means similar changes can be effected in the response to electrical stimuli; and (3) that the direction and magnitude of the response to electrical stimuli are modified by the presence of weak constant currents.

Method.—The electrical response of the eyeball is observed—and if need be recorded—on the following plan:—

To a keyboard having five plugs and plug-holes 1, 2, 3, 4, 5 are connected—

1. A compensator. 2. An inductorium. 3. A condenser. 4. The eyeball. 5. A galvanometer.

Fig. 2.



With 4 and 5 unplugged, any eyeball current that may be present is shown by the galvanometer. Such current is exactly balanced by manipulation of the compensator (which is unplugged at 1) until the galvanometer can be plugged and unplugged without deflection from zero.

With the galvanometer plugged at 5, a single induction shock is sent through the eyeball but not through the galvanometer, which is immediately afterwards unplugged, so as to exhibit deflection only by the excited, and not by the exciting, current.

This excited or after-current may be homodrome or heterodrome to the exciting current. In the heterodrome direction an after-current is not at first sight particularly significant; the direction is that of polarisation which is manifested by non-living, as well as by living, electrolytes. But after-current in the homodrome direction cannot be caused by such polarisation.* It is this clear and evident after-

* The anomalous or positive polarisation of commercial zinc in commercial zinc sulphate, and of amalgamated zinc in water (DU BOIS REYMOND, 'Gesammelte Abhandlungen,' Bd. I., pp. 57 and 67), was

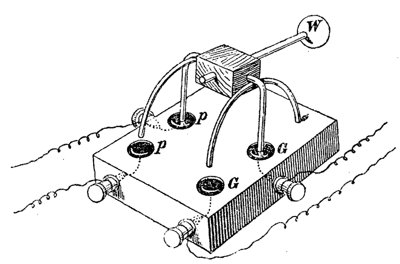
current that first aroused my attention as being an expression of physiological activity, and that has been referred to above as "blaze current of the obvious form."

The magnitude, time-relations, &c., of blaze current will be considered below; at this stage it will be sufficient to say that the electromotive value and the duration of the phenomenon on fresh vigorous eyeballs are such that it can be demonstrated with a galvanometer of less than ordinary sensitiveness (*e.g.*, giving only 1 centim. deflection by $1 \cdot 10^{-8}$ ampere), and at an interval between excitation and galvanometer closure of many seconds or even minutes, *i.e.*, not requiring any rheotome for its demonstration. For its closer investigation an instrument by which that interval may be taken of small and constant value is, however, advantageous and convenient.

A somewhat important condition to fulfil as regards any exact comparison of magnitudes of blaze is to preserve a constant and, if possible, brief interval between excitation and opening of galvanometer circuit.

With induction shocks this was easily effected by connecting primary circuit of coil and galvanometer to the two sides of a Pohl's commutator without cross wires, as figured in the diagram. One pair of pools completes the primary circuit at *pp*; the other pair of pools short-circuits the galvanometer through GG. The lateral

Fig. 3.



pools of mercury and the semicircular wires are adjusted so that circuit is completed at G (*i.e.*, the galvanometer short-circuited) before circuit is completed at *p*. On releasing the commutator cradle the weight, W, lifts the two wires from the mercury, breaking first the primary circuit and subsequently the galvanometer short circuit. Thus the break current is cut out of the galvanometer and its after-effect alone passes through the galvanometer. The time of transfer is constant and may be conveniently adjusted by preliminary measurement; I adjusted it to be as nearly as possible 1/10 second.

Direction of exciting currents should be ascertained by preliminary trial with weak currents sent through the eyeball and galvanometer, *i.e.*, with 4 and 5 unplugged. A reverser is placed in the exciting circuit so that its positions to right and left shall correspond with the deflections of the galvanometer spot right and left.

taken into consideration and found to be out of the question. No trace of this effect was exhibited by any of the unpolarisable electrodes employed throughout these observations.

The nature of an exciting current, and its strength, influence the result, which in any given case is the algebraic sum of blaze current and of polarisation current. The observations of DU BOIS-REYMOND on positive polarisation of muscle, nerve, and electrical organ, those of HERMANN and HERING on the post-anodic action currents of muscle and nerve, were systematically made with the constant current, by which the polarisation factor is elicited in highest degree. By reason of this fact the after-currents observed were very generally diphasic, first negative, then positive, duration of current being favourable to the manifestation of the negative factor, strength of current to that of the positive factor. Thus, on muscle, DU BOIS-REYMOND obtained, *e.g.*, negative maximum after 10 minutes closure of the current from 1 Grove cell, and positive maximum after 0·075 second closure of the current from 20 Grove cells. He incidentally mentions the fact that he obtained pure positive effects by sufficiently strong break induction shocks both upon muscle and upon nerve.

The case of the electrical organ is perhaps of greatest interest in connection with the present investigation. In Malapterurus the natural discharge of the electrical organ is directed from head to tail. A longitudinal strip of organ traversed by a constant current behaves just like muscle or nerve as regards the subsequent after-current, which is diphasic with a predominant negative (polarisation) factor or a predominant positive (action) factor, according as the exciting current has been taken weak and prolonged or strong and brief. But—and this is the point in which the retinal blaze is comparable—the positive factor predominates when the exciting current is directed from head to tail, *i.e.*, the natural discharge swamps the polarisation counter-current.* Similar phenomena obtain in the Torpedo organ, the natural discharge in this case being from ventral to dorsal surface, which is the direction in which the positive after-current, caused by a constant current, is alone manifested.

Precisely similar effects are obtainable on the eyeball, in which the natural direction of discharge when excited by light is from fundus to cornea, which is also the direction in which the positive after current caused by an electrical current is alone manifested (in the normal state of the eyeball).†

The complicating effect of polarisation currents is very greatly reduced by taking as exciting current a strong induction shock in place of the brief closure of a strong galvanic current. A troublesome piece of apparatus is dispensed with, and the chief desiderata for the manifestation of positive after-currents are fulfilled by an induction shock which is "short" and may be taken "strong." I have therefore systematically used as exciting current the break induction shock of a Berne inductorium fed by two Leclanché cells with the secondary pushed home over the primary coil. I have also occasionally in cases where such strength had seemed to be excessive used the coil at

* DU BOIS-REYMOND, 'Gesammelte Abhandlungen,' II., p. 719; 'Arch. f. Physiol.,' 1885, p. 86. (Diagram in summary of changes on p. 121.)

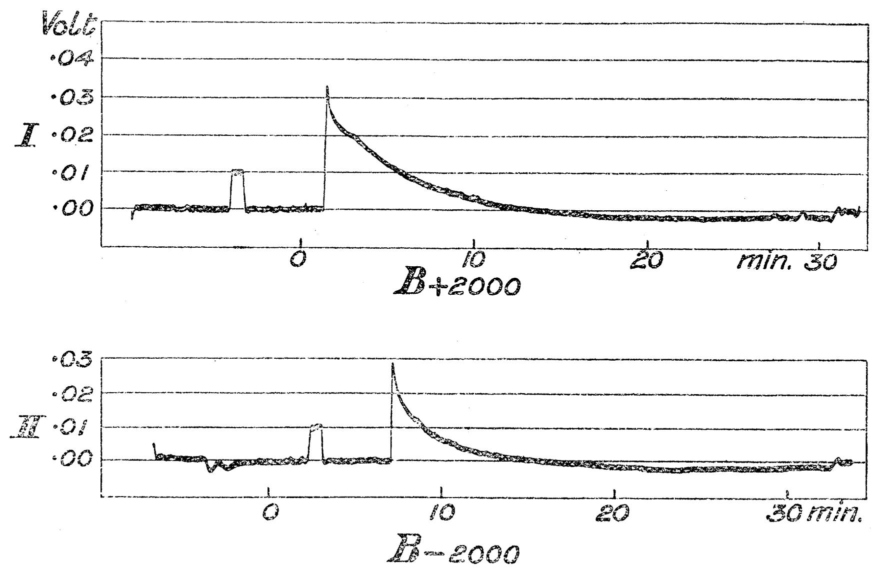
† A. D. W., "The Eyeball as an Electrical Organ," 'Proceedings of the Physiological Society, November, 1900.

three fixed distances corresponding with 1000, 5000, and 10,000 of the Berne graduation. With this instrument polarisation, although still present, was relatively far less obtrusive, and in general far too small to obscure the positive (*i.e.*, homodrome) after-currents in question.

But for closer investigation I have used condenser discharges, because of the great certainty of energy dosage by this means, and the ease with which any given energy may be delivered at various gradients found by preliminary experiment to be the most suitable. By this means polarisation effects can be, if not entirely eliminated, reduced to a minimum and rendered practically insignificant. And in preliminary experiments by means of the condenser, I made frequent use of a method which I had first applied to the case of nerve,* viz., having fixed upon a given energy of excitation at given capacity and voltage, I proceeded at once to two further tests—one at twice the voltage and one quarter the capacity, *i.e.*, with the same energy at eight times the previous rate of discharge—the other at one-half the voltage and four times the capacity, *i.e.*, with the same energy at one-eighth of the original rate of discharge. These two further tests may be briefly denoted as made an octave above or below the first test with reference to the rate of discharge.

Blaze currents are elicited by single induction shocks and by single condenser discharges with a very wide range of varying strengths.

Fig. 4.

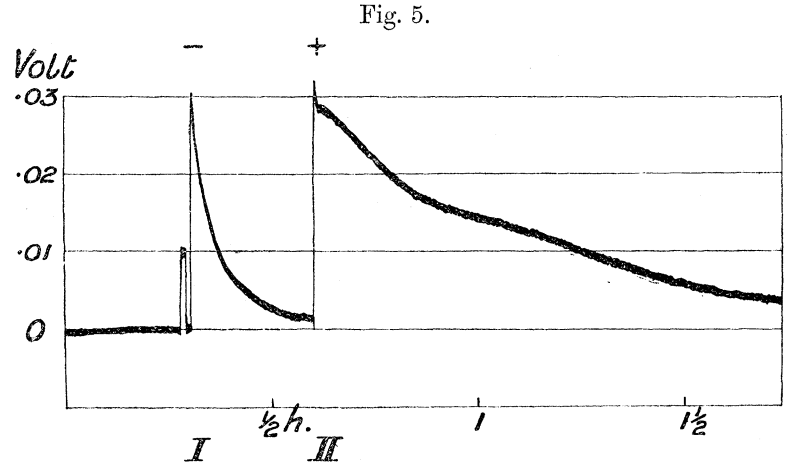


Normal Blaze Currents of a Frog's Eyeball in response to excitation by a single break induction current I. in the positive or homodrome and II. in the negative or heterodrome direction. Berne coil at 2000 units fed by 2 Leclanché cells. Transfer time (*i.e.*, interval between break shock and galvanometer make) = $\frac{1}{10}$th second. Scale in hundredths of a volt.

* 'A. D. W., "The Characteristic of Nerve," 'Roy. Soc. Proc.,' 1897, vol. 52, p. 80.

The typical normal result of a rough preliminary experiment is a pair of responses of invariable direction in response to an induction shock first in one then in the opposite direction, and it is evident that one of these two responses must be homodrome with an exciting current, while the other must be antidrome, *i.e.*, in the polarisation direction. One may feel well assured of the physiological nature of the homodrome effect; it is completely abolished with death of the eyeball. The heterodrome after-effect appears at first sight to be a polarisation current; nevertheless on closer examination it also must be characterised as physiological, for it also is very greatly diminished with death of the eyeball. The fresh eyeball gives a pair of large

Fig. 5.



Normal Blaze Currents in response to single break induction currents at 10,000 units. I. heterodrome or negative, II. homodrome or positive. Transfer time of 2 seconds. II. is more prolonged than I.

responses in response to excitation of both directions. The dead eyeball gives, if anything at all, a small pair of positive and negative responses of contrary direction to excitation.

The organ discharge of a normal eyeball is directed from fundus to cornea, and like the discharge of an electrical organ of Malapterurus or of Torpedo, can be aroused both by a homodrome and by an antidrome exciting current. Seeing that the eyeball current aroused by an electrical stimulus is similar in direction to that aroused by light, it is highly probable that the electromotive origin of both effects is in part identical, *i.e.*, in the deeper layers of the retina, that of the rods and cones, which are rendered physiologically active (*i.e.*, electropositive or galvanometrically negative) by luminous and by electrical stimuli.

One of the most striking features of blaze currents is their very considerable duration—several minutes when the exciting currents have been taken at all strong. I have more than once seen a blaze current evoked by a strong homodrome induction shock last for over an hour; the ordinary duration of a moderately strong reaction is generally between five and ten minutes. This great duration renders it possible to observe the reaction at considerable intervals after excitation, and, if desired, to rheotome it at regular long intervals. On the other hand, this great duration does not permit of an expeditious repetition of a succession of reactions by excitations of any considerable strength.

The most satisfactory and trustworthy means of observation is the photographic record, which brings out far more clearly than unaided observation the character of blaze currents and the particular points of difference between the homodrome after-effect of anodic origin and the antidrome effect of kathodic origin.

The following statements are based upon a review of a considerable number of such records :—

It very commonly (not always, however) occurs that the retinal blaze of a normal eyeball (*i.e.*, of an eyeball manifesting positive response to illumination) is elicited more easily and in greater amount by homodrome than by heterodrome excitation.

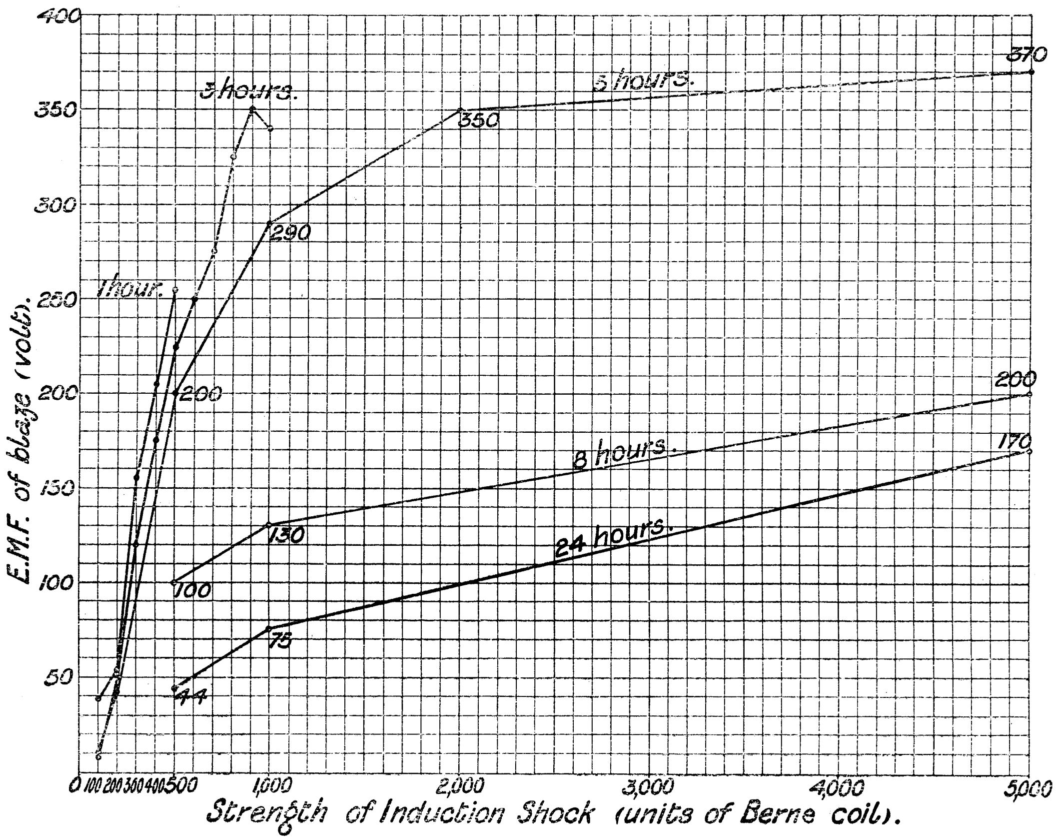
Both effects are small and brief after weak stimuli, large and prolonged after strong stimuli; or, otherwise stated, they increase both in magnitude and in duration with increasing strength of the exciting current. Thus, *e.g.*, to quote some ordinary values, the dimensions one may expect are as follows :—

Strength of break induction.	Duration of blaze.	Electromotive value of blaze.
100 units	1 to 2 minutes	0·0025 to 0·0050 volt
1,000 „	5 „ 10 „	0·0100 „ 0·0150 „
*10,000 „	30 „ 60 „ or more	0·0200 „ 0·0300 „

And whereas the large prolonged effects may not entirely pass off during observation, the small brief effects may fall below the zero value and give place to a small phase of opposite direction.

The eyes of fresh vigorous frogs give much better effects than those of poor half-starved specimens. Moribund frogs give very small effects; the eye shares in the general physiological "misère" which is also evidenced by muscle, nerve, heart, &c. The eyes of frogs found dead in their tank give no effect at all; and, according to my experience, the eyes of *Rana temporaria* have always proved to be more active than those of *Rana esculenta*.

* This strength is far in excess of what I subsequently employed.



BLAZE Currents of a Frog's Eyeball at various strengths of excitation, at various periods after excision.

Frog's eyeball.	1 hour P.M.	3 hours P.M.	5 hours P.M.	8 hours P.M.	24 hours.
Current of rest . .	−0·0190	−0·0200	−0·0170	−0·0080	−0·0020
Response to light .	+0·0007	—	—	—	+0·0002
Response to a break induction shock					
100 +	+0·0038	+0·0008	+0·0010	—	—
200 +	+0·0054	+0·0050	+0·0042	—	—
300 +	+0·0155	+0·0120	—	—	—
400 +	+0·0205	+0·0175	—	—	—
500 +	+0·0255	+0·0225	+0·0200	+0·0100	+0·0044
600 +	—	+0·0250	—	—	—
700 +	—	+0·0275	—	—	—
800 +	—	+0·0325	—	—	—
900 +	—	+0·0350	—	—	—
1,000 +	—	+0·0340	+0·0290	+0·0130	+0·0075
2,000 +	—	—	+0·0350	—	—
5,000 +	—	—	+0·0370	0·0200 +	+0·0170
10,000 +	—	—	+0·0200	0·0055 +	+0·0145

BLAZE currents of a Frog's Eyeball subsequent to excitation by break induction shocks of arithmetically increasing intensity. Berne coil fed by 2 Leclanché cells. Successive excitations at intervals of about 2 minutes. Compensation exactly established just before each excitation. Transfer time, *i.e.* interval between excitation and galvanometer closure, $= \frac{1}{10}$th second. Excitation in alternately opposite directions.

Excitation (units of Berne coil).		Blaze current (voltage).	
100 +	and 100 –	+ 0·0007	and + 0·0005
200 +	200 –	+ 0·0030	+ 0·0020
300 +	300 –	+ 0·0060	+ 0·0030
400 +	400 –	+ 0·0085	+ 0·0080
500 +	500 –	+ 0·0100	+ 0·0100
600 +	600 –	+ 0·0140	+ 0·0130
700 +	700 –	+ 0·0160	+ 0·0150
800 +	800 –	+ 0·0180	+ 0·0170
900 +	900 –	+ 0·0240	+ 0·0190
1000 +	1000 –	+ 0·0265	+ 0·0220

1682–3. *Blaze Currents of a Frog's Eyeball caused by Condenser Discharges of arithmetically increasing quantity.*—The condenser discharged through the eyeball at intervals of about 2 minutes by a Morse key. The transfer time between excitation and galvanometer observation is 2 seconds. Compensation made at outset of each series, and not readjusted between successive excitations. Excitations only in positive direction. In series A the quantity is increased by increasing the capacity of condenser; in series B by increasing the voltage. Excitations are throughout in the positive direction, *i.e.*, from fundus to cornea.

	Voltage.	Capacity.	Quantity.	Energy.	Comparative rate of energy discharge.	Blaze.
	volts.	MF.	MC.	ergs.	V/F.	volt.
A	2·8	2	5·6	80	1·4	+ 0·0022
	,,	4	11·2	160	0·7	+ 0·0028
	,,	6	16·8	240	0·47	+ 0·0032
	,,	8	22·4	320	0·35	+ 0·0034
B	2·8	2	5·6	80	1·4	+ 0·0025
	5·6	,,	11·2	320	2·8	+ 0·0035
	8·4	,,	16·8	720	4·2	+ 0·0050
	11·2	,,	22·4	1180	5·6	+ 0·0015

1684–5. Another eyeball. Excited by discharges of arithmetically increasing quantity by capacity.

volt.	MF.	MC.	ergs.	V/F.	volt.
1·4	2	2·8	20	0·7	+0·0005
,,	4	5·6	40	0·35	+0·0020
,,	6	8·4	60	0·23	+0·0025
,,	8	11·2	80	0·17	+0·0030
,,	10	14·0	100	0·14	+0·0033

And then by arithmetically increasing quantity by voltage.

volts.	MF.	MC.	ergs.	V/F.	volt.
1·4	2	2·8	20	0·7	+0·0007
2·8	,,	5·6	80	1·4	+0·0030
4·2	,,	8·4	180	2·1	+0·0045
5·6	,,	11·2	320	2·8	+0·0050
7·0	,,	14·0	500	3·5	+0·0055

The maximum electromotive value of blaze current that has come under my observation has been $\frac{1}{30}$th volt. I have frequently noted values of between 0·02 and 0·03 volt. These voltages are of the same order as those given by GOTCH for the action current of nerve and for the discharge per disc of an electrical organ, viz., 0·03 in the Skate, 0·04 in Torpedo, 0·045 in Malapterurus.* I think it probable that the maximum value of blaze current that I have observed, 0·033, may be exceeded. My attention was not particularly directed to the observation of maximum values when the best frogs were under experiment, and I did not therefore make any special measurements under *optimum* conditions.

* GOTCH, 'Schäfer's Text-book of Physiology,' vol. 2, p. 584.

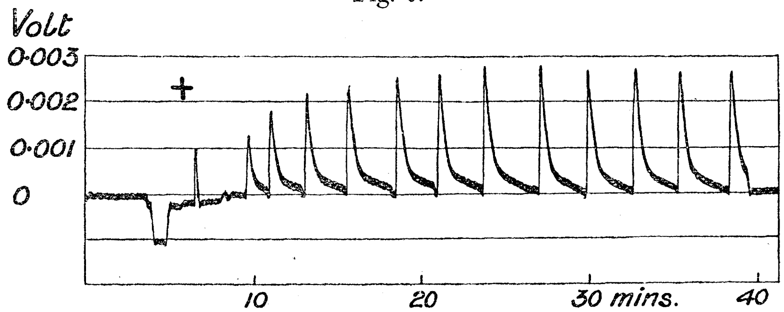
Some Measurements of the Voltage of Blaze Currents of the Frog's Eyeball.

No.	Excitation.	Blaze.	Remarks.
1679	Br. 10000 +	+0·0250	Single effect.
1680	" " +	+0·0045	"
	" " −	−0·0015	"
1681	2L, 1MF +	+0·0050 to +0·0030	Fatigue decline.
1682	2L, 2MF +	+0·0025	Single effect.
1684	1L, 2MF +	+0·0005	"
1685	2L, 2MF +	+0·0030	"
1686	2L, 2MF +	+0·0044	"
1894	Br. 10000 +	+0·0045	"
	" " −	−0·0015	"
1895	Br. 10000 +	+0·0036 to +0·0027	"
	" " −	−0·0012 to −0·0020	"
1897–8	Br. 10000 −	+0·0300 to +0·0200	"
	" " +	+0·0300 to +0·0200	"
1899	Br. 10000 +	+0·0052 to +0·0027	"
	" " −	+0·0038 to +0·0025	"
1914	6L, 0·1MF +	+0·0086	"
	" " −	+0·0070	"
1973	3L, 1MF +	+0·0010	"
	" " −	+0·0009	"
1998	Br. 2000 +	+0·0330	"
	" " −	+0·0290	"
1999	Br. 1000 +	+0·0300	By summation.
4001	Br. 100 +	+0·0040	Single effect.
	Br. 1000 +	+0·0200	"
	Br. 10000 +	+0·0120	"
4002	Br. 100 +	+0·0050 to +0·0072	Staircase increase.
4005–7	Br. 1000 +	+0·0100 to +0·0012	Fatigue decline.
4008	Br. 1000 +	+0·0137	Single effect.
	" " +	+0·0285	By summation.
4009	Br. 1000 +	+0·0016	Single effect.
	" " +	+0·0040	By summation.
	Br. 1000 +	+0·0300	Single effect.
	Br. 1000 +	+0·0200	"

The minute study of the exact relation between magnitude of stimulus and of response will require detailed investigation. At the present stage I shall confine my remarks to one or two principal points.

The statement of evident fact that increasing strength of exciting current evokes increasing strength of blaze can be at once made more precise by the statement that the latter increases more rapidly than the former, at least within the considerable range of what may be termed excitation of medium strength, so that a curve of blaze effects plotted as ordinates with strength of excitation along the abscissa, is concave towards the base, and appears to rise convex towards an asymptote, the position of which one is tempted to determine on the assumption that the curve is logarithmic.

Fig. 6.

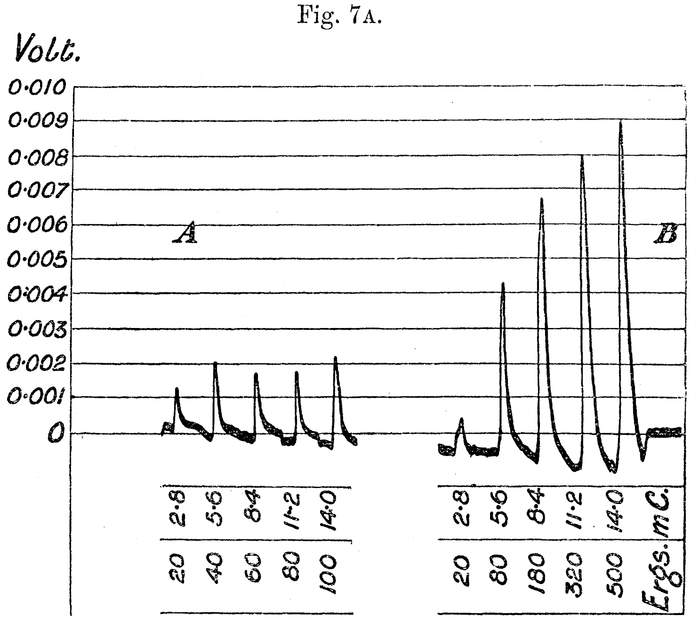


A series of homodrome (positive) blaze currents in response to condenser discharges of arithmetically increasing quantity and energy.

But before actually proceeding to this refinement, I think it is advisable to wait for more numerous and precise data, and above all to settle the fundamental point as to whether it is correct to measure out the abscissa of excitation in units of energy or in units of quantity. I have indeed already* offered reason for concluding that energy rather than quantity is the factor to be considered in the measurement of excitation; but I do not know yet how far I might be held justified in proceeding further from that conclusion assumed as point of departure.

The relation is in any case difficult to examine both above and below the limits of moderate excitation—above by reason of the injuries caused by very strong stimuli, below by reason of the relatively large error of small measurements, and more especially of the relatively large value of polarisation where small blaze effects are in question. The following experiment and numbers taken from my previous paper† will illustrate the preceding remarks.

Fig. 7A.



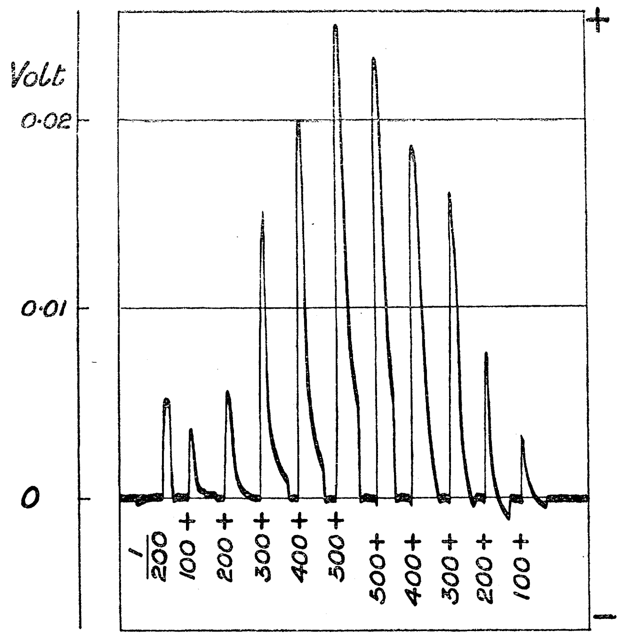
* A. D. W., "Retinal Currents," 'Phil. Trans.,' B, vol. 193, 1900, p. 156.

† A. D. W., "Retinal Currents," 'Phil. Trans.,' B, vol. 193, 1900, p. 156.

A	Capacity, F.	Pressure, V.	Quantity, FV.	Energy, 5FV².	V/F.	Deflection.	
	MF.	volt	MC.	ergs.			volt.
	2	1·4	2·8	20	0·7	+ 5	+ ·0010
	4	1·4	5·6	40	0·35	+10	+ ·0020
	6	1·4	8·4	60	0·23	+ 8·5	+ ·0017
	8	1·4	11·2	80	0·17	+ 9	+ ·0018
	10	1·4	14	100	0·14	+11	+ ·0022
B	2	1·4	2·8	20	0·7	+ 4·5	+ ·0009
	2	2·8	5·6	80	1·4	+22	+ ·0044
	2	4·2	8·4	180	2·1	+33·5	+ ·0067
	2	5·6	11·2	320	2·8	+40	+ ·0080
	2	7·0	14	500	3·5	+45	+ ·0090

Two series of homodrome (positive) blaze effects in response to condenser discharges: A of arithmetically increasing quantity and energy, B of the same arithmetically increasing quantity but of logarithmically increasing energy. The relative rates of energy discharge are indicated by the numbers of the column V/F. Transfer time = 2 seconds.

Fig. 7B.



4044	Excitation.	Blaze.	Blaze.	Mean.
		volt.		
	Break 100+	↓ +0·0038	↑ +0·0032	+0·0035
	200+	+0·0054	+0·0070	+0·0062
	300+	+0·0155	+0·0165	+0·0160
	400+	+0·0205	+0·0195	+0·0200
	500+	+0·0255	+0·0245	+0·0250

Observation upon another eyeball. One hour after death. Excitations only in positive direction, successively from weaker to stronger and *vice versâ*, at intervals of 2 minutes. Current of rest = −0·0190.

Experiment made in order to determine whether Electrical Excitation is Function of Quantity or of Energy.

The eyeball (which gave a small positive response to light) is set up in the usual way, and its blaze currents caused by single condenser discharges are observed at intervals of 5 minutes. The procedure was as follows:—Compensation adjusted—galvanometer plugged at 5 (fig. 2) and condenser unplugged at 4. Discharge sent through the eyeball by a Morse key. Condenser plugged and galvanometer unplugged, the time of transfer being maintained by metronome at 2 seconds.

Time.		Excitation.				V/F.	Blaze.
		Capacity.	Voltage.	Quantity.	Energy.		
	minutes.	MF.		MC.	ergs.		volt.
I.	0	0·2	4·2 +	0·84	18	21	+0·0061
	5	0·2	4·2 −	0·84	18	21	+0·0049
II.	10	0·4	4·2 +	1·68	36	10·5	+0·0087
	15	0·4	4·2 −	1·68	36	10·5	+0·0072
III.	20	0·1	8·4 +	0·84	36	84	+0·0086
	25	0·1	8·4 −	0·84	36	84	+0·0070

Quantities are equal in I. and III., but energies are unequal; the blaze effects are unequal.

Energies are equal in II. and III., but quantities are unequal; the blaze effects are approximately equal.

NOTE.—The rate of discharge, as shown in the column V/F in III. has been eight times that in II.

I have not yet obtained satisfactory measurements of minimum energy of excitation giving maximum energy of blaze effect. But I have repeatedly had occasion to recognise this principal point, that the energy of the excited effect may be in excess of the energy of the exciting cause.

Excessive stimulation, so far from giving a larger, gives a smaller blaze effect than does moderate stimulation. And I have repeatedly been struck by the fact that a single over-strong stimulus not only diminishes the blaze effect provoked by a subsequent moderate stimulus, but that the effect of the excessive stimulus is itself far short of the effect caused by a moderate stimulus. One might have expected that the final explosion provoked by the excessive stimulus should itself be excessive, but one finds that such excessive stimulus, by injury of tissue, sets a limit to the effect which itself produces.

The development of a blaze effect is sudden; its decline is gradual. The culmination appears to outstrip the rate of progress of the deflected galvanometer mirror, more clearly so in the case of a heterodrome than in that of a homodrome blaze. This difference when present is due to polarisation counter-current present in the two cases, which counter-current somewhat accelerates the culmination of heterodrome blaze, and somewhat retards the culmination of homodrome blaze.

From observations on dead eyeballs some indication of the dimensions of this polarisation current may be obtained, and these are found to be such that no fear of confusion by their presence need be entertained, at least in connection with any but the smallest values of blaze currents.

The following values will illustrate this point; they are taken upon an eyeball in which blaze effects were rather below their ordinary value and polarisation, therefore relatively more considerable; moreover, the eyeball was not assuredly "killed," but only "stunned" by repeated shocks from a Ruhmkorff coil.

	Normal.	After violent shocks.
	volt.	volt.
*"Weak" . . 100 +	+0·00400	−0·00005
−	+0·00200	+0·00005
"Medium . . 1,000 +	+0·02000	−0·00020
−	+0·02000	+0·00040
"Strong" . . 10,000 +	+0·02000	−0·00100
−	+0·02000	+0·00200

Thus, although the polarisation contrary to a strong current may be as great as the blaze effect of a weak current, it is evident that of one and the same current polarisation is quite inconsiderable in comparison with blaze, and it is only with strong induction shocks more than sufficient to elicit maximal blaze that polarisation becomes of account, delaying the culmination of homodrome blaze, accelerating that of heterodrome blaze. Moreover the duration of blaze far exceeds that of polarisation in the case of any given current whether weak or strong, although naturally the duration of polarisation is greater in the case of strong than in that of weak currents. This is particularly well seen when, as sometimes happens, a homodrome blaze effect develops more slowly than usual, and is preceded by a short, sharp polarisation effect in the contrary direction.

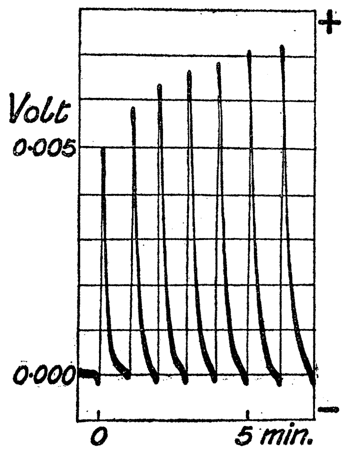
The decline of a blaze current, most rapid at first, progresses more and more slowly, towards zero in the case of strong excitation, beyond zero in that of weak excitation, in either case giving, when photographed, a curve falling convex towards its abscissa. *Cæteris paribus*, particularly after strong excitation, a homodrome generally subsides less rapidly than a heterodrome effect (see fig. 5).

The time during which an excised frog's eyeball remains capable of manifesting the blaze effects is very considerable. I have observed them five days after excision, and have no doubt that they might be seen still later. The feature that most aroused my attention in these late effects was that they were of normal (positive) direction as in the fresh eyeball.

* These terms are purely relative. What is here referred to as a medium stimulus generally gives maximal effect. "Strong" is in reality excessive.

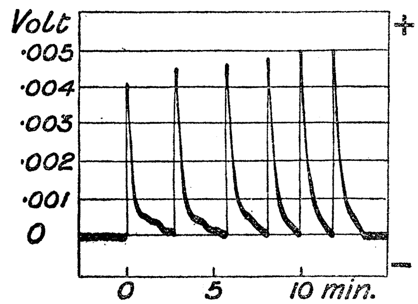
A succession of homonymous blaze currents taken at regular intervals of time by uniform stimulation, exhibits progressive modifications which vary with the nature of the eyeball, the strength of stimulation, and the interval between successive stimuli.

Fig. 8.



Staircase increase of successive blaze currents excited by + break shocks at 100 units.

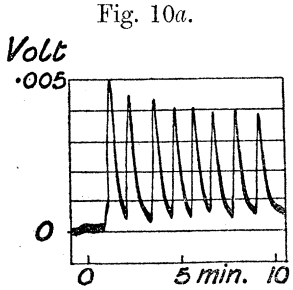
Fig. 9.



Staircase increase, exhibiting decreasing permanence of successive blaze currents.

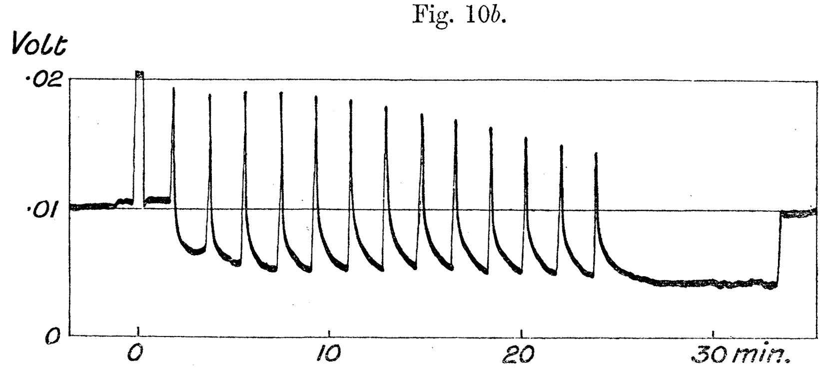
The series of effects may exhibit staircase increase or a decline similar to the decline exhibited by an ordinary fatigue series of muscular contractions. And at appropriate

Fig. 10*a*.



Fatigue decline.

Fig. 10*b*.



Fatigue decline.

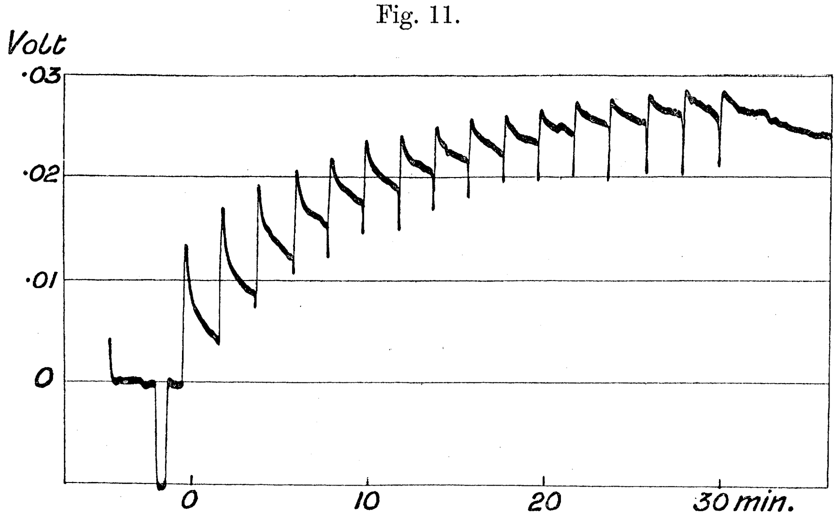
strength and interval of excitation summation of effects may be witnessed similar in general type with the summation of effects manifested by muscle that is excited to contraction by frequently repeated stimuli.

Summation of stimuli as well as summation of effects may be observed upon the frog's eyeball. A stimulus may be fixed upon by trial of such magnitude that it may be indefinitely repeated at long intervals without producing any effect whatever. The same stimulus repeated in rapid succession will produce a considerable effect, This is most readily demonstrated by the difference in effect of single induction shocks and tetanisation with an eyeball and galvanometer in series, as in the experiments described at p. 210. The single shocks produce equal and opposite deflections, *i.e.*, excite no blaze reaction; tetanisation at the same strength gives a considerable positive effect due to a summation of the succession of make and break stimuli. The following numbers were observed on a somewhat sluggish eyeball:—

	Coil at 50 units.	At 75 units.	At 100 units.
Break + . . .	Defl. +3	Defl. + 4·5	Defl. + 6
„ − . . .	−3	− 4·5	− 6
Make + . . .	+3	+ 4·5	+ 6
„ − . . .	−3	− 4·5	− 6
Tetan. {M. + . Br. − .}	+5	+ 8	+10
„ {M. − . Br. + .}	+5	+15	+30

($\frac{1}{1000}$ volt = deflection of 10.)

Fig. 11.



Summation of blaze effects caused by a series of positive (homodrome) break induction shocks of "moderate" strength (1000 units), delivered at regular intervals of 2 minutes. Transfer time = $\frac{1}{10}$th second. Compensation of eyeball current is established at the outset of experiment and not adjusted in its course. Each successive blaze effect is smaller, and starts from a higher level, due to summation of successive residues. (The brief downward strokes are caused by short-circuiting of the galvanometer for about 2 seconds, during the delivery of each excitation to the eyeball.)

Observation of a declining blaze current provoked by strong excitation; break induction current from Berne coil, 2 Leclanchés, 10,000 units alternating in positive and negative directions.

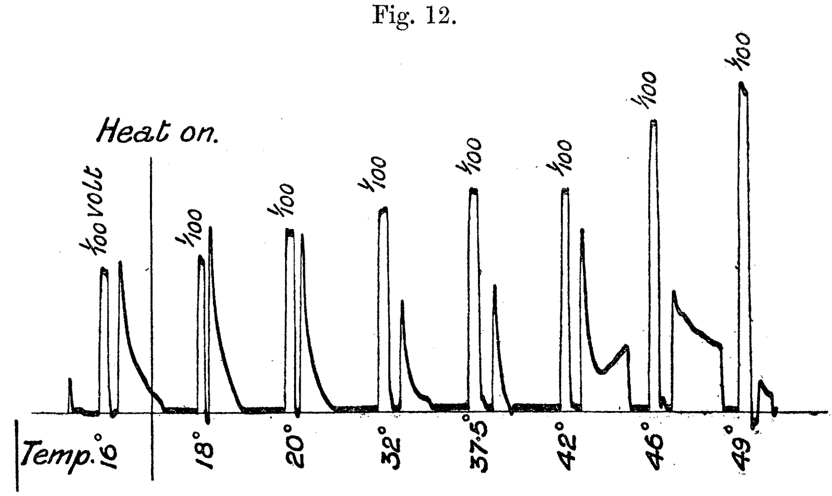
Time.	Direction of break current.	Voltage of blaze effect.
min.		
0	+	+0·0052
5	–	+0·0038
10	+	+0·0035
15	–	+0·0032
20	+	+0·0027
25	–	+0·0025

See also figs. 10*a* and 10*b*.

Influence of Raised Temperature.

In my previous paper* it was stated that the normal electrical response to light is temporarily abolished by rise of temperature. A precisely similar influence is produced upon the blaze current caused by electrical excitation. A series of such responses taken upon an eyeball set up in a moist chamber, of which the temperature is gradually raised up to 50°, exhibits at first a progressive increase, followed very soon after by a progressive decrease. At 35° to 40° the blaze current is at its smallest; at 40° to 45° it commonly reappears, and is then of a prolonged and "sticky" character; at 50° it is completely abolished. If the temperature has not

Fig. 12.



Influence of rise of temperature.

* *Loc. cit.*, p. 4.

been maintained high for too long a period, the response may reappear to some extent, with subsequent fall of temperature to normal.

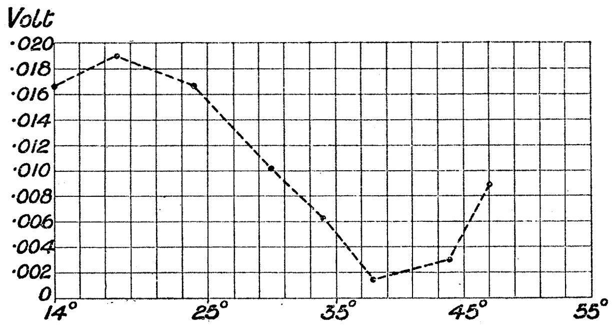
The electromotive value of the response does not fluctuate up and down in ratio with augmentation and diminution of deflection. Rise of temperature causes alterations by resistance, viz., diminution of resistance of the moist warmed electrolyte, and augmentation of resistance in consequence of drying. In order to know which of these two effects predominates at any given time and to obtain electromotive values of the blaze deflections, these must be compared with deflections by a standard electromotive force observed at frequent intervals during experiment.

4020. Break 1000 +.

Time.	Temp.	$\frac{1}{100}$ volt.	Deflection.	Corrected voltage.
min.	°	mm.	mm.	
0	20	34	+8	+0·00235
5	22	34	8	0·00235
10	27	36	7	0·00195
15	32	38	5·5	0·00145
20	35	41	5·5	0·00135
25	38·5	42	7·5	0·00178
30	43	44	7·5	0·00170

4022. Excitation by Break 1000 +.

min.	°	mm.	mm.	
0	14	17	+28	+0·0165
5	19	18	38·5	0·0190
10	24	24	40	0·0165
20	30	27	27·5	0·0102
25	34	27	17	0·0063
30	38	27	4	0·0015
35	44	27	11·5	0·0031
40	47	28	25 (sticky)	0·0088

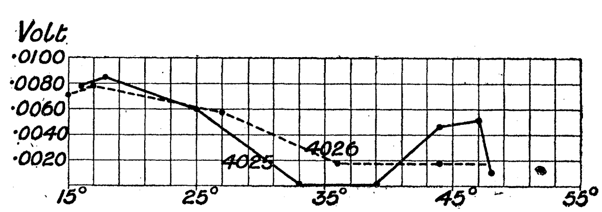


4025. Excitation by Break 1000 +.

Time.	Temp.	$\frac{1}{100}$ volt.	Deflection.	Corrected voltage.
min.	°	mm.	mm.	
0	16	10·5	+8	+0·0076
5	17	10·5	9	0·0085
10	25	12·5	7·5	0·0060
15	34	13·5	0	0·
20	39	13	0	0·
25	44	14	6·5 (sticky)	0·0046
30	47	16·5	8·5	0·0052
35	48	19·5	2	0·0010

4026. Excitation by Break 1000 +.

Time.	Temp.	$\frac{1}{100}$ volt.	Deflection.	Corrected voltage.
min.	°	mm.	mm.	
0	15	11·5	8	+0·0070
5	17	11·5	9	0·0078
10	27	13	7·5	0·0058
15	36	13·5	2·5	0·0019
20	44	13	2·5	0·0019
25	48	16	2·5 (sticky)	0·0016
30	51	17·5	0	0

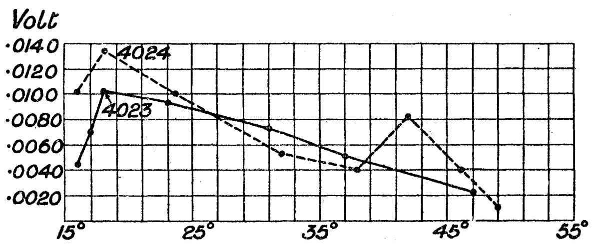


4023. Excitation by Break 1000 +.

Time.	Temp.	$\frac{1}{100}$ volt.	Deflection.	Corrected voltage.
min.	°	mm.	mm.	
0	16	11	5	0·0045
5	17	11	8	0·0072
10	18	11	11·5	0·0104
15	23	13	12·5	0·0096
20	31	15	11 (sticky)	0·0073
25	37	17	9 (,,)	0·0053
30	47	17·5	4	0·0023
35	46	18	2	0·0011

4024. Excitation by Break 1000 +.

min.	°	mm.	mm.	
0	16	18·5	19·5	0·0105
5	18	19·5	25	0·0135
10	20	23·5	23·5	0·0100
15	32	26	14	0·0054
20	37·5	38·5	16	0·0042
25	42	28·5	23 (sticky)	0·0084
30	46	37	15 („)	0·0041
35	49	42	5	0·0012
40	47·5	51	5·5	0·0011
60	20	25	4	0·0016

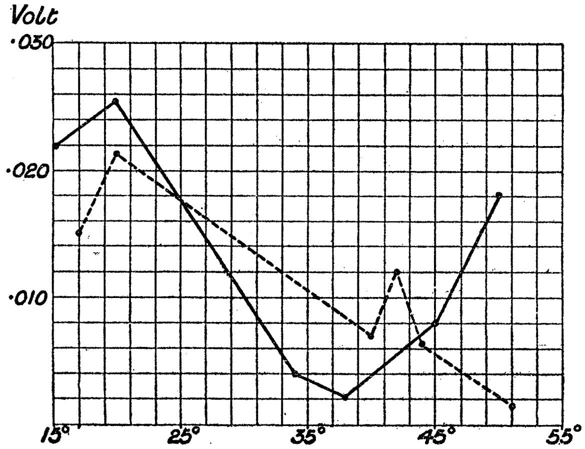


Influence of Rising Temperature upon the Blaze Currents of the Frog's Eyeball.

Excitation by Break + 1000. Berne coil, 2L.

Time.	Temp.	Deflection by $\frac{1}{100}$.	Deflection by blaze.	
min.	°	mm.	mm.	
0	15	10	+22	0·0220
5	20	12·5	+32	0·0255
10	34	17	+7	0·0041
15	37	12·5	+2·5, −5	0·0020
20	38	11	+9	0·0082
25	45	12	+22	0·0183
30	50	17	?	

min.	°	mm.	mm.	
0	17	11·5	+17·5	0·0152
5	20	14	+30	0·0215
10	36	19	−2	0·0015
15	40	18	+3	0·0067
20	42	18	+22	0·0123
25	44	20	+13	0·0065
30	51	30	+4	0·0013



NOTE.—For convenience of inspection, the tabulated numbers are plotted to scale beneath each table.

Experiments exhibiting the Influence of Rise of Temperature upon Blaze Currents of the Frog's Eyeball.

The eyeball is set up as usual in a dark chamber, under which a spirit lamp is placed. Temperatures within the chamber are read at intervals. The resistance in circuit is gauged just before each excitation by the deflection produced by $\frac{1}{100}$ volt. Excitation by a break shock in the positive direction at 10,000 units of a Berne coil fed by two Leclanché cells.

4014

Time.	Temperature of chamber.	Deflection by $\frac{1}{100}$ volt.	Deflection by the blaze current.
min.			
0	18°	3·5	+ 8·5
5	20	—	+ 9·5
10	30	—	+12
15	37	7·5	+11
20	43	7	+ 8·5
25	48	—	+ 6·5
30	50	5	+ 1·5

Excitation by Break + 1000.

4017

min.			
0	20°	10·5	+11
5	25	11·5	+13
10	32	14·5	+10
15	39	16	− 4, +7
20	41	16·5	− 9
25	46	17	− 7

In my previous communication I showed cause for admitting that the positive electrical response of a normal fresh eye has a minor negative component which, with lapse of time and decline of the major positive component, becomes more and more prominent until, in what I have termed the third stage, the response to light becomes frankly negative. I showed further, that by gentle massage of the eyeball, the positive component may be at once abolished, and made to give place to an uncomplicated negative effect. I have found since then that the change may be brought about without massage, by a gradually increased compression of the eyeball, and I think therefore that the change effected by massage is essentially due to compression and increased eyeball tension, producing some modification of the retinal elements, as evidenced by their modified response to light.

The response to electrical stimulation exhibits an analogous change, and I have expended much time in the endeavour to disengage some "law" amid the rather perplexing phenomena presented by "stale" or injured eyeballs. There was never the slightest doubt or uncertainty as regards a fresh and uninjured eyeball; the response was always positive. Difficulties of interpretation arose only in the case of eyes that had undergone manipulation; these, however, have been considerably diminished since I have found means of experimentally modifying at will the character of the response by means of increased eyeball tension. And I may remark in passing that this fact has led me to believe that in the modifications that have sometimes (but not always) supervened with lapse of time, alterations of eyeball tension have been a principal factor. I have witnessed response of the first type two or three days after death, when the eyeballs had become obviously flaccid; and I have witnessed response of the first type very shortly after excision, and I now think it probable that in such case the eyeball had been accidentally compressed more than usual.

The various types of response that may be witnessed on excised eyeballs, are summarised in the accompanying diagram (fig. 13).

Type I. is that presented by the response of a normal fresh eyeball in the great majority of cases—nearly always in fact—to such an extent indeed that I feel assured in the rare cases in which the type is of another form, the eyeball must have suffered compression. According to the terminology used in this paper, both responses are positive; the first being in the same direction as the exciting current, cannot be polarisation, but is obviously blaze effect; the second being opposed in direction to the exciting current, is in the polarisation current, and is therefore of debateable nature.

Type IV. is that presented by an absolutely dead eyeball. The after-currents are counter-currents in relation to excitatory currents, of much smaller electromotive value and of much shorter duration than blaze currents. They are ordinary polarisation effects.

Type III. is that presented by an eyeball towards the close of prolonged observa-

Fig. 13.

Direction of exciting current . . . . .

TYPE I.

The response to excitation in both directions is positive. This is the normal response.

TYPE II.

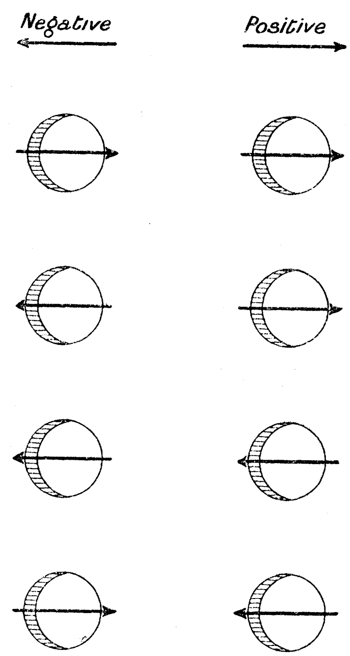
The response to excitation in the negative direction is negative, and in the positive direction positive.

TYPE III.

The response to excitation in both directions is negative.

TYPE IV.

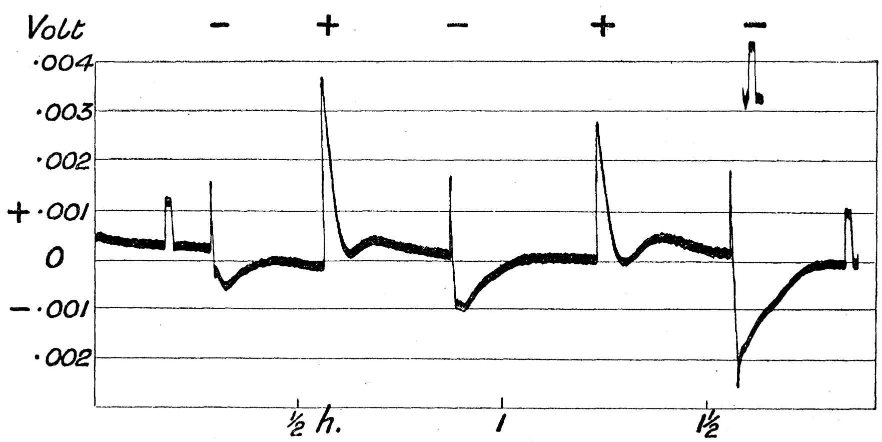
The response to negative excitation is positive and to positive excitation negative.



tion, during which the organ may have been submitted to considerable manipulation, or to strong currents. Both responses are in the negative direction; the first being opposed in direction to the exciting current, is of debateable nature; the second being of the same direction as the exciting current, is an obvious blaze effect.

Type II. is observed under similar conditions to Type III., and I regard it as being intermediate between them. Both responses are of the same direction as their exciting currents, and are therefore obvious blaze effects.

Fig. 14.



An eyeball exhibiting blaze currents of Type II., viz., in the same direction as that of the exciting current. The negative blaze is preceded by a brief positive deflection (= ? a polarisation counter-current).

During the period of observation, positive blaze currents decreased and negative blaze currents increased.

Excitation was made throughout by break induction currents of a Berne coil at 10,000 units, supplied by two Leclanché cells. Blaze currents of this type have been, in my experience, of exceptional occurrence.

NOTE.—Considering the eyeball in the light of an electrical organ, of which the normal direction of discharge is from fundus to cornea (= "positive") the correspondence between the terminology used above and that employed by DU BOIS-REYMOND with reference to electrical organs is as follows :—

	Negative.	Positive.
Direction of exciting current .	←	→
Type I.	→ Absolutely positive and relatively negative.	→ Absolutely positive and relatively positive.
Type IV.	→ Absolutely positive and relatively negative.	← Absolutely negative and relatively negative.

The word "absolutely" in the DU BOIS terminology is used with reference to the organ-discharge, the response being denoted as absolutely positive or absolutely negative according as it is in the same direction as the normal discharge or of opposite direction. The word "relatively," as used by DU BOIS, refers to the direction of response in relation with that of the exciting current, relatively positive and relatively negative, signifying that the response is in the same and in the opposite direction to that of the exciting current.

Retinal responses of Type I. correspond with DU BOIS' organ responses of the first and second stages, both "absolutely positive," but one "relatively positive" and the other "relatively negative."

Retinal responses of Type IV. correspond with DU BOIS' third and fourth stages, and are both in the direction of polarisation current, one being absolutely and relatively negative, the other absolutely positive and relatively negative. Retinal responses of Types II. and III. are not represented in DU BOIS' four stages, which indeed are reducible to only two stages, equivalent as described above to Type I. and Type IV. Type I. is that of a normal living eyeball. Type IV. is that of an exhausted or dead eyeball.*

DU BOIS-REYMOND'S experiments on the electrical organs of Torpedo and of Malapterurus have been repeated by GOTCH and by BURDON-SANDERSON, and extended to the analogous organs of the Skate. The last-named observers distinguish between the normal excitatory reaction caused by induction shocks of either direction, and the "after-effect," also in the normal direction, caused by induction shocks and by voltaic currents of sufficient strength and brevity led through the organ in either direction.†

ALTERATIONS OF RESISTANCE.

Comparing the electrical resistance of an eyeball before and after it has been

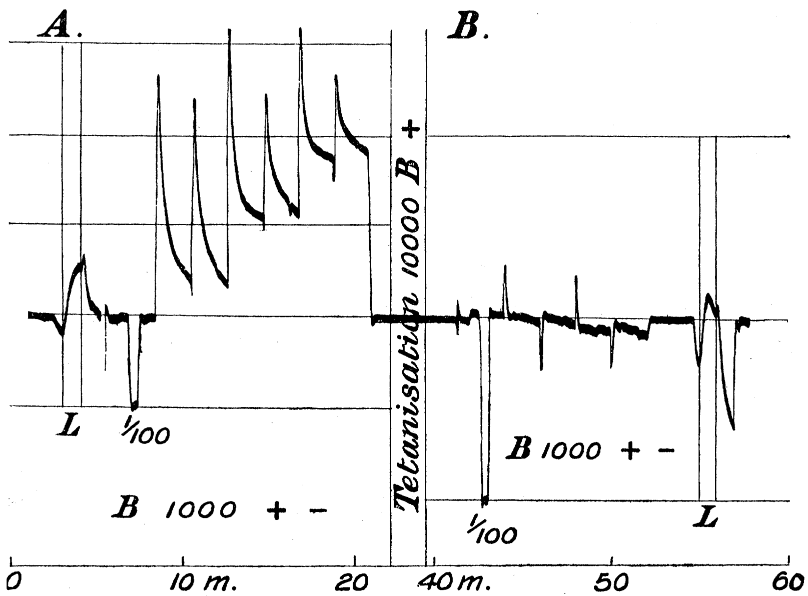
* *Cf.* DU BOIS-REYMOND, 'Arch. f. (Anat. u.) Physiologie,' 1885, p. 121. A. D. W., "The Eyeball as an Electrical Organ," 'Proc. Physiol. Soc.,' November, 1900.

† GOTCH, "The Electromotive Properties of the Electrical Organ of Torpedo Marmorata," 'Phil. Trans.,' B, vol. 178, 1887, p. 487. BURDON-SANDERSON and GOTCH, "On the Electrical Organ of the Skate," 'Journal of Physiology,' vol. 9, 1888, p. 137. GOTCH and BURCH, "The Electromotive Properties of *Malapterurus electricus*," 'Phil. Trans.,' B, vol. 187, 1896, p. 347.

excited to its maximal blaze current, I have always found this latter to be accompanied by a marked increase of conductivity. This alteration was shown by the fact that a standard deflection by $\frac{1}{1000}$ volt was found to be increased sometimes by as much as 50 per 100. In such case, however, since the total resistance in circuit was unknown, it was not possible to translate this obvious increase into its value in ohms. But this much it was possible to see with certainty, 1st, that the altered conductivity was similar to both directions of testing current, and 2nd, that it subsided with subsidence of blaze.

The principal difficulty that stands in the way of exact measurements of resistance arises from the fact that the testing current itself excites retinal discharge in a given ("positive") direction. The phenomenon of apparent "irreciprocal resistance," due to organ discharge in one direction only, is thus presented by the eyeball precisely as by an electrical organ.* Deflection caused by a homonymous induction shock sent through eyeball and galvanometer in series is greater than deflection caused by a similar but heterodrome shock. The algebraic sum of positive shock *plus* positive discharge is greater than the algebraic sum of negative shock *plus* positive discharge.

Fig. 15.



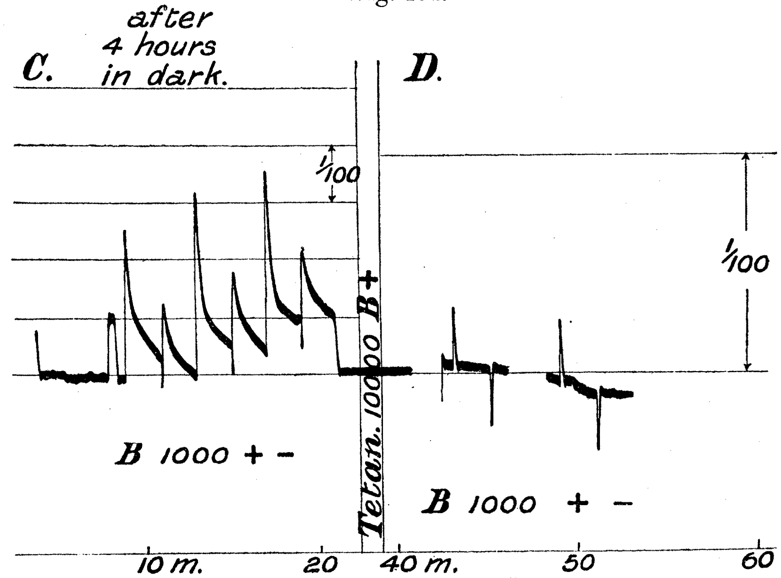
Four groups of excitations, A, B, C, D, by single break induction currents in + and − directions, through an eyeball and a galvanometer in series. The excitation strength throughout = 1000 units of Berne coil.

* "On the Apparent Irreciprocity of Resistance of Electrical Organs," *cf.* DU BOIS-REYMOND, 'Arch. f. (Anat. u.) Physiol.,' 1887, and GOTCH, 'Phil Trans.,' B vols. 178 and 179, 1887 and 1888.

4015–6	Before T.	After T.	4 hours later.	After 2nd T.
Response to light (with galvanometer unshunted)	+0·0008	+0·0007	+ ?	+ ?
Deflection by 0·01 volt	12 millims.	24 millims.	7·5 millims.	28 millims.
Excitation Br. 1000+	+34	+6·5	+19	+7·5
,, ,, −	−2, +24	−6·5	−4, +7	−7·5

The inequality between the effects of Br.+ and Br.−, due to + blaze in the two cases, is completely abolished after tetanisation. The inequality gradually returns, and is abolished after a second tetanisation. The resistance is temporarily diminished after tetanisation. The eyeball gives positive response to light (normal) which is not appreciably altered by tetanisation. As regards the blaze effect it is of Type I. (normal).

Fig. 15*a*.



Nor is the difficulty avoided by placing the eyeball in the x arm of a Wheatstone bridge, for the testing battery is apt to itself provoke a blaze current that greatly complicates the determination of any equilibrium value of balancing resistance. I have therefore postponed the attempt to give definite values to the indubitable diminution of resistance that goes with the state of blaze.

Nevertheless, certain principal points are already clear at this stage of the inquiry—

1. The inequality between + and − break induction shocks (or between + and − condenser discharges) is due to the + discharge of the eyeball itself.

2. While the eyeball is in the state of blaze its electrical resistance is diminished, *e.g.*, from 17,000 down to 12,000 ω; from 8000 down to 6000 ω; from 10,500 down to 7000 ω.

3. The inequality between + and − shocks just referred to is diminished or abolished when the eyeball has been provoked to its maximal electrical discharge.

The diminution is temporary, and the inequality reappears with return of the eyeball to its normal quiescent state.

Regarding the two extreme states of the eyeball as analogous to the two extreme functional states of glands, we may characterise them as—

A. Loaded and ready to discharge when excited.
B. Discharged and refractory to excitation.

The inequality of deflections by equal and opposite electrical shocks is a sign of the loaded state, whereas equality of such deflections is a sign of the discharged state. In the case of a dead eyeball, giving equal and opposite polarisation after-currents, the deflections caused by equal and opposite electrical shocks are themselves equal and opposite. In the case of what may be termed a "stunned" eyeball, *i.e.*, after violent tetanisation, the inequality is diminished or abolished. In a few hours the eyeball recovers more or less perfectly.

In my previous communication* I commented upon the remarkable persistence of the retinal response to light after even violent tetanisation of the eyeball. In view of the comparative ease with which blaze currents are abolished, I was led to repeat the previous experiments, observing upon one and the same eyeball the response to light and the response to electrical stimuli, before and after strong tetanisation. Blaze effects were completely absent while the response to light remained unaltered —if anything, apparently increased by reason of a diminution of resistance. I must refrain from any attempt to explain this remarkable result at present. There can, however, be no mistake as regards the fact itself.

Experiments Exhibiting the Influence of Strong Tetanisation upon the Blaze Currents.

The eyeball is set up as usual in the dark chamber and connected with the keyboard as shown in fig. 2. Compensation is established at the commencement of each group of excitations, and is left unaltered during that group. The exciting currents are not short-circuited from the galvanometer, which is left in series with the eyeball, the compensator, and the induction coil (by unplugging the keyboard of fig. 2 at 1, 2, 4 and 5). The observations are taken before and after tetanisation for ½ minute at 10,000 units of the Berne coil fed by 2 Leclanché cells. Excitation is by a single break induction shock of the same coil at 1000 units. The galvanometer is shunted, except when it is desired to observe response to light.

4011	Before T.	After T.	½ hour later.
Deflection by 0·01 volt . . .	12·5 millims.	30 millims.	28 millims.
Excitation Br. 1000 + . . .	+15	+8	+10
" " − . . .	−4·5, +11	−8	−7

* *Loc. cit.*, p. 26.

4018	Before T.	After T.
Response to light	−0·0002	−0·0002
Deflection by 0·01 volt . . .	20 millims.	40 millims.
Excitation by Br. 1000 + . .	+34	+10
" " − . . .	−5, +21	−10

The eyeball gives negative response to light (3rd Stage), its blaze reactions, producing the inequality of deflection by Br. + and Br. −, are positive (Type I.). The inequality is abolished by tetanisation, and resistance is diminished. The negative response to light is not appreciably altered.

Frog's Eyeball; previously used for other Experiments.

Experiment to Test Influence of Strong Tetanisation upon the Response to Light and upon the Blaze Currents.

Time after excision.		Response to light.	Deflections by		Calculated voltage.	Deflection by $\frac{1}{1000}$ volt.	Remarks.
			B. 1000 −.	B. 1000 +.			
hrs.	min.						
7	—	+39	—	—	+0·0024	16	
7	20	+34	—	—	+0·0023	15	
7	30	+31	—	—	+0·0021	15	
7	40	—	—	+26	+0·0068	3·8*	*Galvanometer shunted.
7	42	—	−13	—	+0·0034	3·8*	
7	45	Tetanisation by coil at 10,000 B. +.					
7	50	+23	—	—	+0·0012	18·5	Conductivity increased after tetanisation.
7	55	—	—	0	0	"	Response to light diminished.
7	57	—	0	—	0	5·5*	Blaze currents abolished; after an hour's interval the response to light has recovered, and small blaze currents are present. The resistance has not increased.
9	—	+36	—	—	+0·0020	18	
9	10	—	—	+5·5	+0·0010	5·6*	
9	12	—	+3	—	+0·0005	"	
10	30	+31	—	—	+0·0017	18	
10	35	—	—	+6	+0·0011	5·2*	
10	37	—	+4	—	+0·0007	5·2*	
11	—	+27	—	—	+0·0015	18	

I may take this opportunity of commenting upon an absence of parallelism that is most commonly observed between the several stages as regards response to light and the several types described above as regards blaze currents.

Experiments Exhibiting the Influence of Pressure upon the Electrical Response to Light, and upon Blaze Effects.

The eyeball is set up in the dark chamber between unpolarisable electrodes which are fixed to the stage and body of a small microscope stand. A handle passing into the dark chamber is fixed to the fine adjustment screw of the microscope, so that the eyeball can be compressed at will by turning the screw from the outside. The ends of the electrodes are covered by two small slabs of pipe-clay, so as to afford the necessary firm pressure of the eyeball when the screw is turned. Illumination of the eyeball is made in the usual way by exposure at regular intervals for a regular period, and between each exposure the compression screw is turned by half a turn, giving a vertical displacement of about ¼ mm.

EXPERIMENT I.—*Influence of Pressure upon the Response to Light. Reversal of the Response.*

Compression.	Response to light.
turn of screw.	volt.
0	+0·0010
1	+0·0008
2	+0·0007
3	+0·0006
4	+0·0006
5	+0·0002, −0·0006
6	−0·0008, permanent
7	−0·0008 ,,
8	−0·0008 ,,

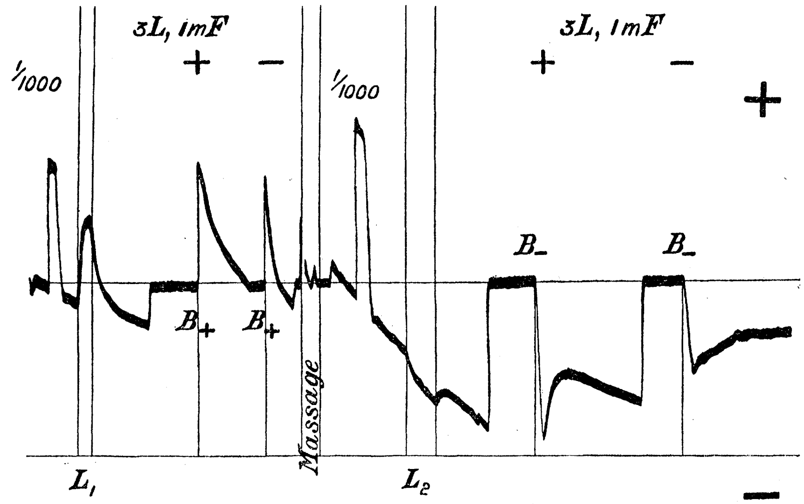
As was stated at the outset of this communication, I found that it was possible to gradually convert a positive (normal) into a negative (reversed) response to light by means of gradually increased compression of the eyeball. I also found that a normal (positive) blaze could be converted into a reversed (negative) blaze by similar means.

But when I came to study the progressive development of the two kinds of change, I found that there was no constant parallelism between them. In some cases—as illustrated, *e.g.*, in fig. 16—the two kinds of change were quite similar and parallel, *i.e.*, positive response to light (Stage 1) was converted into negative response to light (Stage 3), while positive blaze (Type 1) was converted into negative blaze (Type 3). But in the great majority of cases there was no such exact correspondence, and as a rule, indeed, I noticed that an eyeball giving negative response to light of the

EXPERIMENT 2.—Influence of Pressure upon the Blaze Currents—Progressive Modification of Type.

Compression.	Excitation.	Blaze Current.	Type.
0	3L., 1MF. +	+0·0100	I.
	,, −	+0·0070	
1	,, +	+0·0033	
	,, −	+0·0016	
2	,, +	nil	
	,, −	nil	
2	6L., 1MF +	+ small	
	,, −	+ small	
4	,, +	+	II.
	,, −	−	
6	,, +	−	III.
	,, −	−	
Do. 3 hrs. later	,, +	−	IV.
	,, −	+	

Fig. 16.



EXPERIMENT 3.—Influence of Gentle Massage of the Eyeball upon the Electrical Response to Light (L_1 and L_2), and upon the Blaze Currents B + and B. −. Reversal of both Effects, and Diminished Resistance.

	Before massage.	After massage.
Deflection by 0·001 volt . . .	16 mm.	23 mm.
Electrical response to light . .	+0·0007 volt.	−0·0001 volt.
Excitation by 3L, 1MF + . . .	+0·0010 ,,	−0·0009 ,,
Do. do. − . . .	+0·0009 ,,	−0·0005 ,,

3rd Stage, gave still positive blaze of the 1st Type. It is possible that the difference is to a considerable extent a question of strengths of excitation. Nevertheless, it exists and distinctly forbids us to admit an exact correspondence in all cases between the Stages 1, 2, and 3 as regards response to light, and the Types I., II., and III. as regards response to electrical stimuli.

I found also that whereas a positive blaze current could be reversed by negative galvanisation, no such reversal was thereby produced of a positive response to illumination.

CONCERNING THE INFLUENCE OF LIGHT UPON BLAZE CURRENTS.

No portion of this investigation has given me more trouble than that relating to the influence of illumination upon the response to electrical stimuli. Whereas the converse influence of electrical stimulation upon the response to luminous stimulation has been clear and manifest, I am unable to say definitely whether electrical stimuli are more, or are less, effective after prolonged illumination. I should, indeed, have preferred to omit all reference to this doubtful point in the present paper, but the fact that I have carefully examined into the possible parallelism between luminous and electrical stimulation effects in different states of eyeball makes the omission unadvisable, and I think it will be preferable that I should give a brief account of these somewhat unsatisfactory results. Moreover, the very facts that no clear results have been obtained, and that there is very evident defect of parallelism between effects of luminous and of electrical stimuli, are, although negative items of evidence, points of some possible future significance.

At an early stage of the investigation, I noticed more than once that an eyeball put up as usual in a dark box gave larger blaze currents than an eyeball put up on electrodes and exposed to the continuous effect of ordinary light.

I therefore made a set of experiments *ad hoc*—bisecting the heads of pithed frogs, but leaving the eyes *in situ*, one in a dark chamber, the other exposed to light. I could not assure myself of any regular and constant difference between the blaze currents of the dark eye and of the light eye. Moreover, control experiments with both eyes under similar conditions of light and dark exhibited differences between the two eyes of the same order of magnitude as those presented by dark *versus* light eyes. Nevertheless, the currents of dark eyes appeared to be, on the whole, larger than those of the light eyes—but not with convincing regularity—and it appeared that unavoidable differences of disturbance during manipulation might have accounted for the results.

The following experiment was the most apparently satisfactory of this set :—

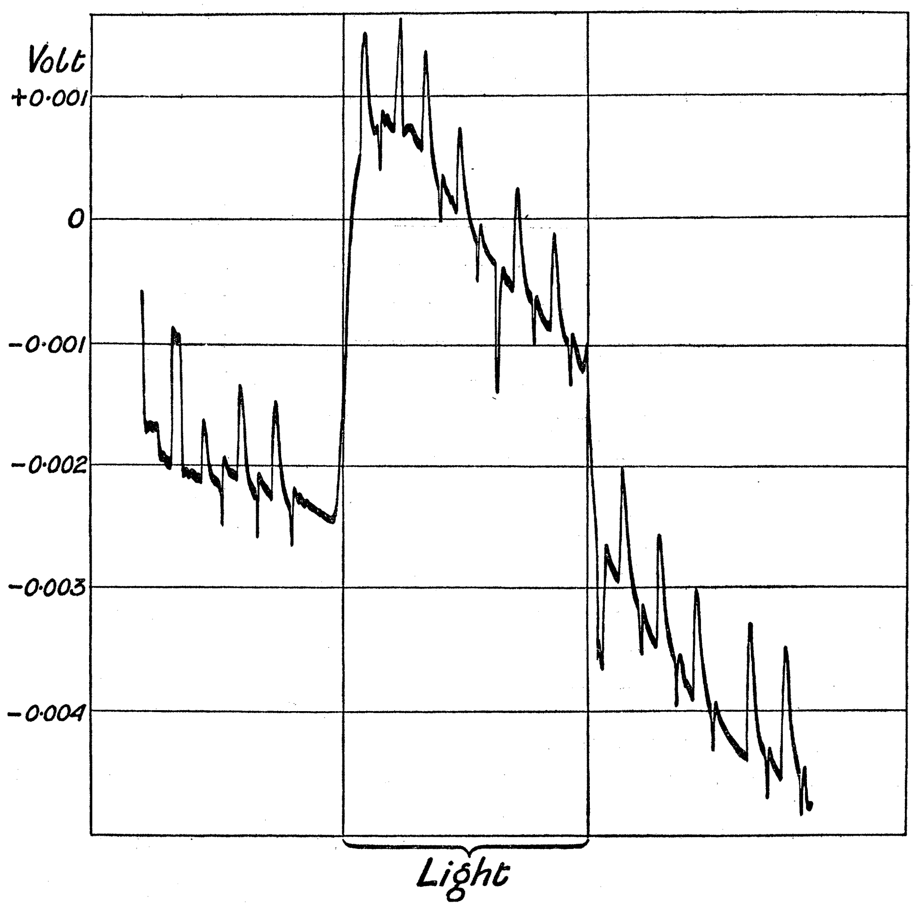
Stimulus.	*Dark Eye.* 2 hours after excision.	*Light Eye.* 2 hours after excision.
	Response.	Response.
Candlelight	+0·0003	+0·0002
Break shock 100 + . .	+0·0050	+0·0007
" " 100 − . .	+0·0025	+0·0009
" " 1,000 + . .	+0·0210	+0·0050
" " 1,000 − . .	+0·0210	+0·0075
" " 10,000 + . .	+0·0270	+0·0062
" " 10,000 − . .	+0·0090	+0·0007

This apparently well-marked difference led me to make trial of a given eye as to its blaze current during prolonged illumination and prolonged darkness. The objection to this plan of procedure is that we may find it difficult to distinguish an effect of altered light from the spontaneous modifications occurring with mere lapse of time, and in such prolonged observations we have to bear in mind that by reason of gradual evaporation, which is apt to take place even in the moist chamber if not fully saturated, an alteration of total resistance of the eyeball may take place, causing the standard deflection to become smaller, and the eyeball response of apparently higher voltage by reason of the smaller derivation by the drying eyeball. With this reservation borne in mind, we may consider the following series of data; it certainly appears from their plotted curves that the magnitude of blaze currents has been better maintained during darkness than during light. The value of blaze current increases for the first hour, or two hours in the case of the dark eye, whereas in that

4042. Excited by break 100 + and − through eyeball and galvanometer. $\frac{1}{1000}$ volt = 17 centims.

	Br. 100 +.	Br. 100 −.
Before	+ 7	− 5
	+ 12	− 5
	+ 12	− 5
During light	+ 12	− 6
	+ 11	− 5
	+ 13	− 6
	+ 12	− 5
After	+ 14	− 5
	+ 13	− 5
	+ 13	− 6
	+ 17	− 6
	+ 16	− 6

Fig. 17.



Absence of effect of light upon the blaze currents, if anything increase of homodrome and decrease of heterodrome.

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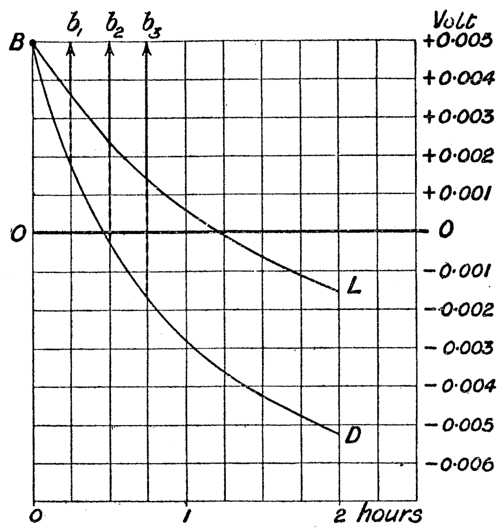
of the light eye it diminishes during that period. I consider this to be a true difference, and find it to be in relation with the course of the so-called current of rest in a dark and light eyeball respectively.

Already, at the time of my previous communication, I had seen reason to believe that the normal eyeball current, or current of rest, or current of darkness—which is generally positive immediately after excision, then declining to and beyond zero, and becoming increasingly negative—is partly an injury current due to electromotivity of the optic nerve section, and partly a blaze current due to the mechanical disturbance necessarily caused by excision. I have subsequently become fully confirmed in this opinion, and am satisfied that the falling positive and rising negative current is essentially a subsiding blaze current. I find that with this fall of current the blaze current that can be elicited by a given electrical stimulus gradually increases. I find further that the fall of current is delayed by light and more rapid during darkness. And, finally, in association with this more rapid fall during darkness, I find that there is a more pronounced increase of successive blaze currents than occurs in association with the less rapid fall during illumination. I regard this difference as an evidence, if not a convincing proof, of an effect of light upon the blaze currents. The point is illustrated, if not very obviously, by the data of the accompanying experiments. It is explained by the accompanying diagrammatic representation, the dimensions of which have been chosen in approximation to observed data.

Fig. 18.



The line OO indicates the galvanometer zero.

The ordinate OB indicates the "normal current" at the outset of observation (= the manipulation blaze).

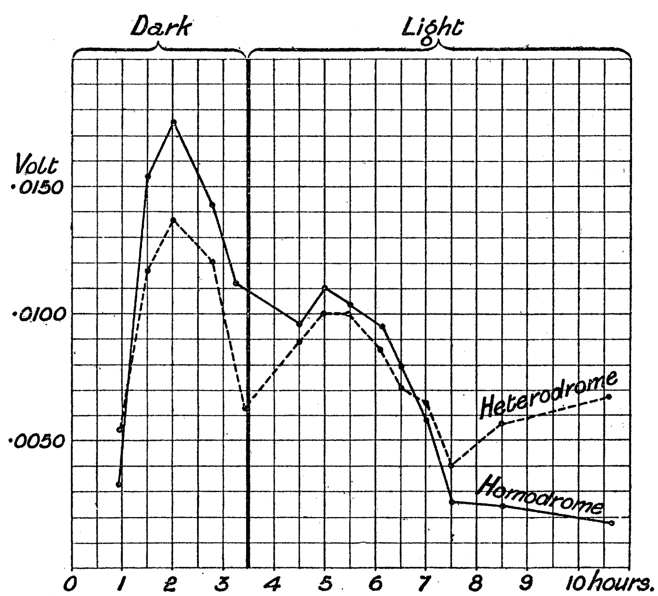
The falling curve BD indicates the altering electromotive value of the "normal current of a dark eyeball."

The falling curve BL indicates the altering electromotive value of the "normal current of a light eyeball."

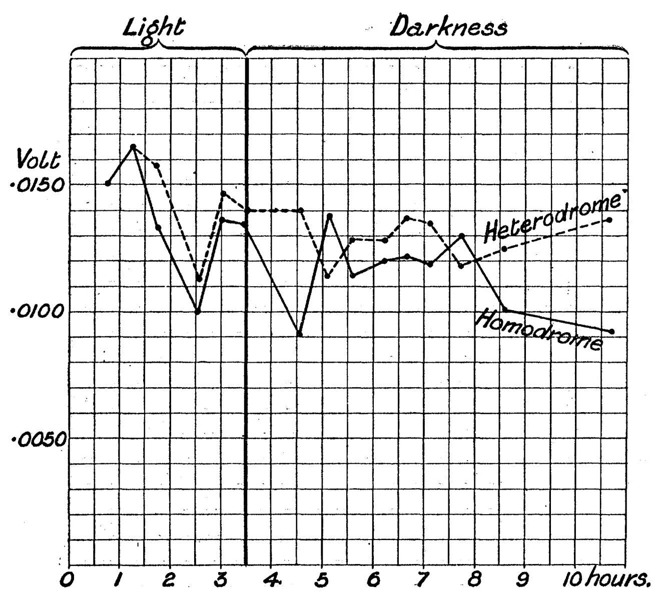
The ordinates b_1, b_2, b_3 indicate successive blaze effects, starting from the levels BD and BL of normal current of the dark and light eyes.

These ordinates will in general be larger from BD than from BL, and will at the outset increase more rapidly from BD than from BL; and if the observation is commenced with a rested eyeball, made to give a rising in place of a falling current, then we may have during the initial period diminishing in place of increasing effects b_1 b_2.

	Time.		Normal current.	Blaze.		Br. 1000.
				Heterodrome. − Exc.	Homodrome. + Exc.	
	hrs.	min.				
D	11	50	+0·0057	+0·0056	+0·0032	12·5
D	12	30	−0·0022	+0·0118	+0·0153	8·5
D	1	0	−0·0048	+0·0137	+0·0175	8
D	1	45	−0·0054	+0·0121	+0·0143	7
D	2	15	−0·0058	+0·0062	+0·0113	8
L	2	30	Eyeball placed in light chamber.			
L	3	00	−0·0060	+0·0089	+0·0095	9
L	4	0	−0·0068	+0·0100	+0·0111	9
L	4	30	−0·0071	+0·0100	+0·0105	9·5
L	5	10	−0·0063	+0·0085	+0·0095	9·5
L	5	30	−0·0055	+0·0071	+0·0081	10·5
L	6	0	−0·0047	+0·0066	+0·0057	10·5
L	6	30	−0·0022	+0·0040	+0·0025	12·5
L	7	30	−0·0028	+0·0057	+0·0024	10·5
L	9	40	−0·0043	+0·0068	+0·0018	11

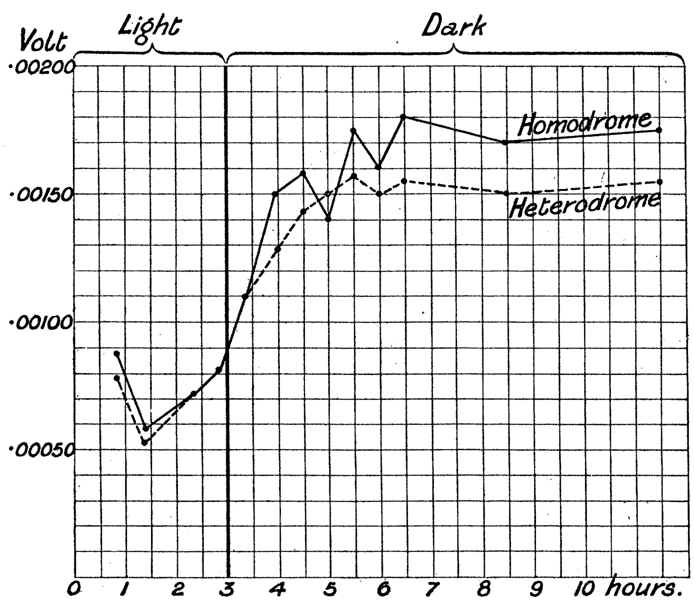


Time.			Normal current.	Blaze.		Br. 1000.
				Homodrome. + Exc.	Heterodrome. – Exc.	
	hrs.	min.				
L	11	45	– 0·0045	+ 0·0150	+ 0·0150	10
	12	15	– 0·0084	+ 0·0167	+ 0·0167	9
	12	45	– 0·0082	+ 0·0132	+ 0·0158	9·5
	1	35	– 0·0071	+ 0·0100	+ 0·0112	9
	2	0	– 0·0096	+ 0·0137	+ 0·0148	9·5
	2	25	– 0·0105	+ 0·0135	+ 0·0140	10
	2	30	Eyeball placed in dark chamber.			
D	3	35	– 0·0090	+ 0·0090	+ 0·0140	10
	4	10	– 0·0105	+ 0·0138	+ 0·0114	10·5
	4	40	– 0·0101	+ 0·0114	+ 0·0129	10·5
	5	15	– 0·0105	+ 0·0119	+ 0·0128	11
	5	40	– 0·0104	+ 0·0123	+ 0·0137	11
	6	10	– 0·0103	+ 0·0118	+ 0·0135	11·5
	6	45	– 0·0098	+ 0·0130	+ 0·0117	11·5
	7	35	– 0·0088	+ 0·0100	+ 0·0125	12
	9	45	– 0·0080	+ 0·0092	+ 0·0138	13



First Frog's Eye. November 23.

Time.	Normal current.	Blaze currents by Br. 1000.	
		Homodrome. + Exc.	Heterodrome. − Exc.
hrs. min.			
0 30	—	—	—
0 50	+0·0047	+0·0087	+0·0078
1 25	+0·0020	+0·0058	+0·0054
2 20	+0·0007	+0·0072	+0·0072
2 50	−0·0024	+0·0082	+0·0082
3 0	Changed from light to dark.		
3 20	−0·0055	+0·0110	+0·0110
4 0	−0·0090	+0·0150	+0·0128
4 30	−0·0100	+0·0158	+0·0143
5 0	−0·0110	+0·0140	+0·0150
5 30	−0·0120	+0·0174	+0·0158
6 0	−0·0120	+0·0160	+0·0150
6 30	−0·0130	+0·0180	+0·0155
8 30	−0·0120	+0·0170	+0·0150
11 30	−0·0126	+0·0175	+0·0155



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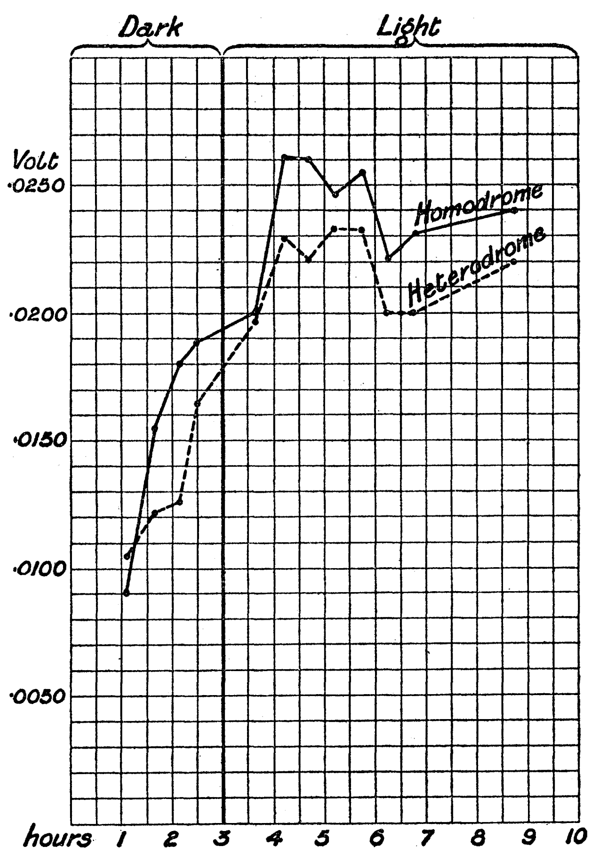
No. 2. November 23.

	Time. hrs.	Time. min.	Normal current.	Homodrome. Br. + 1000.	Heterodome. Br. − 1000.
D	1	10	+0·0020	+0·0090	+0·0105
D	1	40	−0·0030	+0·0155	+0·0122
D	2	10	−0·0060	+0·0180	+0·0125
D	2	35	−0·0080	+0·0188	+0·0165
	3	0	Changed from dark to light.		
L	3	40	−0·0092	+0·0200	+0·0198
L	4	15	−0·0124	+0·0262	+0·0230
L	4	45	−0·0134	+0·0260	+0·0220
L	5	15	−0·0136	+0·0245	+0·0234
L	5	45	−0·0137	+0·0255	+0·0233
L	6	15	−0·0128	+0·0221	+0·0200
L	6	45	−0·0128	+0·0230	+0·0200
L	8	45	−0·0110	+0·0240	+0·0220



I made use of a third plan of trial, with results hardly more satisfactory than before, taking a series of blaze effects for comparatively short periods before, during, and after illumination. But as by previous modes of trial the finding by this method remained in doubt, and although there did appear to be some diminution during, and some augmentation after, illumination, the alteration was not striking and indubitable. I hesitate, therefore, to make any brief assertion based upon data or averages however scrupulously treated, and prefer to give an example of the data themselves. I do not consider that they are such as to justify more than the conclusion that the effect of light upon blaze currents is ill-defined. Finally, I should state that I have failed to detect any alteration of electrical resistance of the eyeball during and after the action of light.

To sum up the points referred to in this paragraph, we may say that the influence of electrical excitation upon the response to light is experimentally clear and unmistakable, whereas the influence of light upon the response to electrical stimulation is little or none. The difference is to some extent intelligible on the supposition that the retina alone is concerned in the response to light; whereas tissues other than retinal are coefficient in the response to strong electrical stimuli.

On the other hand, we have to recognise that, whereas the positive blaze current of an entire eyeball is augmented and diminished and reversed by galvanisation, and abolished by strong tetanisation, the positive response to light suffers little or no modification during galvanisation, and is augmented at a strength of tetanisation sufficient to abolish the blaze current.

This difference is difficult to understand otherwise than on the assumption that response to light is of retinal origin, and response to electrical stimulation of non-retinal source. For this reason, I have felt it necessary to avoid use of the qualification "retinal response," and to use the expression "eyeball response."

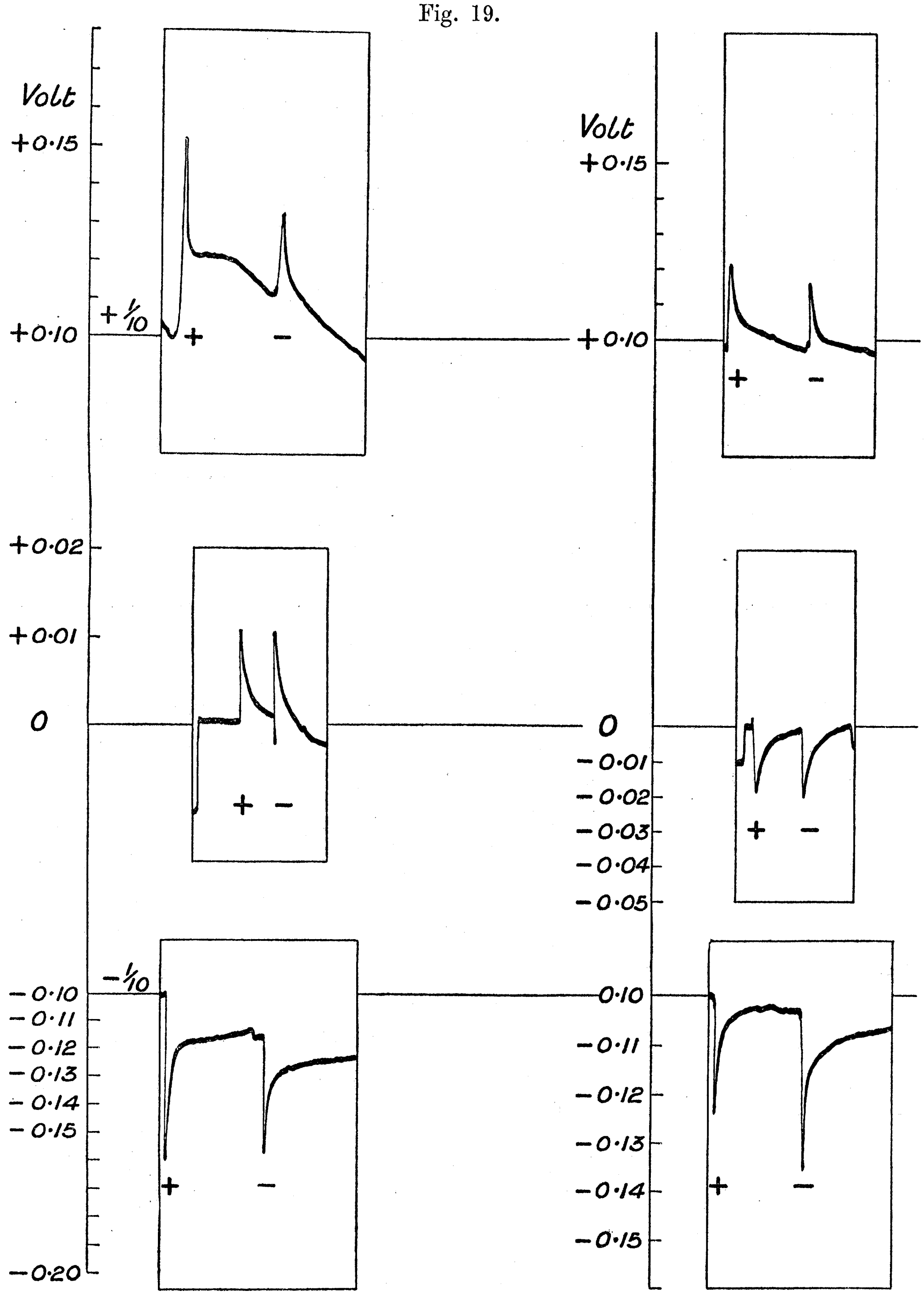
Concerning the Influence of Weak Galvanic Currents upon the Blaze Currents.

Comparatively late in the investigation I noticed that a blaze current was liable to be modified by the compensating current when the latter was at all considerable. I therefore proceeded to investigate the effect of weak galvanic currents sent through the eyeball in the positive and negative directions. Compensation being inadmissible, I used the plan of connections described on p. 210, sending induction shocks through the galvanometer and eyeball in series. This was done (*a*) in the absence of any added galvanic current; (*b*) during the passage of positive current; and (*c*) during the passage of negative current. Inasmuch as the added current has to pass through the galvanometer, we are restricted to weak voltage, and after a few preliminary trials, I took $\frac{1}{10}$th volt, and we are obliged to bring the galvanometer on to the scale or photographic plate by means of the controlling magnet. Alterations of field thereby produced do not invalidate the readings, seeing that in every case the value of deflection is standardised by a known voltage—in this case, by $\frac{1}{100}$th volt.

The result of the experiment is quite regular. During the passage of a galvanic current in the positive direction from fundus to cornea, the positive blaze, whether by homodrome or by heterodrome excitation, is increased. During passage of a galvanic current in the negative direction, it is diminished or reversed.

This effect on the blaze current of a positive and negative galvanic current having been determined, the next obvious step to take was to look for the effect of galvanic currents upon the electrical response to light. So far, however, I have not found the response to light to be modified by galvanic currents in either direction sufficiently strong to markedly influence the electrical responses to electrical stimuli. The effects

Fig. 19.



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are very similar to what may be seen upon nerve under similar conditions, and I shall reserve their more detailed consideration until I shall have found time to systematically re-examine nerve in this connection.

Time.	Excitation.	Response		
		During negative galvanisation by −0·025 volt.	Without galvanisation.	During positive galvanisation by +0·025 volt.
hr. min. 1 0	Light Br. +100 Br. −100	+0·0014 −0·0014 −0·0012	+0·0011 nil nil	+0·0012 nil nil

Remarks.—The eyeball current at the beginning of this observation was +0·0100 volt, and fell during its progress to +0·0067, +0·0025, −0·0020. The response to light was unaltered during + and − galvanisation. Blaze currents of a negative direction were alone apparent during negative galvanisation. Observation continued with stronger currents.

Time.	Excitation.	Response		
		During galvanisation by −0·1 volt.	Without galvanisation.	During galvanisation by +0·1 volt.
hr. min. 1 45	Br. 1000+ Br. 1000−	> −0·0500 −0·0300	+0·0105 +0·0095	> +0·0500 +0·0275

Remarks.—Both directions of excitation give rise to positive blaze currents in the absence of galvanisation; these are increased during positive galvanisation, and reversed during negative galvanisation.

Time.	Excitation.	Response		
		During galvanisation by −0·1 volt.	Without galvanisation.	During galvanisation by +0·1 volt.
hr. min. 3 0	Br. 1000+ Br. 1000−	−0·0575 −0·0410	— —	+0·0500 +0·0220
3 50	Br. 1000+ Br. 1000−	−0·0910 −0·0320	— —	+0·0800 +0·0320
9 0	Br. 1000+ Br. 1000−	−0·0350 −0·0250	— —	+0·0750 +0·0450

Remarks.—The blaze currents remain of the same character, viz., positive during positive galvanisation, and negative during negative galvanisation. The eyeball is now killed by immersion in hot water, after which no blaze effects are witnessed, but only polarisation counter-currents.

Time.	Excitation.	Response		
		During galvanisation by −0·1 volt.	Without galvanisation.	During galvanisation by +0·1 volt.
—	Br. 1000 +	−	—	−
—	Br. 1000 −	+	—	+

The 2nd eyeball, with response of Type III., gave:—

Time.	Excitation.	Response		
		During galvanisation by −0·1 volt.	Without galvanisation.	During galvanisation by +0·1 volt.
hr. 5 min. —	Br. 1000 +	−0·0240	−0·0190	+0·0240
	Br. 1000 −	−0·0330	−0·0190	+0·0190

Observations made to investigate the possible effect of a Galvanic Current upon the Electrical Response of the Frog's Eyeball to Light. Candle at 1 foot from eye; exposure to light for 1 minute.

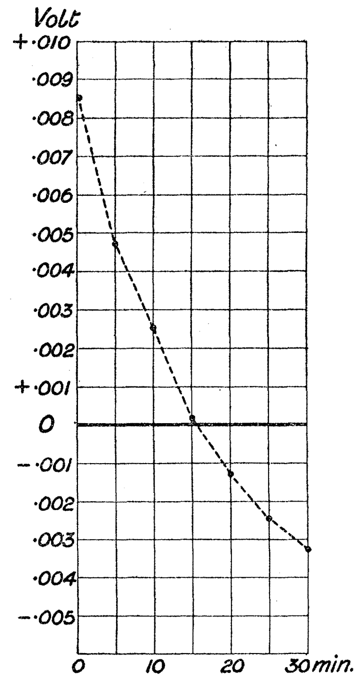
Strength of galvanic current.	Response to Light.		
	I. During G. in − direction.	II. Without.	III. During G. in + direction.
0·100 volt	+0·00120 volt	+0·00090 volt	+0·00160 volt
0·100 ,,	+0·00100 ,,	+0·00100 ,,	+0·00100 ,,
0·025 ,,	+0·00140 ,,	+0·00110 ,,	+0·00120 ,,
0·080 ,,	—	+0·00080 ,,	+0·00100 ,,
0·080 ,,	{ −0·00022 ,, / +0·00044 ,, }	{ −0·00015 ,, / +0·00030 ,, }	{ −0·00012 ,, / +0·00054 ,, }

Concerning the so-called Current of Rest.

I have gradually reached the conclusion that the positive (fundus to cornea) current regularly manifested by a freshly excised eyeball is mainly due to a subsiding disturbance. It is of the nature of blaze current, and therefore in no sense "current of rest" or current of darkness, but action current. It rapidly subsides, and gives place to a negative (cornea to fundus) current, which is the true current of rest, analogous with an ingoing current of rest of the skin. And the positive response to light with reference to this current of rest is its negative variation.

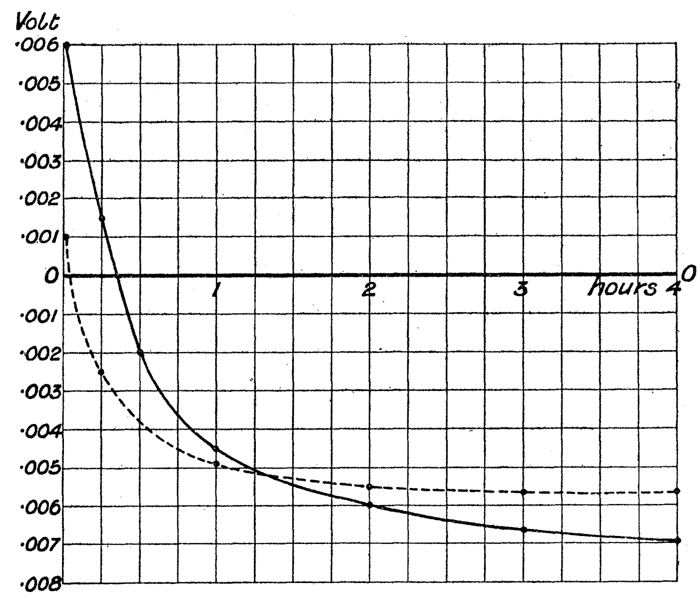
Frog's Eyeball. Natural Decline af the "Current of Rest."

Time.	E.M.F.
0 min.	+0·0084 volt
5 ,,	+0·0047 ,,
10 ,,	+0·0025 ,,
15 ,,	+0·0002 ,,
20 ,,	−0·0013 ,,
25 ,,	−0·0025 ,,
30 ,,	−0·0033 ,,



Normal Decline of "Current of Rest" of a Frog's Eyeball (full line), and of a Dog's Eyeball (dotted line) in Dark Chamber.

Time.	Voltage.	
	Frog.	Dog.
0 hour	+0·0060	+0·0010
¼ ,,	+0·0015	−0·0025
½ ,,	−0·0020	−0·0038
1 ,,	−0·0045	−0·0048
2 ,,	−0·0060	−0·0055
3 ,,	−0·0066	−0·0057
4 ,,	−0·0070	−0·0057



The rate and shape of decline resemble those of a blaze current.

The results of the action of CO_2 and of tetanisation upon the retina and upon nerve are in harmony with this analogy.

Carbonic acid gives primary diminution and secondary augmentation of the

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negative variation of nerve and of the positive variation of the eyeball current. It diminishes the positive variation of nerve and the negative variation of the eyeball.* The typical after-effect of tetanisation as regards nerve is an augmentation of the negative response to electrical stimulation. The typical after-effect of tetanisation as regards the retina is an augmentation of the positive response to luminous stimulation. And I think I may also say that the positive response of nerve and the negative response of the eyeball are both diminished after tetanisation.

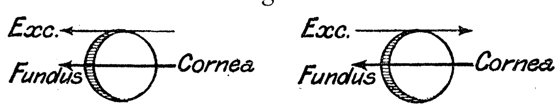
Experiments on the Mammalian Eye.

I have not examined mammalian eyes as systematically as the frog's eye; nevertheless, I have ascertained certain points of similarity and of difference between the two kinds of eye, using for the purpose the eyes of a litter of puppies between the ages of three and five weeks.

Such an eye, disposed between unpolarisable electrodes like a frog's eye, has a much smaller "current of rest," and gives much smaller "blaze currents" in response to electrical stimulation. When first observed, the current of rest may be positive or negative, *e.g.*, + 0·0017, + 0·0032, + 0·0034, giving place to − 0·0013 at the end of two hours, + 0·0012, + 0·0016, 0 giving place to − 0·0056 at the end of eight hours, + 0·0020, + 0·0010. Thus the fall of positive current and increase of negative current which is so well marked and constant in the case of the frog's eye, occurs also, but in less marked degree, in that of the puppy's eye. Its current of rest is comparatively small.

Blaze currents are also less conspicuous than in the case of the frog's eye. With the first eye I tested, as quickly as possible after excision and at ordinary room temperature, they were so small as to be doubtful, and I did not pursue the observation. Subsequently, however, with eyes examined in a warm chamber at about 35° ± 2°, they were quite unmistakable. In all cases they were of considerably lower electromotive value than in the case of the frog, and of negative direction, *i.e.*, from cornea to fundus. I noticed that in the warm chamber they were at their best two or three hours after excision, and I have observed them for as long a period as ten hours, when they gradually gave way to the small currents contrary in direction to that of exciting currents, as in the case of the frog's eye. Thus the puppies' eyes, as regards their blaze current, corresponded with Type III. of the frog's

Fig. 20.



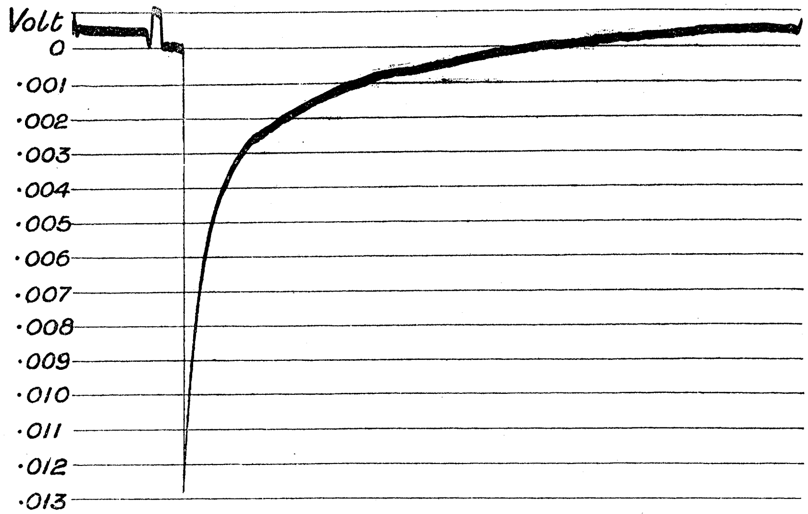
eye. The indubitable and obvious blaze current homodrome with the exciting current was from cornea to fundus. The less obvious, although larger, blaze current

* A. D. W., *loc. cit.*, pp. 146–7–8.

(less obvious by reason of its being opposed to exciting current, and, therefore, conceivably due to polarisation) was also in this same direction from cornea to fundus.

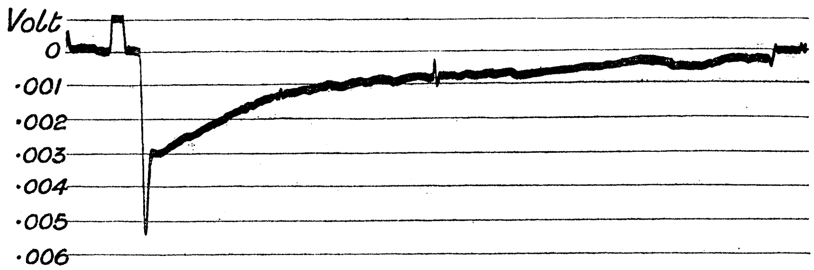
Puppy's Eyeball.

Fig. 20*a*.



A Negative response to positive excitation, *i.e.*, heterodrome effect.

Fig. 20*b*.



B. Negative response to negative excitation, *i.e.*, homodrome effect.

Summation of effects was far less well marked in the case of the mammalian eyes than in that of the frog's eye.

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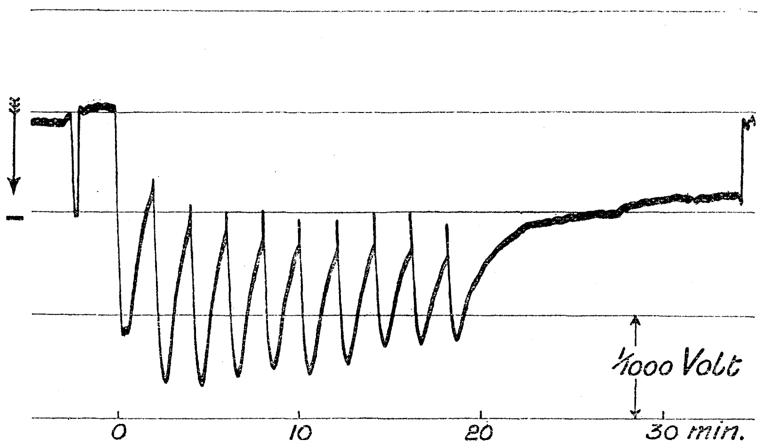
Fig. 21.



Puppy's Eyeball. Excitation by break induction shocks in negative (= cornea to fundus) direction at intervals of 2 minutes—Berne coil at 1000 units, 2 Leclanchés. There is hardly any summation of successive effects. The second response reaches to a lower level than the first, but the third and subsequent excitations produce no further increase of the negative effect.

On the other hand, fatigue and exhaustion by strong stimulation was far more easily effected. Nevertheless, even after complete exhaustion or shock caused by violent tetanisation, a certain amount of recovery may be witnessed.

November 16. 25 days old Puppy's Eyeball.

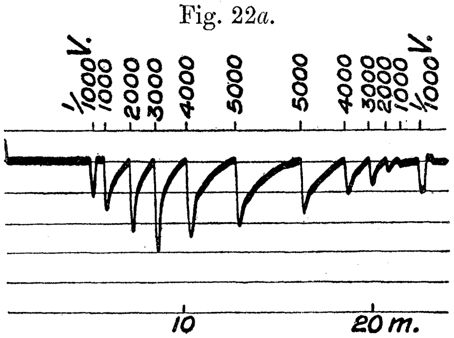
Time.	Excitation.	Current of Rest.	Response.
15 mins.	Br. 5000 +	+ 0·0032 volt.	− 0·0077 volt
	5000 −	—	− 0·0031 "
	10000 +	—	− 0·0230 "
	10000 −	—	− 0·0054 "
	10000 +	—	− 0·0290 "
	10000 −	—	− 0·0115 "
4 hrs.	10000 −	—	− 0·0053 "
	10000 +	—	− 0·0130 "

November 17. 26th day. Puppy's Eye.

Time.	Excitation.	Current of Rest.	Response.
25 mins.	Br. 5000 +	+ 0·0034 volt	− 0·0014 volt
	5000 −	—	− 0·0006
Tetanisation by coil at 10000 Br. + for ½ min.			
	5000 +	—	− 0·0015
	5000 −	—	− 0·0006
2½ hrs.	1000 +	—	− 0·0075
	1000 −	—	− 0·0027
Several strong single shocks by Ruhmkorff coil.			
	1000 +	—	− 0·0012
	1000 −	—	− 0·0005
Tetanisation by Ruhmkorff coil.			
3¾ hrs.	5000 +	—	− 0·0010 } viz., polarisation.
	5000 −	—	+ 0·0010 }
4¼ "	5000 +	—	nil
	5000 −	—	nil
4¾ "	5000 +	—	− 0·0020
	5000 −	—	− 0·0007
5¼ "	5000 +	—	− 0·0019
	5000 −	—	− 0·0006
6¼ "	5000 +	—	− 0·0015
	5000 −	—	− 0·0004

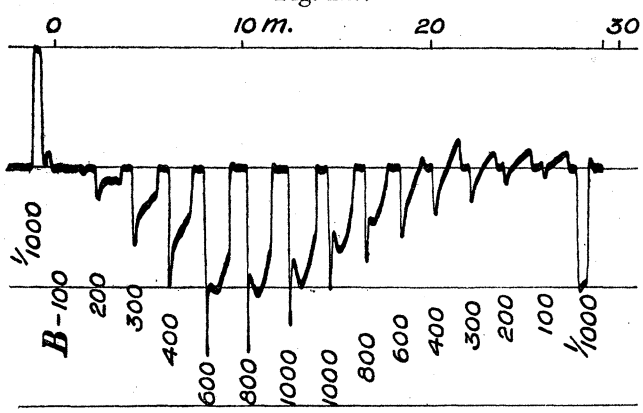
By reason of fatigue, the relation between strength of stimulation and magnitude of effect was far less easy to observe than with frog's eyes, and it was absolutely necessary to strike a mean between pairs of readings taken in an increasing and in a decreasing scale of stimulation strength.

Fig. 22*a*.



Puppy's eyeball. Negative responses to negative excitations of increasing and diminishing strength.

Fig. 22*b*.



Puppy's eyeball. Negative responses to negative excitations of increasing and decreasing strength.

Break induction shocks of Berne coil beginning at 100 units. Transfer time = 0·1 second.

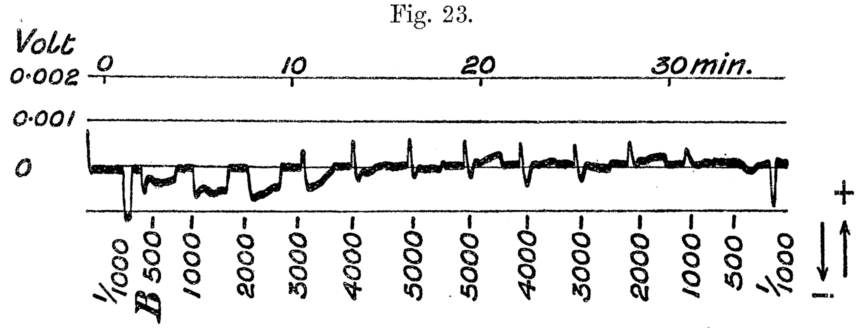
	Excitation.	Response.		Mean.
	Br. 100 –	↓ – 0·0001	↑ 0	– 0·00205
	„ 200 –	– 0·0005	– 0·0001	– 0·00030
	„ 300 –	– 0·0011	– 0·0003	– 0·00070
	„ 400 –	– 0·0014	– 0·0005	– 0·00085
	„ 500 –	– 0·0020	– 0·0012	– 0·00160
4034*	„ 1000 –	↓ – 0·0015	↑ 0	– 0·00075
	„ 2000 –	– 0·0022	– 0·0002	– 0·00120
	„ 3000 –	– 0·0030	– 0·0007	– 0·00185
	„ 4000 –	– 0·0025	– 0·0010	– 0·00175
	„ 5000 –	– 0·0021	– 0·0016	– 0·00185
4038	Br. 200 –	↓ – 0·0002	↑ – 0·0001	– 0·00015
	„ 300 –	– 0·0007	– 0·0003	– 0·00050
	„ 400 –	– 0·0010	– 0·0004	– 0·00070
	„ 600 –	– 0·0016	– 0·0006	– 0·00110
	„ 800 –	– 0·0015	– 0·0007	– 0·00110
	„ 1000 –	– 0·0013	– 0·0010	– 0·00115

* In another galvanometer (not dead beat) in series the readings were—

0·0017	0·0000
0·0027	0·0003
0·0033	0·0007
0·0027	0·0010
0·0023	0·0017

Br. 500 –		– 0·00075	0
1000 –		– 0·00075	0
2000 –		– 0·00075	0·0004
3000 –	+0·002	– 0·0004	
4000 –	+0·004	– 0·0002	
5000 –	+0·004		

Fig. 23.



4037. Puppy's eyeball. Excitation by break induction shock in negative direction. Mixed response in the opposite direction (= polarisation current), and in the same direction (= blaze current).

Puppy's Eye.

	Excitation.	Response.	Current.	
4029–30. Nov. 16 .	B 1000 – 1000 +	– 0·0053 – 0·0130	—	
4031. 1st eye . . Nov. 18	B 5000 + 5000 –	– 0·0010 – 0·0006	+ 0·0016	½ hour.
	B 5000 + 5000 –	– 0·0030 – 0·0008	—	1 hour.
	B 1000 + 1000 –	– 0·0027 – 0·0013	Plate	2½ hours.
4032. 3 P.M. . . .	B 1000 – 1000 –	– 0·0023 – 0·0027	By single shock . By summation .	3 hours.
4033.	B 1000 + 1000 –	– 0·0068 – 0·0062	By single shock . By summation .	4 hours.
4034. Cause/effect .	B 1000 –	– 0·0015	—	8 hours.
4035. 2nd eye . .	1000 +	– 0·0007		
4036.	10000 + 10000 –	– 0·0003 + 0·0004		
Nov. 19.	B 600 –	– 0·0043	—	Polarisation effects. Trace of blaze.