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VI. *On the Retinal Currents of the Frog's Eye, Excited by Light and Excited Electrically.*

By AUGUSTUS D. WALLER, M.D., F.R.S.

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I. INTRODUCTION.

It has been shown by several previous observers (HOLMGREN, DEWAR and M'KENDRICK, KÜHNE and STEINER) that the excised eyeball gives an electrical current, which undergoes variations at illumination, and that these variations of current are due solely to changes occurring in the retina.

All the observers above named describe the variation to be positive at the commencement and at the end of illumination. HOLMGREN makes no distinct statement

with regard to the state during illumination. DEWAR and M'KENDRICK seem to imply that the state during illumination is negative. KÜHNE and STEINER distinctly assert that the state is positive during illumination, and that variations of the type described by DEWAR and M'KENDRICK are characteristic of an injured, fatigued, or dying eyeball.

KÜHNE and STEINER observe further that the variation during illumination is quite independent of the direction of the current of rest.

With regard to the time elapsing between illumination and electrical response, DEWAR and M'KENDRICK observed that it was less than $\frac{1}{10}$ th second; FUCHS, by means of the rheotome, that it was $\cdot 0004$ to $\cdot 006$ second. DEWAR and M'KENDRICK state further that fatigue and recovery occur during illumination and darkness; that coloured lights act in the order—yellow, green, red, blue; that with geometric increase of light-intensity there is an arithmetic increase of deflection; and that the effect on one eye may be traced to the opposite optic lobe.

II. PLAN OF EXPERIMENT.

My purpose was to re-examine more closely, and with the help of photographic records, the phenomena as presented by the frog's eyeball, which KÜHNE and STEINER (with whom I agree) consider to be the most normal object upon which to study retinal effects. The effects manifested by the posterior half of the eyeball or by the isolated retina are, I find, precisely what is obtained on the injured eyeball, and I therefore consider as typical the effect obtained on the uninjured eyeball. Moreover the latter has in my hands proved to be far more sensitive and far more enduring than previous accounts had led me to expect—*e.g.*, a "good" eye will give a large electrical response to illumination by a flash of moonlight lasting $\frac{1}{100}$ th second, and will respond distinctly to exposure to light reflected from a white card 10 feet distant lighted by a standard candle 10 feet from the card, while the period during which response may be witnessed extends to more than 48 hours.

That heat-rays do not contribute to the effect is at once shown by means of an alum cell or a black-hot poker. And the "physiological" nature of the electrical response is proved by the fact that it is subject to the influences of anæsthetics and of raised or lowered temperature.

The eyeball is carefully excised, pressure of the globe being particularly avoided, and placed between the soft clay ends of an ordinary pair of unpolarisable electrodes. A black box with a hole and tube opposite the eye, a candle in a spring stand, wires through the box to a galvanometer, and a sensitive plate to record the movements of the galvanometric spot complete the apparatus.

The connections between eyeball and galvanometer are always such that the nerve stump is to the N. terminal and the cornea to the S. terminal. Normal current in the eyeball is thus always upwards from nerve to cornea, northwards through the

galvanometer. Deflections in this upward direction in the eyeball are given as upward movement in the photograms, and are termed "positive." Deflections downwards are termed "negative." "Up" and "down" on the record signify thus current "up" and "down" through the eyeball, *i.e.*, "up" from choroidal to vitreous surface of the retina, "down" from vitreous to choroidal surface.

The galvanometer, which is nearly, but not quite, dead-beat, is usually adjusted by a shunt to give a deflection across the plate with a standard current from $\frac{1}{10000}$ volt through eyeball, electrodes, and galvanometer. Its sensitiveness, unshunted, was approximately 15 millims. deflection for $1 \cdot 10^{-9}$ ampere on photograms, and 30 millims. on a transparent scale used to take readings.

I also used for recording purposes where less sensitiveness was sufficient a fully dead-beat instrument giving on the photographic plate a deflection of 1 millim. for $1 \cdot 10^{-9}$ ampere.

Fig. 1.

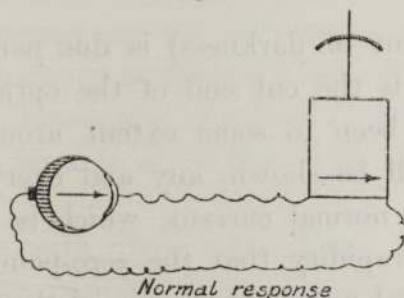


Diagram to show direction of normal current and direction of normal response.

The recording plate was let down by clockwork at speeds varying with particular requirements between 5 millims. per minute to 15 millims. per second. Intermediate speeds frequently used were 25 and 150 millims. per minute.

Excitation was made by brief or prolonged exposure to the light of a standard candle, sliding along a scale 20 feet long, fixed to a shelf in a darkened room. The exposure shutter was an ordinary Thornton-Pickard camera shutter released by air-pressure. To signal the instant of flash or the duration of exposure, the releasing bellows (a small bicycle-pump) was connected by T-piece with the releasing nipple, and with a second nipple that signalled the releasing stroke upon the travelling plate. In the slower records this complication was, however, omitted, and the signal was made by hand.

Units of excitation marked along the candle scale were taken in hundredths of a foot-candle, *viz.*, the light of a standard candle at a distance of 1 foot. Thus at 10 feet distance the stimulus was 1 unit, at 20 feet $\cdot 25$ unit, at 2 feet 25 units, &c.* The eyeball rests upon one electrode with the cornea upwards. Light reaches it

* I have since adopted the metre-candle as unit to facilitate calculation. 1 metre-candle equals $\cdot 0929$ foot-candle, or approximately $\frac{1}{10}$ th.

through a horizontal tube, and there is thus no focussing action by the cornea upon the retina.

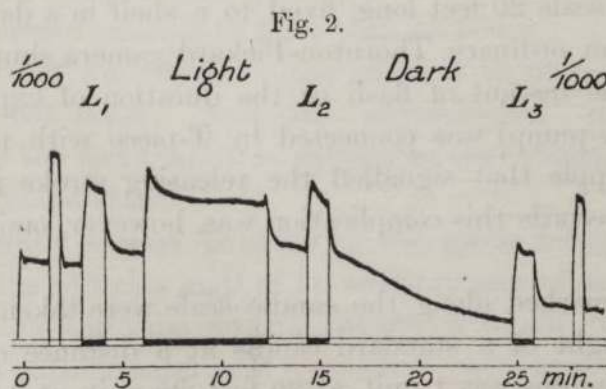
I have also occasionally tested the effects and the after-effects of electrical excitation, viz., of induction shocks and of condenser discharges. In the latter case it was of course necessary to exactly compensate through the galvanometer any current that might be present, and to arrange the circuit in a special manner, described below (p. 155).

III. RESULTS.

The results of the present investigation confirm and extend the results of previous observers, and are summarised under the following heads:—

§ 1. *A Fresh Normal Eyeball, set up as figured, manifests Positive Current, which gradually declines to Zero, and becomes Reversed.*

This normal current (current of darkness) is due partly to current of injury, of which the electromotive spot is the cut end of the optic nerve, partly to the retina itself, which has necessarily been to some extent aroused by the disturbance of removing the eyeball. As will be shown, any and every disturbance of the retina arouses positive current. The normal current, which is the sum of these two components, subsides with such rapidity that the zero-point is reached in 15 minutes or less; e.g., in one case where I measured and timed the fall, it fell from +0.005 volt to zero in the first 15 minutes, and in the next 15 minutes reached a value of -0.002 volt. Not infrequently, when an eyeball has been most carefully removed and kept for a few minutes in the dark, the normal current is negative from the outset of observation. The fall of a subsiding current, whether diminishing from + to 0 or increasing from 0 towards -, is delayed by light and accelerated by darkness



1714. The normal current (connections as in fig. 1) is positive, declining rapidly during darkness, less rapidly during illumination. Positive variations during illumination, L_1, L_2, L_3 . Slight fatigue after light for 5 minutes, $L_2 < L_1$. Slight recovery after obscurity 5 minutes, $L_2 < L_3$.

The absolute value of its E.M.F. is too variable to be of much significance : +·006, +·004, +·012, +·005, +·0006, +·006, +·003, -·004, -·001 are values recorded in notes of my earlier experiments, when I measured the current by compensation at the outset. I have seen it reach to the value of -·012 after the reversal.

§ 2. *On Exposure to Light the Current, whether Upward or Downward, undergoes an Upward Variation.*

The statements contained in §§ 1 and 2 have been previously made in other words by KÜHNE and STEINER, the second being designated by them as the "law of constant alteration of tension," and expressed as follows : "Reversed direction of the current of darkness is without influence upon the magnitude and character of the photo-electrical variations which reverse their signs."

The main effect during illumination is a positive effect, by upward current through the retina, whether the current of rest be at the time upward or downward. An upward variation of a downward current has been described as being a negative variation of a current of injury : it is therefore desirable to clearly understand that the main electrical effect of illumination of a fresh eyeball is always directed through the retina from rod and cone layer to nerve fibre layer (represented by an arrow from fundus to cornea).

The direction of deflection with illumination, when watched on the galvanometer scale, usually appears to be positive at the commencement of illumination and positive at the end of illumination. It has been variously described as being positive or as being negative during illumination.

Thus DEWAR and M'KENDRICK* say : "The action of light on the eye of a frog may be briefly stated as follows : When diffuse light is allowed to impinge on the eye of the frog after it has arrived at a tolerably stable condition, the natural electromotive force is in the first place increased, then diminished ; during the continuance of light it is still slowly diminished to a point where it remains tolerably constant, and on the removal of light there is a sudden increase of the electromotive power nearly up to its original position."

KÜHNE and STEINER† consider this course of events to be characteristic of abnormal eyeballs, and state that the initial augmentation of current suffers no diminution during illumination lasting for some minutes.

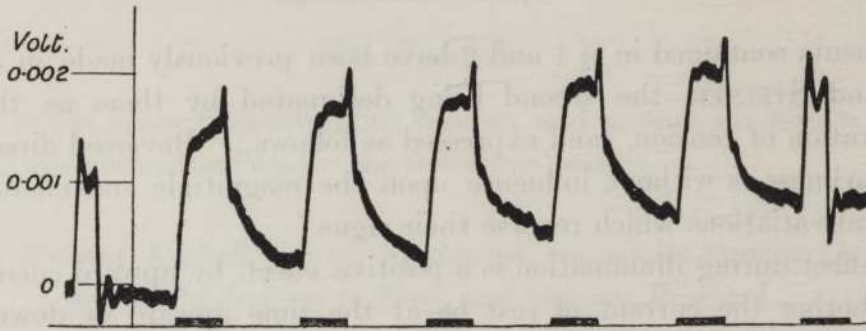
All my observations and records confirm this view, and show that the effect of exposure to light are as described by KÜHNE and STEINER. The puzzling feature that we should have at commencement and at end of illumination, *i.e.*, with the advent of light and with the advent of darkness, a deflection of the same sign, is to some extent cleared up by photographic records, which show that the final

* DEWAR and M'KENDRICK, 'Trans. Roy. Soc. Edin.,' 1873, p. 153.

† KÜHNE and STEINER, 'Sehorgane,' p. 30.

deflection is a subordinate feature of the main change, and justify the simple statement that there is positive (upward) current during illumination and no such current during darkness. Figs. 3 and 11 typically illustrate this fundamental fact. The accessory to the fact, *i.e.*, the terminal positive deflection, will be best considered later, *vide infra*, p. 140.

Fig. 3.



1661. Series of five normal responses. Candle at 2 feet (25 units). Illumination for 1 minute; obscurity for 2 minutes.

Any disturbance of the retina—whether by its normal stimulant, light, or by mechanical pressure, or by electrical stimulation, arouses a more or less considerable and more or less enduring positive current. The original positive current of a freshly excised eyeball has two factors: electromotivity of the cut end of the optic nerve and electromotivity of the disturbed retina. Fall of current by subsidence of such disturbance is therefore delayed by light, or having fallen is made to rise again by light, or by tetanisation, or by mechanical pressure. The general rise of base line in fig. 3 illustrates this gradually rising after-effect accompanying the succession of positive effects directly caused by illumination.

The *electromotive force* of the response to light varies usually between $\cdot 0001$ and $\cdot 0010$ volt. The following values are taken from my note-book:—

$$+ \cdot 00013, + \cdot 0002, + \cdot 0001, \text{ rising to } + \cdot 00015, \\ + \cdot 0005, + \cdot 0003, + \cdot 0013, + \cdot 0003 \text{ volt.}$$

For the third stage (*vide infra*) I find the values—

$$- \cdot 0002, - \cdot 00005, - \cdot 0001, - \cdot 0003 \text{ volt.}$$

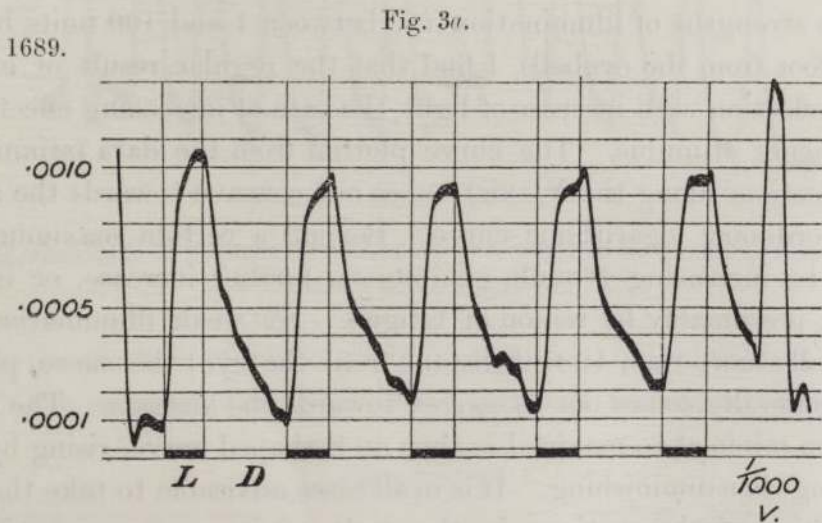
These values refer to responses obtained by exposure for 1 minute to the light of a standard candle at 2 feet (= 25 units).

§ 3. *The Magnitude of Response increases with the Duration of Illumination.*

With the strength of light as before (25 units), the response to a brief exposure by means of a flash shutter (timed at $\frac{1}{100}$ th second); the deflection is generally one-tenth to one-quarter of that provoked by exposure for a period of 1 minute—a time that is sufficient to bring out the maximum effect. The following are values that were noted :—

{	Flash of $\frac{1}{100}$ th second	{ + ·0001	{ + ·00012	{ + ·00003 volt.
	Exposure for 60 seconds	{ + ·0005	{ + ·00048	{ + ·00038
{	Flash *	{ + ·00015	* { + ·000075	{ + ·00004 „
	Exposure	{ + ·00020	* { + ·000150	{ + ·00025
{	Flash	{ + ·0001	{ + ·00033	{ - ·00004 „
	Exposure	{ + ·0008	{ + ·00130	{ - ·00020

The last two pairs of numbers are calculated from the records of figs. 11 and 13. The two starred pairs were observed with eyes of the second stage (*vide infra*). I have learned to associate a relatively large effect of brief illumination with a relatively conspicuous break deflection at the end of prolonged illumination. A conspicuous break effect is characteristic of what will be described below as the second stage. The point is illustrated in fig. 12.



1689. Series of five normal responses taken as in fig. 3, and exhibiting diminution (? fatigue).

The following observations give values of deflection for periods of intermediate length, and show that the effect increases less and less rapidly with arithmetic increase of time.

	Duration of light at 25 units.	Magnitude of deflection.	
			$\frac{3}{4}$ hour later
Exp. I.	·01 second	+ 3 cm. scale	+ 5 cm.
	·10 "	7 "	+ 10 "
	·60 "	14 "	+ 15 "
	4·20 "	25 "	+ 22 "
	60·00 "	30 "	+ 27 "
Exp. II.	·01 second	+ 9 cm. scale = ·00011 volt.	
	·10 "	+ 16 "	·00020 "
	·60 "	+ 30 "	·00037 "
	4·20 "	+ 42 "	·00052 "
	60·00 "	+ off scale	

§ 4. *The Magnitude of Response increases with the Strength of Illumination.*

This relation has been commented upon by all previous observers. DEWAR and M'KENDRICK in particular, regard the data they observed as being in conformity with FECHNER'S logarithmic law. They give, *e.g.*, the effects of a given light at 1, 4, and 8 feet from the eyeball (\therefore strengths as 64, 4, and 1)—

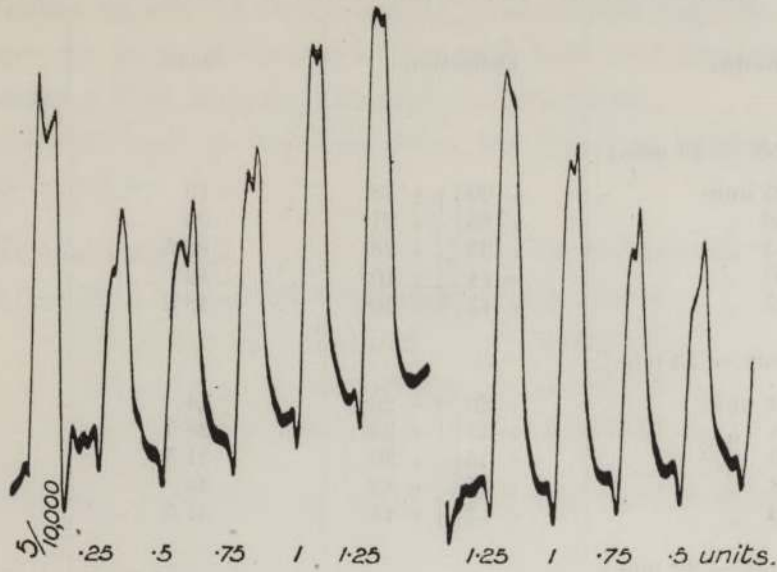
$$\left\{ \begin{array}{l} \text{at make} \\ \text{at break} \end{array} \right\} \begin{array}{l} + 8 \quad + 5 \quad + 1 \\ + 12 \quad + 5 \quad + 5. \end{array}$$

For moderate strengths of illumination (*i.e.*, between 1 and 100 units by a standard candle 10 to 1 foot from the eyeball), I find that the regular result of experiment is an increasing deflection with increase of light, the rate of increasing effect diminishing with the increasing stimulus. The curve plotted from the data (stimulation along the X axis, deflections along the Y axis) comes out concave towards the abscissa, and not unlike an ordinary logarithmic curve. Beyond a certain maximum effect, the response, even to increasing stimuli, exhibits no further increase, or it may be an actual decrease, presumably by reason of fatigue. For weak illumination (*i.e.*, below 1 unit, by a candle more than 10 feet distant from the eye) the curve, plotted in the same manner, generally comes out as convex towards the abscissa. The entire curve of response from minimal to maximal is thus an S-shaped curve, rising by increments at first increasing then diminishing. It is in all cases advisable to take the mean value of a double series of observations in the scale of increasing and of diminishing intensity of stimulation.

These several points are illustrated in the following observations—the first giving a simple series of readings of responses to stimulation in the ascending scale of intensity; the second a more carefully taken series up and down a scale of units. The latter are photographically recorded in figs. 4 and 5, on inspection of which it may be

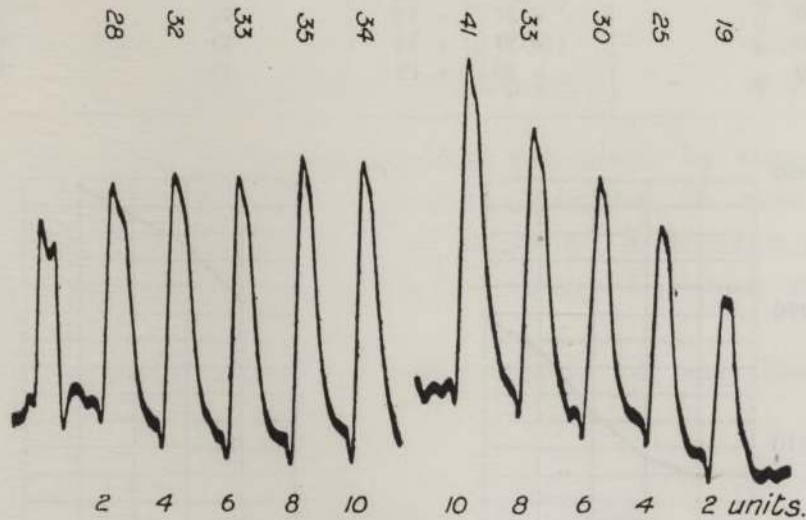
1701.

Fig. 4.



1702.

Fig. 5.



Alterations in magnitude of response by alterations in strength of illumination, from $\frac{1}{4}$ to 10 units on rising and falling scale.

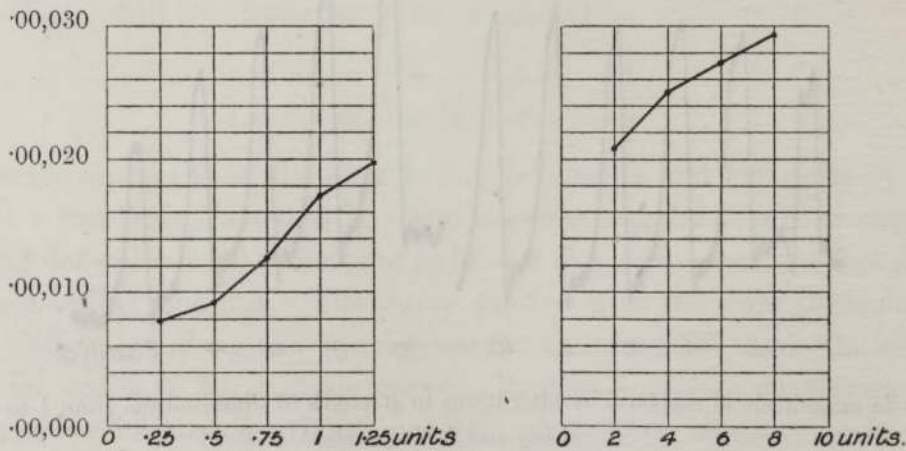
noticed that the decline of response in the group of diminishing stimuli is more striking than the increase of response in the group of increasing stimuli.

Observation 1.

Stimulus.	Deflection.	Stimulus.	Deflection.	Stimulus.	Deflection.
.25 unit	+ 5 cm.	2 units	+ 24 cm.	20 units	+ 42 cm.
.50 "	+ 7 "	4 "	+ 28 "	40 "	+ 50 "
.75 "	+ 10 "	6 "	+ 32 "	60 "	+ 50 "
1.00 "	+ 14 "	8 "	+ 34 "	80 "	+ 48 "
1.25 "	+ 18 "	10 "	+ 36 "	100 "	+ 49 "

Observation 2. (Measurements taken simultaneously with the records Figs. 4 and 5.)

Stimulus.	Deflection.	Mean.	Voltage.
$(\frac{1}{2000}$ volt = 49 mm.)			
0.25 unit	+ 20 + 18	19	·000078
0.50 "	+ 25 + 21	23	·000094
0.75 "	+ 33 + 28	30.5	·000124
1.00 "	+ 44 + 40	42	·000172
1.25 "	+ 47 + 50	48.5	·000198
$(\frac{1}{2000}$ volt = 23 mm.)			
2 unit	+ 28 + 20	24	·000208
4 "	+ 32 + 25	28.5	·000248
6 "	+ 33 + 30	31.5	·000274
8 "	+ 35 + 33	34	·000296
10 "	+ 43 + 41	37.5	·000326
$(\frac{1}{2000}$ volt = 22 mm.)			
20 unit	+ 42 + 30	36	·000328
40 "	+ 38 + 32	35	·000318
60 "	+ 37 + 33	35	·000318
80 "	+ 37 + 33	35	·000318
100 "	+ 36 + 42	39	·000354



First two groups of the above measurements plotted to scale.

§ 5. *Fatigue.*

Fatigue—*i.e.*, a diminution in power consequent upon previous action—is apparent in all experiments where the response to light is observed for any length of time. But the amount of fatigue brought into evidence by illumination is much less than might have been expected. The retina, although to some extent liable to be fatigued by experimental illumination, is much less fatigued than is ordinary muscle by electrical tetanisation. And whereas it is an easy matter to completely exhaust a muscle by repeated tetanisation, the retina cannot be exhausted by repeated illumination—at

least, within the range of intensity that I have employed. Even with electrical tetanisation—by which, as will be shown in § 12, true retinal response is elicited, the signs of fatigue are no more pronounced than with luminous stimulation. On the other hand, the recovery from fatigue is prompt and complete.

Thus in an experiment made to test this point, the following values were observed (illumination at 25 units):—

Normal response	+·00034	volt.
After illumination for 5 minutes	+·00020	„
„ obscurity for 5 minutes	+·00030	„
„ illumination for 5 minutes	+·00016	„
„ obscurity for 5 minutes	+·00038	„

In another experiment in which the eyeball was submitted to direct sunlight the responses were

Candle at 2 feet (25 units)	+·0003	volt	+·00031
Sunlight	+·0007	„	+·00073
Candle at 2 feet	+·0001	„	+·00016
„ „ 2 minutes later	+·0002	„	+·00025

In sum, then, the retina as regards apparent exhaustion by strong stimulation holds a position in the scale intermediate between nerve-fibre, the most resistant, and nerve-terminals (including muscle), the least resistant. A character that is in all probability due to the efficiency of restorative change by which expenditure of substance is made good.

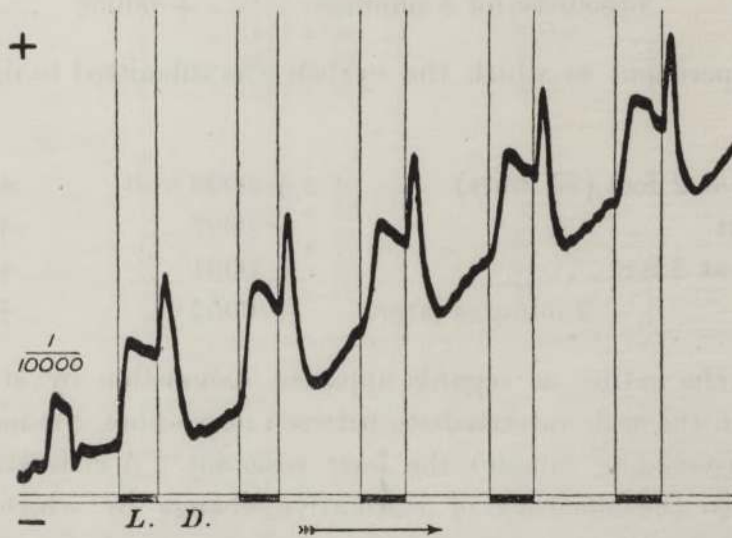
The comparative conditions of the three cases will be best illustrated by an example—

		Nerve-fibre.	Retina.	Muscle.
Five excitations, each lasting for 1 minute and separated by intervals of rest for 2 minutes	1st.	-·00200 volt	+·00051 volt	-·01100 volt
	2nd	-·00215 „	+·00043 „	-·00700 „
	3rd	-·00225 „	+·00040 „	-·00450 „
	4th	-·00235 „	+·00035 „	-·00380 „
	5th	-·00235 „	+·00032 „	-·00250 „

The retinae, like the muscles of different frogs, more or less vigorous, exhibit in more or less pronounced degree the signs of fatigue. In general, the retina of a “poor” frog gives the best marked decline in series of normal positive responses. Nevertheless the response of the third stage (*vide infra*) has, so far as I have seen, proved to be remarkably persistent. And sometimes, particularly with brief stimulation (for 6 seconds at 1 minute intervals), an increasing deflection has come under observation,

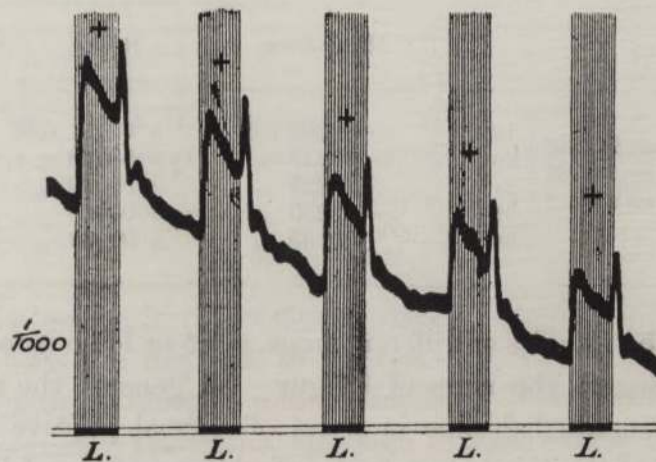
giving a series with "staircase" increase, like that obtained on cardiac and other muscle and on nerve. But whereas in the latter case we may feel assurance that the effect is veritably the result of the stimulation, in the case of the retina this certainty is obscured by the fact that spontaneous gradual increase and diminution of response are apt to be present, in consequence, I believe, of the state of eyeball as regards the internal production of carbonic acid. For this reason I have attached little importance to the detailed examination of fatigue effects and of staircase phenomenon; a general view of the facts, as they have come under observation, may be gathered from the following summary table, and from the records given in figs. 3, 3*a*, 6, 7, and 8.

Fig. 6.



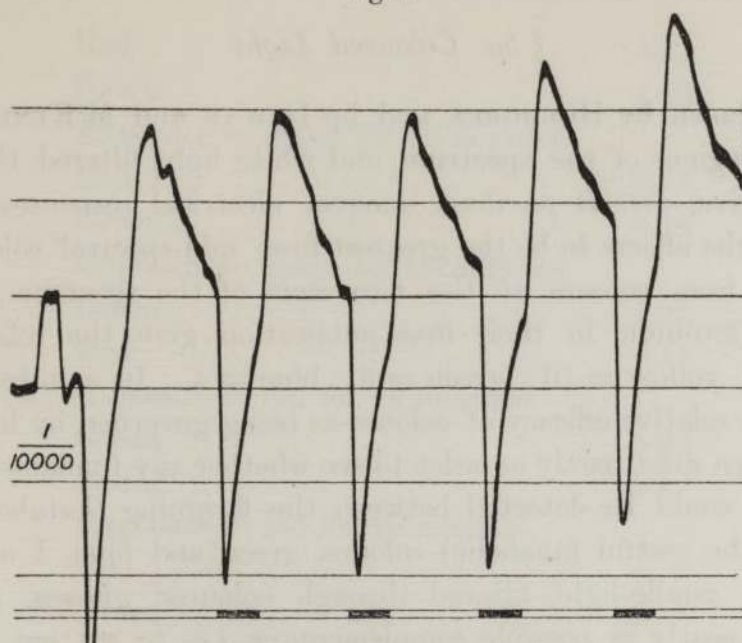
1647. Series of positive responses in an eyeball 6 hours after excision. No appreciable fatigue. Late first stage. Illumination *L* for 1 minute; obscurity *D* for 2 minutes.

Fig. 7.



1650. Similar series, 2 hours after excision. ? Fatigue or ? natural decline. Late first stage.

Fig 8.



1704. Series of negative responses of the third stage. Eyeball 18 hours after excision. No appreciable fatigue.

No. of experiment.		Time after excision.	Strength of light.	Illumination for 1 minute. Obscurity for 2 minutes. Voltage of successive responses.				
				1st.	2nd.	3rd.	4th.	5th.
1	(1647)	Hours. 6	Units. 4	+·00016	+·00018	+·00016	+·00015	+·00015
2	(1650)	2	25	+·00051	+·00043	+·00040	+·00035	+·00032
3	(1652)	6	25	+·00120	+·00095	+·00070	+·00055	+·00045
4	(1656)	6	25	-·00090	-·00095	-·00095	-·00095	-·00090
5	(1660)	1	25	+·00110	+·00100	+·00100	+·00100	+·00100
6	(1674)	2	25	+·00100	+·00110	+·00110	+·00110	+·00100
7	(1689)	2	25	+·00085	+·00075	+·00065	+·00065	+·00065
8	(1704)	18	25	—	-·00032	-·00031	-·00033	-·00033

From these numbers, and still more evidently from the actual records (figs. 3, 6, 7, 8), it is clear that the retina, as compared with muscle, is a very inexhaustible organ. Experiments 5 and 8 (figs. 3 and 8) exhibit hardly any "fatigue." Experiments 2, 3, and 7 (fig. 8) are instances in which "fatigue" is most apparent. But it is possible that even in these cases there may have been a natural decline more pronounced than usual. Similar considerations apply to the mammalian eye, where the positive response rapidly diminishes, while the later negative response persists of undiminishing magnitude (*vide infra*, fig. 37).

§ 5a. Coloured Light.

As previously shown by HOLMGREN and by DEWAR and M'KENDRICK, chromatic light of different regions of the spectrum, and white light filtered through different coloured media, give, *ceteris paribus*, unequal electrical responses of the retina. HOLMGREN found the effects to be the greatest from mid-spectral colours, yellow and green, and least from colours at the two ends of the spectrum, red and blue. DEWAR and M'KENDRICK in their first publication give the relative efficacy as being: red = 10; yellow = 10; green = 8; blue = 4. In a subsequent publication they give the relative efficacy of colours as being governed by luminosity.

Partly for its own sake, partly in order to see whether any fundamental antagonism or even difference could be detected between the fatiguing (katabolic) colours, red and yellow, and the restful (anabolic) colours, green and blue, I made a series of experiments with candle-light filtered through coloured glasses, chosen of such nature as to be as nearly as possible complementary, *i.e.*, to cut out all candle-light when taken in superposed pairs, red + green; yellow + blue.

The relative order of efficacy at 25 units came out—

Red	+ 4
Blue	+ 9
Green	+12
Yellow	+16
“White” (candle)	+33

I next made a series of trials to see whether the joint effect of two complementary (or opposed) colours is greater or smaller than their separate effects, as illustrated by the following experiment:—

Candle at 20 feet. $\frac{1}{4}$ unit.

Red alone	+ 5
Green alone	+10
Red + green	+14
“White” (candle)	+40

Finally I made a series of trials to see whether prolonged stimulation by a given colour produces equal or unequal fatigue to that colour and to its complementary. I chose red and green for this purpose, and after each prolonged exposure reversed the order of testing.

Candle at 1 foot. (100 units.) Stimulus lasts 10 seconds.

Red	+21
Green	+28
Exposure to green for 10 minutes.	
Red	+16
Green	+24
Exposure to green for 10 minutes.	
Green	+22
Red	+15
Exposure to red for 10 minutes.	
Green	+20
Red	+12
Exposure to red for 10 minutes.	
Red	+ 8
Green	+18

No complementary or antagonistic influence as regards retinal response is to be detected in any of these experiments. All colours seem to act in the same direction, more or less powerfully according as they are more or less luminous.

§ 6. *Effect of Temperature.*

Like previous observers, I find that the normal response at first increases with rising temperature and then disappears. To which I have only to add that the abolition may be only temporary if the temperature has not been raised too high for too long a period. For example, in an experiment directed to this point, with the temperature

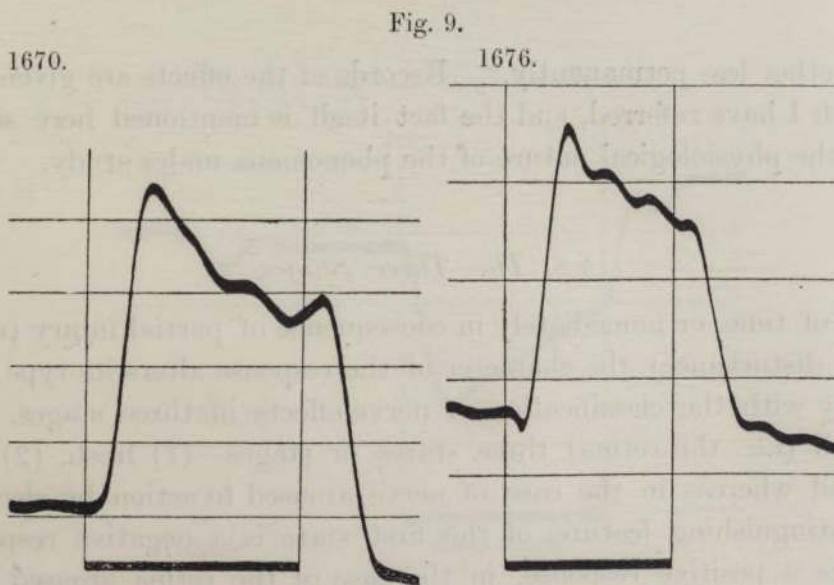


Fig. 9.

Positive responses of two eyeballs at 22°, previously heated to 42°, with temporary abolition of the response.

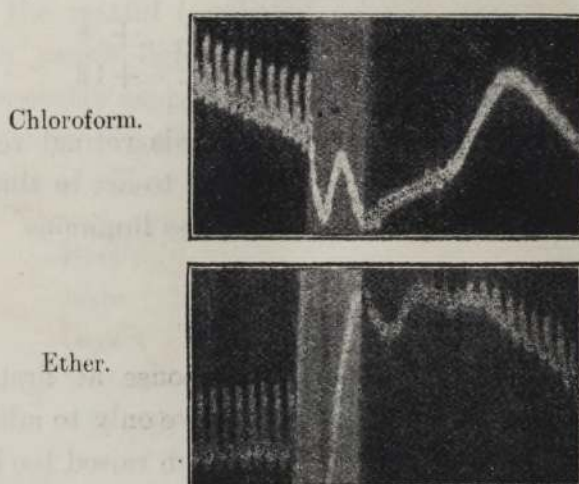
of a box enclosing the eyeball and electrodes standing at 16° , the response to light (candle at 2 feet) was + '00020. At 30° it was at its maximum, + '00030, from which it gradually declined to + '00001 at 42° . On cooling to 20° the response reappeared of its original character and magnitude as + '00020.

The response is immediately abolished by freezing the eyeball, and I have not seen it recover on subsequent thawing.

§ 7. *Effects of Anæsthetics.*

I have previously shown, in connection with a study of ether and chloroform, that these vapours more or less permanently abolish the response—chloroform more

Fig. 10.



Action of ether and of chloroform upon retinal excitability by light. (From 'Brain,' 1896.)

permanently, ether less permanently.* Records of the effects are given in the publication to which I have referred, and the fact itself is mentioned here solely in order to emphasise the physiological nature of the phenomena under study.

§ 8. *The Three Stages.*

With lapse of time, or immediately in consequence of partial injury (*i.e.*, of a more or less violent disturbance), the character of the response alters its type.

Conformably with the classification of nerve-effects in three stages, I distinguish for the eyeball (*i.e.*, the retina) three states or stages—(1) fresh, (2) transitional, (3) stale. And whereas in the case of nerve aroused to action by electrical stimulation the distinguishing feature of the first state is a negative response, and in the third state a positive response, in the case of the retina aroused to action by

* A. D. W., 'Brain,' 1896, p. 571.

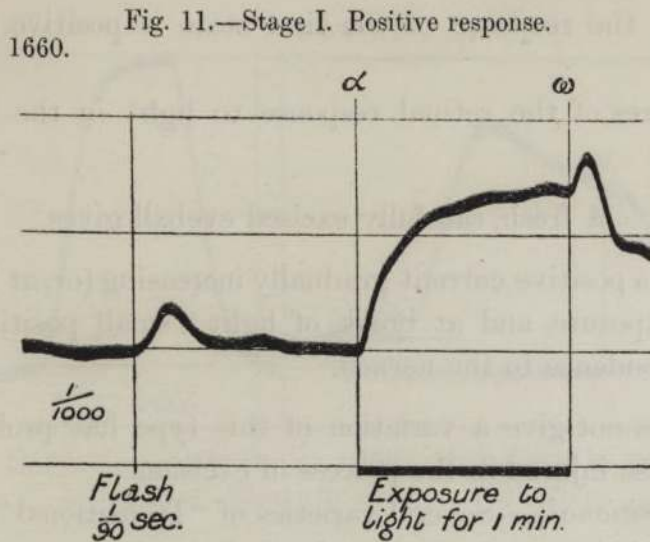


Fig. 12.—Stage II. Positive interrupted by negative response.

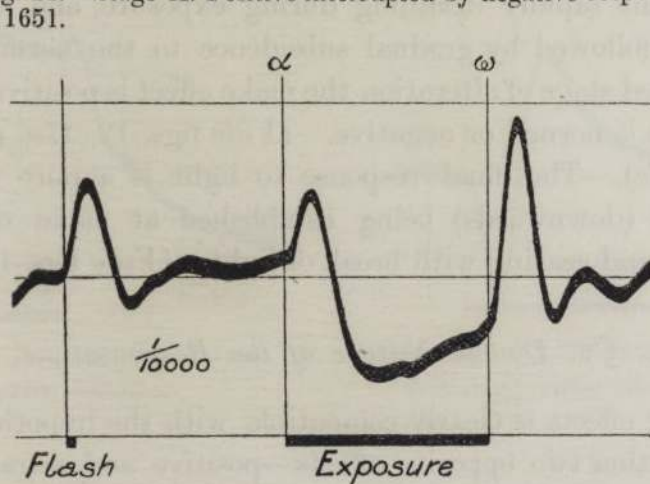
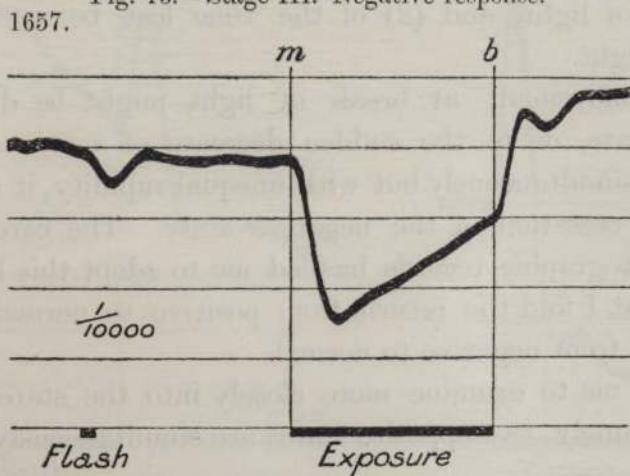


Fig. 13.—Stage III. Negative response.



luminous stimulation, the response of the first state is positive, of the third state negative.*

The principal features of the retinal response to light in the three stages are as follows:—

First Stage (Fresh).—A fresh, carefully excised eyeball gives:

At make of light a positive current gradually increasing (or, at least, not diminishing) during exposure, and at break of light a small positive effect, followed by gradual subsidence to the normal.

An eyeball that does not give a variation of this type has probably been unduly compressed or otherwise injured in the process of excision.

Second Stage (Transitional).—Several varieties of “Transitional” responses present themselves, which shade into each other, and are obviously connecting forms between the first and the third types. (a) The earliest transitional form exhibits at make of light a positive current rapidly declining during exposure, and at break of light a large positive effect, followed by gradual subsidence to the normal. (*Vide* fig. 16.) (b) At a more advanced stage of alteration the make effect is positive, but the electrical state during exposure is normal or negative. (*Vide* figs. 12, 17*a*, and 17*b*.)

Third Stage (Stale).—The final response to light is a pure negative response, the negative current (downwards) being established at make of light, enduring throughout exposure and ceasing with break of light. (*Vide* figs. 13, 35, 36, and 37.)

§ 9. *Double Nature of the Response.*

The entire series of effects is clearly compatible with the hypothesis that illumination arouses in the retina two opposite effects—positive and negative, and that the former dies out more rapidly than the latter.

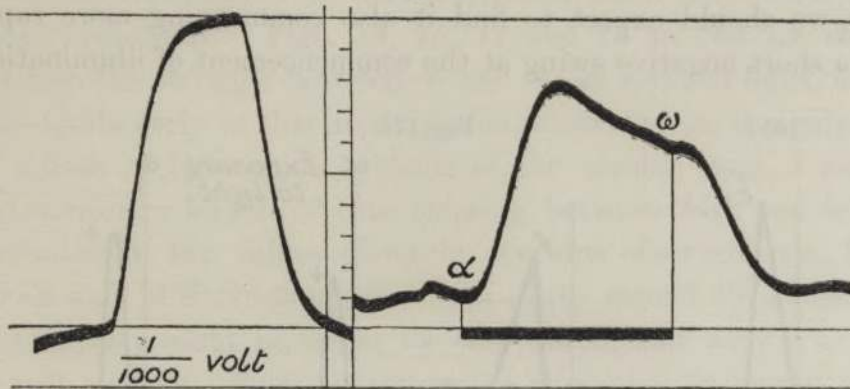
This view is confirmed by the closer consideration (1) of the terminal positive deflection at break of light, and (2) of the time lost between illumination and response at make of light.

(1.) The positive movement at break of light might be due to the sudden increase of a *plus* state, or to the sudden decrease of a *minus* state. Or if two opposite states cease simultaneously but with unequal rapidity, it might be due to the greater sharpness of cessation of the negative state. The careful inspection of a large number of photographic records has led me to adopt this last explanation, by reason of the fact that I find the return from positive to normal to be always less rapid than the return from negative to normal.

This reflection led me to examine more closely into the state of matters at the make of light. If, namely, two opposite states are simultaneously aroused, but with

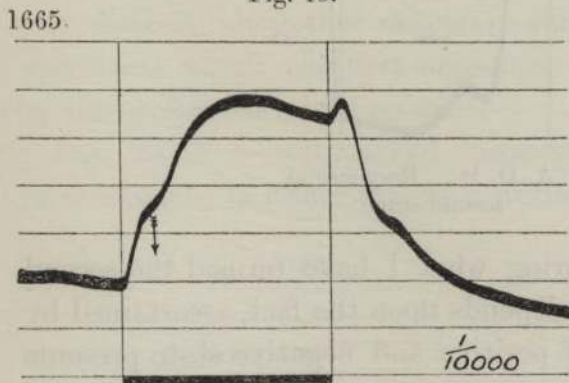
* A. D. W., ‘Phil. Trans.’ B, 1897, pp. 23 and 48. The significance of positive and negative effects is discussed in section 5, p. 62, of that paper.

Fig. 14.



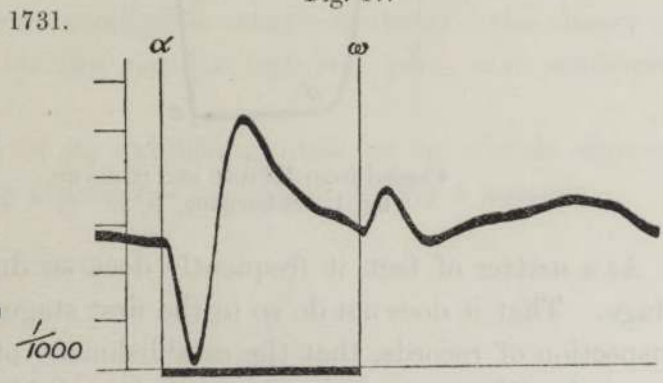
1726. First stage. Standardising deflection by 1/1000 volt, followed by retinal response to light from α to ω. Unusually small terminal effect.

Fig. 15.



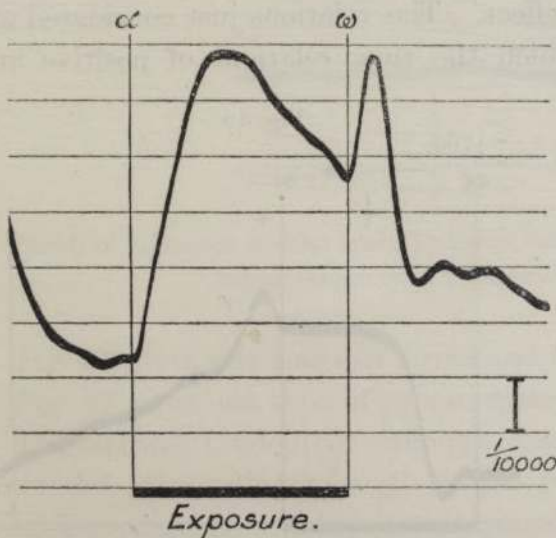
1665. Early second stage. Negative restraint at ↓ of initial positive deflection.

Fig. 17.



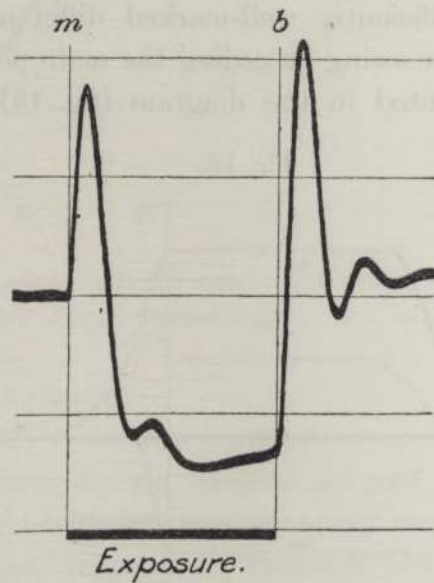
1731. Second stage. Initial negative effect, followed by declining positive effect during exposure.

1646. Fig. 16.



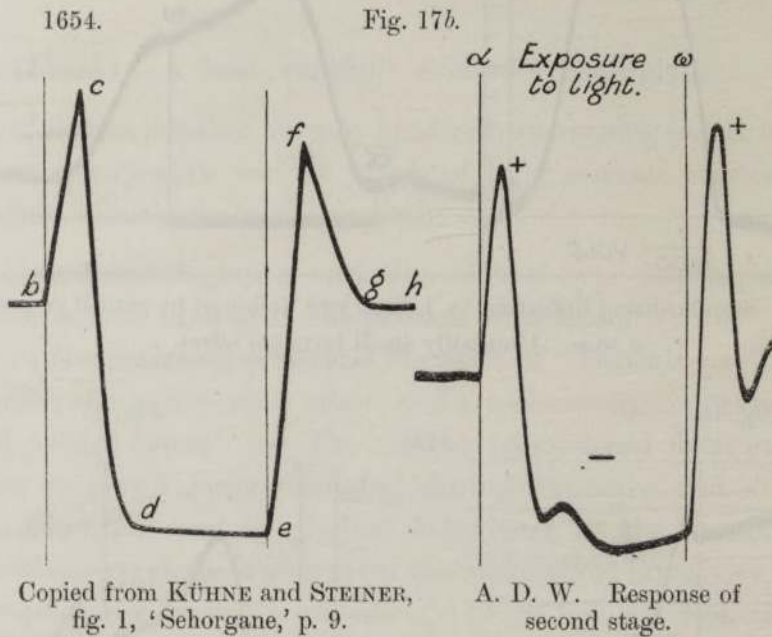
1646. Early second stage or late first stage. Positive effect beginning to give way to negative effect.

1654. Fig. 17a.



1654. Second stage effect. Compared with fig. 1 of KÜHNE and STEINER's second paper ('Sehorgane,' p. 9).

not quite equal rapidity, and if the negative ceases more rapidly, giving a short positive swing, we should expect to find it also commencing more rapidly, and to give therefore a short negative swing at the commencement of illumination.



As a matter of fact, it frequently does so during what I have termed the second stage. That it does not do so in the first stage depends upon the fact, ascertained by inspection of records, that the establishment of positive and negative state presents no such difference of speed as their subsidence. The negative state is indeed established more rapidly than the positive state, but the difference is not sufficient to affect a galvanometer that shows quite distinctly the difference in their rate of subsidence. If, however—and the case presents itself frequently in the second stage—a sufficiently well-marked difference should exist, then we shall have a short negative swing preceding the main positive effect. The relations just considered are represented in the diagram (fig. 18), in which the time relations of positive and

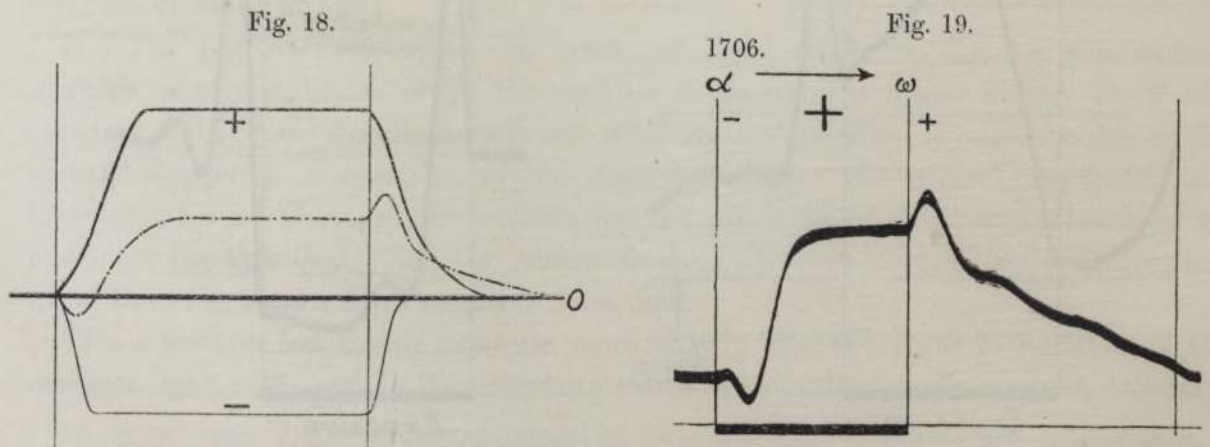


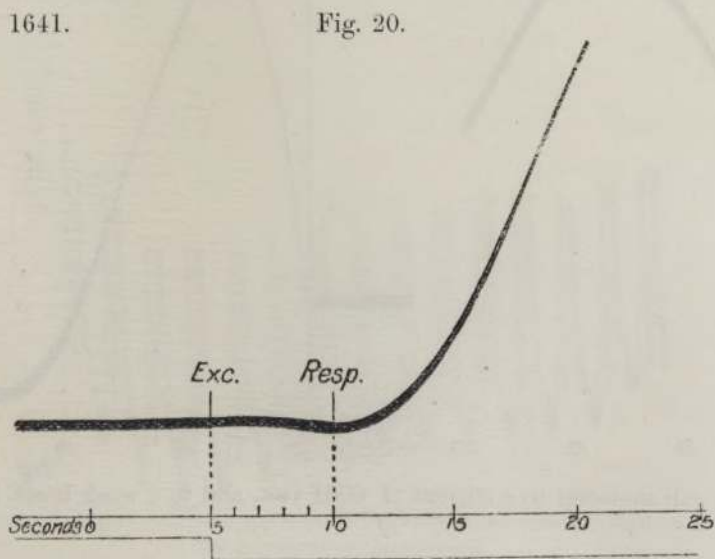
Diagram to illustrate the effect upon a galvanometer (broken line) of a simultaneous larger positive current and smaller negative current, commencing and ending more rapidly.

Retinal response of the second stage, illustrating the double effect of fig. 18.

negative effects are represented by lines above and below zero, while the broken line represents their resultant. Figs. 19, 15, 17 and 23 to 26a are reproductions of instances in which the struggle between + and -, at make of light, is evident.

Lost Time.—Quite early in this investigation, observing on the galvanometer scale the effect of a flash of light upon eyeballs of the second stage, I was surprised to notice the extraordinary length of time elapsing between flash and deflection, extraordinary in relation to the values given by previous observers, viz., less than $\frac{1}{10}$ th second (DEWAR and M'KENDRICK), less than $\frac{1}{100}$ th second (S. FUCHS). The times under my observation could be noted by stop-watch, and were 3 to 5, and in one case as high as 7 seconds. Such an interval is altogether in excess of any possible physiological lost time, and highly suggestive of a period of hesitation, during which two opposed currents were developed from the retina at nearly equal rates. Graphically recorded, this false period of latency or "period of hesitation" is remarkably distinct, altogether deceptive and unintelligible otherwise than on the theory of opposition which was first suggested by the regular terminal *plus*, and confirmed by the occasional initial *minus*.

Fig. 20 is a well-marked instance of it, exhibiting little or no visible sign of predominance in either direction during a period of hesitation lasting 5 seconds.



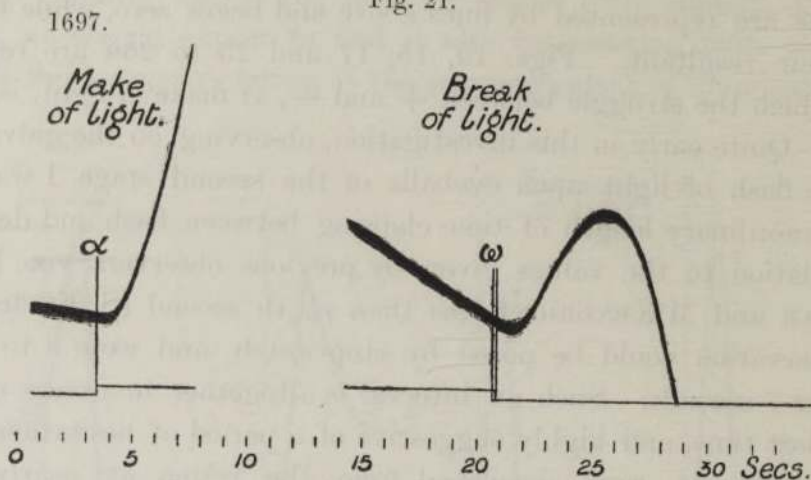
Period of hesitation or false latent period of retinal response to light (25 units). Presumably due to initial congruity of positive and negative effects. Second stage.

Fig. 21 gives lost times of initial and terminal effects.

Fig. 22 gives lost time of galvanometer itself.

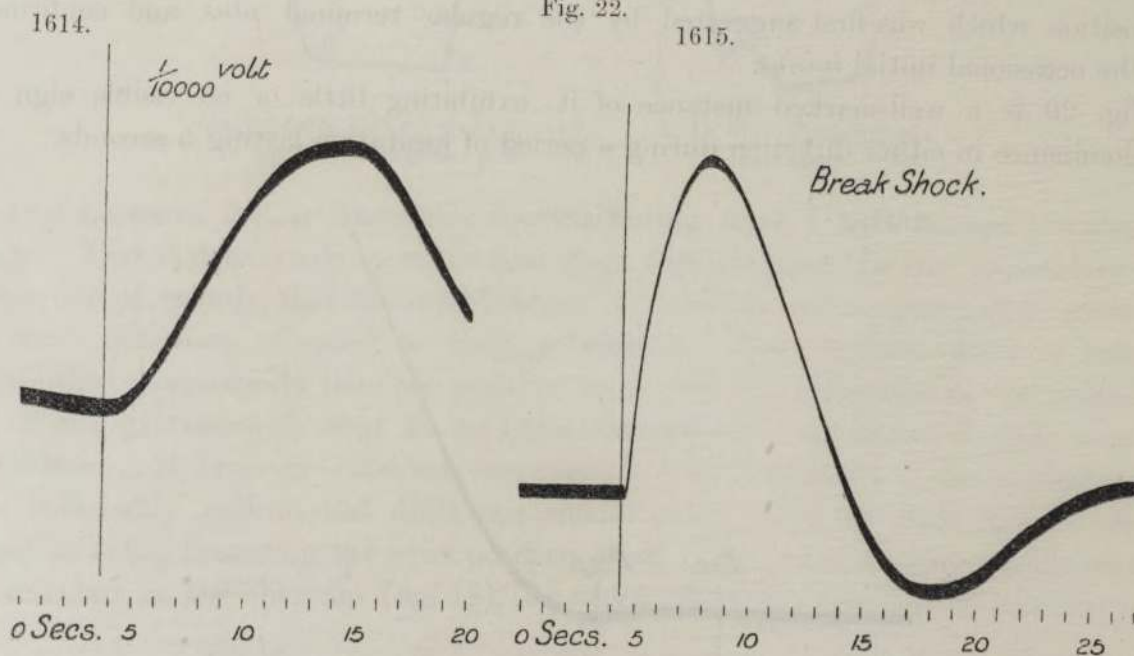
The method I adopted, although amply sufficing for my present purpose, viz., to show the extraordinary length of the period of hesitation, was obviously unadapted to a determination of a true latent period of retinal response by reason of the inertia of the magnet itself, and I accordingly did not attempt to use it for the latter

Fig. 21.



Apparent latency of retinal response at beginning and end of illumination (25 units). First stage.

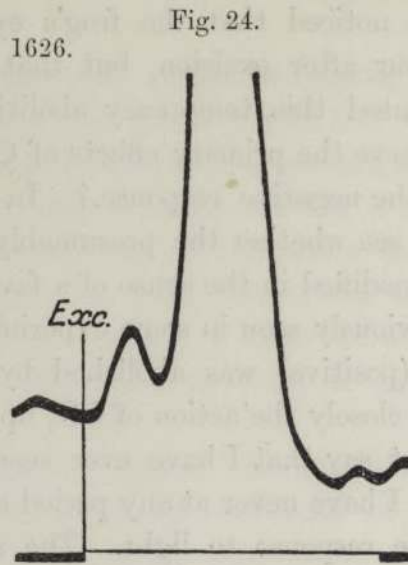
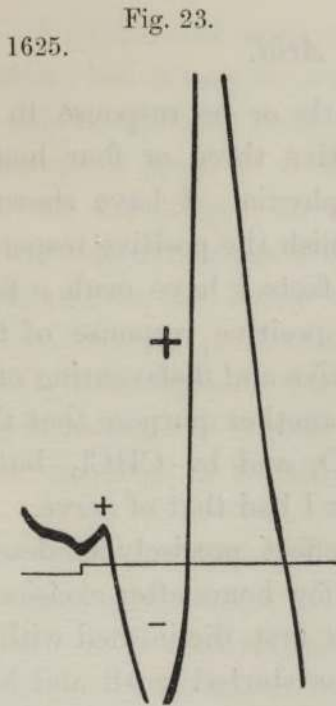
Fig. 22.



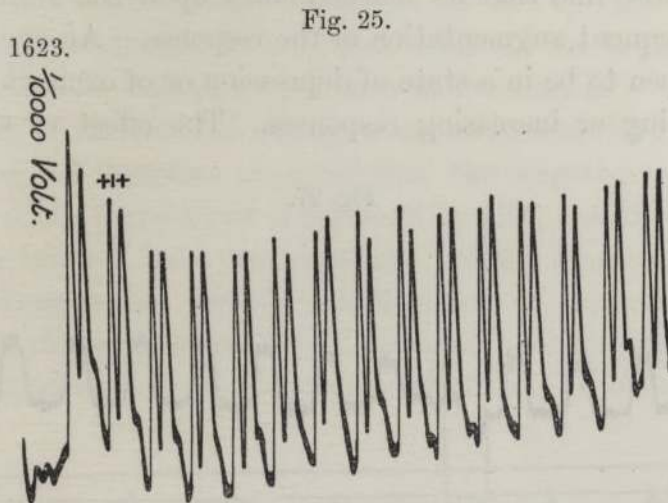
Lost time of the galvanometer to a current of .0001 volt, and to a weak break induction shock.

purpose. At most I have ventured to compare by this means the lost times of make and of break of light, and have found that whereas in the first stage no gross difference is to be detected, in the second stage the lost time of make considerably exceeds the lost time of break—by a gross difference that is to be measured in seconds, and that I have spoken of as the period of hesitation.

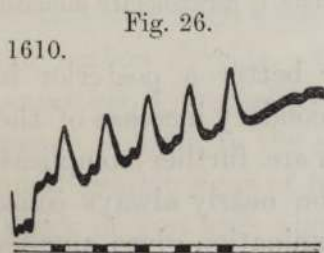
Once recognised, the fact of a struggle of opposite effects taking place at the make of light is recognisable in another form that occasionally presents itself, viz., as an initial + interrupted by a brief -, and then passing into the large + of make. (*Vide* figs. 23, 24, 25, 26.)



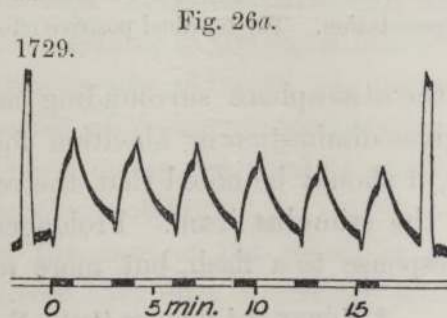
Initial effects at the commencement of illumination, showing evidence of a struggle between positive and negative currents. The first positive movement is interrupted by a negative movement.



Series of retinal responses to light. The apparent reduplication of effect is due to a positive, interrupted by a negative, movement.



Another variety of record, simulating an auriculo-ventricular rhythm, but due to the same cause, viz., an initial positive effect checked by a negative effect. (See also fig. 15.)



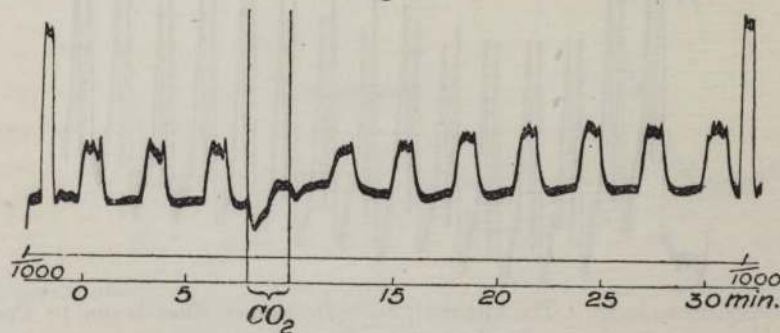
Series of retinal responses on the same type as that of fig. 19. Standard deflection by .001 volt at beginning and end of observation.

§ 10. *Action of Carbonic Acid.*

KÜHNE noticed that the frog's eyeball gave little or no response to light half to one hour after excision, but that it became active three or four hours later.* He attributed this temporary abolition to local asphyxia. I have shown that as regards nerve the primary effects of CO_2 are to diminish the positive response and to increase the negative response.† In view of these facts I have made a few experiments to see whether the presumably negative-cum-positive response of the retina could be modified in the sense of a favouring of negative and disfavouring of positive. I had previously seen in some experiments made for another purpose that the retinal response (positive) was abolished by CO_2 , by Et_2O , and by CHCl_3 , but had not examined closely the action of CO_2 upon the retina as I had that of nerve.

I cannot say that I have ever seen the eyeball effect precisely as described by KÜHNE. I have never at any period during the first few hours after excision failed to obtain the response to light. The response has at first diminished with lapse of time, and subsequently increased. Sometimes it has started small and has subsequently become considerable. The event apparently depends upon the state of the eyeball at the time of excision. Like KÜHNE I find that carbonic acid can abolish the response, but I also find that its marked effect upon the retina as upon nerve is to give rise to subsequent augmentation of the response. An eyeball placed on the electrodes may happen to be in a state of depression or of excitation by CO_2 and give a series of diminishing or increasing responses. The effect of CO_2 experimentally

Fig. 27.



Influence of carbon dioxide upon the normal retinal response to light. Diminution followed by augmentation. The terminal positive effect at break of light is permanently diminished.

added to the atmosphere surrounding an eyeball, or better a posterior half of the eyeball, gives diminution or abolition followed by secondary increase of the response. Moreover, it should be noted that the retinal effects are further complicated by the action of the stimulus itself. Prolonged illumination nearly always causes diminution of response to a flash, but more moderate illumination gives augmentation of

* KÜHNE and STEINER (1st), 'Netzhaut,' p. 359; (2nd), 'Sehorgane,' p. 24.

† A. D. W., 'Phil. Trans.,' B, vol. 188, 1897, p. 21.

response. A rhythmical series of moderately brief stimuli exhibits generally little or no diminution, but it may be reinforced, and then give evidence of fatigue or reduced and then exhibit staircase increase.

One remarkable point of contrast between nerve and retina as regards the action of CO_2 is the following: In the case of nerve the primary effect of CO_2 is to augment the negative response of fresh nerve and to diminish the positive response of stale nerve, and in the latter case the typical and striking effect is a reversal of response by CO_2 from positive to negative.* In the case of the retina the primary effect of CO_2 is to augment the positive response of a fresh retina, and to diminish the negative response of a stale retina. Hitherto, however, I have not witnessed a conversion of retinal $-$ to retinal $+$ analogous with the conversion of nerve $+$ to nerve $-$.

Another difference between nerve and retina as regards the action of CO_2 is obviously dependent upon a difference in the physical conditions of the two experiments. It is relatively easier to obtain the primary augmentation of response in the case of the retina and the full depressant effect in the case of the nerve. Primary augmentation is an effect of little CO_2 , the full depressant effect is produced by much CO_2 , and it is obviously easier to get the full effect upon the naked nerve of small mass than in a retina deeply imbedded in the eyeball. The full effect is accordingly more easily obtained on a fundus than on the intact eyeball, and still more easily obtained on an isolated retina than on the fundus.

The regular effect of carbon dioxide upon nerve in the third stage is to diminish the positive response. I therefore expected that the negative response of retina in the third stage would be found to be diminished by CO_2 . And this was found to be the case in the few trials I have made of the point. Moreover, a very constant feature in all the photographic records that I possess of the action of CO_2 upon the positive deflection is the suppression of the terminal positive kick, which I attribute to the sudden cessation of a masked negative deflection. (*Vide supra*, fig. 27.)

§ 11. *Effects after Tetanisation.*

I have in a previous paper offered evidence that tetanised nerve exhibits signs of metabolism, and that such signs are throughout similar to the signs characteristic of the action of carbon dioxide. Guided by the results obtained on nerve by prolonged tetanisation, I proceeded to test the effect of prolonged tetanisation upon the retinal response to light, in the expectation that a retina provoked to activity in this manner should exhibit signs of increased molecular mobility.

And in point of fact such signs appear in the case of the retina in even more striking degree than in that of nerve. Moreover they offer a distinct advantage in

* *Loc. cit.*, p. 30.

that the stimulus is by light. 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.

The experiment is extremely simple, and I have not yet seen it fail.

With connections as in fig. 33, the response to light is observed (or recorded), then

Fig. 33.

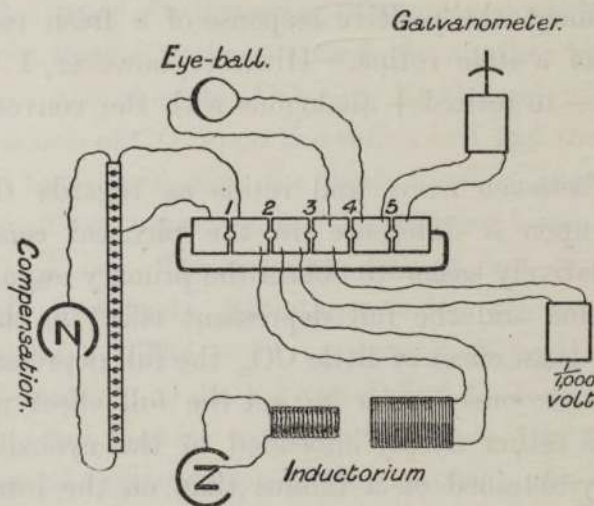
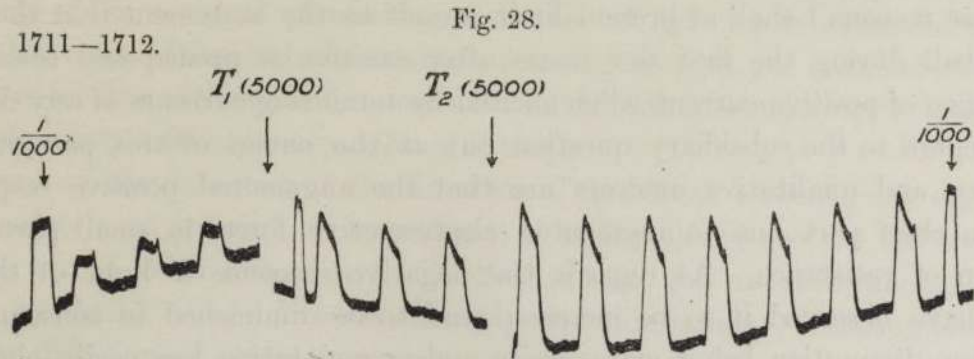


Diagram of connections.

the eyeball is tetanised by alternating make and break induction-currents sent through the eyeball in both pairs of directions, the galvanometer being cut out of circuit at plug 5. At the end of a minute, more or less, the galvanometer is unplugged, current aroused by the disturbance of tetanisation is compensated, and as soon as the spot is steady, the response to light is again observed. The augmentation, which may amount to $\times 2$ or $\times 3$, lasts for a considerable time—half an hour or an hour or more—the effect being indeed even more marked and striking than in the case of nerve. The retina is quite surprisingly resistant, even to strong electrical currents, far in excess of such as are sufficient to diminish or permanently abolish the negative response of nerve. The physical conditions appear to be more favourable in the case of embedded retina than in that of naked nerve to the manifestation of effects caused by internal products of activity. In my hands the strongest currents have failed to permanently abolish the retinal response to light, which has at most been temporarily diminished even by currents with which I sought to effect its abolition.

The following numbers, and the figs. 28 and 31, will sufficiently illustrate the facts :—

					Deflection by light at 25 units for 1 minute.	
Exp. 1.	Tetani-	at 5000	units (Berne coil)	for 1 minute	{ before . . .	+ 14
					{ after . . .	+ 19 + 25
						+ 30 + 28
" 2.	"	"	"	5 minutes	{ before . . .	+ 23
					{ after . . .	+ 8 + 21
						+ 25
" 3.	"	"	"	1 minute	{ before . . .	+ 15
					{ after . . .	+ 30 + 40
" 4.	"	"	"	"	{ before . . .	+ 3
					{ after . . .	+ 35
" 5.	"	"	"	"	{ before . . .	+ 5 .00010 volt.
					{ after . . .	+ 9 .00018 "
" 6.	"	"	"	"	{ before . . .	+ 11 .00011 "
					{ after . . .	+ 37 .00037 "
" 7.	"	"	"	"	{ before . . .	+ 11 .00011 "
					{ after . . .	+ 30 .00030 "



Influence of tetanisation upon the normal retinal response to light. Ordinary arrangement of induction coil, fed by two Leclanché cells. Secondary coil at 9 centims. (5000 units on Berne scale). Two periods of tetanisation, T_1 and T_2 , each lasting 1 minute. After the first tetanisation the positive response is considerably augmented, and falls during illumination. The terminal positive deflection at break of light is abolished. After the second tetanisation the positive response is further augmented.

Augmentation of the positive response to light is the principal and typical after-effect of tetanisation of the retina. Many points of inquiry arise from this principal fact. What are the effects upon the response to light during tetanisation? What are the effects during and after tetanisation upon a retinal response of the third stage? Is the alteration due to an augmentation of electromotive force or to a diminution of resistance, or to both factors concurrently?

I have to some extent investigated all these several points, but in so doing have become involved in a group of considerations that are, in my opinion, important to further study of the electrical activity of the retina, but that cannot be fully disengaged from their non-physiological concomitants without considerable care and labour.

The case stands thus:—In addition to the alterations of response to light, there are produced in the living eyeball in consequence of electrical excitation—(1) An

alteration of the normal current in a positive direction, *i.e.*, in the same direction as its exciting current; and (2) an alteration in a negative direction, *i.e.*, in the opposite direction to its exciting current. The first of these currents is physiological and occurs only on the living eye, the second is physical and occurs with or against the first on the living eye, and alone on the dead eye; it is the ordinary counter-current of electrolytic polarisation.

Tetanisation by alternating makes and breaks is a particularly complicated case, inasmuch as we have unequally exciting currents that elicit unequal polarisation currents. Once outside the clear case of a large positive effect or after-effect caused by *both* directions of tetanisation, matters become exceedingly complicated. We shall find it necessary for further intelligence of the facts to study the effects of single induction shocks and of single condenser discharges. We shall also do well to avoid for the present further complication by considering the effects upon retinal responses of other than the first stage.

For these reasons I shall at present limit myself to the statement that the normal living eyeball during the first few hours after excision is predisposed towards the manifestation of positive current when excited by tetanising currents of any direction.

With regard to the subsidiary question put at the outset of this paragraph, the preliminary and qualitative answers are that the augmented positive response to light is in chief part due to augmented electromotive force, in small part due to diminution of resistance. As regards the negative response to light of the third stage, I have observed it to be increased and to be diminished in consequence of tetanisation, diminution being more easily and augmentation less easily obtained of the negative than of the positive response. The effect *during* tetanisation upon positive response of the first stage will be described in the next paragraph. As regards the points of the present paragraph I repeat as definitely acquired:—

1. That subsequent to tetanisation the positive response to light is augmented.
2. That the eyeball during the first few hours after excision gives after tetanisation of any direction a large after-effect, causing the spot to fly off the scale in the positive direction. Its ordinary designation in my laboratory is the "retinal blaze," and it can be quite easily distinguished from
3. An after effect in the direction of the break-shock, witnessed on the dead and moribund eyeball, reversed by reversal of tetanisation, due to superiority of polarisation by make induction shocks over polarisation by break induction shocks.*

The after-effects of tetanisation as regards retinae in the third and second stages are, by reason of this last complication, reserved for future consideration.

* A. D. W., 'Proc. Physiol. Soc.,' November 12, 1898.

§ 12. *Effects during Tetanisation.*

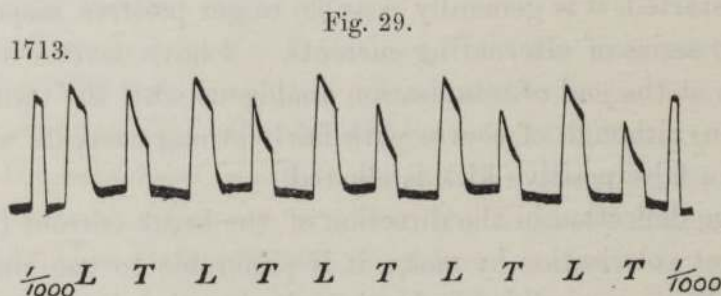
In the course of preliminary trials of the after-effects of tetanisation, it was evident that the positive retinal after-effect was the prolongation of a positive effect occurring during the passage of the tetanising currents.

The practical difficulty in the way of a close examination of the effects produced *during* tetanisation consists in the necessity of conjoining in one circuit the eyeball, inductorium, and galvanometer (fig. 33, by removal of plugs 2, 4, and 5), so that any inequalities of interruptor give an unsteady spot; and in most cases the currents have to be taken of such strength that the galvanometer is influenced by the first make and last break of each series of currents. Nevertheless, with a regular interruptor and by gradual approximation of the secondary to the primary coil after the current has been started, it is generally possible to get positive response to both pairs of direction of the series of alternating currents. I have never witnessed a terminal positive deflection at the end of tetanisation analogous with the terminal effect at the end of illumination, although of course with fairly strong currents with break in the positive direction a false positive kick is elicited.

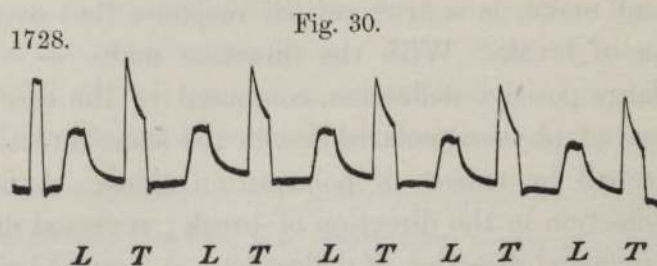
By reason of the deflection in the direction of the break current (*vide supra*, § 11), due to predominant polarisation by make, it is preferable to use the coil with Helmholtz side wire. With unmodified induction shocks, the direction should be taken make $+ \rightarrow$, break $- \leftarrow$, in which case a positive deflection \rightarrow during tetanisation, *i.e.*, in the direction of make, is a true retinal response that overcomes the physical effect in the direction of break. With the direction make $- \leftarrow$, break $+ \rightarrow$, we obtain, it is true, a large positive deflection, composed in the case of a living eyeball of retinal response and of physical polarisation in the same direction, but also obtainable on the dead eyeball by reason of polarisation alone. A dead eyeball during tetanisation gives deflection in the direction of break; reversed direction of tetanisation gives therefore reversed direction of deflection. A normal living eyeball, in spite of this effect, gives positive deflection to both pairs of direction of tetanisation. Intermediate and often complicated effects present themselves in the case of moribund eyeballs, and I have therefore confined my observations to the clear case of positive response to both directions of tetanisation.

The chief point of interest in connection with this true positive response to tetanisation is the following: Comparing the fatigue effects of retina and of muscle (*vide supra*, § 5), it is perhaps not strictly allowable to take effects of electrical excitation in the case of muscle and effects of luminous excitation in the case of retina. Nevertheless I regard the comparison as a legitimate confrontation of two definite physiological processes—one in muscle aroused from nerve *via* the end-organ of nerve in muscle, the other in the retina directly excited by its natural physiological excitant light. The apparent fatigue in muscle excited

through its nerve is in reality, as I have urged elsewhere,* fatigue of the motor-end plate. The fatigue of muscle directly excited electrically is not, however, *markedly* different as regards its rate of development from the fatigue of muscle excited by electrical stimulation. The fatigue in either case is the expression of physiological change. The fatigue of the retina by light is equally certainly the expression of a physiological change. And now I find that fatigue of the retina by tetanisation runs a nearly parallel course with fatigue of the retina by luminous stimulation. This last comparison justifies then a study of fatigue of the retina by tetanisation, which has as its closest counterpart fatigue of muscle by tetanisation. And from the whole of the preceding argument it follows that we may legitimately compare, on the one hand, the apparent fatigue of muscle, whether directly tetanised or physiologically excited through its nerve, and, on the other hand, fatigue of the retina directly tetanised or physiologically excited.



Series of normal positive responses to light and to tetanisation, alternating. Light at 25 units. Coil at 75 units of Berne scale.



Similar experiment ; coil at 40 units. The numerical measurements of these two records are given in the text.

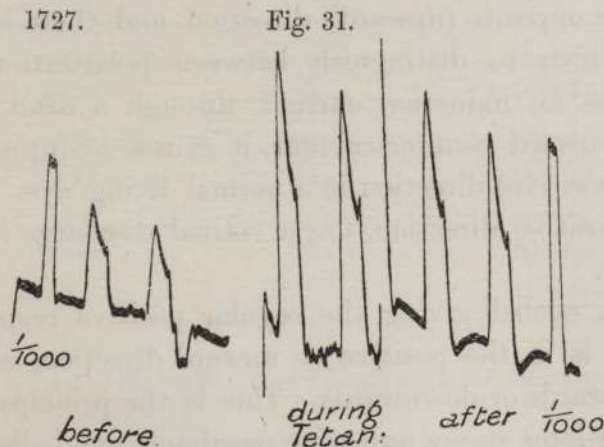
In any case, however, and quite apart from any comparison with signs of expenditure in other tissue, the bare fact as regards the retina considered alone preserves all its interest, viz., that tetanisation like light provokes positive response, and that the two kinds of response wear out in a parallel manner. I should add that the parallelism is not always absolute, that sometimes I have found large response to light with small response to tetanisation, and at other times a reversed relation. These exceptions do not, however, disturb the evidential value of instances in which parallelism has been clear. They have probably had their origin in polarisation, which had more or less added to or subtracted from the physiological response.

* Reports to the Scientific Grants Committee of the British Medical Association, 'B. M. J.,' July 1885 and July 1886.

	(1713.)		(1728.)		(1730.)	
	Defl.	Volt.	Defl.	Volt.	Defl.	Volt.
Light . . .	+ 15.5	.00115	+ 7.5	.00053	+ 8	.00089
Tetan. . .	+ 13	.00096	+ 16	.00115	+ 25	.00278
Light . . .	+ 15	.00112	+ 7	.00050	+ 11.5	.00128
Tetan. . .	+ 11.5	.00085	+ 14	.00110	+ 21.5	.00239
Light . . .	+ 15.5	.00115	+ 6.5	.00046	+ 10	.00110
Tetan. . .	+ 11	.00082	+ 13	.00093	+ 21.5	.00239
Light . . .	+ 15	.00112	+ 6	.00043	+ 10	.00110
Tetan. . .	+ 10.5	.00078	+ 12.5	.00090	+ 21	.00234
Light . . .	+ 15	.00112	+ 6	.00043	+ 10	.00110
Tetan. . .	+ 10	.00074	+ 12	.00086	+ 20.5	.00229

Three observations of retinal response to alternate illumination and tetanisation for periods of 1 minute each at 2-minute intervals. Break induction current in positive direction. Berne coil fed by two Leclanché cells. Secondary coil 245 millims. distant from primary (= 40 units). Illumination by standard candle at 2 feet (= 25 units).

Up to this point I have described the retinal responses to electrical excitations. We have next to consider the influence of tetanisation upon the retinal response to illumination. The results of this kind of experiment quite clearly demonstrate the "mobilisation" of retinal matter by tetanisation, and are obviously free from complication or fallacy. With eyeball, galvanometer, and secondary coil in series (fig. 33, p. 148, keyboard unplugged at 2, 4, and 5) the effects of light are observed (or recorded) before, during, and after the passage of tetanising currents. The latter arouse in the retina a large and steady positive current. Illumination of the retina during this condition gives a largely augmented positive response. Subsequently to tetanisation the response to light remains considerably augmented as a rule, or, if the tetanisation has been long and strong, and the eye poor, it is temporarily diminished.



Augmentation of the normal positive response to light *during* (and *after*) tetanisation (1000 units).
 (NOTE.—The record incidentally illustrates a feature that I have not yet investigated. The standard deflection of $\frac{1}{1000}$ volt at outset of experiment = 17, at end of experiment = 27.5; this implies, if referred to diminution of resistance alone, an alteration of more than 50 per cent. The total resistance in circuit is approximately 25,000, of which the eyeball constitutes less than one-tenth. The alteration cannot therefore be referred to altered resistance. It is probably due to an electromotive effect in the same direction as the standardising current.)

	Illumin. for 1 min. by candle at 2 feet.
<i>E.g.</i> , tetanisation at 1000 units for several minutes	before . . + 20
	during . . + 58
	after . . + 15
" " "	before . . + 12
	during . . + 36
	after . . + 27

The effect produced during tetanisation by alternating induction shocks might be characterised by saying that the retina is mobilised in the positive direction, and at the same time rendered more mobile in the same direction to the stimulus of light.

§ 13. *After-effects of Single Induction Shocks.*

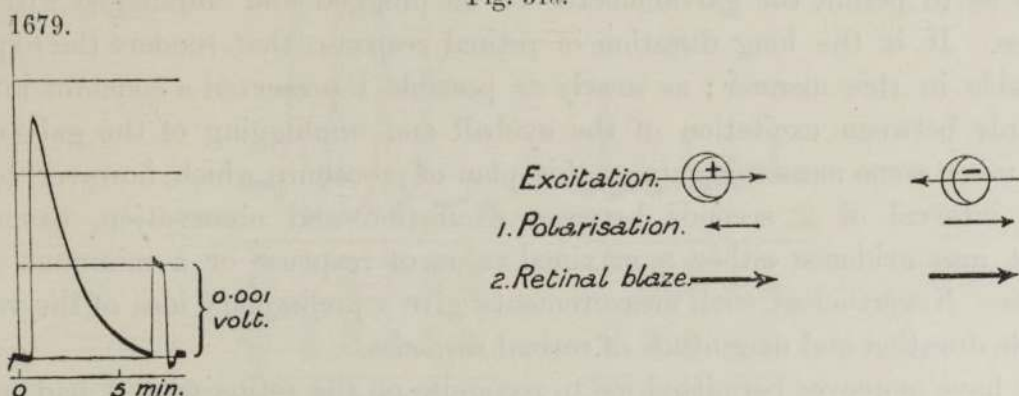
Connections are established as shown in fig. 33 (see back, p. 148). The galvanometer spot is brought exactly upon its zero mark by adjusting the compensator current, so that plugging and unplugging at 5 cause no deflection. A single induction shock is sent through the eyeball while the galvanometer is plugged out of circuit, and immediately afterwards the galvanometer is unplugged.

With a dead eyeball the deflection on unplugging the galvanometer, after a strong induction current, is of contrary direction to the direction of exciting current, indicating an ordinary polarisation counter-current. But with a living normal eyeball similarly treated the deflection is positive (*i.e.*, from fundus to cornea) whatever the direction of the exciting current. An induction current sent through an eye, whether living or dead, in the downward or negative direction causes counter-current in the opposite (upward) direction, and there is in this reaction no absolute token by which to distinguish between polarisation and physiological response. But whereas an induction current through a dead eye in the upward direction causes a downward counter-current, it causes an upward after-current in the same (upward or positive) direction in a normal living eye. In this case there is after-effect in the positive direction, *i.e.*, a retinal discharge in the same direction as the exciting current.

With a normal fresh eyeball giving the regular positive response to illumination this retinal discharge is in the positive or upward direction, whether the exciting current be directed upwards or downwards. This is the principal and most certainly demonstrable fact. At later stages and with moribund eye-balls the effects become variable. We may then witness retinal discharge upward in response to upward excitation, and downward in response to downward excitation, and finally I have once or twice obtained a downward retinal discharge in response to both directions of excitation. But I have bestowed little attention as yet upon these varieties, and I do not associate them with the three types of response to light.

They are in any case less striking and invariable than the normal positive response which I have described as the principal effect, and which is of such regularity, magnitude, and duration as to suggest comparison with the discharge of an electrical organ. I designate it as the "retinal blaze" or the "retinal discharge," and find that the normal retinal discharge in response to an induction current is positive.

Fig. 31a.



Positive retinal response to a single induction shock sent through the eyeball in the positive (upward) direction.

EXPERIMENT.—Eyeball 6 hours after Excision, giving Response to Light of Early Second Stage. Break induction shocks from a Berne Coil, fed by two Leclanché Cells.

Direction and strength of exciting current.	Deflection 2 seconds later.	Voltage.
1000 +	+ 7	+ ·000050
1000 -	+ 9	+ ·000064
2000 +	+ 28	+ ·000200
2000 -	+ 25	+ ·000179
5000 +	+ 36 × 10	+ ·002575
5000 -	+ 23 × 10	+ ·001650

§ 14. *After-effects of Condenser Discharges.*

Precisely similar after-effects are produced by condenser discharges. Positive or upward retinal response is provoked in a normal living eyeball by condenser discharges, directed either upwards or downwards. Polarisation currents of contrary direction to exciting discharges are alone elicited in the case of a dead eyeball. The experiment is most simply realised by connecting electrodes from a condenser with the keyboard of fig. 33. The condenser, battery, and Morse key are set up to deliver

discharge alone into the key-board circuit, the plugs of which are manipulated so as to excite the retina with the galvanometer cut out of the circuit, and subsequently complete the circuit of compensator, retina, and galvanometer to witness the retinal discharge that has been provoked by a previous condenser discharge. The chief case is of course positive retinal current consequent upon positive condenser current. Previous to each test any current in circuit must be exactly neutralised by compensation, so as to permit the galvanometer to be plugged and unplugged without disturbance. It is the long duration of retinal response that renders the experiment practicable in this manner; as nearly as possible I preserved a constant interval of 2 seconds between excitation of the eyeball and unplugging of the galvanometer. I have taken some measurements on this plan of procedure which, however, by reason of the interval of 2 seconds between excitation and observation, cannot have brought into evidence either a maximal value of response or a minimum value of stimulus. Nevertheless, such measurements give a preliminary idea of the very considerable duration and magnitude of retinal response.

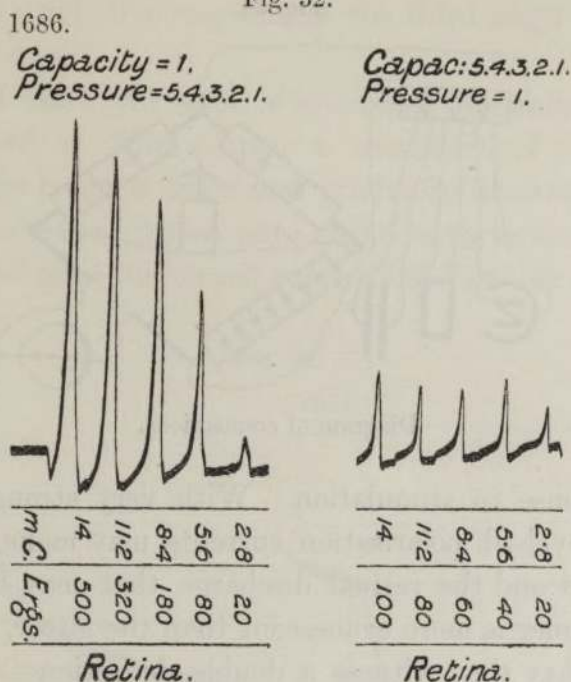
They have moreover permitted me to recognise on the retina what I had assumed, but not proved, to be the case in the electrical stimulation of nerve.* My assumption was to the effect that energy, not quantity, is the important factor in electrical stimulation. I have now made the following experiment upon the retina—delivering to it two series of stimuli by discharges through the eyeball as first described:—(A) of arithmetically increasing quantity and energy; and (B) of the same arithmetically increasing quantity, but with geometrically increasing energy. The first series of stimuli is supplied from a condenser of 2, 4, 6, 8, 10 micro-farads charged at the constant pressure of 1 Leclanché cell. The second series of stimuli by a condenser of 2 micro-farads charged at the rising scale of 1, 2, 3, 4, 5 Leclanchés. The results were as follows:—

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

* A. D. W., "The Characteristic of Nerve," 'Roy. Soc. Proc.,' 1899, p. 207.

† Taking the voltage of a Leclanché = $\sqrt{2}$ volt.

Fig. 32.



A better method of studying the positive effect of induction currents and of condenser discharges is, however, that which I first adopted to demonstrate the unequal polarisation counter-currents of make and break induced currents sent through nerve,* but which is generally applicable to any case where we desire to bring into evidence the electrical state immediately after a single short electrical stimulus. The eyeball is placed in the α arm of a Wheatstone bridge. The balancing resistance, R, is adjusted as if for a measurement of resistance, until the exciting induction shock or condenser discharge gives little or no deflection of the galvanometer. The adjustment is roughly made with weak currents, and more and more exactly with stronger and stronger currents.

And as the latter are increased, there is no difficulty in distinguishing a small sharp "inequality kick" from a comparatively large and prolonged deflection by a polarisation current or by a retinal discharge. The varying magnitudes and time-relations of the three kinds of change are such that all three may at certain current-strengths be made apparent. The inequality kick by the stimulating current is sharp, and can be taken as small as we wish, and in any desired direction, by slight variations in "too much" and "too little" at the balancing resistance. A considerable advantage of this method is that it permits us to dispense with compensation. In my first trials of the method I used carbon resistances to form the bridge, for fear of self-induction.

But I find that the Post-Office pattern of bridge answers very well for the purpose, being (at least in the two instruments I possess) apparently free from self-induction. Polarisation counter-currents in a normal living eyeball are masked by the true

* A. D. W., 'Proc. Physiol. Soc.,' November 12, 1898.

Fig. 34.

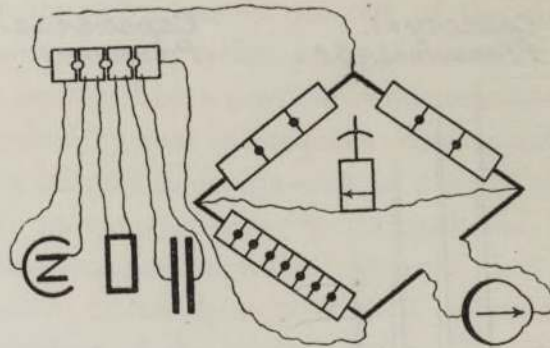


Diagram of connections.

retinal current in response to stimulation. With very strong stimuli, or with progressive death of the eyeball, polarisation currents may make their appearance. Of the polarisation current and the retinal discharge that may then be provoked by a given stimulus, the former is more evanescent than the latter, and makes its appearance first, so that we may then witness a double deflection—a first brief movement contrary to the direction of stimulation, a second prolonged movement in the direction of retinal discharge.

Another advantage of this method is that we are able at the same time to take observations of resistance under various circumstances, and to various forms of current. Without having systematically examined into this matter, I have incidentally observed that the apparent resistance (eyeball + electrodes) is higher to a make than to the corresponding break shock (*e.g.*, 19300 *versus* 18000 ω), and that it is diminished by tetanisation. The diminution (*e.g.*, 18500 *versus* 18000 ω) is, however, insufficient to account for the augmented effect of light during and after tetanisation (*vide supra*, p. 148).

§ 15. *Effect of Massage.*

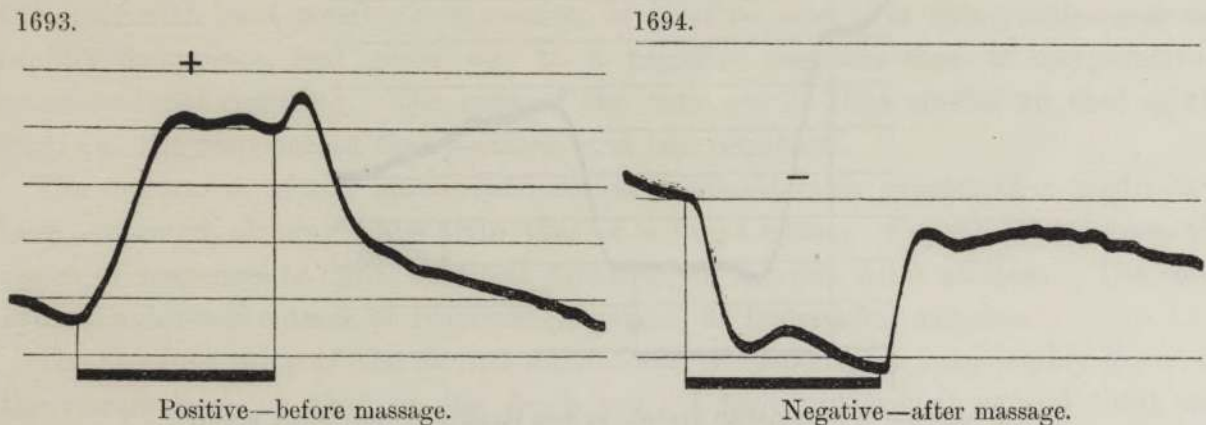
At an early stage of this investigation, and frequently during its course, I sought to obtain experimental control over the retinal response to light, and especially to find means of unmasking the negative effect which I recognised to be latent in the apparent positive response. I tried various drugs and reagents without success. I tried rise of temperature, and found that a positive response was either abolished permanently, or if temporarily abolished, that it reappeared of similar character. I tried tetanisation, and found that the positive response was thereby augmented. Finally, I tried massage, and found in this simple and apparently rough proceeding an unfailling means of effecting the desired change.

A fresh eyeball giving the typical positive response to light, if removed from the electrodes, gently rolled and pressed between the finger and thumb, and replaced upon the electrodes, will give a pure negative effect. Positive response of the first

stage has been abolished ; negative response of the third stage has been established, or rather, unmasked.

The result, as far as I have yet seen, is invariably the same, and on one occasion I carried it out without a failure upon a succession of six fresh eyeballs, the regular effect of massage being a large and gradually diminishing positive current due to disturbance of the retina, with a pure negative variation on exposure to light. If an eyeball be massaged after its normal current has become negative, the latter is

Fig. 35.



Response to light (25 units). The horizontal lines in both these records denote a scale in $\frac{1}{10000}$ ths of a volt ; *i.e.*, the resistance of the eyeball has been much diminished by massage.

greatly diminished or reversed, *i.e.*, the retina is always aroused in the direction of a positive current by massage as by tetanisation. The resistance of an eyeball after massage is always much diminished. Much stress may not be laid upon this diminution of resistance, since the eyeball has been removed from and replaced upon the electrodes. Nevertheless, the alteration is so marked and unfailing, that it can hardly be an accident of irregular contact. I regard it as being due to the same cause as the diminution of resistance by tetanisation, *viz.*, to a dissociation of retinal matter.

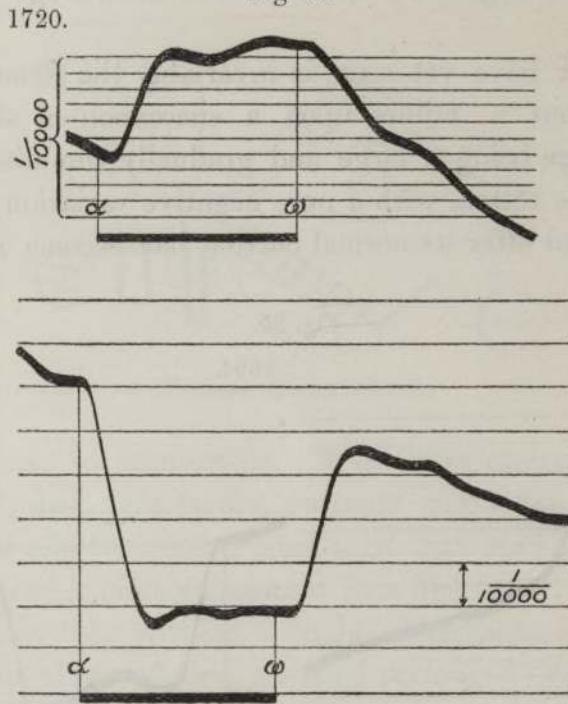
It is possible, but difficult, to massage the eyeball "too much," and to completely abolish not only the positive, but also the negative, response. It is difficult, but possible, to massage the eyeball too little, and to imperfectly convert the positive into a negative response. It is very easy to convert a positive into a negative by moderately rough manipulation.

§ 16. *Response of the Mammalian Retina.*

HOLMGREN* found the response of the mammalian eyeball (rabbit, dog, cat) to be negative at the commencement of illumination, and positive at the end of illumination, whereas in the frog's eyeball he had found the response to be positive at beginning and end of illumination. DEWAR and M'KENDRICK, in their first obser-

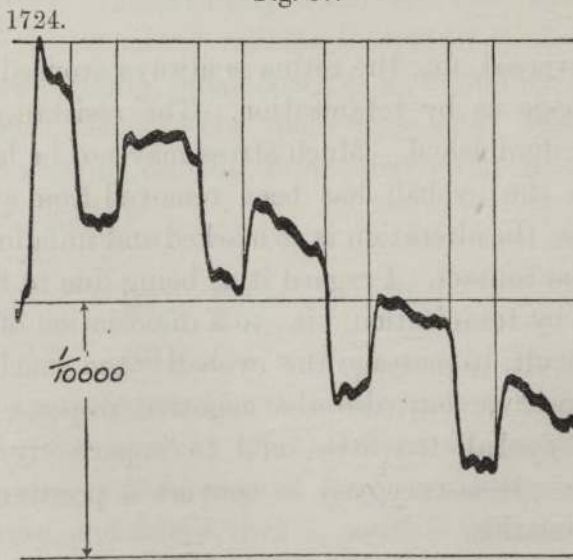
* HOLMGREN, 'Unters. Heidelberg,' vol. 3, p. 314.

Fig. 36.



Retinal response of mammalian eyeball, at first positive, subsequently negative.

Fig. 37.



Series of negative responses to light (100 units) of mammalian eyeball 9½ hours after excision. 1 minute illumination ; 2 minutes darkness. No sign of fatigue.

vations,* obtained the same effects, but in a subsequent publication† state that the action of light is the same in warm-blooded and in cold-blooded animals, viz., that

* DEWAR and M'KENDRICK, 'Trans. Roy. Soc. Edin.,' 1873, p. 149.

† DEWAR, 'Proc. Roy. Inst.,' March 31, 1876.

in all cases the response is positive on impact and positive on removal. KÜHNE and STEINER* confirm HOLMGREN'S statement that the response of the frog's eye is positive, and of mammalian eyes negative; but, commenting upon the improbability of any fundamental difference of character in the retinal excitation aroused in the two cases, are of opinion that the simple negative response of a mammalian eye signifies that the organ is moribund.

The few observations I have made upon mammalian eyes (cat) quite bear out this view, and at the same time reconcile the apparent discrepancies in the statements quoted above. I find that the response of a fresh eye (cat), carefully removed from the orbit with least possible compression, is positive, and that this positive response rapidly disappears, and gives way to a negative response that is comparatively prominent and enduring. The case of the cat's eye is thus similar to that of the frog, *i.e.*, the response, at first positive, is at last negative.

The endurance of the mammalian retina is considerably greater than might have been expected, although less than that of a frog's retina. Fig. 37 (1724) gives the series of responses to light, obtained upwards of 9 hours after excision. The same eyeball exhibited a trace of response (negative) 24 hours after excision.

The absolute value of the electromotive force of response is considerably lower on the mammalian eye than on the frog's eye. I have not seen it exceed '0001 volt in the former, whereas in the latter I have frequently found it to be above '0010 volt. I attribute the difference to the greater size of the mammalian eyeball, and consequent shunting of the galvanometer.

IV. CONCLUSIONS.

As regards the facts themselves, the principal conclusions are set forth in the paragraph headings which precede, and which may be recapitulated as follows:—

A fresh normal eyeball manifests positive current, which gradually declines to zero, and becomes reversed (p. 126).

On exposure to light the normal current, whether positive or negative, undergoes a positive variation (p. 127).

The magnitude of the response to light increases with the duration of illumination (p. 129).

The magnitude of the response to light increases with the strength of illumination (p. 130).

Fatigue—*i.e.*, diminution of response by reason of previous activity—is less pronounced in the case of the retina than in that of muscle. It is manifested in nearly the same degree to stimulation by light, and to stimulation by tetanising currents (pp. 132 and 151).

* KÜHNE and STEINER, 'I. Netzhaut,' p. 357.

Coloured lights act in the same direction, and in accordance with their luminosity. No electrical evidence is obtained of antagonistic influence (p. 136).

The response is temporarily abolished at moderately high temperature, and permanently abolished by freezing (p. 137).

The response is temporarily abolished by anæsthetics (p. 138).

With lapse of time—or immediately in consequence of partial injury, the character of the response to light alters its type. Three stages are to be recognised in accordance with the state of the retina, as (*a*) fresh; (*b*) transitional; (*c*) stale (p. 140).

In the first stage the response is positive.

In the second stage the response is mixed.

In the third stage the response is negative.

The interval of time between stimulus and response is much in excess of a physiological latent period. In the second stage this "period of hesitation" may amount to 5 seconds (p. 143).

Under the influence of carbonic acid the response to light undergoes diminution or abolition followed by secondary augmentation (p. 146).

Subsequent to tetanisation in either direction the normal current becomes strongly positive (or less negative). This positive change gradually subsides (p. 147).

The positive response to light subsequent to such tetanisation is much augmented (p. 147).

During tetanisation of moderate strength and of whatever direction the normal current becomes positive (or less negative). This positive change gradually subsides (p. 151).

Strong single induction shocks of whatever direction arouse prolonged positive after-effects, that gradually subside (p. 154).

Single condenser discharges (2 to 10 M.F., 1 to 7 volts), of whatever direction, arouse prolonged positive after-effects (p. 155).

In consequence of gentle massage of the eyeball, the normal current becomes strongly positive (or less negative). This positive change gradually subsides (p. 158).

In consequence of gentle massage of the eyeball, the positive response gives place to a negative response (p. 158).

The response of mammalian (cat's) retina to light is similar in type with that of frog's retina—viz., positive at first, subsequently negative (p. 159).

The positive response to light, the positive effect of tetanisation, and the positive after-effect of condenser discharges are suppressed by anæsthetics (ether and chloroform) and by rise of temperature (to 40–45°). The suppression may be permanent or temporary. An anæsthetised like a dead eyeball tested by single currents manifests only polarisation effects negative in direction to the exciting currents. Tetanisation then gives only polarisation effect in the direction of the break shocks, negative to the direction of the make shocks.

As regards inferences from the facts, and the theoretical signification of the latter, I am very unwilling to commit myself too absolutely to any theoretical conclusions. I believe it to be proved by these observations that the retina is the seat of a double electrical movement, a simultaneous positive and negative effect, but whether this double effect is the expression of duplex change in one substance, or of two changes in two different components, cannot be strictly demonstrated, and must remain matter of opinion. I am of the opinion that we have to do with a duplex change, constructive and disruptive, in one substance. The further question as to the correspondence of the two hypothetical movements with the two obvious electrical movements appears to me to be an open question. KÜHNE and STEINER, without committing themselves very absolutely, indicate as their opinion that a positive electrical effect is the token of regeneration, and a negative electrical effect the token of decomposition. I have no serious objection to this view, nevertheless I hesitate to adopt it, by reason of the effects of carbon dioxide and of tetanisation upon the electrical signs. These, as far as I have yet seen, are in the sense of an analogy between positive variations in retina with negative variations in nerve, and between negative effects in retina with positive effects in nerve. Positive and negative are, however, purely relative and conventional qualifications, of no essential significance.

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