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# THE RELATIONSHIP BETWEEN THE CHANGE IN THE ELECTRORETINOGRAM AND THE SUBJECTIVE DARK-ADAPTATION CURVE

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It is well known that the electroretinogram (E.R.G.) changes appreciably during dark adaptation. Granit (1938) has shown that the nature of the change depends to some extent on whether the eye in question possesses an E- or I-type of retina and he has further demonstrated (Granit, 1933) that, so far as the electroretinogram is concerned, the human eye has an E-retina. In the human electroretinogram dark adaptation reduces or obliterates the small negative *a*-wave and causes a considerable increase in the size of the *b*-wave, while the whole electrical response is much prolonged (Cooper, Creed & Granit, 1933; Karpe, 1945). These changes can be seen in Fig. 1.

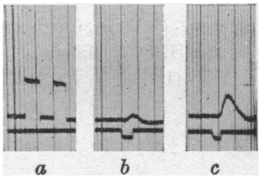

Fig. 1. The effect of the state of adaptation on the *b*-wave of the human electroretinogram. *a*, Calibration to 0·5 mV. *b*, E.R.G. of an eye adapted to 5 m.c. *c*, E.R.G. of an eye adapted to about 0·05 m.c. Stimulus 20 m.c. restricted to a central retinal area subtending 8°.

The increase in sensitivity of an eye which occurs during dark adaptation is usually expressed in terms of the light intensity just visible (the threshold) at any given moment, and when the threshold is plotted against the duration of dark adaptation the well-known dark-adaptation curve shown in Fig. 2 is obtained. This curve is made up of two parts, the first, lasting for about 7 min. in Fig. 2, being generally considered to represent cone adaptation and the second rod adaptation.

Great improvements in the technique of recording the human electroretinogram have now made it possible to follow its changes during dark adaptation with fair accuracy, and the time seems to have come to consider the relationship between these changes and the subjective dark-adaptation curve. Is any relationship, in fact, demonstrable and, if so, what does it mean in terms of the process of dark adaptation?

## METHOD

The subjective dark-adaptation curve and the change in size of the *b*-wave were recorded simultaneously for the left eye of one of us (G. K.).

Gullstrand's method, using Carle's apparatus (Carle, 1937), was used to determine the subjective curve; this method measures the light threshold only; no form or brightness discrimination is required. The technique recently described by one of us (Karpe, 1945) was used for recording the electroretinogram.

In order to ensure that the initial condition of light adaptation was as constant as possible from one experiment to another, the experiment was begun by a preliminary period of dark adaptation which was continued until a fairly constant threshold value was obtained. The light adaptation consisted of exposure to 5000 m.c. for 30 sec. followed by 10,000 m.c. for 5 min. The final dark-adaptation curves were then taken.

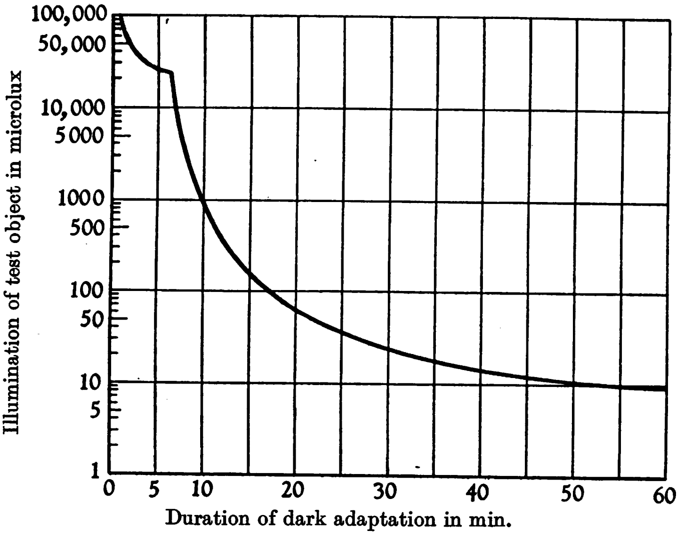

Fig. 2. The subjective dark-adaptation curve. Abscissae: duration of dark adaptation in min. Ordinates: the smallest visible illumination in microlux (1,000,000 microlux = 1 m.c.). (After Kohlrausch (1931). See Wright & Granit (1938).)

After the subject had been prepared for electroretinography with a contact glass on the eye to be investigated, the white screen of Carle's apparatus was placed in front of him with a red fixation light so that the subjective stimulus fell 12° from the fovea on one side and the E.R.G. stimulus 8° on the other. The room lights were then extinguished and the subject indicated as soon as the subjective stimulus became visible. This was then reduced, the time having been noted, and he again indicated as soon as he could see it. At the same time the E.R.G. to a constant stimulus of 1·25 m.c. was recorded, first at intervals of 1 min., later at 2 min. intervals and finally (after 30 min.) at 5 min. intervals.

When dark adaptation seemed to be reasonably complete a triple ground glass screen was placed close to the subject's face and a 500 W. bulb lit behind it, followed after 30 sec. by another 500 W. bulb. One bulb alone gave an illumination of 5000 m.c. and both together 10,000 m.c. evenly distributed over practically the whole field of vision. After 5 min. both lamps were put out, the ground glass removed and the final recording of the two dark-adaptation curves begun. This usually lasted for 40–60 min.

## RESULTS

The results are shown in the curves given in Fig. 3, which illustrate the course of one whole experiment comprising two dark adaptations separated by as intense a light adaptation as we could produce.

The plotting of two curves concerned with such different values as the subjective threshold illumination and the height of the *b*-wave of the electroretinogram on one figure is certain to present some difficulty in the selection of the scales to be compared. However, in the present instance, we have one common point in the asymptotic value finally reached by both curves: the maximum *b*-potential of nearly 0·30 mV. and the subjective threshold of about 0·001 m.c. (the high subjective threshold is due to the presence of the contact glass with possibly some corneal oedema; without a contact glass the same eye normally had a threshold of 0·00003 m.c.). There is a good deal of evidence (see

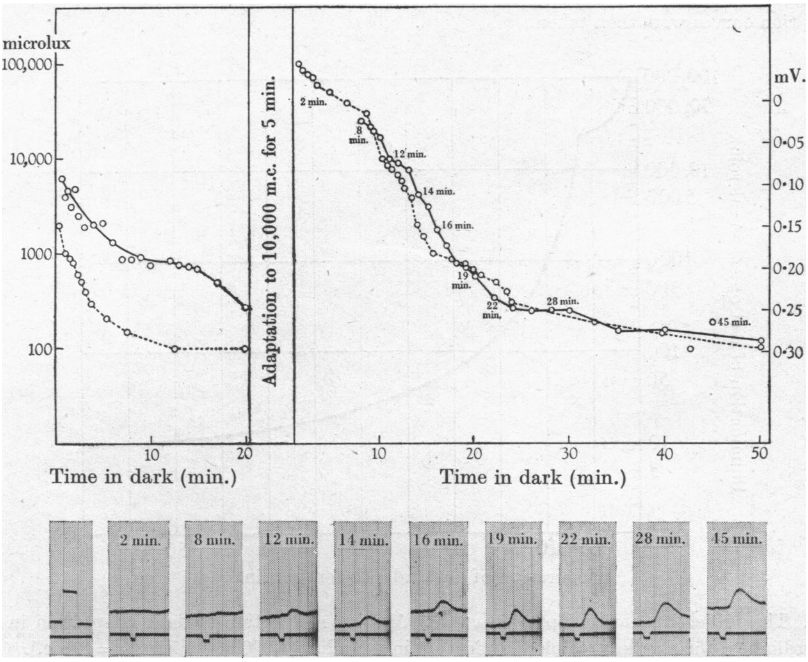

Fig. 3. Comparison of the subjective dark-adaptation curve and the *b*-potential dark-adaptation curve of the same eye before and after intense light adaptation. o- - - - - -o subjective curve; o———o *b*-potential curve. Abscissae: duration of dark adaptation. Ordinates: *Left*, Log illumination in microlux; *Right*, *b*-potential in mV. 5 min. light adaptation to 10,000 m.c. between the two dark adaptations. A selection of the E.R.G.'s recorded after the light adaptation preceded by a calibration to 0·5 mV. is given at the bottom of the figure. The times at which these were recorded are given both on the records and on the curve. Stimulus for E.R.G., 1·25 m.c.

Granit, 1947) suggesting that there is a particularly close association between the *b*-potential and rod activity, and this seemed a good reason for placing the 0 value of the *b*-potential curve at the position of the kink in the subjective curve, where rod adaptation is generally thought first to become manifest. When these two points on each curve are placed together, the *b*-wave and subjective dark-adaptation curves following an efficient light adaptation show a surprisingly good empirical fit. When stronger stimuli (20 or 80 m.c.) were used, however, the two curves did not fit so well, for after light adaptation the *b*-wave curve fell more rapidly than the subjective one. With the 80 m.c. stimulus, there was, on the other hand, a fairly good fit between the two curves taken *before* light adaptation (Fig. 4).

## DISCUSSION

Although other stimuli were occasionally used to produce an electroretinogram, our standard stimulus was 1·25 m.c. In recording a dark-adaptation curve in terms of the size of the *b*-potential it is important to use a stimulus which is neither too strong nor too weak. Under reasonably constant conditions of adaptation, the size of the *b*-wave increases with increased stimulus intensity (Dewar & McKendrick, 1873; de Haas, 1903; Chaffee & Hampson, 1924; Granit, 1947), so that if the stimulus is weak and lies too near the threshold for the electroretinogram, it will not be possible to obtain a *b*-wave which alters with adaptation. If, on the other hand, the stimulus is too strong, the *b*-wave will reach its maximum before the adaptation process is complete. We, therefore, investigated the effect of the strength of the stimulus on the size of the *b*-potential of the dark-adapted subject. The results are shown in the curve of Fig. 5 and indicate that a stimulus of 1·25 m.c. from the rising part of the curve should be suitable for our present purpose.

It is clear from the curves given in Fig. 3 that the increase in the size of the *b*-potential evoked by a constant stimulus can be used as a measure of the course of dark adaptation in man. With an efficient preceding light adaptation and a suitably selected stimulus, the curve relating the size of the *b*-potential to time in the dark follows at least the latter part of the sensory dark-adaptation curve very closely indeed. Under these conditions this curve does appear to correspond to what is generally known as the rod part of the ordinary subjective dark-adaptation curve.

In this connexion it is of interest to mention some other reasons for supposing that the electroretinogram, taken with this apparatus and this stimulus (1·25 lux), is probably dominated by the reactions of the rods. For instance, the presence of macular degeneration is not associated with an abnormal electroretinogram whereas retinitis pigmentosa, even where good central vision is still present, is characterized by a response which is very much diminished or even absent. Perhaps of greater significance is the fact that we

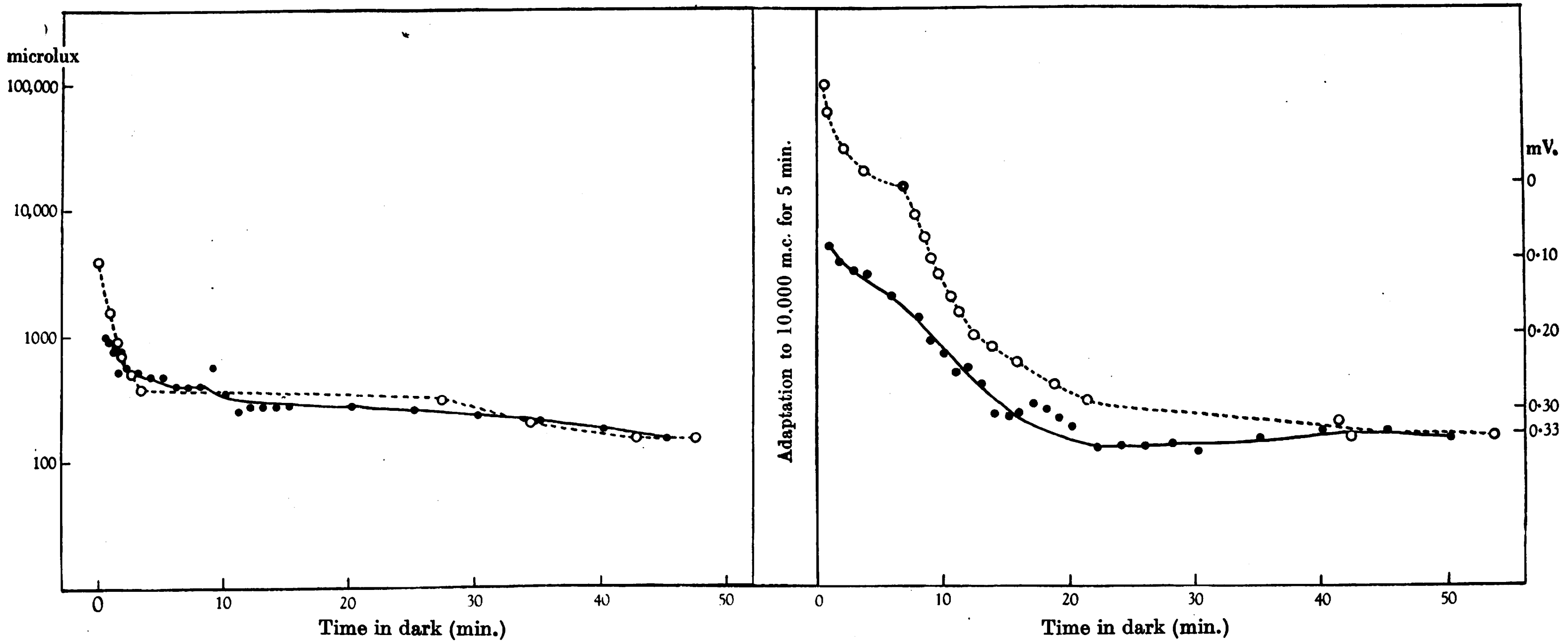

Fig. 4. Effect of a higher stimulus strength on the relation between the *b*-potential dark-adaptation curve and the subjective dark-adaptation curve. Stimulus for E.R.G. 80 m.c. Other details as in Fig. 3.

were unable to evoke any measurable response to a red stimulus (700 mμ) of about this intensity, even though the flash was clearly seen and easily recognized as being red. It is not, therefore, very surprising to find that, during dark adaptation, the electroretinogram only becomes measurable at a time when

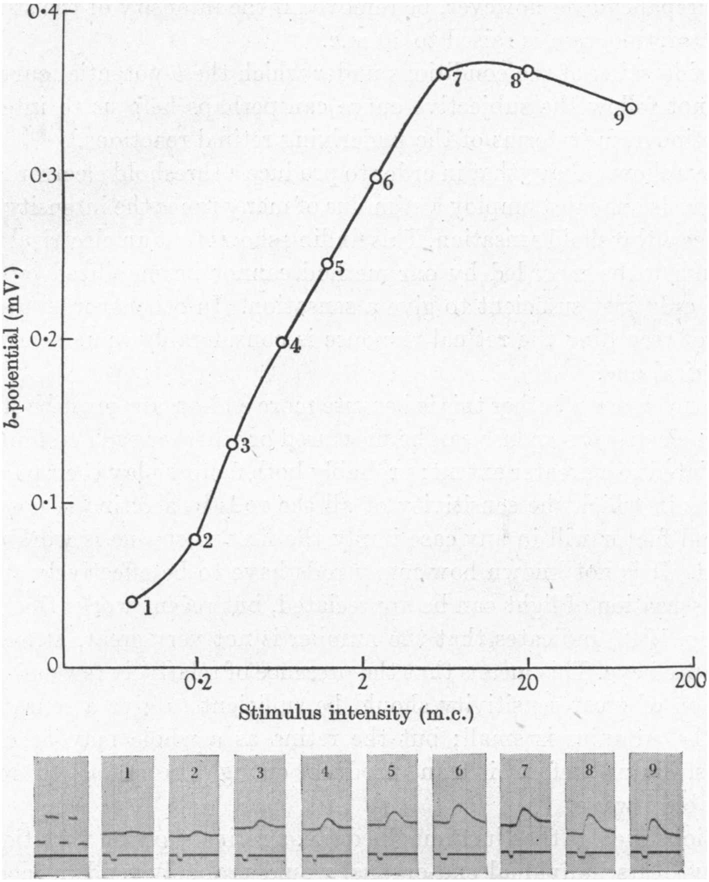

Fig. 5. The effect of stimulus strength on the size of the *b*-potential of the dark-adapted eye. The first E.R.G. was recorded after complete dark adaptation for 40 min.; the intensity of the stimulus was changed by means of neutral tint filters; no stimulus was applied until the eye had recovered its dark-adapted subjective sensitivity. Abscissae: log stimulus intensity. Ordinates: *b*-potential in mV. The E.R.G.'s recorded for each stimulus are given at the bottom of the figure preceded by the calibration to 0·5 mV.

there is at least a likelihood that the rods are beginning to react and that, thereafter, the increase in the *b*-wave follows a curve which can also represent the increase in rod sensitivity.

Difficulties in interpreting the relationship between the *b*-potential and the sensory curves arise, however, when one comes to consider those taken at the beginning of an experiment and not preceded by any special light adaptation. Under these conditions the *b*-potential curve does not follow the rod part of the sensory dark-adaptation curve; a final threshold for the latter may be reached before a maximum *b*-wave can be recorded on the electroretinogram. This discrepancy can, however, be removed if the intensity of the stimulus for the electroretinogram is raised to 80 m.c.

A consideration of the conditions under which the *b*-potential curve follows or does not follow the subjective curve can perhaps help us to interpret the electroretinogram in terms of the underlying retinal reactions.

We have shown above that in order to produce a threshold electroretinogram from the rods one must employ a stimulus of many times the intensity required to produce a threshold sensation. This finding shows that an electrical potential big enough to be recorded by our method cannot be mobilized by a retinal response only just sufficient to give a sensation. In other words, the sensory method of recording the retinal response is considerably more sensitive than the electrical one.

We do not know whether this is because more end-organs must be stimulated before an electrical response can be measured or whether each end-organ must be stimulated to a greater extent; probably both factors play their part. Under conditions in which the sensitivity of all the rods in a retina is not identical the second factor will in any case imply the first when one is working at the threshold. It is not known how many rods have to be effectively stimulated before a sensation of light can be appreciated, but recent work (Hecht, Shlaer & Pirenne, 1942) indicates that the number is not very great, at least in the dark-adapted eye. This means that the presence of relatively few end-organs in a condition of great sensitivity should be sufficient to give a sensation even though the stimulus is small; but the retina as a whole may need a much greater stimulus before it can produce enough potential to register a recognizable *b*-wave.

Conditions such as that just imagined (i.e. a retina showing variations in the sensitivity of its individual end-organs) would probably tend to increase the difference between the sensitiveness of the sensory threshold and that of the electrical method as a measure of the actual retinal response. Now a drastic light adaptation, such as the one we used, will have the effect (and, indeed, this is one of the reasons for its use) of making the initial state of all the rods as uniform as possible and should, therefore, decrease the difference in sensitiveness of the two methods. The same effect would also be achieved by increasing the strength of the stimulus used for producing the electroretinograms, since this would bring in rods too insensitive to play a part when a weaker stimulus is used.

Theoretically, a more satisfactory comparison between the subjective and the E.R.G. curves would be obtained if the latter represented the stimulus intensity necessary just to evoke a recognizable *b*-potential at different times during dark adaptation. We attempted to make such a curve, but found that the difficulty of determining the moment at which such a *b*-potential first appeared rendered the method too inaccurate to be practicable with our apparatus.

## SUMMARY

1. Curves relating the size of the *b*-potential of the electroretinogram to the duration of dark adaptation were compared with subjective dark-adaptation curves taken simultaneously from the same eye.

2. It was found that the *b*-potential curve showed a good agreement with the rod part of the subjective dark-adaptation curve if the E.R.G. stimulus was of moderate strength and the experiment was preceded by an efficient light adaptation.

3. There was also good agreement without the preceding light adaptation if the E.R.G. stimulus was made strong enough, but in this case the two curves did not fit well after light adaptation, the *b*-potential reaching its maximum too soon.

4. The significance of these findings is discussed.

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