

## EVIDENCE FOR THE EQUIVALENT-BACKGROUND HYPOTHESIS IN CONES

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**Abstract**—The equivalent-background hypothesis was tested in the cone system for increment-field diameters of 3.5', 10' and 50'. The wavelength composition of the increment field was also varied; it was either white (color temperature 3000 K) or red (657 nm). The dark-adaptation thresholds were obtained following full bleaches. Using an analysis which corrected all the data for the effects of photopigment depletion, the equivalent-background hypothesis was found to hold fairly accurately across all conditions. The results suggest that the long-term adaptation mechanisms in the rod and cone systems are very similar.

### INTRODUCTION

According to the equivalent-background hypothesis, the effects of bleaching observed during dark adaptation are equivalent to those obtained by presenting some continuous and stabilized background of light that has the same spatial dimensions and retinal locus as the bleaching field. This hypothesis has played an important role in the development of recent theories of dark adaptation (Barlow, 1964, 1972; Rushton, 1965b), since it provides a simple link between the mechanisms underlying the effects of bleaching and those underlying the effects of steady backgrounds. A great deal of evidence supports the equivalent-background hypothesis for the human rod system (Crawford, 1937, 1947; Blakemore and Rushton, 1965a, b; Barlow and Sparrock, 1964; Alpern and Ohba, 1972).

In contrast, there have been very few experimental tests of the equivalent-background hypothesis in cones. One experiment (DuCroz and Rushton, 1966) showed that real backgrounds and equivalent backgrounds produced by bleaching are additive in their effects on cone threshold. Since this additivity property had already been demonstrated in rods (Blake-

more and Rushton, 1965b), the adaptation mechanisms in rods and cones appeared to be similar. Unfortunately, the apparent similarity between rod and cone adaptation seemed to break down when Rinalducci, Higgins and Cramer (1970) attempted to extend the classical equivalent-background experiments of Crawford (1937, 1947) and Blakemore and Rushton (1965a) to the cone system. Crawford, and Blakemore and Rushton, showed that in rods, the equivalent-background hypothesis holds accurately with respect to spatial summation. In particular, they showed that when a state of adaptation (at a given time after bleaching) and a continuous background have the same effect on threshold for detecting an increment field of one size, they also have identical effects on threshold for increment fields of any size.<sup>1</sup> In contrast, Rinalducci *et al.* found that the equivalent-background hypothesis failed drastically for increment field diameters varied within the narrow range of 8' to 20'.

However, the results of a recent study by Hollins and Alpern (1973) suggest a different interpretation of the study by Rinalducci *et al.* Hollins and Alpern measured absolute threshold and cone pigment density during dark adaptation for a wide range of bleaching-field intensities and durations. The primary purpose of their study was to test the generality of the Dowling—Rushton relation (Dowling, 1960; Rushton, 1961),

$$\log \frac{\Delta I}{\Delta I_0} = \alpha q. \quad (1)$$

In this equation,  $\Delta I_0$  is absolute threshold in the dark-adapted eye,  $q$  is the proportion of bleached cone pigment, and  $\alpha$  is a constant whose value is usually about 3.0 for the human cone system (Rushton, 1963, 1965a). Hollins and Alpern found that with  $\alpha = 3.3$ , equation (1) accurately described all their results except those obtained during the first 30–60 sec after relatively weak bleaches (less than about 60%).<sup>2</sup> During this initial period the thresholds exceeded those predicted by equation (1). The fact that a single value of  $\alpha$  was sufficient, implies that the sensitivity of the cone system during dark adap-

<sup>1</sup> In these studies and in the present one, the background field was not stabilized on the retina. However, Burkhardt (1966) and Sparrock (1969) have shown that increment thresholds obtained on uniform stabilized and unstabilized backgrounds are almost identical.

<sup>2</sup> Hollins and Alpern also included a condition in which saturating bleaches were obtained with a brief (<0.001 sec) xenon flash. Due to photoreversal, it is impossible under such conditions to bleach more than about 60% of the cone photopigment (Rushton, 1964; Rushton and Henry, 1968). Hollins and Alpern found that their data could not be accounted for by equation (1) with  $\alpha = 3.3$ . On the basis of similar experiments in rods, Pugh (1975) has concluded that the recovery of rod sensitivity may be governed by the proportion of photopigment molecules that effectively absorb at least one quantum and not by the proportion bleached. Pugh shows that this hypothesis can apparently account for all his results, but it suggests the existence of an unknown substance in the receptor with about the same rate of regeneration as rhodopsin.

tation (excluding the initial period after weak bleaches) is predicted by the proportion of pigment bleached no matter how that state of bleaching is reached. This property strongly suggests that the underlying adaptation mechanism is controlled by the bleached photopigment or by some closely related substance within the receptor (see footnote 2). Hollins and Alpern's results therefore support the hypothesis that there are at least two mechanisms that govern the recovery of cone sensitivity during dark adaptation: (1) a short-term mechanism whose effects are revealed during the first 30–60 sec after weak bleaches and (2) a long-term mechanism which is dominant at all other times and controlled by the bleached photopigment (or a closely related substance). Results similar to those of Hollins and Alpern have been reported, for example, for the human rod system (Rushton and Powell, 1972a, b), for the rat ERG (Dowling, 1963), and for ganglion-cell responses in skate (Green, Dowling, Siegel and Ripps, 1975).

Rinalducci *et al.* used weak bleaching fields that could not have bleached more than 40% of the cone photopigments. Indeed, for some of their conditions bleaching must have been considerably less. Furthermore, most of their dark-adaptation curves were at or near asymptote within 60 sec. Thus, their study apparently shows that the short-term mechanism does not satisfy the equivalent-background hypothesis, but it seems to leave open the question of whether the long-term mechanism satisfies the hypothesis.

A more general problem that no previous equivalent-background studies have considered is that simple photopigment depletion makes a significant contribution to photopic dark-adaptation curves obtained with intense bleaches (Rodieck, 1974; Geisler, 1978). Obviously, any losses in sensitivity that are accounted for by photopigment depletion are not due to the long-term or short-term mechanisms. Thus, in order to test the equivalent-background hypothesis one must first correct the dark-adaptation curves for the effects of photopigment depletion. Corrections for depletion effects have been successfully applied in the analysis of a variety of other experiments employing intense stimuli (Brindley, 1955; Cornsweet, 1962; Alpern, Rushton, and Torii, 1970c; Boynton and Whitten, 1970; Boynton and Baron, 1975; Geisler, 1978).

The purpose of the present experiment was to test the equivalent-background hypothesis in the photopic long-term mechanism as a function of increment field diameter, using a method (Geisler, 1978) that takes into account the effects of photopigment depletion.

#### METHODS

Two channels of a 4-channel Maxwellian-view optical system were used to present the bleaching, background

and increment fields to the subjects right eye. The circular bleaching and background fields subtended 5', and were composed of white light from a tungsten source (3000 K). An infrared-blocking filter was always interposed in the beam used for the bleaching and background fields.

Dark-adaptation and increment-threshold curves were obtained for increment-field diameters of 3.5', 10' and 50'. The increment fields were always presented in the center of the bleaching and background fields. The subjects fixated the center of an imaginary cross formed by four dim fixation lights that surrounded the background field. In addition to varying increment-field diameter, wavelength composition was also varied; the increment field was either a tungsten white (3000 K), or a 657 nm red that was obtained with a narrow-band interference filter. For the red increment field, thresholds were only obtained for diameters of 3.5' and 50'. The thresholds measured with the white increment field probably reflected the combined sensitivity of the red ( $\pi 5$ ) and green ( $\pi 4$ ) cone mechanisms, and those measured with the red increment field probably reflected the sensitivity of the red ( $\pi 5$ ) cone mechanism alone (Stiles, 1939, 1959; DuCroz and Rushton, 1966). In all conditions, the increment field was flashed for 30 msec, once every two seconds. All stimuli were turned on and off with electromagnetic shutters that produced rise and decay times of less than 1 msec. Retinal illuminances were determined by the method recommended by Westheimer (1966). The image of the tungsten filament at the subject's pupil, which was dilated with 1% Mydriacyl<sup>3</sup>, was less than 2.0 mm in diameter.

After aligning the bite bar so that the image of the filament passed through the center of the pupil, a 6.0 log td bleaching field was presented for 2 min. At this illuminance nearly 100% bleaching of the cone pigments is obtained (Rushton and Henry, 1968). For 15 min following the bleach, dark-adaptation thresholds were obtained using the method of adjustment. Immediately after the dark-adaptation run increment thresholds were obtained starting with the lowest background intensity. The subject adapted to each successively more intense background for 2–3 min before adjusting the increment field to threshold. The session ended by completing another dark-adaptation run. Two highly practiced observers, one of them the author, served as subjects. Both observers completed two sessions for each increment-field diameter. Observer MB was tested with the white increment fields, and observer WG with both the white and red fields.

#### RESULTS

The dark-adaptation and increment-threshold functions obtained with the white increment fields are shown in Figs 1 and 2. Each symbol represents a single threshold setting. Comparison of the data obtained at different times for the same condition revealed no systematic differences in thresholds across sessions or across the first and second dark-adaptation runs within a session. The functions obtained with the 657 nm increment field appeared very similar to those in Fig. 2.

#### *Correction for photopigment depletion*

The traditional method of testing the equivalent-background hypothesis involves deriving an equivalent-background function (background intensity as a function of time) for each increment field diameter. These equivalent-background functions could be obtained graphically from Fig. 1 (or 2) by reading off the background intensity that produced the same threshold as that observed at each point in time after

<sup>3</sup> Subject WG used 1% Mydriacyl (Alcon Laboratories, Inc., Fort Worth, Texas) throughout the experiment. However, control conditions showed that it was not necessary, so subject MB was not required to use it. It was also feared that slight variations in accommodation would seriously affect threshold for the 3.5' test flash. In order to test this, a control condition was run in which accommodation was paralyzed with 1% Cyclogyl (Alcon Laboratories). The results were the same as without the Cyclogyl.

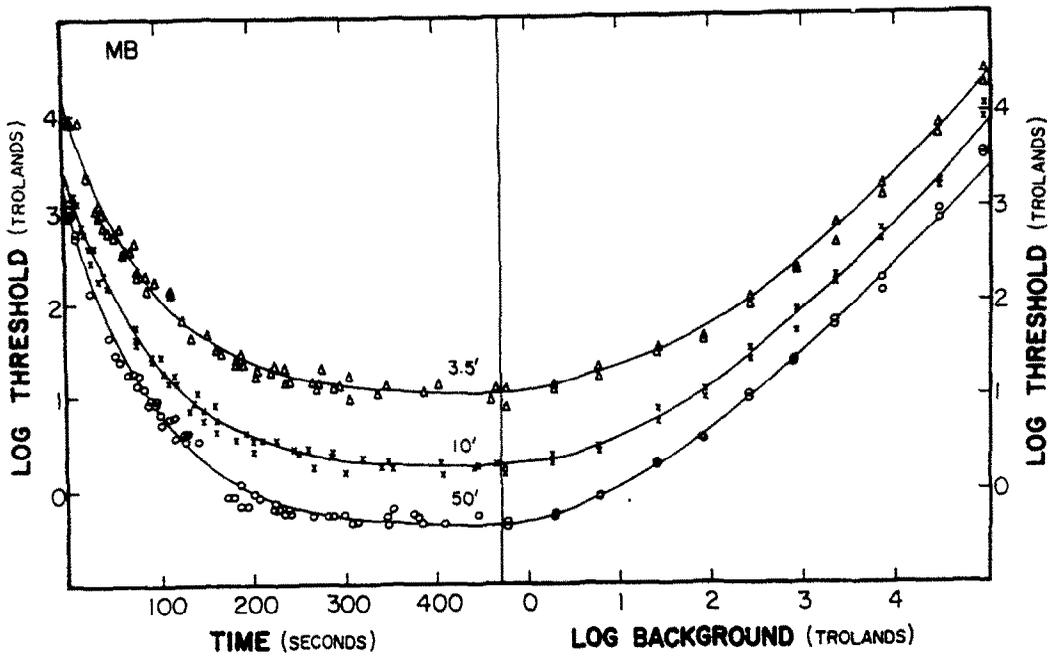


Fig. 1. Dark-adaptation and increment-threshold curves for subject MB. The increment field was white (3000 K), and the increment-field diameters were as indicated. Each symbol represents a single threshold setting.

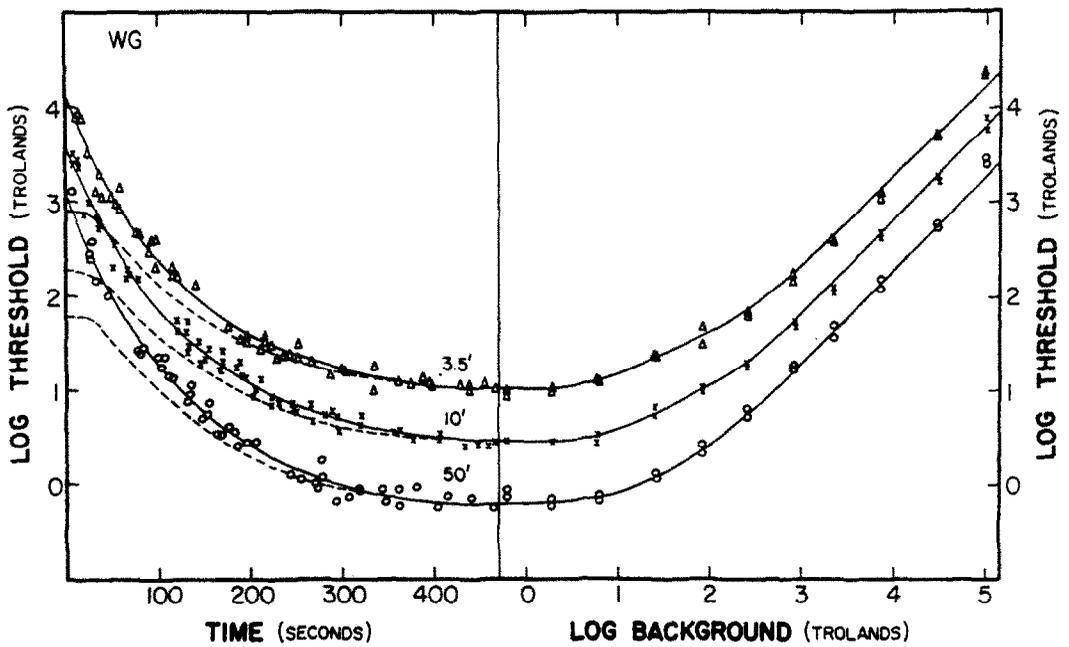


Fig. 2. Dark-adaptation and increment-threshold curves for subject WG (the author). The increment field was white (3000 K), and the increment-field diameters were as indicated. Each symbol represents a single threshold setting. The dashed curves are the solid curves after correction for the effects of photopigment depletion.

bleaching. If the three equivalent-background functions turned out to be superimposed it would be interpreted as confirmation of the hypothesis.

This analysis, however, is not logically correct in the cone system since photopigment depletion accounts for a sizable component of the dark-adaptation curves, and only a much smaller component of the increment-threshold curves. Fortunately, the effects of photopigment depletion can be parceled out by expressing all intensities in terms of effective absorbed quanta. Once the dark-adaptation and increment-threshold data are expressed in these units, the equivalent-background hypothesis can be tested with the usual graphical method. Actually, it is sufficient to use any intensity unit that is proportional to absorbed quanta. The easiest such unit to use is the one that will be referred to here as the *corrected troland*. If a light has an intensity of  $I$  trolands, and if the proportion of pigment present is  $p$ , then we will define its intensity, in corrected trolands, to be  $pI$ . (This definition assumes that self-screening effects are negligible.)

In order to transform the data into corrected trolands, two functions are needed: (1) the proportion ( $p$ ) of photopigment present as a function of the time ( $t$ ) after bleaching, and (2) the proportion ( $p^*$ ) of photopigment present as a function of the steady background intensity ( $I$ ). These two functions have been measured directly by reflection-densitometry techniques, and agree with those derived from Rushton's differential equation for bleaching and regeneration of cone pigments (Rushton, 1963, 1965a; Rushton and Henry, 1968; Hollins and Alpern, 1973). In particular

$$p = 1 - q_0 \exp(-t/t_0) \quad (2)$$

and

$$p^* = \frac{I_0}{I_0 + I} \quad (3)$$

where  $t_0$  is the time constant of regeneration,  $q_0$  is the initial proportion of pigment bleached, and  $I_0$  is the half-bleaching constant. To use these equations,  $I_0$  and  $t_0$  must be specified. Once these parameters are specified,  $q_0$  can be calculated from Rushton's differential equation. One way to proceed would be to use the values of  $I_0$  and  $t_0$  reported by Rushton and Henry (1968) since they are the most recent values published by Rushton, and they were obtained for bleaching with white tungsten light. The drawback to this approach is that the values of  $I_0$  and  $t_0$  are somewhat variable across subjects and experiments. For example, Alpern and Wake (1977) have found values of  $I_0$  as low as 3.3 log td and as high as 4.6 log td, and values of  $t_0$  as small as 84 sec and as large as 146 sec. (Undoubtedly, much of this variability

is due to individual differences.) Fortunately, variations of  $I_0$  within the range of 3.3–4.6 log td do not have much effect on the present analysis, so a value of 4.3 log td was used throughout. The reasons for this insensitivity to variations in  $I_0$  are first, that the effects of photopigment depletion are simply very small for the relevant background intensities, and second, that the bleaching field was so intense that the value of  $q_0$  can safely be assumed to be 1.0 as long as  $I_0$  is any value less than 4.6 log td.

In order to take into account individual differences in  $t_0$ , its value was estimated from each subject's dark-adaptation curve. To begin with, it was assumed that equation (1) accurately describes the relationship between relative threshold and the proportion of pigment bleached. Using equation (2) to replace  $q$  (i.e.  $1 - p$ ) in equation (1), we have

$$\log \frac{\Delta I}{\Delta I_0} = \alpha q_0 \exp(-t/t_0). \quad (4)$$

The values of  $t_0$  were estimated by finding least-squares fits of equation (4) to the dark-adaptation data obtained with the 50' increment field. These best-fitting functions are the solid curves drawn through the open circles in Figs 1 and 2. For the white increment field, the estimates of  $t_0$  were 90 and 129 sec for subjects MB and WG, respectively. (The estimates of  $\alpha$ , assuming  $q_0 = 1.0$ , were 3.6 and 3.5.) For the 657 nm increment field, the estimated value of  $t_0$  was 122 sec. (The estimate of  $\alpha$  was 3.4.)<sup>4</sup>

With the above parameter values, equations (2) and (3) were used to transform all the data into corrected trolands. The transformed data from Fig. 2 are plotted in Fig. 3. The solid curves drawn through the data in Fig. 2 were also transformed and then plotted as the solid curves in Fig. 3.

In order to illustrate the effects of photopigment depletion, the solid curves in Fig. 3 are also plotted as dashed curves in Fig. 2. The difference between the solid and dashed curves shows the component of the dark-adaptation curve accounted for by photopigment depletion.

#### *Test of the equivalent-background hypothesis*

The left-hand side of Fig. 3 shows the dark-adaptation curves for the long-term adaptation mechanism alone. Does the equivalent-background hypothesis hold for the photopic long-term mechanism? This was tested by using the customary graphic method to calculate equivalent-background functions from the smooth curves drawn through the data (as in Fig. 3). One minor difficulty arose with this approach. The photopigment-depletion analysis, when applied to equation (4) or equation (1), predicts that threshold in corrected trolands is constant (or increasing) during the first several seconds after bleaching (see the solid curves in Fig. 3). In fact, the data do not support this prediction. The dashed line segments in Fig. 3 were added in order to better represent the data for purposes of calculating the equivalent-background functions. It is legitimate to add the dashed line segments because at this point the curves are only being used for graphical purposes. The poor fit between the data and the solid curves suggests that equation (1) does not hold for the first several seconds after

<sup>4</sup> In order to obtain the smooth curves that pass through the data, equation (4) was also fit to the dark-adaptation data obtained with the 3.5' and 10' increment fields. However, the values of  $t_0$  were not used in the photopigment-depletion analysis, since the validity of equation (1) has only been demonstrated for large increment fields.

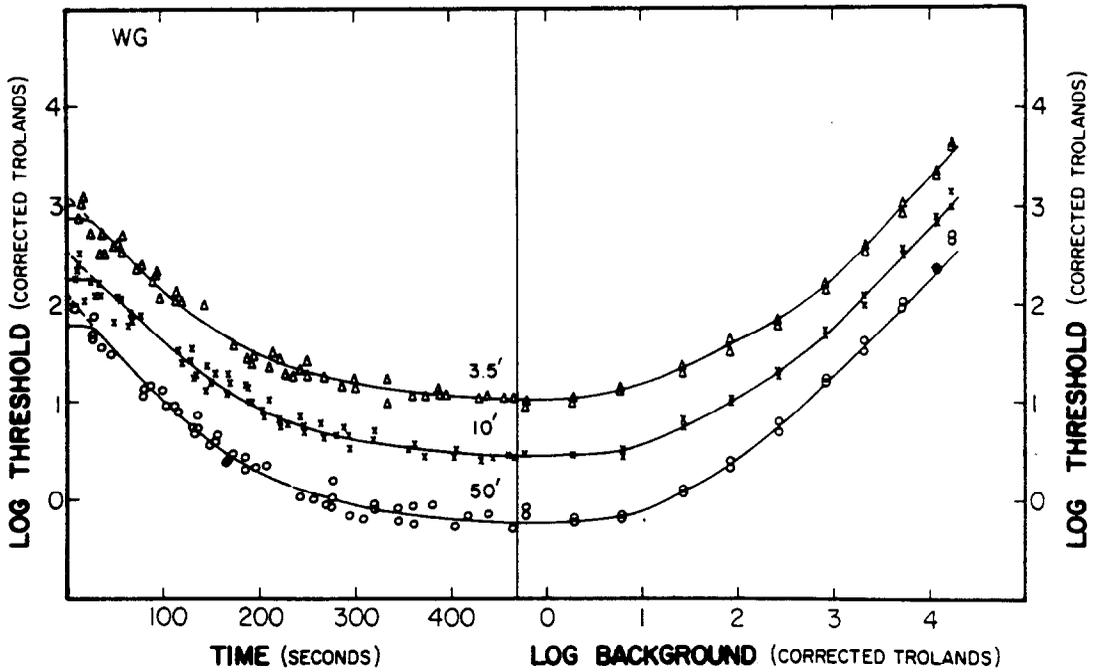


Fig. 3. The dark-adaptation and increment-threshold curves that are obtained after correcting all intensities in Fig. 2 for the effects of photopigment depletion. The solid curves drawn through the dark-adaptation thresholds are the same as dashed curves in Fig. 2. See text for explanation of the dashed lines.

bleaching. This point will be discussed below. The equivalent-background functions obtained for the white increment fields are shown in Fig. 4, and those obtained for the red increment fields are shown in Fig. 5.

DISCUSSION

The equivalent-background functions obtained with the 3.5', 10', and 50' increment fields are very nearly superimposed for both subjects and for both

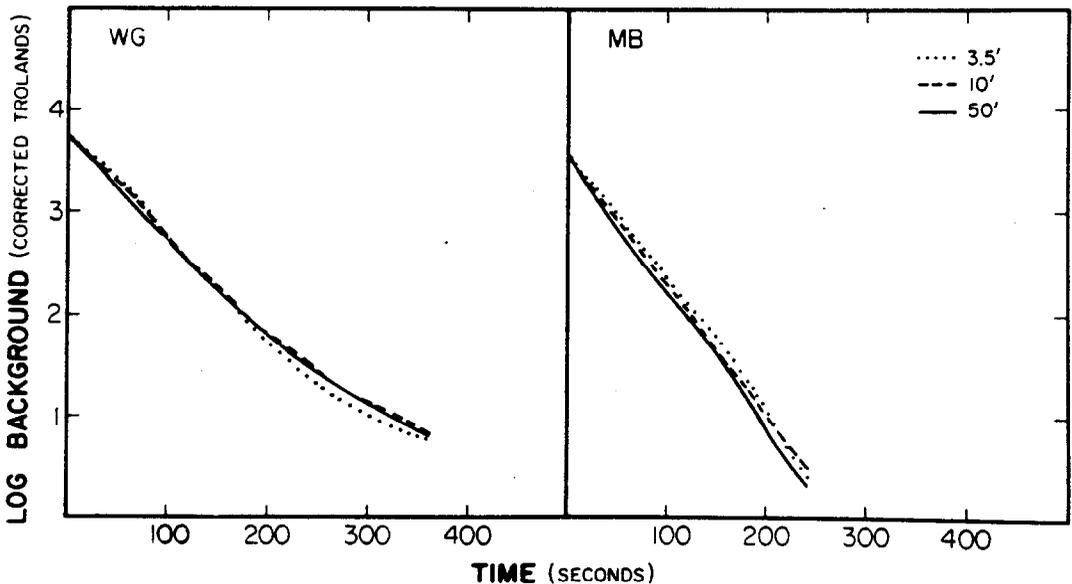


Fig. 4. Equivalent-background functions (white test field) for subjects MB and WG.

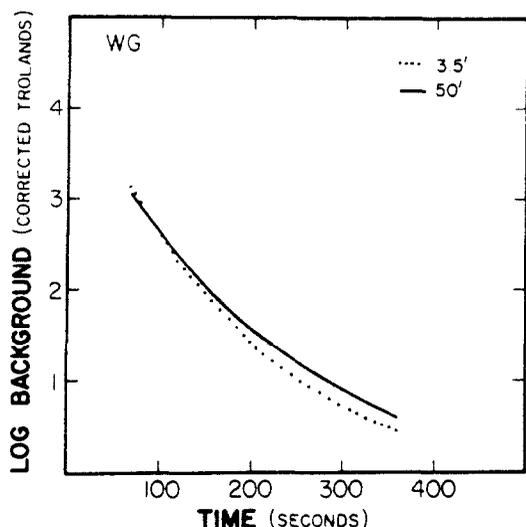


Fig. 5. Equivalent-background functions (red test field) for subject WG.

wavelength compositions. There do appear to be some small systematic differences between the functions, but they hardly exceed the variability of the data. Thus, it appears as if the long-term mechanism in cones satisfies the equivalent-background hypothesis with respect to spatial summation. The fact that the hypothesis holds equally well for subjects MB and WG despite the apparently large difference in their rates of photopigment regeneration is particularly convincing.

If an equivalent-background analysis is carried out on the present data without first correcting for the effects of photopigment depletion, the equivalent-background functions obtained are differently shaped than those in Figs 4 and 5, but they are superimposed almost equally as well. In other words, we would have concluded that the equivalent-background hypothesis holds, even if the photopigment-depletion analysis were not used. The reason is that the increment-threshold functions obtained for different test-field diameters are nearly parallel at high background intensities, where the depletion correction has its greatest effect. (In the present discussion, the term "parallel" will mean that the curves are superimposable by some vertical translation.) It is easy to show that if the increment-threshold functions are parallel, then the equivalent-background functions obtained with the correction for photopigment depletion are identical if, and only if, those obtained without the correction are identical. To see this, suppose first of all that the increment-threshold functions are parallel and that the equivalent-background functions obtained without the depletion correction are identical. It follows that the dark-adaptation curves must also be parallel and have the same vertical separations as the increment-threshold curves. Now, if the uncorrected increment-threshold curves are parallel, then the corrected curves will be parallel and will have the same vertical separations they had prior to the correction. This follows since at any given background intensity the depletion correction translates

the points on all the increment-threshold curves equally. By the same argument, the corrected dark-adaptation curves will also be parallel and have the same vertical separations. Consequently, all the equivalent-background curves obtained from the corrected data will be identical, just as they were when obtained from the uncorrected data. A similar argument proves the assertion in the other direction. On the other hand, if the increment-threshold functions are *not* parallel, then the two methods are not equivalent for testing the equivalent-background hypothesis. For example, if all the equivalent-background functions derived from the corrected data are identical, then those derived from the uncorrected data cannot be identical. Fortunately, correcting for the effects of photopigment depletion also has little effect on the conclusions of DuCroz and Rushton's (1966) equivalent-background study.

Although in the rod system the equivalent-background hypothesis has been confirmed under many conditions, there are conditions under which it has failed (Rushton and Westheimer, 1962; Westheimer, 1968). The implications of these studies have been questioned (Barlow and Sakitt, 1973; Barlow and Andrews, 1973), but it seems certain that there are some aspects of visual processing in the rod system not equally affected by bleaches and backgrounds (Alpern, Rushton and Torii, 1970a, b). The present results in conjunction with previous work suggest that the long-term adaptation mechanisms in rods and cones are very similar. Thus, further research may find that the equivalent-background hypothesis fails in the cone system under the same conditions that it fails in the rod system.

It was mentioned earlier that applying the correction for photopigment depletion to equation (1) predicts a dark-adaptation curve that is bent over sharply for the first few seconds after bleaching and that the data do not support this prediction (see Fig. 3). The data are, however, consistent with the suggestion made by Hollins and Alpern (1973) that equation (1) holds (in cones and rods) for relative threshold expressed in corrected trolands:

$$\log \frac{\Delta I'}{\Delta I'_0} = \alpha' q \quad (1')$$

where  $\Delta I' = p\Delta I$ , and  $\alpha'$  is a constant. (Note that  $\Delta I'_0 = \Delta I_0$  since  $p = 1.0$  in the dark-adapted eye.) By picking  $\alpha'$  appropriately (it will be smaller than  $\alpha$ ) equations (1) and (1') can be made to closely coincide except during the first few seconds after a full bleach. Equation (1') predicts that log threshold in corrected trolands will decrease exponentially, thus at the moment it seems to be the better description of the relationship between absolute threshold and the proportion of pigment bleached. The conclusions that were drawn from the equivalent-background analyses presented here are same whether equation (1) or equation (1') is used.

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## REFERENCES

- Alpern M. and Ohba N. (1972) The effect of bleaching and background on pupil size. *Vision Res.* **12**, 943-951.
- Alpern M., Rushton W. A. H. and Torii S. (1970a) Attenuation of rod signals by backgrounds. *J. Physiol. Lond.* **206**, 209-227.
- Alpern M., Rushton W. A. H. and Torii S. (1970b) The attenuation of rod signals by bleachings. *J. Physiol. Lond.* **207**, 449-461.
- Alpern M., Rushton W. A. H. and Torii S. (1970c) Signals from cones. *J. Physiol. Lond.* **207**, 463-475.
- Alpern M. and Wake T. (1977) Cone pigment in human deutan colour vision defects. *J. Physiol. Lond.* **266**, 595-612.
- Barlow H. B. (1964) Dark adaptation: A new hypothesis. *Vision Res.* **4**, 47-57.
- Barlow H. B. (1972) In *Handbook of Sensory Physiology—Visual Psychophysics* (Edited by Jameson D. and Hurvich L. M.). Springer, Berlin.
- Barlow H. B. and Andrews D. P. (1973) The site at which rhodopsin bleaching raises the scotopic threshold. *Vision Res.* **13**, 903-908.
- Barlow H. B. and Sakitt B. (1973) Doubts about scotopic interactions in stabilized vision. *Vision Res.* **13**, 523-524.
- Barlow H. B. and Sparrock J. M. B. (1964) The role of afterimages in dark adaptation. *Science* **144**, 1309-1314.
- Blakemore C. B. and Rushton W. A. H. (1965a) Dark adaptation and increment threshold in a rod monochromat. *J. Physiol. Lond.* **181**, 612-628.
- Blakemore C. B. and Rushton W. A. H. (1965b) The rod increment threshold during dark adaptation in normal and rod monochromat. *J. Physiol. Lond.* **181**, 629-640.
- Boynton R. M. and Baron W. S. (1975) Sinusoidal flicker characteristics of primate cones in response to heterochromatic stimuli. *J. opt. Soc. Am.* **65**, 1091-1100.
- Boynton R. M. and Whitten D. N. (1970) Visual adaptation in monkey cones: Recordings of later receptor potentials. *Science* **190**, 1423-1426.
- Burkhardt D. A. (1966) Brightness and the increment threshold. *J. opt. Soc. Am.* **56**, 979-981.
- Cornsweet T. (1962) Changes in the appearance of stimuli of very high luminance. *Psychol. Rev.* **69**, 257-273.
- Crawford B. H. (1937) The change of visual sensitivity with time. *Proc. R. Soc.* **B123**, 69-89.
- Crawford B. H. (1947) Visual adaptation in relation to brief conditioning stimuli. *Proc. R. Soc.* **B134**, 283-302.
- Dowling J. E. (1960) Chemistry of visual adaptation in the rat. *Nature* **188**, 114-118.
- Dowling J. E. (1963) Neural and photochemical mechanisms of visual adaptation in the rat. *J. gen. Physiol.* **46**, 1287-1301.
- DuCroz J. J. and Rushton W. A. H. (1966) The separation of cone mechanisms in dark adaptation. *J. Physiol. Lond.* **183**, 481-496.
- Geisler W. S. (1978) The effects of photopigment depletion on brightness and threshold. *Vision Res.* **18**, 269-278.
- Green D. G., Dowling J. E., Siegel I. M. and Ripps H. (1975) Retinal mechanisms of visual adaptation in the skate. *J. gen. Physiol.* **65**, 483-502.
- Hecht S. (1937) Rods, cones and the chemical basis of vision. *Physiol. Rev.* **17**, 239-290.
- Hollins M. and Alpern M. (1973) Dark adaptation and visual pigment regeneration in human cones. *J. gen. Physiol.* **62**, 430-447.
- Pugh E. H. (1975) Rushton's paradox: Rod dark adaptation after flash photolysis. *J. Physiol. Lond.* **278**, 413-431.
- Rinalducci E. J., Higgins K. E. and Cramer J. A. (1970) Nonequivalence of backgrounds during photopic dark adaptation. *J. opt. Soc. Am.* **60**, 1518-1524.
- Rodieck R. W. (1974) *The vertebrate retina*. Freeman, San Francisco.
- Rushton W. A. H. (1961) Rhodopsin measurement and dark adaptation in a subject deficient in cone vision. *J. Physiol. Lond.* **156**, 193-205.
- Rushton W. A. H. (1963) A cone pigment in the protanope. *J. Physiol. Lond.* **168**, 345-359.
- Rushton W. A. H. (1964) Flash photolysis in human cones. *Photochem. Photobiol.* **3**, 561-577.
- Rushton W. A. H. (1965a) Cone pigment kinetics in the deuteranope. *J. Physiol. Lond.* **176**, 38-45.
- Rushton W. A. H. (1965b) Bleached rhodopsin and visual adaptation. *J. Physiol. Lond.* **181**, 645-655.
- Rushton W. A. H. (1965c) The Ferrier lecture: Visual adaptation. *Proc. R. Soc.* **B162**, 20-46.
- Rushton W. A. H. and Henry G. H. (1968) Bleaching and regeneration of cone pigments in man. *Vision Res.* **8**, 617-631.
- Rushton W. A. H. and Powell Diane S. (1972a) The rhodopsin content and visual threshold of human rods. *Vision Res.* **12**, 1073-1081.
- Rushton W. A. H. and Powell Diane S. (1972b) The early phase of dark adaptation. *Vision Res.* **12**, 1083-1093.
- Rushton W. A. H. and Westheimer G. (1962) The effect upon the rod threshold of bleaching neighbouring rods. *J. Physiol. Lond.* **164**, 318-329.
- Sparrock J. M. B. (1969) Stabilized images: Increment and the spectral sensitivities of the rods and cones. *Proc. R. Soc.* **B127**, 64-105.
- Stiles W. S. (1939) The directional sensitivity of the retina and the spectral sensitivities of the rods and cones. *Proc. R. Soc.* **B 127**, 64-105.
- Stiles W. S. (1959) Color vision: The approach through increment-threshold sensitivity. *Proc. natn. Acad. Sci. U.S.A.* **45**, 100-114.
- Westheimer G. (1966) The Maxwellian view. *Vision Res.* **6**, 669-682.
- Wysszecki G. & Stiles W. S. (1967) *Color science: Concepts and Methods. Quantitative Data and Formulas*. Wiley, New York.