J. Physiol. (1952) 118, 289–298

THE SCOTOPIC *A*-WAVE IN THE ELECTRICAL RESPONSE OF THE HUMAN RETINA

By J. C. ARMINGTON, *Brown University*,
E. P. JOHNSON, *Bowdoin College*, and L. A. RIGGS, *Brown University*[*]

(*Received* 10 *March* 1952)

The electrical response of the retina is conventionally described as comprising several 'waves' known since the time of Einthoven & Jolly (1908) as the *A*, *B*, *C* and *D* waves. These are described in terms of the polarity of the cornea. The *A*-wave, first observed when Gotch (1903) used a magnifying glass to examine some records from the eye of a frog, is portrayed as a brief, negative deflexion of short latency, ending with the inception of the first positive component or *B*-wave. With the subsidence of the *B*-wave there appears in some records a second positive component, slowly rising and diminishing. This is the *C*-wave. These three waves are 'on-effects', appearing in response either to the turning on of light or to stimulation by brief flashes. The fourth component, the *D*-wave, is a rapid, positive 'off-response'. These several waves have been attributed by Granit (1933) to the interaction of three basic processes: *Process I*, a sluggish positive process, responsible for the *C*-wave; *Process II*, the principal positive process, accounting for the *B*-wave; and *Process III*, the negative process, producing the *A*-wave and also, through its cessation of activity at the termination of the stimulus, contributing the larger part of the *D*-wave.

Though this general picture has for some time been accepted as the normal or typical form of the retinal response, it has been recognized that the precise configuration of the response varies considerably with circumstances. Important variables include the degree of light-adaptation, the character of the stimulus, the condition of the eye (whether moribund, anoxic, drugged, or 'normal'), the species of organism, etc. Investigators, varying these conditions, have sought to analyse the retinal response either into 'basic processes', as Granit has done, or into 'photopic' and 'scotopic' portions.

---

[*] This research was carried out in the Psychology Laboratory of Brown University under contract between the Office of Naval Research and Brown University, Providence, R.I., U.S.A.

With regard to the human response, the principal *B*-wave is thus now considered to reflect activity within the scotopic visual system. This has been inferred by Adrian (1944, 1945), Johnson (1949), Riggs, Berry & Wayner (1949) and by others. *C*-waves and *D*-waves are not evident in human responses. *C*-waves occasionally reported are probably artifacts attributable to the intrinsic muscles of the eye. The negative *A*-wave, however, appears under many conditions, the principal requisite being a stimulus of high intensity.

According to Granit (1947), all negative phases of the response are referable to his *Process III* and, in discussing the '*E*-retina', in which class he places the human retina, he suggests that *Process III* (hence also the *A*-wave) represents cone-function. He supports this view by citing the experimental work of Adrian.

Adrian (1944, 1945), besides contributing the hypothesis that the negative *A*-wave is part of the photopic response, has demonstrated the existence of another small positive component, occurring earlier than the *B*-wave. This component, because it is most evident in responses to red light, has also been assigned tentatively to the photopic system. The current picture of the human retinal response, then, as described by Adrian (1945, p. 103), is as follows:

> '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.
>
> '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.'

It has been our observation that the *A*-wave may be considerably augmented by dark-adaptation. This is not true of Adrian's brief positive component. Using higher intensities of stimulation than those available to Adrian, we were able to elicit *A*-waves in response to monochromatic stimuli ranging from red through blue. It thus appeared possible, upon determining the energy required at each wave-length to produce some 'standard *A*-wave', to define the spectral sensitivity curve for this component. The results are reported below. We have also made exploratory studies of the course of development of the *A*-wave during the period of dark-adaptation and of its relationship to stimulus-intensity. We conclude that the negative portion of the response is not a simple, unitary phenomenon. The main *A*-wave, if such may be identified, seems contaminated by other components, positive or negative, which confuse the picture. One conclusion which seems inescapable is that the *A*-wave, as grossly observed, is not a purely photopic effect.

METHOD

The apparatus is similar to that previously described by Johnson (1949). It comprises an optical system for stimulating the eye, recording electrodes, an amplifier, and a photographic-recording device. The eye is kept in position with a biting-board and a central fixation point. The active electrode is a silver disk mounted in a contact lens. The inactive electrode is applied to the forehead. The responses are led into an amplifier which activates a monitoring cathode ray oscillograph and a G.E. loop oscillograph. The excursions of the latter are recorded photographically on tape. Responses may be recorded using either direct-coupled or condenser-coupled amplification. Measurements have been made only on direct-coupled records.

The stimulus, presented in Maxwellian view, is a circular patch with a diameter of 7° 30′. Its maximum luminance, with no filters inserted, is about $1\frac{1}{2}$ million footlamberts. Filters used were Wratten neutral density filters and Farrand monochromatic filters with transmission peaks (adjusted for the scotopic visibility function) at 564, 541, 529, 509, 466, and 434 mμ, referred to below as *E*, *F*, *G*, *H*, *I* and *K* filters, respectively. Three additional filters used were: *FR* (ethyl cellulose, red, cutting off at about 600 mμ); W 44 (Wratten no. 44, minus-red, cutting off the red end at about 580 mμ); and W 49 (Wratten no. 49, blue, cutting off at about 510 mμ). Spectral transmissions of all filters have been determined with a Beckman DU spectrophotometer. The light source, a 50 c.p. tungsten lamp, burns at a temperature of 3300° K, from which its spectral emission may be calculated. The method by which the scotopic luminosities of the various filter combinations are computed has been described by Riggs *et al.* (1949).

Conditions of light-adaptation are maintained with a white-illuminated hemispheric field. The stimulus is presented through a hole in the centre of this field. A two-footlambert field was used while recording responses of the 'light-adapted eye'. In sessions devoted to a study of dark-adaptation the subject, after donning electrodes, spent 15 min in darkness followed by 15 min of exposure to a 40-footlambert field. The field light was then extinguished and dark-adaptation began. Stimuli were presented after 5 sec; 1, 2, 3, 4 and 5 min; and at intervals of 2–5 min thereafter. Records reported as being taken with the eye 'dark-adapted' were recorded after at least 40 min of dark-adaptation.

RESULTS

Fig. 1 shows responses to red and white flashes under conditions of light- and dark-adaptation. *A*-waves are present in all four records but, whereas the two different stimuli yield approximately matched responses in the light, the response to *white* has much the larger *A*-wave when the eye is dark-adapted. This comparison invites the suspicion that the *A*-wave recorded in the dark reflects scotopic activity to some degree. Attention should be drawn to the fact that the dark-adapted red- and white-*A*-waves differ in character as well as in amplitude. Reduction in the intensity of the 40 msec white flash, though it decreases the overall amplitude of the *A*-wave, does not result in a flat-bottomed response such as that obtained with the red. It would be manifestly impossible, then, to determine the intensities required for each of these stimuli to elicit some 'standard *A*-wave'. Fortunately, though perhaps fortuitously, the responses to colours other than red are considerably less individualistic in appearance. The degree of similarity may be seen by referring to Fig. 2 where are shown roughly matched responses to stimuli of different colours ranging from yellow through blue.

Assuming some validity in the making of such matches, we have attempted to determine the spectral sensitivity of the *A*-wave of the dark-adapted eye.

Three colour-normal subjects were used. Each of the monochromatic stimuli was presented at several intensities so as to record *A*-waves ranging from zero amplitude to waves of moderate size. The intensity was varied with neutral filters in 0·3 or 0·4 log. unit steps. The *A*-waves were then measured and their magnitudes plotted against intensity. By interpolation from these graphs, intensity values such as would be requisite for the elicitation of 'standard'

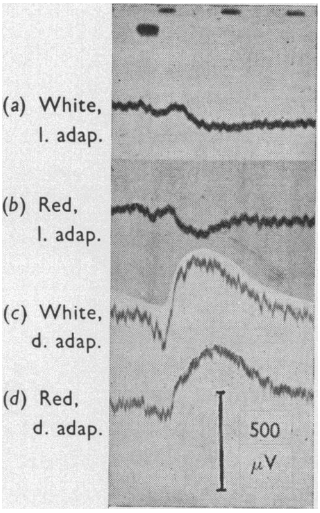

Fig. 1

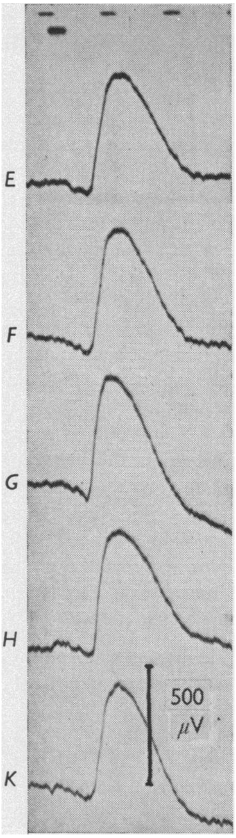

Fig. 2

Fig. 1. Responses to red and white stimuli under conditions of light- and dark-adaptation: (*a*) response to white (1·3 log density neutral filter) recorded during continuous exposure to a 2-footlambert field; (*b*) response to red (*FR* filter) under the same conditions; (*c*) response to same white stimulus, but with the eye dark-adapted; (*d*) response to the same red with eye dark-adapted. 40 msec flashes. Time marks, 0·1 sec. Subject E.P.J.

Fig. 2. Approximately matched responses of the dark-adapted eye to 'monochromatic' stimuli: filters *E* (yellow), *F*, *G*, *H* and *K* (blue). Varying strengths of neutral density filter were employed. Time marks, 0·1 sec. Subject E.P.J.

A-waves of moderate size were determined. Relative photopic and scotopic luminosity values of such stimuli were then computed. The computed photopic values were obviously unequal. The fit to a scotopic function turned out much better, as may be seen in Fig. 3. Here the scotopic luminosity values obtained for the several colours have been plotted as deviations from the scotopic sensitivity function. The scotopic curve used is that of Stiles & Smith (1944). The luminosity value of the *H* filter, and its corresponding position on the scotopic sensitivity curve (509 mμ), have been assigned an arbitrary value of 1·00. The result is a 'spectral sensitivity curve' for the *A*-wave which shows

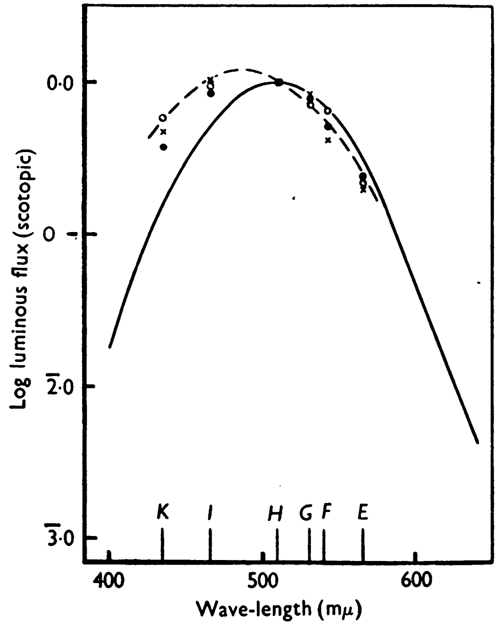

Fig. 3. 'Spectral sensitivity curve' of the *A*-wave (experimental points plotted for three individual subjects at six points on the spectrum) compared with the sensitivity curve for the *B*-wave (broken line) and with the scotopic luminosity function (solid line). The letters designate the 'monochromatic' filters employed.

relatively more sensitivity to blue, less to yellow, than would be predicted even on the assumption that the phenomenon is scotopic. This is similar to what was earlier found true of the *B*-wave (Riggs *et al.* 1949). The curve drawn through the experimental points in Fig. 3 is, in fact, the *B*-wave sensitivity curve from the earlier study. The argument which has been applied by Boynton & Riggs (1951) to explain the discrepancy in the case of the *B*-wave data is that the shorter wave-lengths are scattered more by the ocular media so as to stimulate an effectively greater area. This reasoning would seem to apply equally to the case of the *A*-wave.

This does not mean that the *A*-wave may now be summarily assigned to the scotopic visual system. There are several arguments against this. In the first place, the response to red light undeniably exhibits an *A*-wave, an initial negative deflexion. From a computation of the scotopic luminosity value of our red stimulus we should predict none—the scotopic value of the red is much too low by comparison with the other colours. The *A*-wave, furthermore, frequently appears duplex in character. The typical *A*-wave, in response to high-intensity stimuli, shows a momentary 'levelling off' midway through the response. The slope then increases again, abruptly, continuing until it is interrupted by the rise of the positive *B*-wave. Such a response may be seen in Fig. 2 (*E* filter, yellow), in Fig. 4 (toward the end of dark-adaptation in the blue series), or in Fig. 7, where it is illustrated schematically.

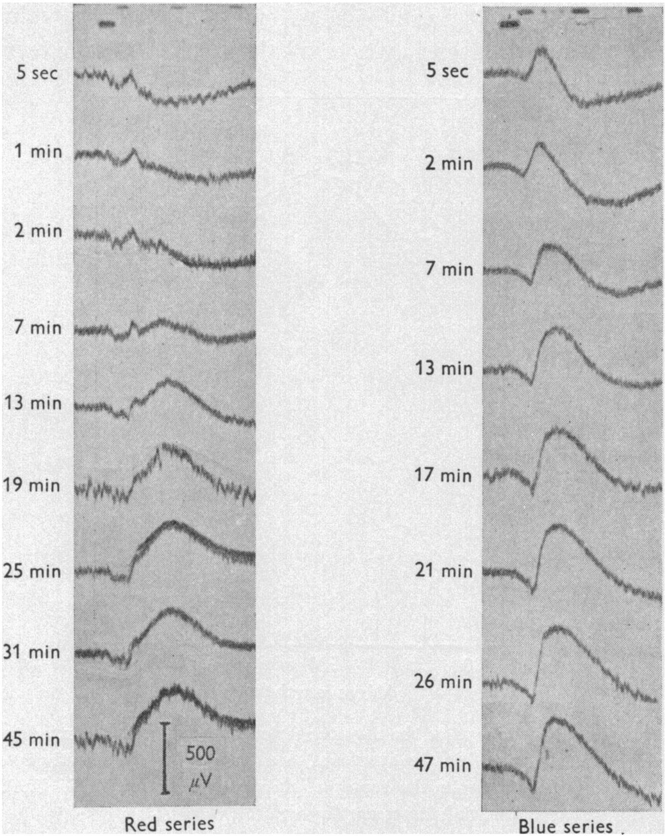

Fig. 4. Responses to blue (W 49) and red (*FR*) stimuli recorded during the course of dark-adaptation. Times given are from the turning-off of the 40-footlambert light-adaptation field. Time marks, 0·1 sec. Subject E.P.J.

Fig. 4 shows responses to blue light and red light, recorded during the course of dark-adaptation. Similar series of responses were recorded using white and minus-red stimuli. In Fig. 5 the magnitude of the *A*-wave, in microvolts, is plotted as a function of time-in-the-dark for each of these stimuli. The red-*A*-wave, though it alters somewhat in appearance, does not grow in amplitude. The blue-, white-, and minus-red-responses, on the other hand, begin increasing noticeably in size after the eye has been 4–7 min in darkness. This growth continues until the end of the session, thus paralleling the development of the *B*-wave as revealed in earlier studies. The heavy broken line in Fig. 5 represents the growth of the *B*-wave, as reported by Johnson (1949). Only the general form of the curve is pertinent, inasmuch as conditions were somewhat different during the *B*-wave experiment. The stimuli, in that study, were less intense and the preliminary light-adaptation level was lower.

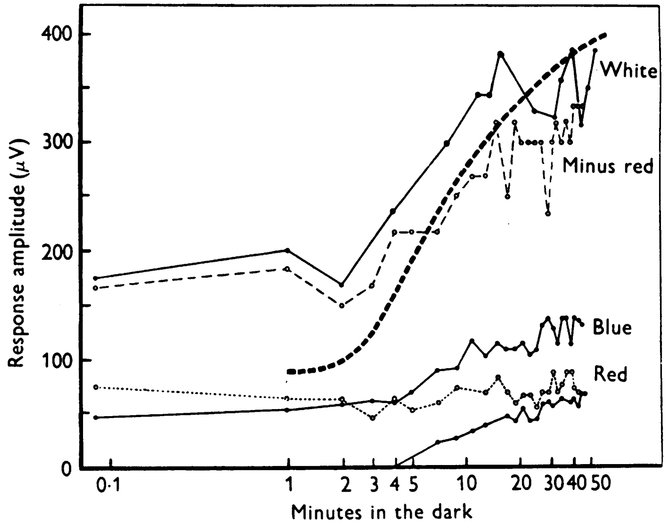

Fig. 5. Magnitude of the *A*-wave plotted against minutes of dark-adaptation for stimuli of four different colours: white (0·6 log unit neutral density filter), minus red (W 44), blue (W 49), and red (*FR*). The heavy broken line represents the growth of the *B*-wave under similar circumstances. The bottom curve (unlabelled) shows the contribution of the secondary 'spurt' to the total magnitude of the blue-response. Subject E.P.J.

The growth of the *A*-wave in the later stages of dark-adaptation appears, on inspection, to be related to the appearance of the secondary 'spurt' of negativity which we have described as coming directly before the *B*-wave. This 'spurt' is not characteristic of the red-responses but it may be differentiated easily in the blue series, as seen in Fig. 4. Although it is probably futile to try to estimate, quantitatively, how much of the *A*-wave is produced by the activity underlying this 'spurt', inasmuch as only the combined effect or resultant of response processes appears in the record, we have attempted to measure the magnitude of the 'spurt' treating it as though it were a discrete component and as though any other, residual, negativity were maintained at a constant level during its occurrence. The bottom curve in Fig. 5 shows the actual increase in negativity during the 'spurt' portion of the response as measured on records of the blue series in which the beginning and the end of the 'spurt' could be discerned clearly. It may be seen that the increase in the size of this component accounts for most of the growth of the *A*-wave during dark-adaptation.

In Fig. 6 there is shown a series of responses to progressively increasing intensities of white light. The eye was dark-adapted. The stimulus flashes had a duration of 5 msec. The double nature of the *A*-wave is very evident. Use of the shorter flash (others were 40 msec) seems to give emphasis to the duplicity. A possible explanation of this is discussed below.

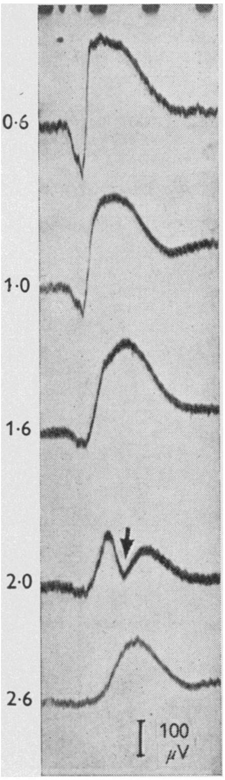

Fig. 6. Response of the dark-adapted eye to different intensities of white light. The values given are the log units of neutral density filter inserted in the stimulus-beam. Maximum intensity (no filter) is assessed at about 1½ million footlamberts. Arrow indicates a 'wink-artifact' in the 2·0 record. 5 msec flashes. Time marks, 0·1 sec. Subject J.W.

DISCUSSION

The early negative phase of the electrical response of the human eye has hitherto been regarded as dependent on a retinal process which is (1) simple and unitary, and (2) primarily photopic. In view of the results presented here, neither of these ideas is tenable. Evidence for the existence of a scotopic component includes the fact that the *A*-waves recorded in response to stimuli of high scotopic luminosity show a progressive increment in magnitude as dark-adaptation proceeds. Further, the effectiveness of different colours of light in eliciting *A*-waves from the dark-adapted eye may be calculated with fair accuracy from the scotopic luminosity function. Although the scotopic function does not provide a perfect fit to the data, the divergence is such as to indicate excess blue-sensitivity—lending no encouragement to the view that the process is photopic. Most significant, perhaps, is the fact that the spectral sensitivity of the *A*-wave matches that of the *B*-wave, which most investigators agree to be scotopic. The divergence of *B*-wave-sensitivity from the scotopic curve has been explained by Boynton & Riggs (1951) as resulting from the greater scattering of blue light within the eye; the departure is less when larger stimulus-areas are employed.

That the *A*-wave is not entirely scotopic, however, is shown by the fact that red light, even though low in scotopic luminosity, produces a definite negative potential. The red-*A*-wave fails to increase appreciably in amplitude during dark-adaptation, having, after 5 sec in the dark, about the same amplitude as when the eye has been dark-adapted for 45 min. There would appear to be two negative processes: one scotopic, the other, perhaps, photopic. Our tentative appraisal of the situation is indicated in Fig. 7. Here we suggest that there may be a 'photopic' *A*-wave, a negative potential with a latency of 10 msec or less, which attains its maximum level of evocability or excitability within a few seconds after dark-adaptation has commenced. A second negative component, the 'scotopic' *A*-wave, does not appear until the eye has been dark-adapted for several minutes. It has a longer latency than the 'photopic' potential, coming in only 10–20 msec ahead of the *B*-wave. Its magnitude is dependent on the scotopic luminosity value of the stimulus and on the degree of dark-adaptation.

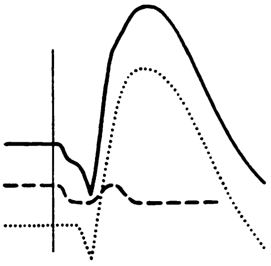

Fig. 7. Analysis of the retinal response of the dark-adapted eye into 'photopic' and 'scotopic' components. The solid line represents the typical response to a high-intensity flash of white or mid-spectral light. The broken line depicts the supposed photopic response (cf. light-adapted responses in Fig. 1 or the earlier red-responses in Fig. 4). The dotted line shows what would then remain as the scotopic contribution. A response of the latter form has not been experimentally isolated, though a sufficiently intense violet flash might be expected to evoke it.

Although the 'photopic' and 'scotopic' components are drawn as single, diphasic elements in Fig. 7, it is not meant to imply that the negative and positive phases of each cannot vary independently of each other. The positive components have been sketched in partially to cover our ignorance of the later course of the negative processes. There is some evidence that the 'photopic' *A*-wave returns rather quickly to the base-line, once the stimulus has been removed. We may point, for instance, to the responses shown in Fig. 6, where the break between the two negative portions of the response is very evident. The stimulus, here, lasted but 5 msec. With longer flashes, the early *A*-component maintains its level of negativity longer, passing more smoothly into the later 'scotopic' phase. What appears to be a tiny positive peak occurring in the trough of the *A*-wave in the lower-intensity responses of this series may be interpreted as an 'off-effect' resulting from the cessation of the 'photopic' A-process. It would thus be somewhat comparable to the D-wave observed in lower animals.

There is a possibility, of course, that this peak is a genuine positive component whose conditions of occurrence are such as to bring about the 'broken' appearance of the A-wave which has concerned us in this report. For the present, however, we are content to accept the analysis which we have proposed. As the next step in our investigation we intend to check on the supposed photopic nature of the early A-component by working in the early period of dark-adaptation where, if our analysis is correct, we will find it uncontaminated by the scotopic phase.

SUMMARY

1. A-waves elicited from the human eye by light-flashes of high intensity have been analysed into two components.

2. The earlier component, best observed in response to red light, is tentatively designated the 'photopic A-wave'.

3. A slightly later component, which develops during prolonged dark-adaptation, shows spectral sensitivity characteristics which identify it as scotopic in nature.

REFERENCES

ADRIAN, E. D. (1944). Rod and cone responses in the human eye. *Nature, Lond.*, **154**, 361–362.

ADRIAN, E. D. (1945). The electric response of the human eye. *J. Physiol.* **104**, 84–104.

BOYNTON, R. M. & RIGGS, L. A. (1951). The effect of stimulus area and intensity upon the human retinal response. *J. exp. Psychol.* **42**, 217–226.

EINTHOVEN, W. & JOLLY, W. A. (1908). The form and magnitude of the electrical response of the eye to stimulation by light at various intensities. *Quart. J. exp. Physiol.* **1**, 373–416.

GOTCH, F. (1903). The time relations of the photo-electric changes in the eyeball of the frog. *J. Physiol.* **29**, 388–410.

GRANIT, R. (1933). The components of the retinal action potential in mammals and their relation to the discharge in the optic nerve. *J. Physiol.* **77**, 207–239.

GRANIT, R. (1947). *Sensory Mechanisms of the Retina*, pp. 126, 135. Oxford University Press.

JOHNSON, E. P. (1949). The electrical response of the human retina during dark-adaptation. *J. exp. Psychol.* **39**, 597–609.

RIGGS, L. A., BERRY, R. N. & WAYNER, M. (1949). A comparison of electrical and psychophysical determinations of the spectral sensitivity of the human eye. *J. opt. Soc. Amer.* **39**, 427–436.

STILES, W. S. & SMITH, T. (1944). A mean scotopic visibility curve. *Proc. phys. Soc. Lond.* **56**, 251–255.