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THE ELECTRIC RESPONSE OF THE HUMAN EYE

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The present work arose from an investigation of the electrical changes in the human brain, particularly those produced by the exposure of the eyes to a flickering light. Some years ago Adrian & Matthews (1934) found that potential waves, in phase with the flicker, could be recorded from the occipital part of the head. As a rule, the frequency of the occipital waves agreed with that of the flicker, but sometimes it occurred at double the rate and, as this doubling complicated the analysis of the cerebral events, it seemed necessary to find out how it arose and, in particular, whether it arose in the brain or in the eye. The simplest method of attack was to try to record the potential waves generated in the retina as well as those in the brain. The attempt has been successful to the extent of showing that a double response may certainly arise in the eye, but the more important finding is that the human electroretinogram can be recorded without much difficulty and can give fresh information about the retinal mechanism.

What follows is mainly concerned with the potential changes occurring in the eye in response to single flashes of light. Responses to flickering light are described in a later section. The doubling of the cerebral flicker rhythm will be dealt with elsewhere, although, in fact, it was the starting-point of the investigation.

Previous work on the human electroretinogram is summarized in a paper by Cooper, Creed & Granit (1933). It has been established that the response of the human eye has the same general form as that recorded from other vertebrate eyes, isolated or *in situ*, or from the exposed retina, but technical difficulties have prevented any further study of it. One of the chief difficulties has been that eye movements are hard to avoid and give rise to potential changes resembling those of the electroretinogram. In the present experiments they have not caused much trouble, partly no doubt because the subject learnt to control them, but mainly because of the shortness of the period of illumination. As a rule the stimulus was a flash lasting not more than 1/20 sec., and no serious attempt was made to record with exposures lasting more than a second. Thus the inconveniences of a wandering base-line have not been serious.

METHOD

Electrical recording. A simple electrode system and a standard recording instrument have been used from the beginning. The electrodes are (1) a clip fastened to the lower part of the cheek, and (2) a moist thread making contact with the exposed part of the eye-ball on the nasal side of the cornea. The thread protrudes 2–3 mm. from a narrow glass tube filled with saline and fixed with plasticene between the bridge and the lens rim of a pair of spectacles. One end of a fine silver wire is coiled round the thread near its exit from the tube; the other end connects with an insulated lead fastened to the side member of the spectacle frame. The coil of silver wire in the tube is coated electrolytically with silver chloride. To protect it from the light the tube has sometimes been shielded by a wrapping of black paper or a coat of black paint. This precaution has not always been taken and is unnecessary except with very strong illumination, for the potentials arising in an unshielded electrode on exposure to a flash of light are very much smaller than those produced by the eye.

The electrode is fixed so that when the spectacle frame is in its proper place the moist thread touches the conjunctiva somewhere between the margin of the cornea and the inner canthus of the eye. There is no discomfort if care is taken not to move the eye after the contact is made and there has been no need to use local anaesthetics. Between each set of recordings the electrode is moved away from the eye, since the desire to blink becomes imperative. When it is replaced there is no guarantee that the thread will touch exactly the same point on the eye as before, but it is found that this makes very little difference to the size of the potential waves (cf. Fig. 2B).

The chief drawback with this method of leading from the eye is that eye movements, and especially blinking, disarrange the electrode. Consequently, the records must all be made in less than 2 or 3 min. after the electrode has been adjusted. The adjustment has to be done in the light before a mirror, and, though a red light can be used, there is bound to be some interference with the progress of dark-adaptation. For exploratory work this does not matter very much, but it would be troublesome if exact measurements had to be made of the rate of dark-adaptation.

The potential changes were recorded by a Grass three-channel ink-writing oscillograph of standard pattern. This has amplifiers with resistance-capacity coupling which can be set so that, if a steady potential difference is applied, the deflexion falls to half its initial value in 0·1 or 0·4 sec. Even with the longer coupling the instrument could only be used for recording the response to a relatively brief exposure, but changes occurring in the first $\frac{1}{10}$ sec. will be more or less faithfully reproduced. Since it gave a steadier base-line it was often more convenient to use the shorter coupling for preliminary observations, checking them afterwards with the longer. An ink-writing oscillograph is, of course, unable to follow extremely rapid changes of potential, but the electroretinogram is slow enough to be within its range. Indeed, for the short exposures used in these experiments, it is doubtful whether an instrument with direct-coupled amplifiers and photographic recording would have revealed more, and certain that the difficulties of the experiments would have been much more formidable.

Optical system. In the earliest experiments the source of light was a 75 W., 12 V. headlight bulb, in series with a variable resistance and connected with the 100 V. mains, so that it could be overloaded if necessary. Later, the range of illumination was extended by using either a 1000 c.p. 'Pointolite' lamp or an arc lamp, the intensity being controlled by neutral filters. The light was collected by a condenser, passed through a cooling trough and brought to a focus in the plane of a large wooden disk rotated at a constant speed by a gramophone motor, and having a slit which could be varied in width. A shutter in front of the disk could be raised and lowered so as to give a single flash or a series. Beyond the rotating disk the beam passed through a second condensing lens to illuminate the screen which was viewed by the subject. A small part of the beam was deflected on to a photoelectric cell leading to one channel of the oscillograph, so that the duration and intensity of the flash could be recorded, as well as the electric response of the eye.

Wratten and Ilford colour filters were used for producing approximately monochromatic light. The optical properties of these filters are well known and they have often been used in similar experiments (cf. Graham & Hartline, 1935). Though they are not strictly monochromatic, only a narrow band of wave-lengths is passed by each filter, and the energy value of the light does not vary too greatly from one to another. The transmission of the different filters is shown in Fig. 1 in relation to the scotopic and photopic luminosity curves of the eye.

Two arrangements of viewing screen were used. One was a large white surface, 4 ft. square. On this the light could be thrown in a disk up to 2 ft. in diameter, and the size and shape of the field could be varied by suitable diaphragms and stops. The screen was fixed to the wall of a small dark room, the light was admitted through an opening in the opposite wall, and the subject sat facing the screen with his chin supported in a rest 2 ft. away from it. The other arrangement was that originally devised for work on the flicker potentials of the brain where a large uniform field is needed. An opal glass bowl 11 in. in diameter was fixed in the opening in the wall of the dark room with its convex side facing the beam of light. The subject sat inside the room with his head in the concavity of the bowl, his chin resting on its rim. When the whole of the bowl was illuminated, only the extreme periphery of the visual field was in obscurity, and over most of the field the brightness was even. As the bright surface was very close to the eyes, fixation was impossible and attempted fixation movements did not intervene to spoil the record. This was the more convenient arrangement for all experiments in which the size of the field was not to be varied, but the results were substantially the same whichever screen was used. With the bowl, the brightness is given in equivalent foot candles (e.ft.c.) obtained by dividing the illumination on the convex surface by the transmission factor of the opal glass.

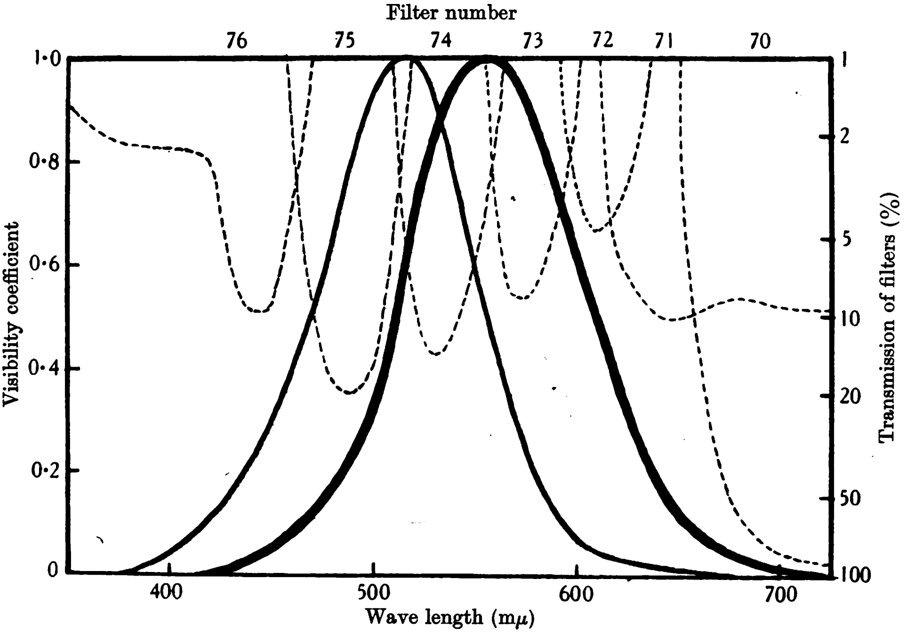

Fig. 1. Wave-lengths transmitted by Wratten colour filters, nos. 70–76, compared with the scotopic and photopic visibility curves of the human eye.

Experimental procedure. In most of the work the experimenter was his own subject, operating the oscillograph motor and the light shutter by strings led into the dark room. Between each series of recordings the light was switched on, and the subject disconnected the leads and went to the outer room to inspect the records, alter the light, etc. If the routine was as regular as possible, the eye could be brought to a fairly steady degree of dark-adaptation, so that, for a given flash after a given period in complete darkness, the responses would be reasonably constant. As the rooms were never brightly lit the normal state of the eye was one of moderate dark-adaptation. Light-adaptation was produced by viewing a large opal screen lit from behind by a 200 W. lamp or by going outside the laboratory and looking at the bright sky. With the latter method at least half a minute had to elapse before a record could be taken. Records have also been made with the screen continuously illuminated, the flash increasing the brightness momentarily.

Results

1. *The response to single flashes*

Nature of records. The accuracy of recording with the foregoing technique may be judged from Fig. 2. In Fig. 2A the eye was exposed to a flash of white light lasting 1/40 sec. with a brightness of the screen of 32 e.ft.c. The response is a diphasic potential change with the conjunctival lead becoming first negative and then positive to that on the cheek. The maximum change of potential is 0·12 mV. Below the record from the eye is that from the photoelectric cell illuminated by the same flash. The calibration curve which follows shows the degree of accuracy to be expected from the record. The sensitivity is that usually employed, for the greatest potential changes encountered are of the order of 0·3–0·4 mV., and the unsteadiness of the base-line (probably due to slight eye movements) prevents the recording of potential changes less than 0·01 mV.

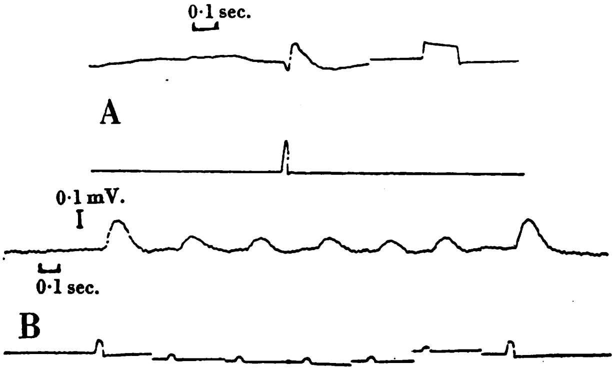

Fig. 2. A. Response to flash of white light followed by calibration curve (0·1 mV.). The photoelectric cell record below signals the duration and intensity of the flash, in this case 0·025 sec. with a brightness of the screen of 32 e.ft.c. B. To show consistency of recording. Blue light (Wratten screen 76). The conjunctival electrode was removed and replaced after each record. Brightness 1·2 e.ft.c. for first and last response, 0·24 e.ft.c. for the five smaller responses.

Fig. 2B shows that the potential changes stay reasonably constant in spite of readjustment of the electrodes. In this case, blue light was used, and the intensity of the flash was chosen to give responses of about two-thirds or one-third of the maximum potential obtainable with the particular arrangement in use. Between each response the conjunctival electrode was removed and replaced, the record being made after 20 sec. in darkness. Records made on successive days show just as little variation, provided that the degree of dark-adaptation is the same. To secure this a few small holes and cracks in the chamber wall were used as sources of very feeble illumination which would become visible when the standard degree of dark-adaptation was reached.

Photopic and scotopic responses. The principal result has been the demonstration that the electric response to a flash may show two distinct components, one of which seems to be mainly due to the photopic mechanism and the other to the scotopic. The appearance of these two components is illustrated in Fig. 3, which gives the response to a brief flash (*a*) of deep red light which should stimulate mainly the photopic system, (*b*) of blue light which should stimulate mainly the scotopic, and (*c*) of orange-red light which should stimulate both, but the photopic more than the scotopic. It will be seen that in (*a*) the response is a brief diphasic potential change lasting about 0·1 sec., with the conjunctival electrode becoming initially negative, in (*b*) it is a monophasic change, positive in sign and lasting at least twice as long, and in (*c*) it is a complex change which could be produced by adding the brief and the slow responses together.

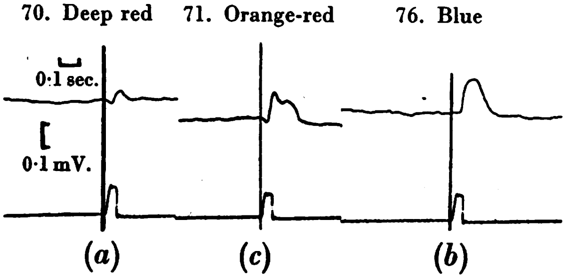

Fig. 3. Records showing the dual character of the response. Brief diphasic response with red light (screen 70, 5 e.ft.c.), longer monophasic response with blue (screen 76, 7 e.ft.c.) and composite with orange-red (screen 71, 11 e.ft.c.).

Fig. 4 summarizes the chief evidence for regarding the brief response as characteristic of the photopic mechanism and the longer monophasic response as characteristic of the scotopic. Fig. 4A shows the responses of the light-adapted eye to brief flashes of various wave-lengths. In the fully light-adapted eye the threshold of the scotopic receptors would be greatly raised, whilst that of the photopic would be much less affected, so that we should expect that the response would be mainly that of the photopic mechanism. It is, in fact, for all colours except deep blue, the same kind of brief change as that shown in Fig. 3 (*a*). With the particular brightness employed the response to blue is so small that its form cannot be made out. This, too, is to be expected, since blue light would not stimulate the photopic receptors, and the threshold of the scotopic has been raised by the light adaptation so that in fact only a very slight visual sensation is produced.

Fig. 4B shows the effect of similar flashes when the eye is moderately dark-adapted. The responses of the scotopic mechanism should now be in evidence with every colour except deep red, which does not stimulate it, and the response of the photopic mechanism should be present also with every colour except blue. It will be seen that the responses to red and blue have the contrasting forms already described, whilst the responses to intermediate wave-lengths seem to be compounded of both types. In the response to orange-red the slow and rapid positive waves are easily separated; with yellow, yellow-green and blue-green the slower positive wave is larger and is merged more or less with the rapid wave.

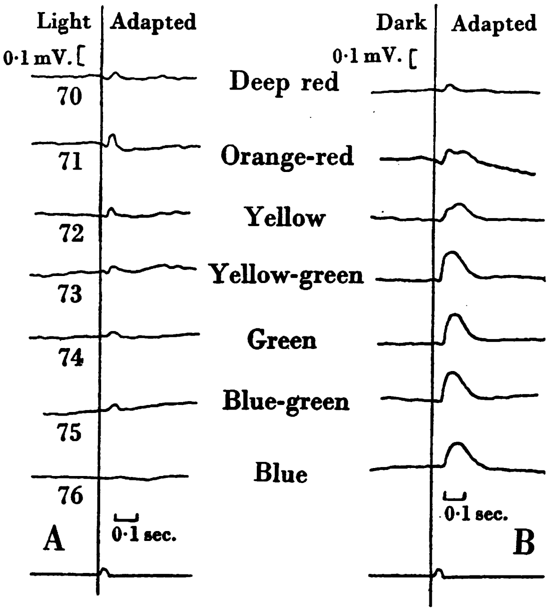

Fig. 4. Response to various wave-lengths in (A) light-adapted and (B) dark-adapted eye. The slower component is only present in B. The light source has the same intensity throughout but the brightness of the screen varies with the colour filter in use.

Changes of intensity. These records are enough to establish a *prima facie* case for regarding the two components as due to the photopic and scotopic mechanisms respectively, but there are several points which need closer examination. In Fig. 4 the intensity of the light falling on the colour filters was the same throughout, but as the transmission factor is not alike for all the filters the energy value of the different flashes of coloured light was not the same. It could have been made so easily enough, but what is really needed is an answer to the question whether the appearances shown in Fig. 4 are to be found only over a narrow and selected range of intensities, or over most of the range to which the eye is normally exposed.

It is not easy to produce a very bright flash of monochromatic light over a large field, yet, if the light is dim, the field must be large if it is to produce a measurable potential change. However, the intensity of the light can be readily increased if the field is made smaller, and, with a bright light, a measurable potential change can still be produced. A reduction in the area of the retina stimulated by a red or a blue flash has no effect on the form of the potential change though it naturally reduces its magnitude (if the intensity of the light is not altered). Thus we can secure a reasonably wide range of stimuli by using a large field for the dimmer light and a much smaller field lit by a concentrated beam when we need the highest intensity.

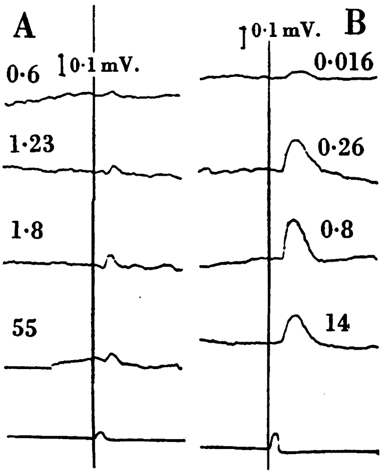

Fig. 5. The form of the response to red and blue is not affected by changes of intensity. A. Response to red (screen 70) with brightness of 0·6, 1·23, 1·8 and 55 e.ft.c. Field reduced in last record. B. Response to blue (screen 76) with brightness of 0·016, 0·26, 0·8 and 14 e.ft.c. Field reduced in last record.

With the largest possible field (the concave opal bowl) and an exposure of 1/30 sec. the minimum intensity of blue light (Wratten screen 76) required to give a measurable response has been 0·003–0·004 e.ft.c. This value could no doubt be lowered by more prolonged dark-adaptation, but it must be well above the visibility threshold, since the potential change must be large enough to stand out against the base-line fluctuations. With deep red light (screen 70) the minimum intensity needed for a response is much higher (about 0·5 e.ft.c.), partly, no doubt, because the photopic mechanism sets up smaller potential changes, but mainly because the visibility threshold is also much higher.

With the largest field, the intensity could not be raised to more than 1·2 e.ft.c. for blue light or 3·7 for red, but with a field reduced to 2 cm. diameter the brightness could be raised to 15 e.ft.c. for blue and 70 for red. Records made at various intensities within this range are given in Fig. 5. They show that the characteristic form of the response to red is quite unaffected by a 100-fold increase in intensity and that to blue by a 900-fold increase. Other experiments have given the same result with a 1–4000 fold increase in the blue light.

With the strongest red light and the eye dark-adapted, there is sometimes a small slower component following the initial diphasic effect, and with strong blue light there is sometimes an initial negative swing, though it is scarcely larger than the random fluctuations in the base-line. It is not surprising that strong red light should be able to affect the scotopic receptors or strong blue light the photopic, yet it can be said that the distinctive form is preserved over a fairly wide range of stimulus intensities and a corresponding range in the size of the response. With light of intermediate wave-length the form of the response ought to change with increasing brightness if it is produced by two components of different threshold. That it does so is shown in Fig. 6 which gives responses to blue, green and orange-red. A feeble green light gives no sign of the initial rapid effect, but it becomes more and more prominent as the intensity is raised. With orange-red light it is the slower component which is absent at low intensities. It should be emphasized that it is the short duration of the positive wave which is the main distinguishing feature of the photopic component. The initial negativity may be very small, and though it only appears when the stimulus would be likely to affect the photopic mechanism there is reason to believe that it may be due to a process not directly concerned with the excitation of the receptors (cf. p. 97).

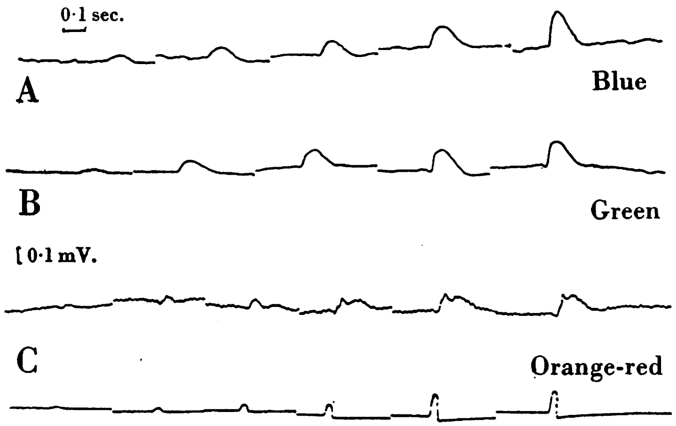

Fig. 6. The form of the response to intermediate wave-lengths varies with the intensity. A. Responses to blue (screen 76), showing no change in form. Brightness 0·03, 0·20, 0·28, 0·48, 1·1 e.ft.c. B. Responses to green (screen 74). The photopic component appears at higher intensities. Brightness 0·015, 0·08, 0·22, 0·54, 1·1 e.ft.c. C. Responses to orange-red (screen 71). The scotopic component appears at higher intensities. Brightness 0·78, 1·6, 3·12, 7·8, 15·6 e.ft.c.

Effect of dark-adaptation. Another point to be considered is the extent to which the prominence of the longer 'scotopic' response can be correlated with the degree of dark-adaptation. It has been shown that it appears when the eye is dark-adapted, but if it is really the response of the scotopic mechanism we should expect that its rate of increase would run parallel to the increasing sensitivity of the eye. If it appeared abruptly at a certain stage of dark-adaptation or reached its maximum long before dark-adaptation was complete, it would be more difficult to accept it as the scotopic response.

Owing to the need for some illumination of the eye when the electrode is adjusted, it is impossible to record the response immediately after a long period in complete darkness; but records may be taken after 2 or 3 min., and the red light, by which the adjustment is carried out, need not be bright enough to interfere much with the general progress of dark-adaptation. The development of the slow response certainly runs parallel to that of dark-adaptation in that the increase begins at once and continues for half an hour or longer. This is illustrated in Fig. 7. In Fig. 7A, for instance, the response to blue light begins to increase in the first 2 min., and it is still increasing, though much more slowly, half an hour later. In Fig. 7B, with orange-red light, the slow component of the dual response increases progressively in the same way. To obtain accurate figures for the whole course of dark-adaptation would involve a change of technique. In spite of this, we can be fairly sure that the increase in the response follows the same general time course as the increase in sensitivity of the eye, for it is found that at all stages of dark-adaptation one can confidently expect to find an electric response just large enough to detect, whenever the sensation produced by the flash exceeds a certain small luminosity.

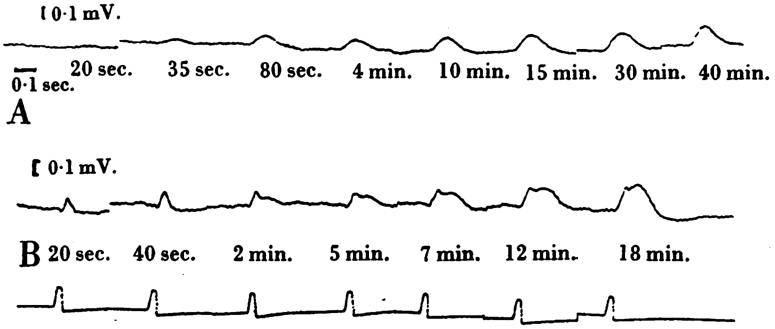

Fig. 7. Progressive increase in slow component with dark-adaptation. A. Responses to blue (screen 76) at various times after beginning of dark-adaptation. Brightness 0·09 e.ft.c. B. Responses to orange-red (screen 71). Brightness 5·2 e.ft.c.

Changes in duration of flash. Since the eye (in animals) and the optic nerve both respond to darkening as well as to illumination, it is worth considering whether the later part of the human electroretinogram in records such as those in Fig. 7B might be partly or wholly an 'off effect', instead of the response of the scotopic mechanism. This would leave unexplained the difference in the responses to red and blue light, but there are two more arguments against it. One is that the slower component of the response still appears though the duration of the flash is reduced to 1/100 sec. (Fig. 8A). The other, and more conclusive, is that the slower component appears in its usual position although the flash is prolonged for half a second or more (Fig. 8B). Indeed, with a flash of long duration, it is possible to make out a small 'off effect' at the end of the electroretinogram, separate from the positive wave nearer the beginning.

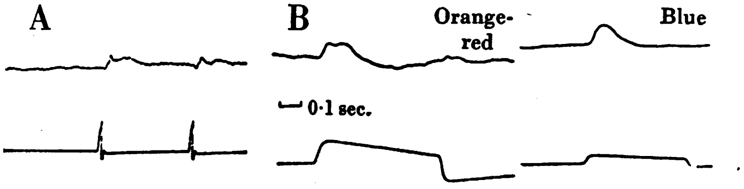

Fig. 8. Records showing that the slower component is not an 'off' response. A. Orange-red flash lasting 0·01 sec., 15·5 e.ft.c. B. Orange-red and blue flashes lasting 0·5 sec., 7·8 and 0·9 e.ft.c.

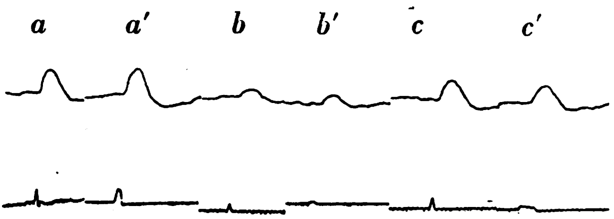

Fig. 9. Parallel effect of changes in intensity and duration. Blue light (screen 76):

	Brightness (e.ft.c.)	Duration (sec.)	Product
a	0·6	0·007	42
a′	0·2	0·028	56
b	0·2	0·007	14
b′	0·04	0·028	11
c	0·2	0·014	28
c′	0·04	0·084	33

When the duration of the flash is short, the size of the response, like the resulting sensation, is determined by the product of the intensity and the duration of the light, i.e. by the quantity reaching the eye. Fig. 9 gives a series of records illustrating this, and Fig. 10 shows the relation between the intensity and duration required for responses of equal size with blue light. The response ceases to depend on the product of intensity and duration when the flash is longer than about 1/15 sec. for blue light and 1/20 sec. for red. A reduction in intensity cannot then be compensated for by a further increase in the length of the flash, for it is the duration of the response and not its size which is increased. It is noteworthy that, when the flash lasts long enough to cause this lengthening in the retinal response, there is also a marked change in the sensation, which now seems to last an appreciable time. The critical duration is certainly shorter for red light than for blue, but there is a considerable margin of error in determining it.

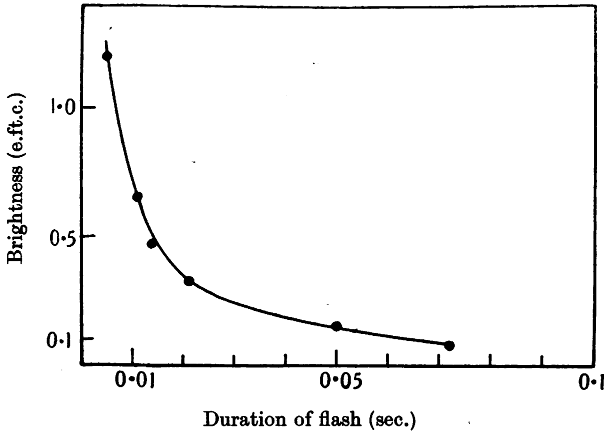

Fig. 10. Relation between intensity and duration of flashes giving a response of fixed size. Blue light (screen 76).

Localization. Since the photopic receptors are more concentrated in the centre of the retina and the scotopic at the periphery, we might expect that the brief response would be more dependent on the brightness of the central part of the visual field and the slower component on that of the periphery. It is not possible to obtain a measurable response when the illumination is restricted to the rod-free area of the retina, but we can use a large field divided into central and peripheral parts and compare the responses due to either of them. The arrangement finally adopted was one in which the light fell in a disk 2 ft. 6 in. diameter on an opaque white screen 2 ft. from the eye. Diaphragms were arranged so that the illumination could be confined to a central disk 6 in. in diameter or to the annulus round it. With blue light the response due to the whole field was not much larger than that due to the peripheral annulus and the response to the central disk was much smaller (Fig. 11 A). With red light, on the other hand, the responses due to the annulus and to the central area were nearly equal (Fig. 11 B).

This indicates that the receptors sensitive to blue and giving the slower monophasic response are less concentrated at the centre than those sensitive to red and giving the shorter diphasic response. To complete the evidence, however, the same sort of difference must be established for the two components of the response to an intermediate wave-length which would stimulate both photopic and scotopic receptors. Results with orange-red are given in Fig. 12. The contrasting effects of the central and peripheral fields on the two components are not as striking as they are on the responses to red and blue, yet there is certainly some favouring of the initial diphasic effect by central vision and of the slower monophasic by peripheral.

From one point of view it is unfortunate that the retina cannot be regarded as a surface of uniform sensitivity and structure, for, if it were so, the relation between the potential developed at the electrode and the distance and size of the stimulated area would have more significance. In all probability the lead on the eyeball is so far forward that there are no great differences in the resistances between it and different parts of the retina. One would expect that larger potentials would be developed by illuminating a peripheral area on the nasal side of the eyeball (near the electrode) than by illuminating a similar area on the temporal side. Actually the potential is larger, but by not more than 50%. This result may be due in part to stray light affecting other parts of the retina than those directly illuminated. Attempts to lead from nearer the retina in the hope that finer details of the electroretinogram could be studied (cf. Fry & Bartley, 1934) have been so far unsuccessful.

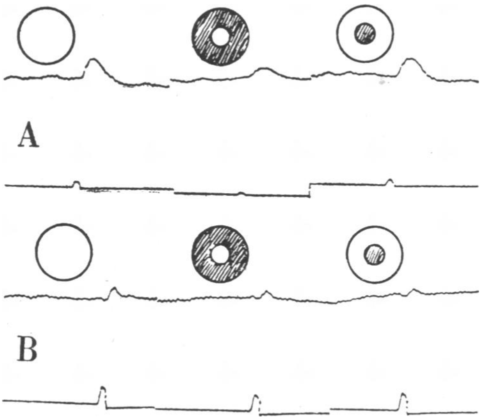

Fig. 11. Effect of restricting illumination to the central or peripheral part of the field A, blue light (screen 76); B, red (screen 70).

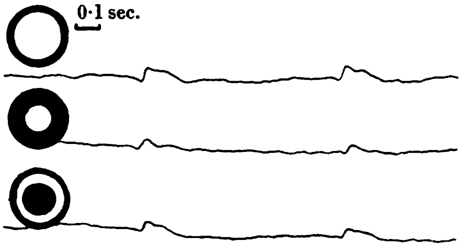

Fig. 12. Effect of restriction to central or peripheral field with orange-red light (screen 71, 14 e.ft.c.). The slow component is relatively smaller when the peripheral field is not lit.

The response to white light. With white light the stimulating effect of a flash can be made far greater than with coloured light, and at high intensities the photopic type of response becomes much more prominent. At very low intensities the response seems to be a pure monophasic effect, a brighter flash gives the primary negativity and the more abrupt rise of the positive wave and finally at very high intensities the initial negativity may become almost as large as the succeeding positive wave (Fig. 13).

In a preliminary account (Adrian, 1944) it was stated that at high intensities the slower part of the response was definitely reduced, as though there were an inhibition of the rod by the cone mechanism. But further work has shown that this reduction was due, mainly at any rate, to unsuspected light-adaptation. A single bright flash may reduce the degree of dark-adaptation for several minutes, and it is therefore essential to expose the eye as little as possible and to allow long periods in darkness between successive flashes. When this is done the response does not show an appreciable curtailment of the positive phase, but if the flashes are repeated at intervals of 10 sec. or less the later part of the response soon disappears as dark-adaptation is lost. Even with all precautions to maintain the dark-adapted state, the maximum potential developed in the positive swing is not as large as one might expect. This alone, however, is not enough to prove an inhibitory effect, for it might have many other explanations.

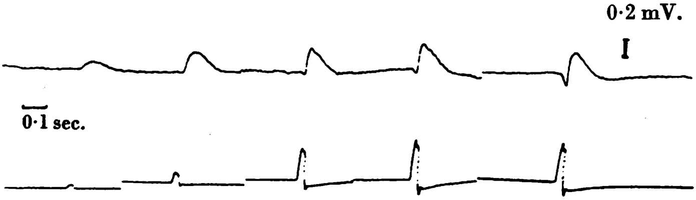

Fig. 13. Response to flashes of white light of increasing intensity. Brightness 0·1, 1·0, 10, 20, 103 e.ft.c. The responses are not strictly comparable, as the degree of dark-adaptation is not constant.

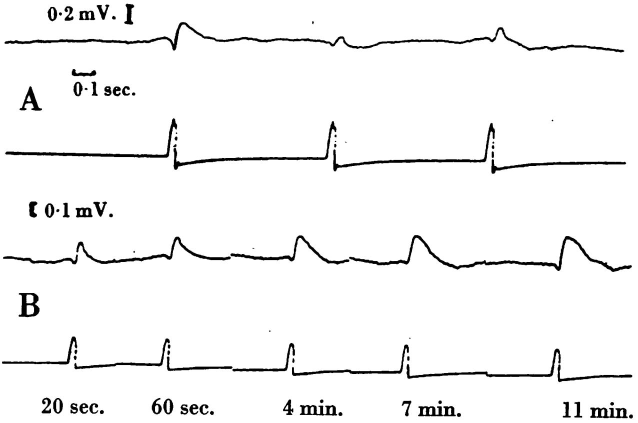

Fig. 14. A. Response of moderately dark-adapted eye to flashes of 103 e.ft.c., showing reduction after the first flash. B. Response at various times after the beginning of dark-adaptation. Flash, 13·5 e.ft.c.

The effect of light- and dark-adaptation can be seen in Fig. 14. In Fig. 14A the moderately dark-adapted eye was exposed to a series of bright flashes at intervals of 1 sec., and at the second flash the slower part of the positive wave has disappeared. The initial negativity is also reduced, but only by about 50%. In Fig. 14B the eye was first light-adapted and was then tested by a flash after various periods in darkness. The initial negativity shows little alteration, but the positive wave is still increasing after 11 min. These records were made with the pupil dilated with 'Paredrine' to avoid the changes which might result from alterations in the amount of light entering the eye.

The relation between the intensity of the flash and the magnitude of the response in the light-adapted eye is not easy to formulate. Judged by the size of the initial negative deflexion there is no sign that the response is near its maximum even with the brightest light possible, but the positive deflexion does not share the same continued increase. In this respect, therefore, the two phases seem to behave differently. In dark-adaptation, too, the negative and positive phases may not increase in size at the same rate. The most likely explanation is that they represent two distinct processes in the retina, as they are supposed to do in the analyses of the electroretinogram proposed by Einthoven & Jolly (1908) and by Granit (1933). The initial negative deflexion may be considered part of the photopic response, in that it is absent with feeble illumination and is not much increased by dark-adaptation, but it is known to occur in eyes which have very few cones and so is unlikely to be specially connected with cones rather than rods.

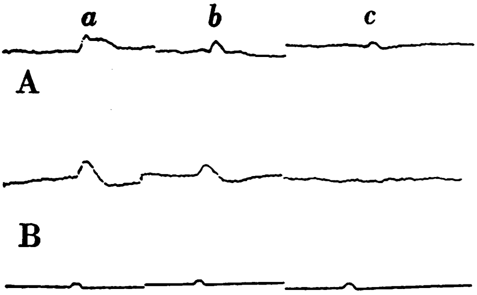

Fig. 15. Response to a flash thrown on a dimly or brightly lit field. A. Orange-red flash of 30 e.ft.c. thrown on field (*a*) in darkness, (*b*) lit by 0·3 e.ft.c., and (*c*) lit by 2 e.ft.c. B. Green flash of 3·5 e.ft.c. on fields as in A.

The response of the eye in light and darkness. In the foregoing experiments the eye has always been in darkness for some seconds before the flash occurs. As the period in darkness would favour the scotopic response, some records were made with the field dimly or brightly lit throughout from another light source. These give some idea of the contribution which would be made by the scotopic mechanism under more normal conditions of vision. Results are given in Fig. 15 with the field (*a*) in darkness, (*b*) having a brightness of 0·3 e.ft.c., and (*c*) of 2 e.ft.c. With a flash of orange-red light which raises the brightness momentarily to 30–35 e.ft.c., the slow component is present when the field is initially dark but not when it is dimly lit. With green light the slow component appears with the dimly lit field although the flash adds only 3·5 e.ft.c. to the brightness. With the brighter field only the photopic type of response could be recorded; an added flash of blue light could be seen, but it was not possible to use an intensity of illumination great enough to produce a measurable electric response, and white light gave only the brief diphasic effect.

2. *The response of different subjects*

Although most of the information has been derived from one eye (E.D.A., left eye), records have been made from five other subjects with similar results. The responses to red, orange-red and blue in three of them are given in

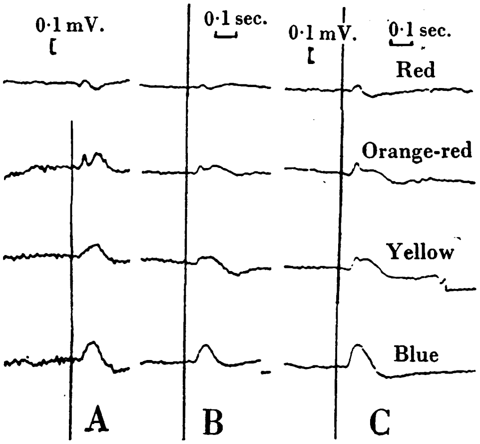

Fig. 16. Responses to red, orange-red, yellow and blue from three different subjects A, B and C, showing composite effect with orange-red and yellow. Records somewhat distorted owing to use of shorter time constant in oscillograph.

Fig. 16. There is the same contrast between the brief response to red and the longer response to blue, whilst orange-red gives the response compounded of both types. Light-adaptation had the same effect, abolishing the slower component of the compound response, but having a relatively small effect on the brief response to red light.

Records were made from one subject who complained of night blindness, but all that could be established was an unusually slow rate of dark-adaptation, judged by the subject's visual sensations and by the progressive increase in the retinal response to blue. Otherwise the scotopic mechanism seemed to act normally, for the response to blue had the usual duration and reached 0·3 mV. after half an hour in the dark, and the response to orange-red showed both the rapid and slow components.

3. *The response to flicker*

With flashes repeated at intervals of half a second or less the compound nature of the response (except to deep red and deep blue) stands out very clearly, since the two components are very differently affected by an increase in frequency. This applies particularly to the responses at the beginning of a series. The two types of behaviour can be seen from the records in Fig. 17 which were made with flashes of red and blue light repeated at various rates. With red light the successive responses are all alike as long as the frequency is less than about 20/sec.: above this rate the first of the series is larger than the rest though the difference in size is not very great. With blue light, however, unless the illumination is very low, the frequency has only to be raised to 3/sec. to cause a considerable reduction in the second and later responses, and above 15/sec. all but the first are so reduced as to be only just visible in the record. Now, if for red or blue we substitute white light, or light of some intermediate wave-length, the records obtained could be reproduced by merely adding together the two types shown in Fig. 17. Examples are given in Fig. 18. At frequencies of 10/sec. or more, the first response of each series has a large positive wave, as in the records with blue light, but after this there is only a series of brief spikes like those in the records with red.

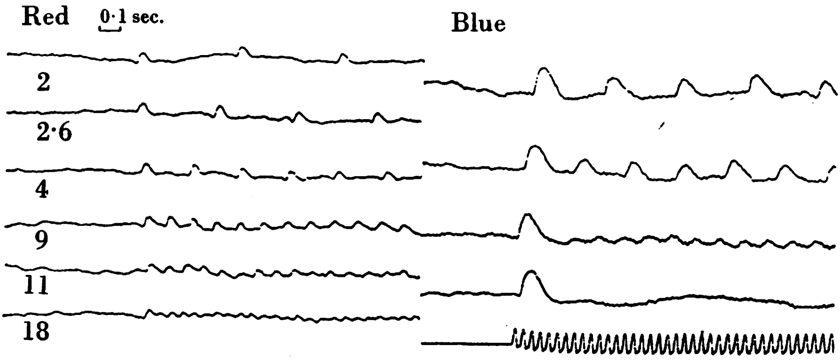

Fig. 17. Response to repeated flashes of red (Ilford screen 609, 1·2 e.ft.c.) and blue light (Wratten screen 76, 0·9 e.ft.c.) at various frequencies, showing reduction after the first response to blue but not to red.

The reduction of the scotopic component after the first response is presumably due mainly to light-adaptation. It is not due, except perhaps to a small extent, to contraction of the pupil, for it is equally marked after dilatation of the pupil with a mydriatic. It is greater when the stimulating effect of the light is high than when it is low, whether the alteration is produced by changing the intensity of the light or by changing the degree of dark-adaptation of the eye. But, although this suggests a dependence on photochemical factors, the rate of recovery after stimulation might well depend on neural factors also, and its relation to the process of dark-adaptation remains to be worked out.

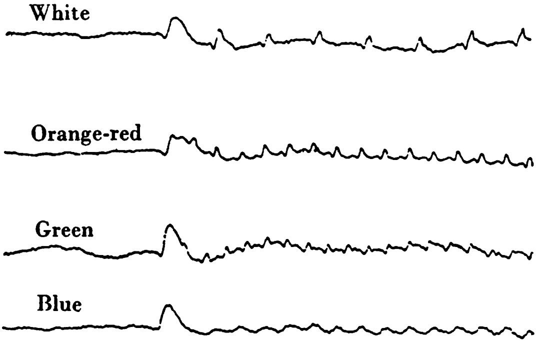

Fig. 18. Response to repeated flashes of white (22 e.ft.c.), orange-red (6·8 e.ft.c.), green (3·1 e.ft.c.) and blue light (1·2 e.ft.c.), eye moderately dark-adapted. The scotopic component of the response is greatly reduced after the first flash. Pupil dilated with 'Paredrine'.

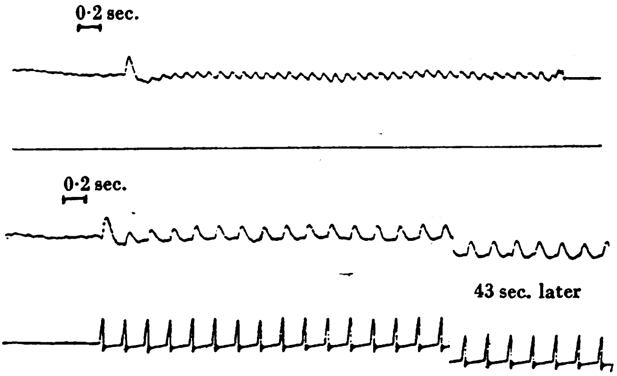

Fig. 19. Initial reduction of the scotopic response followed by return to a steady value. Repeated flashes of violet light (Ilford screen 601, 0·9 e.ft.c.). N.B. The speed of the recording paper is lower in these records than in the other figures.

It is to be noted that with blue light the responses do not become progressively smaller and smaller as stimulation continues. Instead of this the reduction is greatest for the second response, and there is then a progressive return to a steady value, as though the retina discharged its accumulated reserves at the first stimulus, but could then revert to a state of dynamic equilibrium where the supply keeps pace with the demand (Fig. 19). Though it has not been possible to make continuous records for more than 2 or 3 min. there has been no sign during that period of any alteration in the response after the initial changes in size. This might, perhaps, have been expected in view of the fact that there is no decided reduction in the sensation aroused by the flicker after the first few flashes.

With longer intervals between the flashes, and particularly with yellow, orange-red or white light over a certain intensity range, the reduction of the scotopic component may occur progressively during the first few flashes instead of abruptly (Fig. 20). Records of this are interesting chiefly because they indicate what sort of contribution may be made by the scotopic mechanism to the sensation of colour. With a yellow or orange-red filter there is a decided change in hue (from yellow to white and from orange to pink) during the first few flashes, and it is during this period that the scotopic component becomes very much smaller. With the green filters an initial change in hue can sometimes be detected, but it is rarely as clear as with orange.

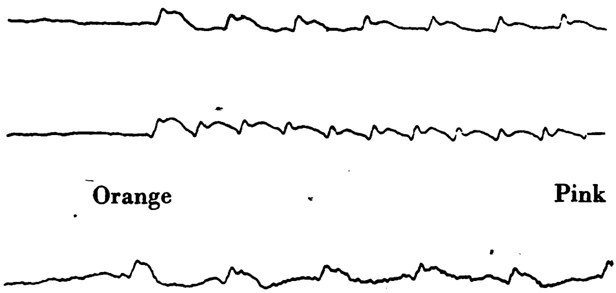

Fig. 20. Progressive reduction of the scotopic component with flashes of orange and orange-red light accompanied by change of hue.

DISCUSSION

In animals, the dual receptor mechanism of the retina and the complex form of its electrical response are both well known. There have been many comparisons of the response in light- and dark-adaptation and in diurnal and nocturnal animals; light-adaptation has always been found to cause a shortening of the positive wave, and Chaffee, Bovie & Hampson (1923) have suggested an analysis of the frog's electroretinogram which is almost identical with that given here. Yet it cannot be said that a definite separation of the response into a scotopic and a photopic component has been established for any animal but man. In man the dual nature of the response to orange light could scarcely be missed, and the identification of the two components can be made with greater certainty, because there is already so much information about the sensory performance of the scotopic and photopic mechanisms of the human eye. There is also the advantage that the eye is in a completely normal state during the observations.

It has been found that there are two distinct types of electric response which can be produced in the human eye by a flash of light. One of them behaves in all respects as though it reflected the activity of the scotopic receptor mechanism. It is evoked by light of short but not of long wave-length, it is greatly enhanced by dark-adaptation, and it is absent or very small when the eye is light-adapted. The other type of response seems to reflect the activity of the photopic mechanism, for it is more prominent with bright light, it is evoked by the longer wave-lengths, is mainly derived from the central regions of the retina, and is not much affected by dark-adaptation. At first sight, it is natural to think of these two kinds of response as due to the activity of the rods and cones respectively. For the dark-adapted eye this would be a reasonable conclusion: the photopic type of response is presumably due to a receptor system without visual purple, and in the dark-adapted eye the receptors without visual purple are the cones. In the light-adapted eye, however, we cannot be sure that the response is due entirely to them. It is at least conceivable that the rods can still react to a bright light, but that with the disappearance of the visual purple the electric response set up by a brief illumination of the rods is reduced in size and duration till it comes to resemble that set up by the cones. We may be justified, therefore, in concluding that in the dark-adapted eye the photopic type of response (e.g. that to red light) is due to the cone mechanism and the scotopic type (e.g. to blue) to the rod mechanism, but it is much less certain that the brief responses of the light-adapted eye are due exclusively to the cone mechanism. The brief response after light-adaptation seems to be found in all kinds of vertebrate eye regardless of the proportion of rods to cones; we can say that it must be due to photoreceptors without visual purple, but we cannot be sure that they are all of one histological type. It is for this reason that the terms rod response and cone response have been avoided. It is scarcely necessary to add that the present results do not show whether the potentials are developed in the receptor cells or in some other part of the retinal mechanism.

The photopic response to a brief flash is a diphasic potential change with an initial negativity (which may be very small), succeeded by a brief positive wave. The scotopic response is a larger and longer positive change with no appreciable negativity in front of it. The greater size and different duration might have been expected, but it is more difficult to see why the scotopic response should be monophasic when the photopic appears to be diphasic. One suggestion might be that the different form of the response is caused by the greater concentration of one kind of receptor at the fovea and of the other at the periphery, but this can be tested by confining the stimulus to different parts of the retina, and it is found that the scotopic and photopic responses retain their usual form wherever they come from. A more likely explanation is that the initial negativity is due to a retinal activity different in kind from that giving the positive phase, for the two phases do not always preserve the same size ratio when the intensity or rate of repetition of the stimulus is altered. This would agree with Granit's analysis of the electroretinogram into three processes, the first of which produces a negative potential and is not associated with the discharge of impulses in the optic nerve fibres.

Observations with longer periods of illumination must be made before these results can be properly assessed in relation to Granit's analysis, and more accurate recording is needed for precise statements of latency and time relations. But the main purpose of the present experiments has been to investigate the apparent duality of the electric response. If it can really show us how much activity is occurring in the scotopic mechanism and how much in the photopic, it will be worth trying to improve the technique. If it had been found that the two components of the response did not behave in accordance with what we should expect of receptors with and without visual purple, then a further investigation would have much less immediate promise. On the whole, the agreement has been very good. Confirmatory evidence is being sought from other types of eye, and it has been found that the monkey agrees with man in giving records in which the two components can be clearly distinguished. We may conclude that there is a good case for regarding the two components in the human response as due to the scotopic and photopic mechanisms and for investigating them in greater detail.

SUMMARY

1. The electric response of the human eye to a brief flash of light can be separated into two components due to the scotopic and photopic mechanisms of the retina.

2. The photopic component is a brief diphasic potential change. There is an initial negativity of the cornea (which may represent a different form of activity) followed by a brief positive wave. The response is produced by white light or by monochromatic light of all colours except blue. It is present in the fully light-adapted eye and is not much increased by dark-adaptation.

3. The scotopic component is a slower monophasic change reaching 0·3–0·4 mV., with the cornea positive. It is produced by light of all colours except deep red. It is absent in the light-adapted eye and is greatly increased by dark-adaptation. The increase continues for half an hour or more and runs parallel with the increased sensitivity of vision.

4. Deep red light gives the simple photopic response and deep blue light the scotopic. Over the range investigated, changes in the intensity of the

light alter the magnitude of these responses but not the form. This is so for a 100-fold increase with red light and a 4000-fold increase with blue. White light and light of intermediate wave-length give a compound response in which the relative magnitudes of the two components vary with the wave-length and intensity of the light and with the degree of dark-adaptation of the eye.

5. The photopic response is more dependent on the brightness of the central part of the retina and the scotopic on that of the periphery.

6. The scotopic component has not been detected when the flash is thrown on a field which is already lit with a brightness of 2 equivalent foot-candles. It is present when the illumination of the field is reduced to 0·3 e.ft.c.

7. If flashes are repeated at short intervals, the two components are easily distinguished because the scotopic responses may be greatly reduced after the first flash, whereas the photopic responses remain the same size. The reduction is probably due to light-adaptation. It occurs initially and there is usually no further change after the first few responses.

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