COMMUNICATIONS

THE ELECTRICAL RESPONSE OF THE EYE TO LIGHT

BY

SIR JOHN PARSONS, F.R.S.

The researches of Keith Lucas (1909-1914), extended by Adrian, have shown that every nerve impulse in the body is accompanied by an electrical response. After a short latent period the stimulus sets up a train of changes in potential following each other in rapid succession, varying from 10 to 300 per second. Each response is followed by a short refractory period of 2-3 $\sigma \left( \sigma = \frac{1}{1000} \text{th. sec.} \right)$ during which no stimulus, however strong, produces any response. The response is of the "all-or-none" type, i.e., if it is above the threshold it produces the same change in potential. Increase in strength of the stimulus merely increases the frequency of the waves of electrical change. The normal, so-called "adequate," stimulus of any sensory end organ produces exactly the same type of discharge in the nerve as stimulation of the nerve by artificial means, e.g., an electric shock. These comparatively simple laws are found to hold good for all nerves, both efferent and afferent. The changes are so rapid that abolition of inertia in the recording apparatus is of the greatest importance. The replacement of the capillary electrometer, used in the early experiments, by the string galvanometer was a great advance, further improved by the enormous magnification which thermionic valve amplifiers provide.
If non-polarizable electrodes are placed on the cornea and optic nerve of an animal and are joined by a wire, with a galvanometer in the circuit, it is found that a current flows from the cornea through the galvanometer towards the optic nerve (du Bois-Reymond, 1849). This, the *current of rest*, has a difference of potential of 7 to 9 millivolts, and is probably the integration of several changes of potential, some of which are purely physical, others physiological. The Donnan difference of potential between blood and aqueous is probably one purely physical factor. It is found, however, that, so far as the retina is concerned, the retinal factor is always of such a nature that the neuroepithelial layer is negative to the nerve-fibre layer; so that the direction of the current outside the retina is in opposite directions in vertebrates and invertebrates (Brücke and Garten, 1907; Riedel, 1918), since the neuroepithelium is directed away from and towards the anterior part of the eye respectively in these groups.

If the current of rest is compensated for and light is thrown upon the eye a *current of action* is induced (Holmgren, 1865), but only so long as the eye survives: it is abolished by removal of the retina from the eye (Dewar and M’Kendrick, 1873), and by anaesthetics. The first accurate measurements were made by Gotch (1903-4) with the capillary electrometer. He showed that in the frog monochromatic red light gave a latent period of 0.3 sec. and a difference of potential of 0.4 millivolt; green 0.2 sec. and 0.5 m v; violet 0.25 sec. and 0.24 m v. The researches of many observers, especially those of Piper (1904-11), Einthoven and Jolly (1909), Kohlrausch (1913-25), Adrian and Matthews (1927) and Granit and his co-workers (1933), have shown that the typical response is as follows (Fig. 1). (1) A latent period; (2) a very brief negative phase (a); (3) a rapid steep initial positive phase (b); (4) a slow depression; (5) a slow secondary positive
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phase \((c)\), persisting for a long time under continued stimulation. On removal of the light there is \((6)\) a short latent period; \((7)\) a sharp positive phase \((d)\) gradually diminishing to the resting state.

The general trend of the responses and especially the unexpected negative phase \((a)\) and the strong positive phase \((d)\) on removal of the light, indicate that the reaction is of a composite character. This is not surprising in view of the fact that at least three, and probably far more, neurones are involved. It cannot be doubted that complete analysis of the response would throw a flood of light on the physiology of vision, and the preliminary steps, taken particularly by Piper, Einthoven and Jolly, Adrian, and Granit, confirm this expectation.

In the first place, there is no doubt that the current originates in the retina, for it is abolished if the retina is removed (Dewar and M‘Kendrick, 1873), but remains unchanged if the anterior part of the eye is removed (Bowie, Chaffee and Hampson, 1923). The curve is much simpler in cephalopods (Beck, 1899; Piper, 1911; Fröhlich, 1913), probably owing to the greater simplicity of the retina and the aggregation of the ganglion cells in a mass posterior to the eyeball. Arthropod eyes show transitions towards the mammalian type of curve (Hartline, 1927). The \(a\) and \(d\) responses are more marked in fishes, amphibia, reptiles, and birds than in mammals. In extirpated frog’s eyes the difference of potential may reach 2-8 m v, but is usually less than 1 m v in warm-blooded animals.

The difference of potential varies with the position of electrodes (de Haas, 1903; Westerlund, 1912), being greatest between the anterior and posterior poles (Westerlund). Loss of vitality (Kühne and Steiner, 1880) injury massage (e.g., Waller, 1903, 1909; Jolly, 1909), cold (Nikiforowsky, 1911), some drugs, e.g., K, Ba, in less degree Mg, and Ca salts added to the Ringer’s solution (Beuchelt, 1921), tend to eliminate the \(b\) response and emphasize the \(a\) and \(d\) responses. With temperature and drugs the reactions are reversible. Asphyxia eliminates the \(b\) response, but the \(c\) response is retained if the eye is dark-adapted (Kohlrausch, 1918); this reaction is also reversible. With progressive narcotization in the decerebrate cat the \(c\) response disappears first; the other responses are diminished (vide infra).

Adaptation. The sensitivity of the retina to light is enormously increased by prolonged \((\frac{1}{2}\) hr. or more) exclusion of light from the eye. When in a condition of dark-adaptation vision is said to be scotopic, in light-adaptation photopic.

The effect on the electroretinogram of change from dark- to light-adaptation differs in different anima’s. Generally speaking the reaction is greater in scotopia (Kühne and Steiner, 1880; Brücke & Garten, 1907). As the eye becomes light-adapted the
latent period is increased, the a response is generally increased, the b wave is diminished and rises less steeply, the c wave is abolished, and the d wave enhanced (cf. Fig. 10).

An almost pure b curve can be obtained with the frog’s eye by good dark-adaptation and a stimulus of 0.5-1 sec. with very weak light (Einthoven and Jolly, 1909). With a strong stimulus applied to the photopic eye the a and d waves are always manifest, and under all circumstances these vary together.

Variations of great theoretical interest occur in different animals. These appear to be related to their evolutionary status, retinal structure, and habits of life. It is impossible at present to correlate the electrical reactions with retinal structure, but it cannot be doubted that these reactions, however apparently contradictory at present, will throw much light on the problem.

It has been found by Kohlrausch (1918) that in pigeons and fowls, which are essentially diurnal birds, the c wave is present only in the condition of light-adaptation, and diminishes with dark-adaptation, the reaction being reversible. Other diurnal animals, such as the turtle (Emys europæa), buzzard, and probably the dog behave similarly; whereas nocturnal animals, such as the pike, salamander, owl, and rabbit behave like the frog. It has already been pointed out that the secondary positive c response is abolished by light-adaptation in amphibian and mammalian eyes. The other phases are more difficult to eliminate. Waller (1909) showed that after massage it was possible to obtain a purely negative response in the frog—an initial fall with the latent period of the a wave and a quick rise to the base line on cessation of stimulation. Granit and Riddell (1934) confirmed this observation except that they failed to obtain complete cessation of the b response. It has been shown by Nikiforowsky (1912) and Tirala (1917) that the b and d responses may vary independently. During light-adaptation the b wave remains practically constant; adaptation is essentially associated with the a wave.
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Narcotization affords another means of analysis of the curve. Working on the dark-adapted eye of the decerebrate cat Granit (1933) used two intensities of stimulation, viz., 14 millilamberts and 0.14 ml. The a and d waves are present only with high intensities or large areas of stimulation. Diminution of area stimulated acts like diminution of intensity, showing abolition of the a, c, and d waves. The c wave is eliminated by small doses of ether, leaving the more rapid a and b waves unaltered, the d effect being enhanced. The c wave itself, however, is composite, for though the major part is abolished by slight anaesthesia,

![Graph](http://bjo.bmj.com/)

**Fig. 3.**
Decerebrate cat. Progressive effect of anaesthesia with stimulus of 1.4 millilambert. A, before narcotization; B, after 21 minutes of anaesthesia; C, after 31 minutes b-wave in A = 0.417 mv. (Granit, 1933.)

deeper anaesthesia is necessary to abolish the remainder. At high intensity of stimulus ether abolishes 50 per cent. of the rise, whereas at low intensities only about 8 per cent. diminution occurs. Further narcotization slows and diminishes the b wave and lengthens its latent period. Similarly the negative a response becomes slower with longer latent period. In the final stage only the negative component persists (Fig. 3).

**Wave-length.** It has already been mentioned that Gotch (1903-4) measured the electrical reactions of the frog's eye to prolonged stimulation with white and monochromatic red, green and violet lights. The reactions of the dark-adapted frog's eye to momentary (1/15 sec.) stimulation with white, red, and blue lights are shown in Fig. 4 (Kohlrausch, 1925). The filters were so arranged that the b waves were practically equal; it will be noted that the c wave is negligible with red, and much enhanced with blue light.
The photoelectric effects of monochromatic spectral lights have been studied by Dewar and M’Kendrick (1876), Holmgren (1880), and Waller (1903) on the frog, and by Chatin (1880) on insects, crustacea, and molluscs. They found that the brighter parts of the spectrum, yellow and green, give stronger responses than the red or blue. Himstedt and Nagel (1900) and Piper (1904-5) made comparative estimates throughout the spectrum. Himstedt and Nagel found that the maximum with fairly strong stimuli for the light-adapted frog was at about 586 mm; feeble stimuli for the dark-adapted frog about 550 mm. The photoelectric response curves resemble nearly the photopic and scotopic luminosity curves of man. The shift of the maximum is the same in each case, thus proving that the Purkinje phenomenon manifests itself already in the retina and is therefore not fundamentally dependent upon central nervous processes. Piper showed that diurnal birds (pigeon, fowl, buzzard) gave the photopic reaction; nocturnal birds (owls) the scotopic reaction, as did also dogs, cats and rabbits irrespective of the condition of adaptation. There is a still further striking shift of the curve in the cephalopod eye (Piper).

Kohlrausch and Brossa (1914) and Kohlrausch (1918) found that with diminishing wave-length the a and c waves become enhanced, markedly in the photopic frog and diurnal birds, very slightly in the scotopic frog and nocturnal birds. Kahn and Löwenstein (1924), Hartline (1925), and Sachs (1929) have demonstrated the same fact for man.
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It is interesting to note that Kohlrausch (1918) has shown that the response with purple light in the pigeon is an exact interference curve due to summation of the red and blue responses.

The Optic nerve Response. Before discussing the more complex problem of the effects of variations in intensity, area, and time of exposure of the stimulus upon the electroretinogram it will be well to review our knowledge of the simpler problem of the response in the optic nerve—knowledge which we owe chiefly to Adrian.

Ishihara (1906) and Westerlund (1912) had already shown that the typical positive "on" and "off" effects of the retinal response also occurred in the nerve response. Adrian's experiments were made chiefly upon the optic nerve of the conger eel, which is specially long and well suited for the purpose. In many of the experiments only the posterior part of the eye was retained, the retina was stimulated with light, and both electrodes were applied to the nerve, with an interval between them. Adrian and Matthews (1927-8), as already mentioned, showed that the responses in the optic nerve agreed in all respects with the responses in other nerves. Changes in intensity of the stimulus therefore do not cause changes in intensity of the reaction, but manifest themselves as changes in the frequency of periodic oscillations.

Fig. 5 shows the typical response of a dark-adapted eye to steady (3 secs.) illumination and the effect of altering the area of retina illuminated. There is a latent period of about 0.2 sec., followed by a sudden outburst of very rapid oscillations. The oscillations diminish in frequency, rapidly at first and then more slowly, whilst the stimulus is still acting. Cessation of the excitation causes a small fall in frequency, followed by a well-marked

![Graph showing frequency of impulses per second during and after stimulation.](http://bjo.bmj.com/)
rise, after which the frequency rapidly diminishes to zero. Clearly we have here the optic nerve expression of the $b$ and $d$ waves of the electroretinogram. There is no manifest evidence of the $a$ and $c$ curves. Increase of the area or intensity of the stimulus causes shortening of the latent period and increased frequency of the oscillations.

The fall of the curve during the continuance of steady illumination is evidence of adaptation, and may be directly correlated with visual sensation; for it is well known that prolonged fixation of an illuminated surface leads to a diminution of the subjective brightness. If during exposure, a shadow is moved across the visual field, the discharge during the movement is far greater than during continuous exposure. This is already correlated with the great sensitivity of the eyes of lower animals and of the peripheral field in man to movement of objects within the field of vision.

A short stimulus (e.g., 0.125 sec.) causes a discharge of similar form lasting about 1 sec. after a latent period of about 0.2 sec. from the beginning of the stimulus. The fall of the curve is more rapid and there is no "off" effect. Feeble illumination or small area stimulated will give a similar curve with a continuous illumination, but with stronger lights and larger areas there is always

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**FIG. 6.**

Conger eel. Evolution of discharge with different intensities of illumination. Disc diameter = 36 mm. (Adrian and Matthews, 1927.)
a definite "off" effect provided that the stimulus has lasted for a second or more.

Increase of intensity of the stimulus causes reduced latent period, increased maximum frequency of the discharge and more rapid rise of the frequency curve (Fig. 6). The maximum frequency curves show that the frequency is some exponential function of the intensity (cf. Weber-Fechner Law).

Increase of area stimulated, with constant intensity, has exactly similar effects. Since the maximum frequency is not directly proportional to the area stimulated and the latent period is reduced when the area is increased, it follows that the retina is not a mosaic of isolated points, but that there is interaction between the points stimulated. This interaction is of such a nature that for areas of less than about 1 mm. in diameter the response depends upon the total quantity of light falling upon the area in unit time, i.e., \( i \times a \times t = \text{a constant} \). There is good anatomical evidence for the probability of such interaction especially in the periphery of the human retina, in the ratio of rods and cones to one ganglion cell and in the presence of amacrine and horizontal cells, but one would expect the result to be most evident at the periphery. If we can regard the threshold response to light stimulus as directly correlated with the photoelectric response we should expect a similar result in the human retina. Curiously enough the law is valid for foveal stimulation only (Riccò and others).

**Analysis of the Electroretinogram.** Piper (1911), confirmed by Kohlrausch (1918), found that vertebrates (fish, amphibians, and reptiles) which had large \( a \) waves also had good off-effects (\( d \)), whereas those (e.g., rabbit, cat and dog) which gave small and inconstant \( a \) waves also had similar \( d \) waves. They therefore ascribed the \( a \) and \( d \) waves to the same process. The same conclusion has been reached by Einthoven and Jolly (1908), and is further confirmed by Adrian and Matthews (1927).

Adrian and Matthews proved that the discharge in the optic nerve commences at a fixed time (about 0.1 sec.) after the beginning of the retinal response, irrespective of the length of the latent period of the latter. This constant delay must be due to changes in the retina, and may be due either to photo-chemical changes or to delay in the two sets of retinal synapses through which the impulse must pass. They further showed that the retinal nerve intervals for \( a \) and \( d \) were the same, and that therefore both must be of the same nature.

There can be no doubt that the electrical response is of a composite nature (Kühne and Steiner, 1880), and various attempts have been made to analyse the curve into its fundamental constituents. These attempts are highly theoretical, and must be regarded as suggestions on which to base further research rather
Einthoven's analysis of the electroretinogram.

Einthoven's analysis is shown in Fig. 7. The component A is responsible for the a and d waves. The component B is responsible for the b wave, which is most marked with feeble illumination. The slow c wave, often persisting beyond the end of excitation, is subserved by the C component. The least satisfactory of these components is A, for Waller's experiment, as well as many other observations since, have emphatically indicated that the A process is entirely negative, in spite of the positive off-effect (d).

Piper's analysis is shown in Fig. 8. His component II corresponds to Einthoven's A, and is seen to be purely negative. I corresponds with B, and II with C.

The most recent and exhaustive attempt is that of Granit, which is a modification of Piper's. He has adduced evidence to show that c is itself composite, and that a large proportion of it can be easily eliminated with ether. This part he calls PI. The positive component of the total curve remaining after the elimination of PI reacts uniformly and simultaneously to ether at all intensities of stimulation, and is PII. The negative component is PIII. These are combined as shown in Fig. 9.
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The response to a weak stimulus gives an almost pure PII. "By using ether it was possible to obtain PII alone at low intensities, PIII alone at high intensities, and also to produce the response PII + PIII. By interfering with the oxygen supply it was possible to produce the response PI + PIII. It has not been possible to obtain PI alone. Thus it follows that PII and PIII are very directly related to the stimulus. It does not seem probable that the one elicits the other. As to PI, it may, of course, merely be a matter of finding the right procedure in order to obtain it alone, but so far it seems as if PI required PIII. It does not require PII to judge from the large PI in the response PI + PIII."

The ether experiments often show an enhanced off-effect after removal of PI. On the other hand, removal of PII at high intensities regularly increases the off-effect (Kohlrausch, Granit). Hence, the component necessary for the relatively positive d wave to appear is the negative PIII plus either PI or PII. For the alternative explanation that PIII actually rises above the base line at the end of stimulation (cf. Einthoven) there is no evidence. Since PI and PII drop at the cessation of the stimulus, it follows that the absence of either counter-acting fall must make the off-effect caused by the return to zero of PIII more marked. PII drops faster than PI; therefore the removal of PII must cause particularly large off-effects, which actually is the case.

FIG. 9.

* Granit's analyses of the electrotetinogram with different intensities of stimulation—14 ml and 0'14 ml. and area of 1661 sq. mm. at a distance of 70 mm. (Granit, 1933.)
The schematic analyses of the responses of the frog's eye in dark- and light-adaptation are shown in Fig. 10.

**Intermittent Light.** The response to stimulation with intermittent light has been studied by Kühne and Steiner (1880), Piper (1911), Day (1915), Creed and Granit (1933), and Granit and Riddell (1934). Piper found that the response consists of undulations during the slow phase (i.e., on the c wave), which disappear above a certain frequency. This critical frequency is low in eyes containing mainly rods (cat), and much higher in eyes in which cones predominate (pigeon). Renqvist (1924) noted that flashes superposed upon steady illumination of the frog's eye gave rise to small a and b waves superposed upon the slow c wave. Adrian and Matthews (1928) recorded the impulses in the optic nerve of the conger eel, and found that below a certain frequency, increasing with the area or intensity of the stimuli, the discharge waxed and waned at the same rhythm as the stimulation, but that
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above that frequency there was a steady stream of impulses such as is given with continuous illumination.

Creed and Granit (1933), working with the decerebrate cat, confirmed Piper's results. With intense stimuli and a well-developed $b$ wave, the undulations only became visible on the fall of the $b$ wave, and are smaller during the first second than afterwards. With weaker stimuli and a smaller $b$ wave the ripples corresponding to the rate of stimulation appear at the beginning and may be actually larger and steeper than the $b$ wave elicited by continuous stimulation of the same intensity (e.g., 0.011 ml). As the frequency is increased the ripples become smaller and finally fuse. The fusion frequency varies directly as the logarithm of the brightness and the logarithm of the area over at least a hundredfold range (Ferry-Porter Law). The product of fusion frequency and latent period of ripples is approximately constant.

The retinal process chiefly responsible for the ripples is PII, but there may be some interaction with PIII. At the fusion frequency the smooth curve of action potential approximates closely to that of a steady stimulus of half the intensity (Talbot-Plateau Law).

Granit and Riddell (1934) have analysed very thoroughly the effects of single flashes superimposed upon the eye at various intervals after the cessation of an initial stimulus of approximately constant duration. Fig. 11 shows the effect of a flash of about 40 $\sigma$ superimposed upon the off-effect ($d$ wave) of a light adapted retina.

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**Fig. 11.**

Effect of flashes (40$\sigma$) at various intervals after cessation of initial stimulus. Time marking $\frac{1}{50}$th second. (Granit and Riddell, 1934.)
In every case there is a negative dip (a wave), which is small at short and at long intervals and largest when at the top of the initial d wave. It would seem that intermittent ripples are produced by a, b, and d waves. At fast rates of stimulation fast ripples are produced by small a waves interrupting the off-effect produced by negative PIII returning towards the base line. At slow rates the waves become very brisk owing to increased negative dips followed by positive peaks (b waves) above the level of the off-effect.

In dark-adapted eyes fusion occurs at less than 6-8 flashes per second; in light-adapted eyes at 12-21.

The Electrical Response of the Human Eye. The first record was obtained by Dewar and M’Kendrick (Dewar, 1877); subsequent records have been obtained by Kahn and Löwenstein (1924), Hartline (1925), Sachs (1929), and Cooper, Creed, and Granit (1933). The last-named found that the curve of potential is of the same type for central and peripheral retina, but the peripheral curve shows lower development of potential. Intermittent stimulation gives rise to corresponding ripples on the curve.

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VARICELLA OF THE CORNEA

By
Ransom Pickard
Exeter

The occurrence of a corneal affection in varicella is a great rarity. Of the references given by Sir John Parsons in his work on the Pathology of the Eye none concerns the cornea, in the bibliography of an article by Dr. J. D. Rolleston on ocular complications in varicella (Medical Chronicle, p. 356, 1909) only two cases of varicella of the cornea are given, one of which is here cited (Oppenheimer's case). The writer of this note has not had access to the remaining case. Comby (Traité des Maladies de l’Enfance, Grancher et Comby, p. 380-1, 1904), writes:—

"J’ai vu aussi la varicelle atteindre . . . même la cornée, déterminant . . . kératite varicelluse qui peut avoir sa gravité et laisser à sa suite une plaie indélébile." He does not state the number of cases he has seen nor does he give any details.

E. H. Oppenheimer (Deutsche Med. Wochenschr., Vol. XXXI, p. 833, 1905), gives a detailed account of a case of varicella of the cornea. It occurred in a two-year-old girl. She and three siblings had had chicken-pox. The eye affection began in the left eye on the sixth day of the disease. In the outer lower quadrant, 3 mm. from the centre of the cornea, was a vesicle two pinheads in width, which had perforated. To the perforation was attached a small mucoid string. The upper lid and conjunctiva were much swollen and injected, and had muco-pus adherent to them. There was very little circum-corneal injection, although the bulbar conjunctiva was very red. The pupil was round, small, and reacted only slightly.
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John Parsons

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