

THE FIELD ADAPTATION OF THE HUMAN ROD VISUAL SYSTEM

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SUMMARY

1. Incremental thresholds were measured in a retinal region 12 deg temporal from the fovea with a target of 200 ms in duration and 6 deg in diameter superimposed on background fields of various intensities and wavelengths. Measurements were made under rod-isolation conditions in five normal observers and in a typical, complete achromat observer who had no cone function.

2. The rise in threshold with background intensity changes with background wavelength in the normal trichromat observers. On 450, 520 and 560 nm backgrounds the average slope in logarithmic co-ordinates (0.78 ± 0.04 , s.d.) is similar to that found for the achromat – whose slope is independent of background wavelength (0.79 ± 0.03) – but on a 640 nm background it more nearly approaches Weber's law (0.91 ± 0.02). This indicates that the sensitivity of the rods to an incremental target is not determined by quantal absorptions in the rods alone but by quantal absorptions in both the rods and the cones.

3. Rod incremental thresholds were also measured in various colour-blind observers lacking one or more of the cone classes: a blue-cone monochromat, four deuteranopes and a protanope. For the blue-cone monochromat, like the achromat, the slope of the increment threshold curve is constant with background wavelength. For the deuteranopes and the protanope, like the normal, the slope increases with wavelength. The protanope, however, shows a smaller increase in slope, consistent with the lower sensitivity of his cones to long-wavelength light.

4. The dependence of the field adaptation of the rods on the cones was confirmed by field-mixture experiments, in which the incremental threshold was measured against bichromatic backgrounds, and in silent substitution experiments, in which backgrounds equated for their effects on either the cones or the rods but not both were instantaneously substituted for one another.

INTRODUCTION

The visual system adapts to variations in ambient illumination by adjusting its sensitivity. This change in sensitivity is typically monitored by measuring the change in detection threshold for a small target flash as a function of the intensity of a larger adapting background (Stiles, 1939). Here we exploit this classical

incremental threshold method, as well as several modifications of it, to determine the extent to which the rod visual system adapts independently of the cone systems. In making our measurements, we used not only normal observers, but also a typical, complete achromat, a blue-cone monochromat, a protanope and four deuteranopes.

Rod adaptation can be assumed to be more or less independent of the cones on dim adapting backgrounds that elevate rod threshold but have little or no direct effect on the cones (e.g. Flamant & Stiles, 1948). As the intensity of the 'rod' adapting background is increased however, it eventually begins to desensitize cones as well as rods. When this happens, *rod adaptive independence* can no longer be safely assumed (see Makous & Boothe, 1974; Makous & Peeples, 1979).

The sensitivity difference between rods and cones decreases with increasing wavelength (Wald, 1945), so that it is 'rod' adapting backgrounds of long wavelength that most severely desensitize the cones. For this reason, long-wavelength backgrounds are typically used to characterize rod adaptation at high scotopic intensities (e.g. Aguilar & Stiles, 1954), where the rod threshold response would be obscured by cones if shorter wavelength backgrounds were used. However, because they strongly adapt the cones, long-wavelength backgrounds are precisely the ones on which failures of rod adaptive independence are most likely to be found.

Consistent with earlier reports (e.g. Makous & Boothe, 1974; Sternheim & Glass, 1975; Frumkes & Temme, 1977; Ingling, Lewis, Loose & Meyers, 1977; Latch & Lennie, 1977; Buck, Peeples & Makous, 1979; Makous & Peeples, 1979), we find that varying background wavelength, but keeping the retinal illuminance in scotopic trolands (td) constant (which varies cone excitation, but not rod) changes rod threshold and that the deviations are associated with long-wavelength backgrounds. This implies a failure of rod adaptive independence. These findings are complemented by thresholds measured in a typical, complete achromat, who had no cone vision, and in other colour-blind observers; and they are confirmed by field additivity and field substitution experiments.

METHODS

Subjects

Several subjects were tested in these experiments. The five trichromat observers, C.F., U.M., R.T., T.A. and J.O., had normal colour vision. The first three were emmetropic, the last two myopic. The target and background field stops were positioned for each observer's best focus.

Observer K.N. was a typical, complete achromat. He displayed all the classic symptoms of typical, complete achromatopsia (for details, see Sharpe & Nordby, 1990). No evidence has been found for cone function in his dark-adaptation, fundal reflectometry, spectral sensitivity, spatial and temporal sensitivity and directional sensitivity to light. During the experiments, he wore a +9.0 dioptre convex lens. This lens magnified the retinal image so that the effective visual angles for him were 1.22 times larger than those stated below.

Observer P.S. was a blue-cone monochromat or X-chromosome-linked incomplete achromat (Blackwell & Blackwell, 1961). His vision was fully described in terms of the participation of only two types of receptor, namely normally functioning rods under scotopic conditions and normally functioning short-wave absorbing (S) cones under photopic conditions. His ophthalmological and psychophysical characteristics were reported in detail elsewhere (Zrenner, Magnussen & Lorenz, 1988; Hess, Mullen, Sharpe & Zrenner, 1989).

Observers L.H., G.L., H.S. and V.S. were deuteranopes and M.W. was a protanope. Their vision was tested using the Ishihara (1976) pseudo-isochromatic plates, the Rayleigh match on the Nagel anomaloscope and the Farnsworth-Munsell 100-Hue test. All tests indicated that these subjects

were dichromats: in addition to S-cones and rods, L.H., G.L., H.S. and W.S. possessed only functioning long-wave absorbing (L) cones, whereas M.W. possessed only functioning middle-wave absorbing (M) cones. Following classical procedures, the colour tests were performed using central vision. It is possible that our dichromats possessed a small number of anomalous cones in their peripheral retinae (see Nagy, 1980; Breton & Cowen, 1981). Even if some of these were present in our observers (and we have no evidence to suggest that this was the case), they should have little effect on our results.

Stimuli

Our basic experimental conditions were similar to those used by Aguilar and Stiles (1954). A target, 6 deg in diameter, exposed for 200 ms every 2000 ms was centred 12 deg from the fovea in the nasal field of view and presented in the centre of an adapting field 18 deg in diameter. To favour rod detection of the target, we used a wavelength of 520 nm, and for the normal observers, in the incremental threshold measurements, we offset its entry point in the pupil by 3 mm from the pupillary centre (because oblique entry light is less effective for the cones than for the rods (Stiles & Crawford, 1933; Stiles, 1939)). The entry point of the adapting field was central. We used background wavelengths of 450, 520, 560 and 640 nm.

Apparatus

The stimuli were produced by a three-channel Maxwellian view, optical system, interfaced with a computer. Earlier versions of the system have been described before (Nordby & Sharpe, 1988). One channel provided the 6 deg diameter incremental target. Its wavelength was shaped by a grating monochromator (Jobin-Yvon V-10, Longjumeau, France) into a triangular profile, peaking at 520 nm and having a half-bandwidth of 5.9 nm. A second and a third channel provided the 18 deg diameter adapting fields. They were rendered monochromatic by interference filters (Schott, Mainz, Germany) having a half-bandwidth at half-height of less than 5.5 nm. The luminances in the three channels were attenuated by neutral density filters and wedges; the latter were controlled by stepping motors (Berger, Lahr, Germany). The quantal flux densities of the light beams were measured with a silicon Pin-10 photodiode coupled to an operational amplifier (United Detector Technology, Model 80X Optometer).

The durations of the test flashes and exposures of the background fields (during the silent substitution experiments) were controlled by computer-operated electromagnetic shutters cutting the filament images in each channel. The shutters had rise and fall times of less than 0.1 ms. Aperture stops in each channel served to restrict the filament images entering the observer's eye to less than 2.0 mm in diameter at the plane of the pupil.

Procedure

Incremental threshold versus background intensity (t.v.i.) measurements. If the Stiles-Crawford effect was to be used, the subject's left pupil was dilated with 0.5% tropicamide (Mydriaticum Roche, Hoffmann-La Roche, Basel) about 60 min before beginning an experimental session. Following 40 min of dark adaptation, the subject positioned himself in the optical system by biting into a silicone-base, dental-wax impression of his teeth mounted in a machine tool rest and fixated an illuminated cross situated 12 deg to the left of the target's centre. Threshold was first measured on a zero background (the absolute threshold) and then on a series of adapting fields of increasing intensity. At each new intensity level the observer adapted for at least 3 min. The threshold measuring method for the t.v.i., field additivity and field substitution experiments was a computer-controlled, single-staircase procedure (Cornsweet, 1962), with a step size of $1/25 \log_{10}$ unit in intensity. Threshold was defined as the mean wedge setting of twelve staircase reversals.

On each background cone thresholds were also obtained by making measurements during the plateau that terminates the cone phase of recovery from a white (3100 K, absolute scale of temperature) bleaching light of $7.7 \log_{10}$ photopic troland seconds (tds) (i.e. between 4 and 10 min following the end of the bleach).

Field additivity measurements. In these experiments, thresholds were first measured against a single background (called μ_1) up to an intensity of $0.0 \log_{10}$ scotopic td. Thresholds were then measured against a mixed background composed of μ_1 , which was held constant at an intensity of $0.0 \log_{10}$ scotopic td, and a second background μ_2 , which was added to μ_1 in steps of 0.25 or $0.5 \log_{10}$ units.

Field substitution measurements. In these experiments, target thresholds were measured following the temporal transition between two backgrounds of different wavelength (506 and 640 nm) that were equated either photopically or scotopically. The substitution was seen mainly either by rods or by cones (the substitution is only truly 'silent' for the rods, see below).

Data treatment

Threshold versus intensity curves. To estimate the slopes of the rod-detected portions of the incremental threshold curves, the thresholds were fitted by means of a computerized curve-fitting programme (Sigmaplot, Jandel Scientific, Corte-Madera, CA, USA) using the logarithmic form of the following equation:

$$\Delta I = \kappa(I_{\mu}^n + I_0^n)^{1/m}. \quad (1)$$

This equation is an extension of the basic Weber–Fechner equation (after Fechner, 1860). In eqn (1), ΔI is the incremental threshold intensity and I_{μ} is the background field intensity of wavelength μ and I_0 is a 'dark noise' constant. In logarithmic co-ordinates, changing the value of I_0 has the effect of shifting the curve laterally along the $\log_{10} I_{\mu}$ axis. Increasing or decreasing the exponent n has the effect of increasing or decreasing, respectively, the rate of transition from the asymptotic absolute threshold to the asymptotic final slope. Varying exponent m also affects the rate of transition, but it primarily determines the final asymptotic slope of the incremental threshold curve (n/m). Finally, κ is a vertical positioning constant.

For each individual observer, the fitting of eqn (1) was completed in two iterative stages. In the first stage, all four parameters, I_0 , κ , m and n , were allowed to vary freely and individual fits were determined for each of the t.v.i. curves measured against the four (450, 520, 560 and 640 nm) field wavelengths, μ . The values determined for $\log_{10} I_0$ and n for each observer were then averaged over μ . In the second fitting stage, I_0 and n were held fixed at their average values and only $\log_{10} \kappa$ and m were allowed to vary.

For each observer, the fits at 450, 520 and 560 nm (and the secondary fit at 640 nm, see below) were made over the same range of background intensities from absolute threshold to an upper limit lying between 0.4 and 1.0 \log_{10} unit below cone threshold. This range was increased at 640 nm, since rod isolation extends to higher scotopic intensities at that wavelength. The precise range of background intensities over which each fit was made is indicated by the horizontal extent of the continuous curves shown in Figs. 1–3. We should point out that the estimates of the t.v.i. slope (n/m) at 640 nm obtained from eqn (1) tend to be slightly less than those obtained solely from the final asymptotic part of the t.v.i. function (the method used, for example, by Sharpe, Fach, Nordby & Stockman, 1989).

Field additivity curves. The logarithmic form of eqn (2) was used to determine the slopes of the rod-detected portions of the incremental threshold curves measured in the bichromatic field additivity experiments:

$$\Delta I = \kappa [(I_x + I_{\mu_2})/I_x]^s. \quad (2)$$

In logarithmic coordinates, κ has the effect of shifting the whole function vertically. I_x , like I_0 in eqn (1), shifts the curves laterally along the background intensity axis (if adaptation to the bichromatic field were purely scotopic, then I_x should equal 0.0 \log_{10} scotopic td, the scotopic illuminance of the fixed background μ_1). Finally, s is the slope of the function in logarithmic co-ordinates, and I_{μ_2} is the intensity of the second (added) background field μ_2 . ($I_x + I_{\mu_2}$) is divided by I_x in eqn (2), so that when I_{μ_2} is small, ΔI is approximately equal to κ (i.e. κ is the threshold on μ_1 alone).

RESULTS

Incremental thresholds

Normal data. A preliminary report of some of the findings illustrated in Figs 1 and 2 precedes this paper (Sharpe *et al.* 1989). Figure 1 shows the incremental threshold or t.v.i. curves (open symbols) measured in five normal trichromats, T.A., C.F., U.M., J.O. and R.T. Thresholds measured against a long-wavelength background (640 nm, open diamonds) – the adapting condition chosen by Aguilar & Stiles (1954) to favour rod isolation for detection of the target – are shown, along with data for

backgrounds of 450 (open circles), 520 (open squares) and 560 (open triangles) nm. Cone thresholds, which were measured for the same target and background conditions but during the plateau terminating the cone phase of recovery after a bleach of $7.7 \log_{10}$ photopic tds are shown as filled symbols.

If the assumption of receptor independence is valid and rod light adaptation proceeds independently of the cones, then the shape and position of the four threshold curves (below the cone thresholds) should be identical, since backgrounds having the same intensity in scotopic trolands have identical effects on the rods. Clearly, though, the slope of the function changes with background wavelength. For all five normal observers, rod thresholds on the 640 nm field rise more steeply than on the other fields. The change can be assessed by comparing the final logarithmic slopes of the t.v.i. functions; these are shown to the right of each set of incremental threshold data. These slopes refer to the curves (continuous lines) fitted to the rod-detected incremental thresholds, according to eqn (1) (see above). The final slopes are listed along with the other curve-fitting parameters in Table 1.

It can be seen in Fig. 1 that the rods determine threshold up to higher scotopic background intensities on the 640 nm background than on the shorter wavelength backgrounds. Thus, we were able to fit eqn (1) over a more extended range of background intensities at 640 nm. We also fitted eqn (1) over the same range of scotopic background intensities at 640 nm as we used for the fits at shorter wavelengths. The resulting slopes are tabulated in the far right-hand column of Table 1. The slopes are markedly higher at 640 nm than at shorter wavelengths, whichever range is used.

The effect of field wavelength shown in Fig. 1 and quantified in Table 1 is robust: it has been replicated in other normal observers (not shown) and has been statistically confirmed by a one-way analysis of variance (see Sharpe *et al.* 1989). Although less pronounced than those measured with the 200 ms, 6 deg target, differences in slope are also found for briefer, smaller targets (see L. T. Sharpe, C. C. Fach, U. Markstahler & A. Stockman, unpublished observations).

Achromat data. Since the cones are most strongly desensitized by the 640 nm field, it seems reasonable to suppose that failures of rod adaptative independence are most likely to be found in the 640 nm threshold data, rather than in the shorter wavelength data. If this is correct, then it is the shallow shorter wavelength rod t.v.i. curves that best characterize the adaptation of the isolated rod visual system, not the steep 640 nm curves. It could be argued, on the other hand, on the grounds, perhaps, that rod target isolation is better on the 640 nm field (compare open and filled symbols, Fig 1), that the opposite is the case and it is the steep 640 nm t.v.i. curve that best characterizes rod adaptation. A clear way to resolve this issue is to measure the four t.v.i. functions in an observer who lacks cone function. The results of such measurements in a typical, complete achromat observer K.N. are shown in Fig. 2A. The slope for K.N. remains constant regardless of wavelength (0.79 ± 0.03 ; see Table 2). Thus for him, rod adaptation is independent of field wavelength; and it proceeds at the same rate as in the normal observers when their thresholds are measured on the 450, 520, 560 nm backgrounds, but not on the 640 nm background (compare Tables 1 and 2). These results force the conclusion that the 640 nm curves for our five normals, as well as the classic curve measured on a long-wavelength background for

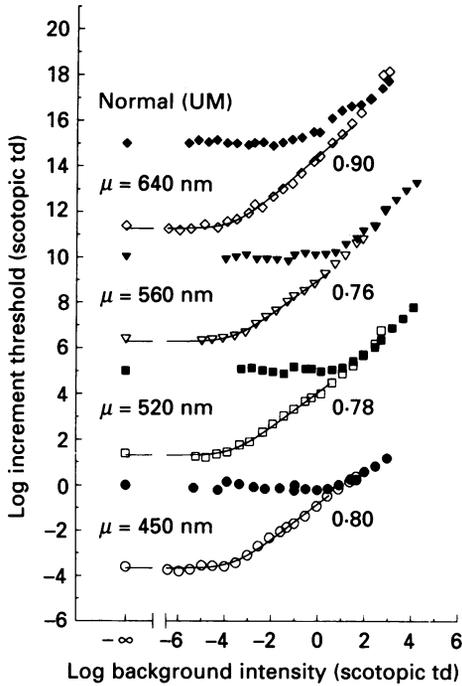
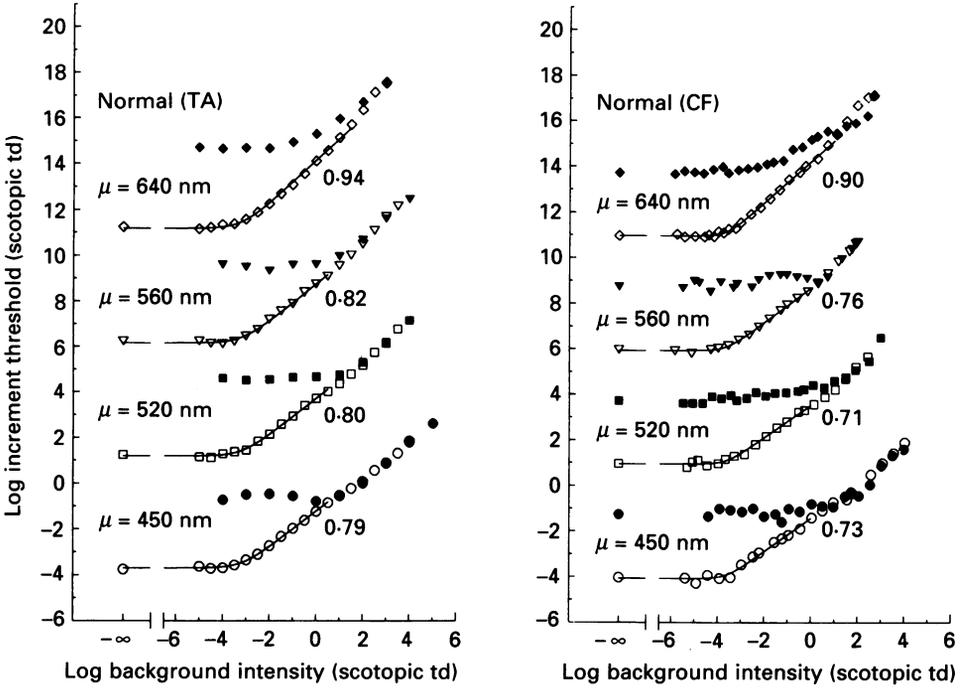


Fig. 1. For legend see facing page.

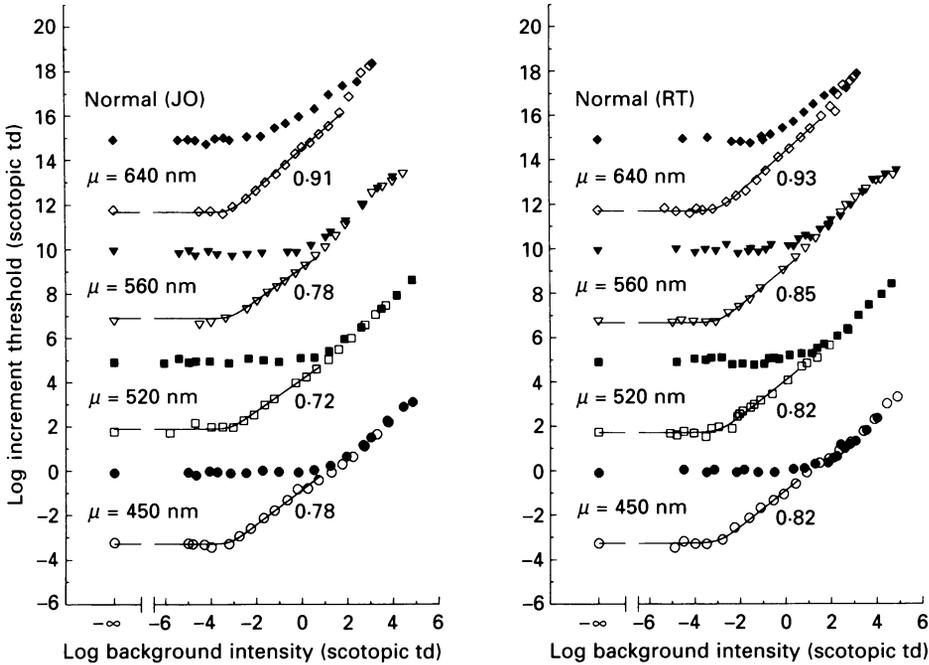


Fig. 1. The effect of background wavelength (μ) on the form of the rod t.v.i. curve for five normal observers, T. A., C. F., U. M., J. O and R. T. The target conditions were chosen to favour the rods relative to the cones (see text, for details). Four background wavelengths were used: 450 (circles), 520 (squares), 560 (triangles) and 640 (diamonds) nm. The open symbols represent the thresholds measured against steady backgrounds; the filled symbols, those measured for the same stimulus conditions during the plateau that terminates the cone phase of recovery from a white (3100 K) bleaching light of $7.7 \log_{10}$ photopic tds. All the curves are correctly placed with respect to the axis of the abscissae, but the axis of the ordinates is correct only for the lowest curve in each of the five panels; the other curves are displaced upward in intervals of five \log_{10} units. Each data point is a mean based on at least three sets of measurements made on different days. The continuous lines drawn through each set of incremental threshold data, below the point at which the cone plateau thresholds intersect the steady-state thresholds, are the best-fitting forms of eqn (1). The slope in logarithmic co-ordinates derived from the parameters of the equation (n/m) is shown to the right of each curve (see Table 1).

four normal observers by Aguilar and Stiles (1954), do not characterize the adaptive behaviour of the isolated rod visual system, but rather are influenced by the cones.

Colour-deficient observers. Figures 2 and 3 show rod incremental threshold curves for various partially colour-blind observers. The thresholds were measured under the same conditions as those used in Fig. 1, except that the Stiles-Crawford effect was not used. The results for these observers, who lacked either M-cones, L-cones or both should reveal which cones are responsible for elevating rod threshold on the 640 nm field. The slopes of the threshold functions, shown to the right of each curve, were determined by eqn (1) and are listed in Table 2.

The threshold curves in Fig. 2B show data for a blue-cone monochromat P. S., who has, besides rods, only S-cones. Since neither the 450 nor the 640 nm field has any marked effect on S-cone sensitivity (filled symbols) until rod saturating levels

($2.0 \log_{10}$ scotopic td), the S-cones should have little or no influence on rod sensitivity in the range of intensities in which we fit eqn (1). This seems to be the case: for P.S., like the achromat, the rod t.v.i. slopes vary little with wavelength and fall well short of Weber's law (they are 0.82 on the 450 nm field and 0.81 on the 640 nm field).

TABLE 1. The parameters of the curves (eqn 1) fitted to the rod incremental threshold responses of five normal trichromat observers

Field wavelength (μ)	$\log_{10} \kappa^*$	Slope (n/m)	Slope (n/m) [†]
Observer T. A. ($n = 0.94$, $\log_{10} I_0 = -3.170$)			
450 nm	-1.206	0.786	—
520 nm	-1.253	0.803	—
560 nm	-1.229	0.819	—
640 nm	-0.815	0.944	0.909
Observer C. F. ($n = 1.417$, $\log_{10} I_0 = -3.634$)			
450 nm	-1.437	0.725	—
520 nm	-1.472	0.710	—
560 nm	-1.303	0.759	—
640 nm	-0.755	0.903	0.895
Observer U. M. ($n = 0.761$, $\log_{10} I_0 = -3.565$)			
450 nm	-0.835	0.795	—
520 nm	-0.922	0.775	—
560 nm	-0.981	0.762	—
640 nm	-0.501	0.902	0.877
Observer J. O. ($n = 1.993$, $\log_{10} I_0 = -3.123$)			
450 nm	-0.848	0.781	—
520 nm	-0.843	0.724	—
560 nm	-0.835	0.775	—
640 nm	-0.508	0.905	0.894
Observer R. T. ($n = 1.490$, $\log_{10} I_0 = -2.897$)			
450 nm	-0.889	0.821	—
520 nm	-0.914	0.820	—
560 nm	-0.868	0.846	—
640 nm	-0.628	0.925	0.902
Means ($n = 1.327$, $\log_{10} I_0 = -3.279$)			
450 nm	-1.043	0.782 (± 0.035) [‡]	—
520 nm	-1.081	0.766 (± 0.048) [‡]	—
560 nm	-1.043	0.792 (± 0.039) [‡]	—
640 nm	-0.647	0.916 (± 0.018) [‡]	0.895 (± 0.012) [†]

* To correspond to the curves shown in Fig. 1, the values of $\log_{10} \kappa$ for the 520, 560 and 640 nm data should be increased by 5, 10 and 15, respectively. Each observer's absolute threshold can be calculated for the relation $\log_{10} \kappa + n/m(\log_{10} I_0)$.

† This column tabulates the 640 nm slopes estimated over the same range of background intensities for each subject as the 450, 520 and 560 nm slopes.

‡ Values (± 1 S.D.)

Fig. 2. The effect of background wavelength (μ) on the form of the rod t.v.i. curve for a typical, complete achromat K. N., a blue-cone monochromat P. S. and a protanope M. W. Same details and conditions as in Fig. 1, except no cone plateau thresholds are shown for the achromat who lacks functioning cone vision. (Data for $\mu = 520$ nm and 560 nm were not measured for observer P.S.) The continuous lines drawn through each set of incremental threshold data are best-fitting forms of eqn (1). The best-fitting parameters are given in Table 2.

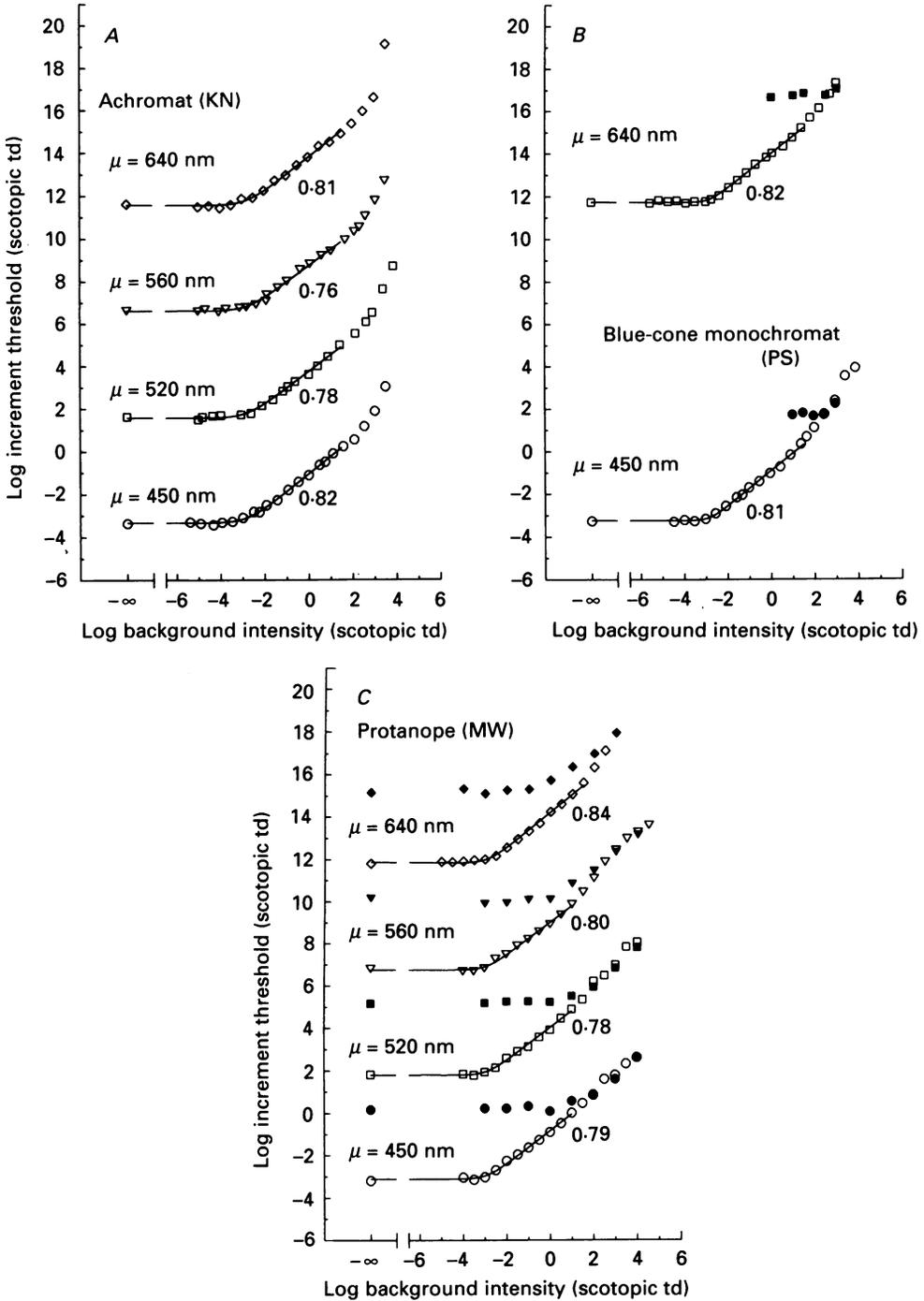


Fig. 2. For legend see facing page.

Figure 2C shows data for protanope M.W., who had M-cones, S-cones and rods, but who lacked L-cones. The M-cones are less sensitive to long wavelengths than the L-cones, and so are less strongly light-adapted by the 640 nm field. Consequently, if the M- and L-cones both elevate rod threshold roughly according to the number of

TABLE 2. The parameters of the curves (eqn 1) fitted to the rod incremental threshold responses of a typical, complete achromat, a blue-cone monochromat, three deuteranopes and a protanope

Field wavelength (μ)	$\text{Log}_{10} \kappa^*$	Slope (n/m)	Slope (n/m) \dagger
Achromat K.N. (0.963, -2.766)			
450 nm	-1.050	0.823	—
520 nm	-1.244	0.784	—
560 nm	-1.269	0.761	—
640 nm	-1.172	0.813	0.813
Blue-cone monochromat P.S. (1.622, -2.828)			
450 nm	-0.907	0.823	—
520 nm	—	—	—
560 nm	—	—	—
640 nm	-0.960	0.812	0.812
Protanope M.W. (1.233, -2.890)			
450 nm	-0.813	0.793	—
520 nm	-0.944	0.779	—
560 nm	-0.939	0.798	—
640 nm	-0.709	0.836	0.820
Deuteranope G.L. (0.741, -3.196)			
450 nm	-0.975	0.765	—
520 nm	-1.069	0.727	—
560 nm	-0.913	0.773	—
640 nm	-0.816	0.849	0.839
Deuteranope H.S. (0.636, -2.723)			
450 nm	-0.877	0.808	—
520 nm	-1.019	0.836	—
560 nm	-1.033	0.770	—
640 nm	-0.738	0.925	0.921
Deuteranope W.S. (0.590, -3.094)			
450 nm	-0.902	0.852	—
520 nm	—	—	—
560 nm	—	—	—
640 nm	-0.539	0.978	0.958

* To correspond to the curves shown in Figs 2 and 3, the values of $\log_{10} \kappa$ for the 520, 560 and 640 nm data should be increased by 5, 10 and 15, respectively. Each observer's absolute threshold can be calculated from the relation $\log_{10} \kappa + n/m(\log_{10} I_0)$.

\dagger This column tabulates the 640 nm slopes estimated over the same range of background intensities for each subject as the 450, 520 and 560 nm slopes.

quanta they receive from the background, then the extra elevation caused by a 640 nm field will be much less for a protanope than for a normal observer or for a deuteranope. We estimate, using data from Wald (1945) and Stiles (1978), that the ratio of rod to cone sensitivity to a 640 nm field for a protanope is approximately equivalent to that to a 610 nm field for a normal observer or a deuteranope. Consistent with less cone excitation in the protanope, the slope of the rod threshold

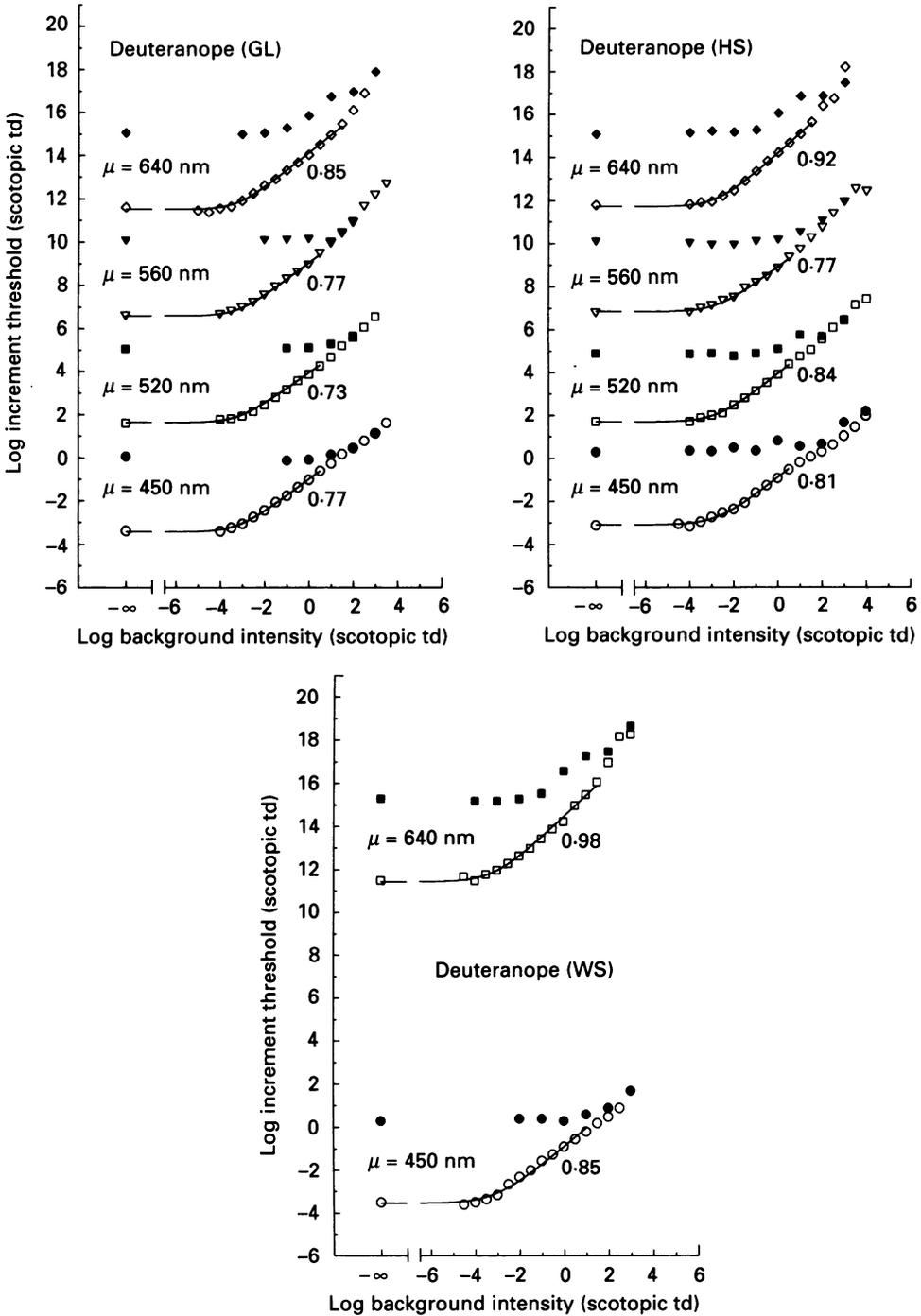


Fig. 3. The effect of background wavelength (μ) on the form of the rod t.v.i. curve for three deuteranopes, G.L., H.S. and W.S. Same details and conditions as in Fig. 1. (Data for $\mu = 520$ nm and 560 nm were not measured for observer W.S.) The continuous lines drawn through each set of t.v.i. data are best-fitting forms of eqn (1). The best-fitting parameters are given in Table 2.

curve increases little with field wavelength (from 0.79 to 0.84), less so than for the five colour normals (compare the values in Tables 1 and 2).

The three panels of Fig. 3 show data for three deuteranopes, G. L., H. S. and W. S., who had L-cones, S-cones and rods, but who lacked M-cones. The slope of the rod threshold curves for H. S. and W. S. changes with field wavelength as it does for our five normal, trichromatic subjects (compare the slopes in Tables 1 and 2). On the other hand, the slope change for G. L. is more similar to the protanope M. W. We do not understand the reason for this discrepancy. A fourth deuteranope L. J. used in the field substitution experiments gave results similar to the normals (see below). G. L. notwithstanding, the overall similarity between the deuteranopes and the normals implicates L-cone excitation as a major cause of the additional rod threshold elevation found on long-wavelength fields.

It is of some interest to compare the cone plateau thresholds in Figs 1–3. For the normal and the protanope the cone thresholds are predominantly M-cone thresholds, and for the deuteranopes L-cone thresholds. Moreover, for the deuteranopes, a second branch appears at higher 640 nm background levels that may be a S-cone branch (compare with the cone data for the blue-cone monochromat).

Field-mixture experiments

The cone dependence of the slope of the rod-detected incremental threshold curve is confirmed by field-mixture experiments, in which incremental threshold was measured against bichromatic backgrounds (see Figs 4–6).

In the four panels of Figs 4 and 5, thresholds in two normal observers, T. A. and C. F., were first measured against a single long-wavelength background up to a background luminance of $0.0 \log_{10}$ scotopic td ($\mu_1 = 640$ nm, open circles, left ordinate). The luminance of μ_1 was then held constant, and threshold was measured as a function of the luminance of a second added background ($\mu_2 = 450, 520, 560$ or 629 nm; open triangles, squares, diamonds and circles, respectively; right abscissa). In Fig. 6 another condition is shown ($\mu_1 = 520$ nm, $\mu_2 = 640$ nm). The cone thresholds measured during the cone phase of dark adaptation are shown for each condition (filled symbols).

As in Fig. 1, against the single 640 nm background (open circles, left), the rise in threshold approaches a logarithmic slope of nearly 0.95 in the range -2.0 to $0.0 \log_{10}$ scotopic td. On the right in each panel, we have used a separate abscissa for the

Fig. 4. Bichromatic field-mixture experiments for normal trichromat observer T. A. Incremental threshold as a function of background intensity was first measured against a single adapting wavelength ($\mu_1 = 640$ nm; \circ), up until a background intensity of $0.0 \log_{10}$ scotopic td. Thereafter light from a second adapting wavelength ($\mu_2 = 450$ (\triangle), 520 (\square), 560 (\diamond) or 629 (\circ) nm, was added in $0.5 \log_{10}$ unit steps from -3.0 to $4.0 \log_{10}$ scotopic td and the threshold further measured against the combined background field. The continuous lines drawn through each set of bichromatic field data, below the point at which the cone plateau thresholds intersect the steady-state thresholds, were determined according to eqn (2). The logarithmic slope is shown to the right of each bichromatic field curve (see Table 3). The filled symbols represent cone thresholds measured against the combined background fields during the plateau that terminates the cone phase of recovery from a white bleaching light.

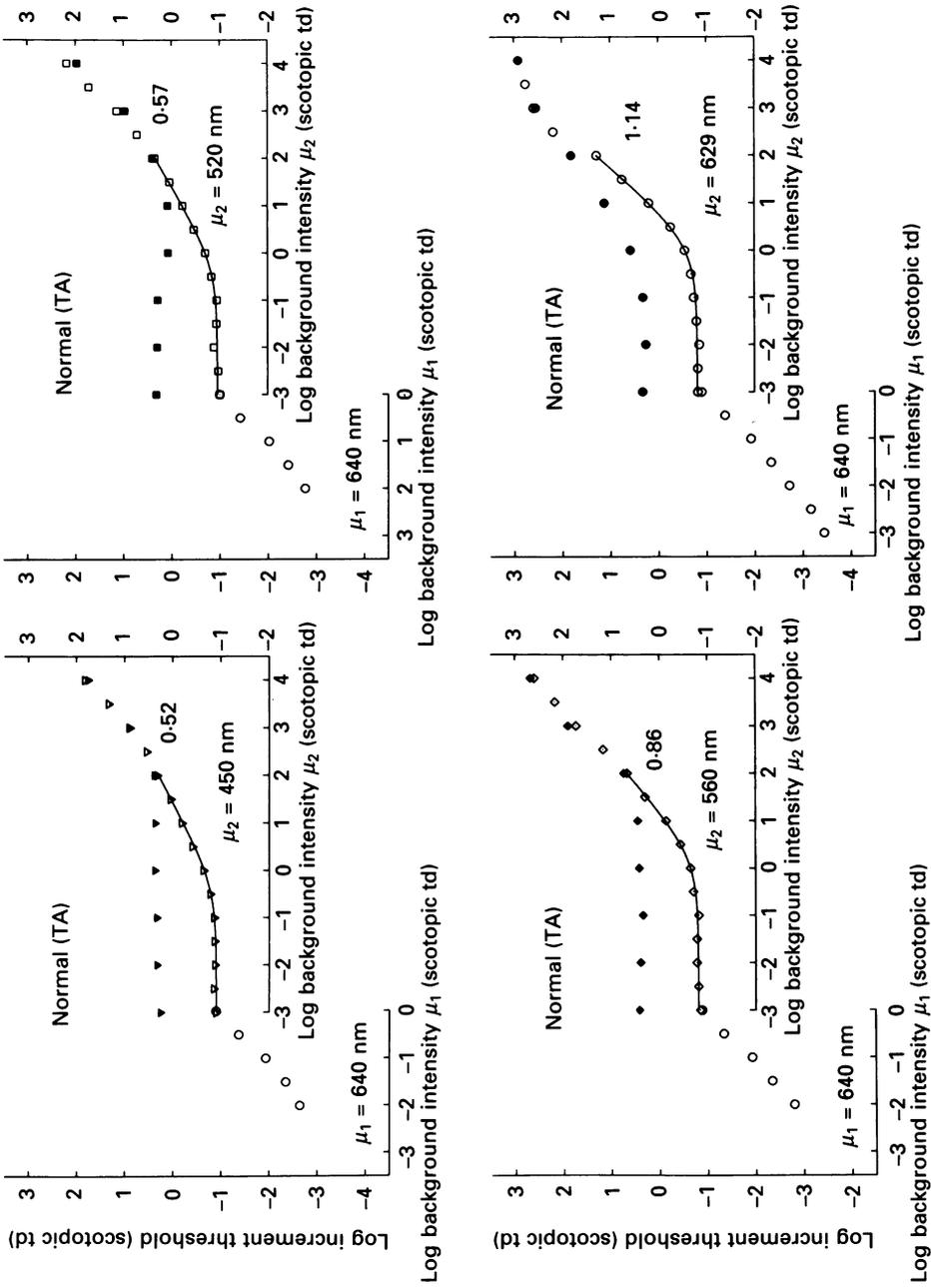


Fig. 4. For legend see facing page.

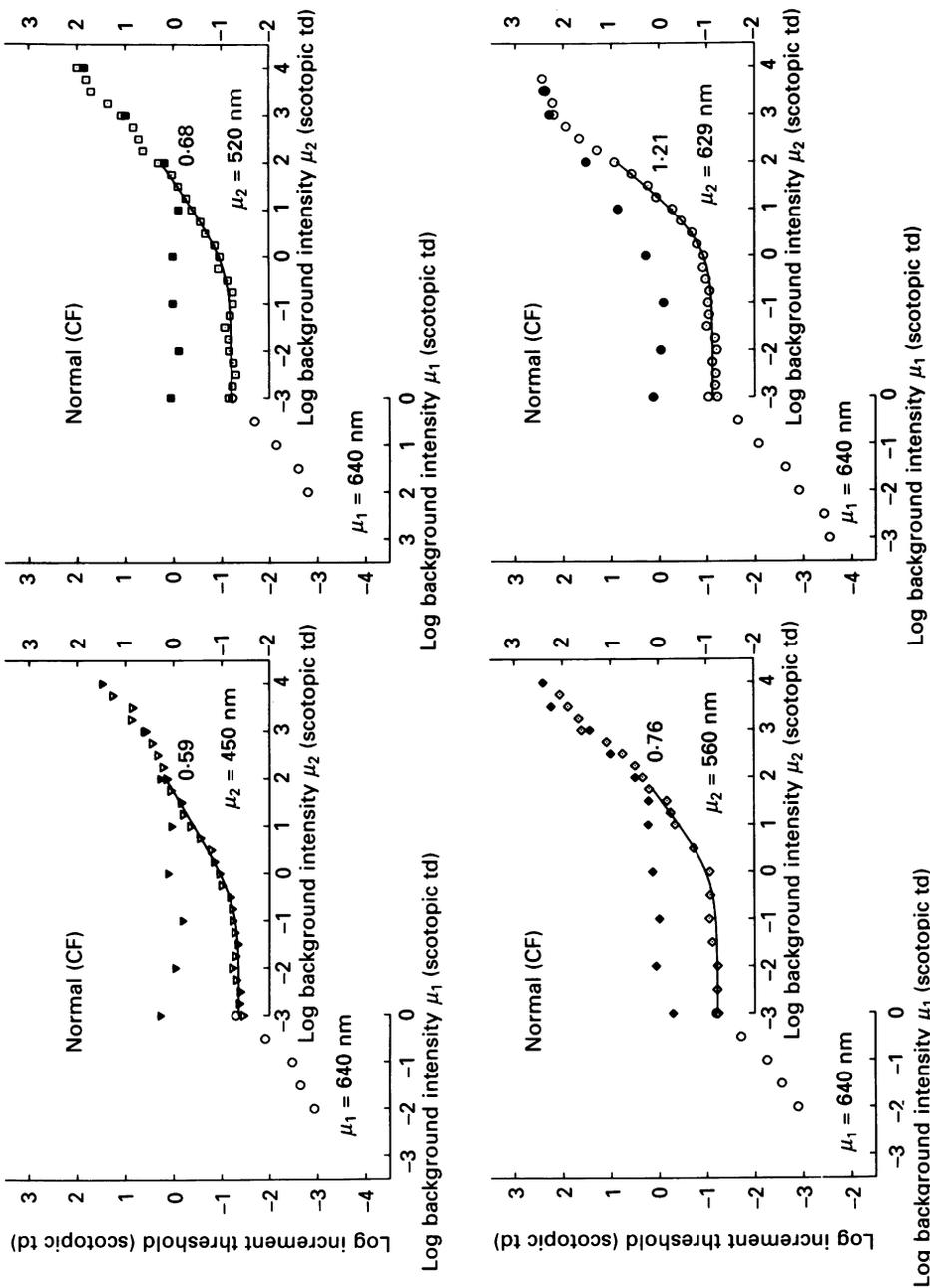


Fig. 5. Bichromatic field-mixture experiments for normal trichromat observer C. F. Same conditions and details as in Fig. 4, except that the intensity of the second adapting field was varied in 0.25 log₁₀ unit steps for the rod threshold measurements.

intensity of the added μ_2 background. This way of plotting the data yields a scalloped slope on the divided logarithmic axes, even though threshold may actually be rising (with respect to the total background intensity of the combined fields, μ_1 and μ_2) at the same rate as on the 640 nm field.

TABLE 3. The parameters of the curves (eqn 2) fitted to the rod incremental threshold responses obtained for two normal trichromat observers in the bichromatic field-mixture experiments

Field combination ($\mu_1 + \mu_2$)	Slope (s)	$\text{Log}_{10} I_x$	$\text{Log}_{10} \kappa$
Observer C. F.			
640 + 450 nm	0.590	-0.576	-1.365
640 + 520 nm	0.684	-0.133	-1.207
640 + 560 nm	0.757	-0.030	-1.222
640 + 629 nm	1.211	0.358	-1.121
520 + 640 nm	1.083	-0.220	-1.499
Observer T. A.			
640 + 450 nm	0.517	-0.318	-0.905
640 + 520 nm	0.572	-0.256	-0.954
640 + 560 nm	0.856	0.267	-0.808
640 + 629 nm	1.144	0.175	-0.809
520 + 640 nm	1.146	-0.226	-1.214

The curves are shown in Figs 4-6.

One advantage of the field mixture method in the context of rod-cone experiments is that μ_1 and μ_2 can be chosen so that increasing the intensity of the added field at first desensitizes mainly rods or mainly cones. For $\mu_1 = 640$ nm, $\mu_2 = 450, 520$ or 560 nm, the added fields at first desensitize primarily rods, and have little effect on the cones. In fact, to achieve a doubling in *photopic* trolands of the fixed $0.0 \log_{10}$ scotopic td, 640 nm μ_1 field requires a $3.15 \log_{10}$ scotopic td 450 nm μ_2 field, a $2.19 \log_{10}$ scotopic td 520 nm μ_2 field or a $1.59 \log_{10}$ scotopic td 560 nm μ_2 field. Consequently, the additional rise in rod threshold caused by the added fields should be due to their effects on rods, not on cones - up to rod saturating levels for the 450 and 520 nm fields. In contrast, the effect of adding 629 nm light should be similar to increasing the intensity of the 640 nm background alone, since to achieve a doubling in photopic trolands of the fixed 640 nm light requires only a $0.17 \log_{10}$ scotopic td 629 nm light. (These values are calculated on the basis of the CIE photopic and scotopic luminosity functions, see Wyszecki & Stiles, 1982). Another important advantage of the field mixture method here is that on a 640 nm μ_1 field, the effects of a short wavelength μ_2 field on rod sensitivity can be measured to much higher scotopic background intensities than if the μ_2 field were presented alone.

The continuous curves shown fitted to each set of bichromatic field thresholds are the best-fitting forms of eqn (2). The main parameter of interest, the slope (s), is shown to the right of each set of bichromatic field thresholds and is listed in Table 3. The curves were fitted between -3.0 and $2.0 \log_{10}$ scotopic td. The upper limit of the fit, which is below the background intensity at which the cone-detected thresholds intersect the rod-detected ones, is near the background intensity at which the rod-detected threshold first begins to exhibit saturation behaviour (see Aguilar & Stiles, 1954; Sharpe, 1990).

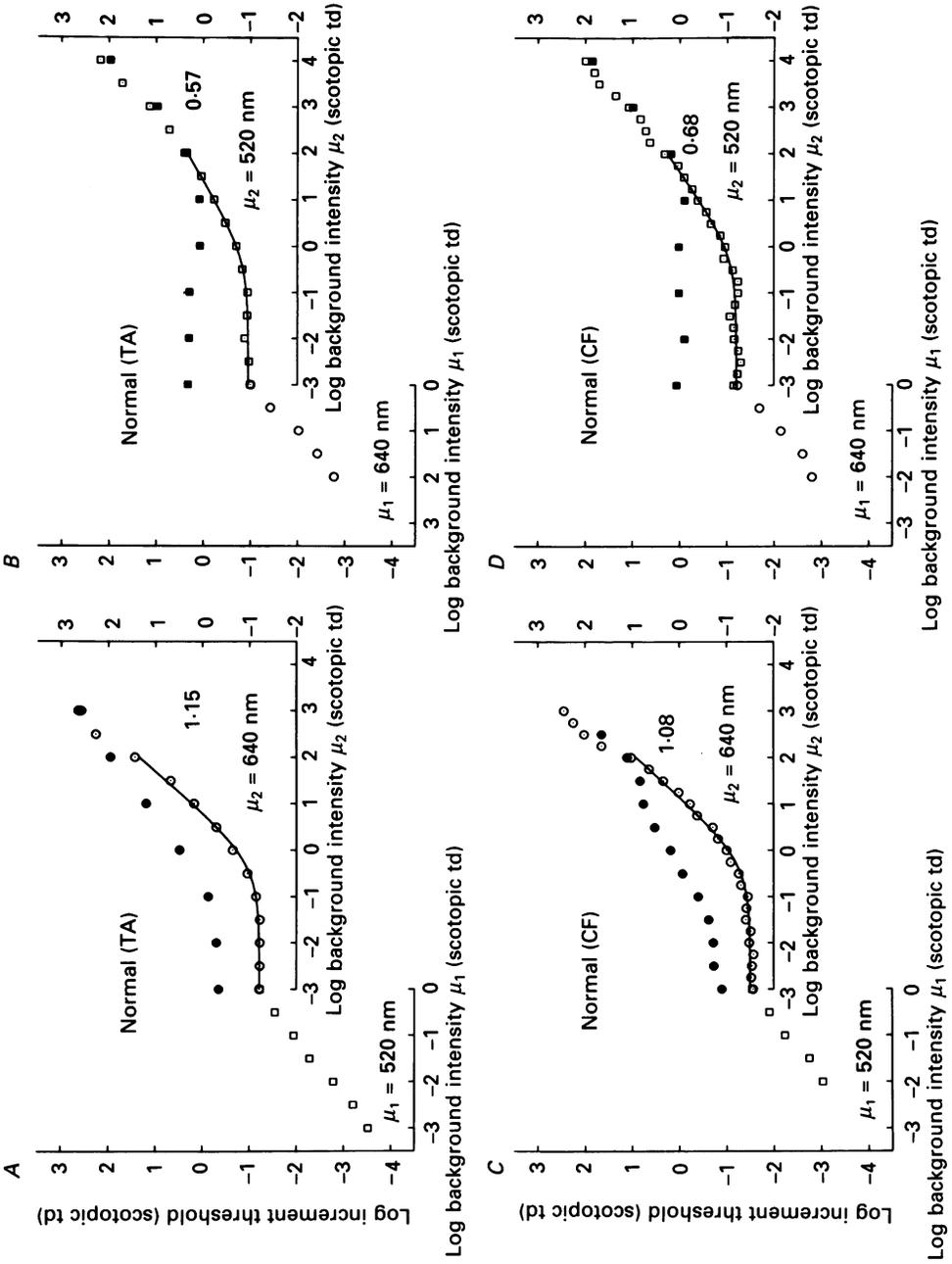


Fig. 6. For legend see facing page.

The second parameter that is of interest is I_x . Varying I_x has the effect of moving the entire curve (in logarithmic co-ordinates) along the $\log_{10} I_{\mu_2}$ axis. If rod adaptive independence holds, $\log_{10} I_x$ should be equal to 0.0, the actual intensity of the fixed μ_1 field in \log_{10} scotopic trolands (see above). But if the added μ_2 field raises rod threshold by its effect on cones the curve may displace horizontally and thus $\log_{10} I_x$ will deviate from 0.0. The best-fitting values of $\log_{10} I_x$ are also listed in Table 3.

It can be seen quite clearly in Figs 4 and 5 that the slope of the field-mixture threshold curves depends upon the auxiliary field wavelength μ_2 . As we would predict from our single field t.v.i. measurements, when the added field affects mainly rods the slope is shallower than when it affects both rods and cones. Unexpectedly, though, the slopes are more extreme than on the single fields: on the 450 and 520 nm μ_2 fields, the slope is shallower (0.59 *versus* 0.78) and on the 629 nm μ_2 field, steeper (1.18 *versus* 0.92). Another unexpected result is that, for short μ_2 wavelengths, $\log_{10} I_x$ is less than 0.0 \log_{10} scotopic troland, particularly at 450 nm (see Table 3). Thus rod threshold starts to rise on these fields at lower μ_2 luminances than a purely scotopic spectral sensitivity requires. This shift, as well as the decreased slope at $\mu_2 = 450$ nm, could be explained by supposing that the S-cones cause a relatively small but constant elevation of rod threshold at low 450 nm luminances (which would decrease s and $\log_{10} I_x$), but the single field t.v.i. functions for the blue-cone monochromat P.S. show no effect of S-cones at these luminances.

The increased slope at $\mu_2 = 629$ nm may reflect the fact that it is estimated only at high rod threshold elevations including some at near-saturating levels. The finding for both subjects that $\log_{10} I_x$ is greater than 0.0 for this field suggests that the added 629 nm field is less effective in raising rod threshold than a scotopically equated 640 nm field. This finding would be expected if cones regulate rod sensitivity on long-wavelength fields, since a scotopically equated 629 nm field is, in fact, photopically less effective than a 640 nm one, and by an amount roughly consistent with the deviation of $\log_{10} I_x$ from 0 (0.36 (C.F.) and 0.18 (T.A.) compared to a photopic difference of 0.19).

Figure 6 shows the results of another field-mixture combination in the two normal trichromats T. A. and C. F. In the left panels, a 640 nm background field (μ_2) is added to a 520 nm one (μ_1). For comparison, the right panels show the reverse condition, which was shown before in Figs 4 and 5. Consistent with Fig. 1, rod-detected thresholds on the single 520 nm field (open squares) rise with a shallow slope. However, on the added 640 nm field, which more strongly adapts the cones, they rise with a slope greater than 1.0 (see Table 3). These slopes are similar to those obtained at $\mu_1 = 640$ nm, $\mu_2 = 629$ nm. Once again, the steepness probably reflects the fact that the slope was estimated at high threshold elevations. For $\mu_1 = 520$ nm, $\mu_2 =$

Fig. 6. Bichromatic field-mixture experiments (*A* and *C*) for normal trichromat observers T. A. and C. F. Same conditions and details as in Fig. 4, except the first adapting field μ_1 had a wavelength of 520 nm (thresholds measured against it are shown as open squares) and the added adapting field μ_2 had a wavelength of 640 nm (thresholds measured against the combined fields are shown as open circles). ● represent cone thresholds measured against the combined wavelength components during the plateau that terminates the cone phase of recovery from a white bleaching light. For comparison the bichromatic field-mixture curves ($\mu_1 = 640$; $\mu_2 = 520$ nm) from Figs 4 and 5 are shown in *B* and *D*.

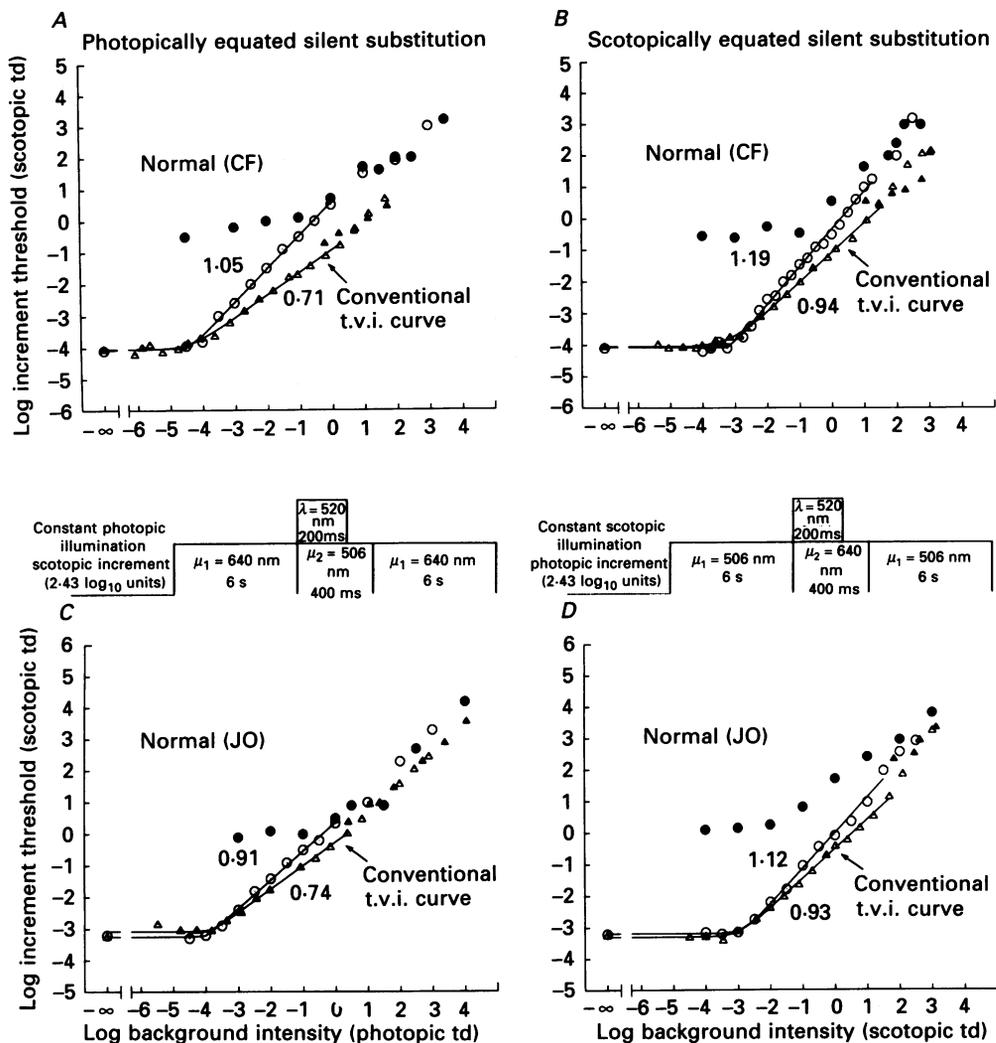


Fig. 7. Field-substitution experiments for two normal trichromat observers C. F. and J. O. In *A* and *C*, the effects on rod threshold during photopically equated silent substitution are shown. Incremental thresholds (○) were measured as a function of intensity following the brief (400 ms) substitution of a 506 nm background (μ_2) for a 640 nm background (μ_1 , see inset between the panels). The field exchange represented a small change in quantal absorptions in the cones, but a much larger increase in the quantal absorptions in the rods (see text). For comparison, the thresholds measured on a steady 506 nm field are shown as Δ (conventional t.v.i. curve). ● represent cone thresholds measured for the background substitution condition during the plateau that terminates the cone phase of recovery from a white bleaching light; \blacktriangle , the cone thresholds measured for the steady 506 nm condition. In *B* and *D*, the effects on rod threshold during scotopically equated silent substitution is shown. Increment thresholds (○) were measured as a function of intensity following the brief substitution (400 ms) of a 640 nm background (μ_2) for a 506 nm background (μ_1 , see inset between the panels). The field exchange represented no change in the quantal absorptions in the rods, but a large change in the quantal absorptions in the cones. For comparison, the thresholds measured on steady 640 nm backgrounds are shown as Δ (conventional t.v.i. curve). ● represent cone thresholds

640 nm, $\log_{10} I_x$ is less than 0.0. Such a shift in $\log_{10} I_x$ would be expected if the cones raise rod threshold, since a scotopically equated 640 nm field is more effective photopically than a 520 nm one. However, the shift is only small (about 0.22), implying only a moderate deviation from a scotopic spectral sensitivity at low $\log_{10} I_{\mu 2}$. Overall, then, the results of these field-mixture experiments leave us in little doubt: rods do not adapt independently of cones.

Field-substitution experiments

Further confirmation that rod adaptation is not independent of cones is provided by the result of field-substitution experiments, in which thresholds were measured following the transition from a 506 to a 640 nm background and *vice versa*. The results for two normal observers are shown in Fig. 7 and (for the 506 to 640 nm transition only) for a protanope and a deuteranope in Fig. 8.

Normal data. For the normal observers C.F. and T.A., the 506 and 640 nm backgrounds were either photopically equated (Fig. 7A and C) or scotopically equated (Fig. 7B and D). When equated in photopic trolands, the 506 nm field was substituted for the 640 nm field once every 6 s for 400 ms; and the 520 nm incremental flash was presented during the first 200 ms following the transition to the 506 nm field (the temporal conditions are shown in the insert between the panels for the two observers). For the rods, the 506 nm field was 270 times more intense than the 640 nm field; for the cones the change in intensity was much smaller: to the L-cones the 640 nm field appeared about 1.8 times more intense than the 506 nm field and to the M-cones about 6.8 times less intense.

When scotopically equated, the 640 nm field was substituted for the 506 nm field once every 6 s for 400 ms; and the 520 nm incremental flash was presented during the first 200 ms following the transition to the 640 nm field (see insert). For the rods this was a silent substitution. For the L-cones the 640 nm field was approximately 470 times brighter than the 506 nm one and for the M-cones it was approximately 40 times brighter. (These estimates are based on the Smith & Pokorny M- and L-cone fundamentals and the CIE photopic and scotopic luminosity functions, all of which are tabulated in Wyszecki & Stiles, 1982.)

The thresholds measured following the field substitutions are shown as open circles in Fig. 7. The thresholds measured against the 400 ms component presented as a single steady field are shown as open triangles and labelled as the 'Conventional t.v.i. curve'. The filled circles are cone thresholds measured under the silent substitution conditions; the filled triangles are the comparable cone thresholds measured under the single steady field conditions.

Clearly, rod threshold is elevated above its steady-state level by either a transient

measured for the background substitution condition during the plateau that terminates the cone phase of recovery from a white bleaching light; \blacktriangle , the cone thresholds measured for the steady 640 nm condition. In both groups of panels, the continuous lines drawn through each set of rod incremental threshold data, below the point at which the cone plateau thresholds intersect them, were fitted according to eqn (1). The slope in logarithmic co-ordinates derived from the parameters of the equation (n/m) is shown adjacent to each curve.

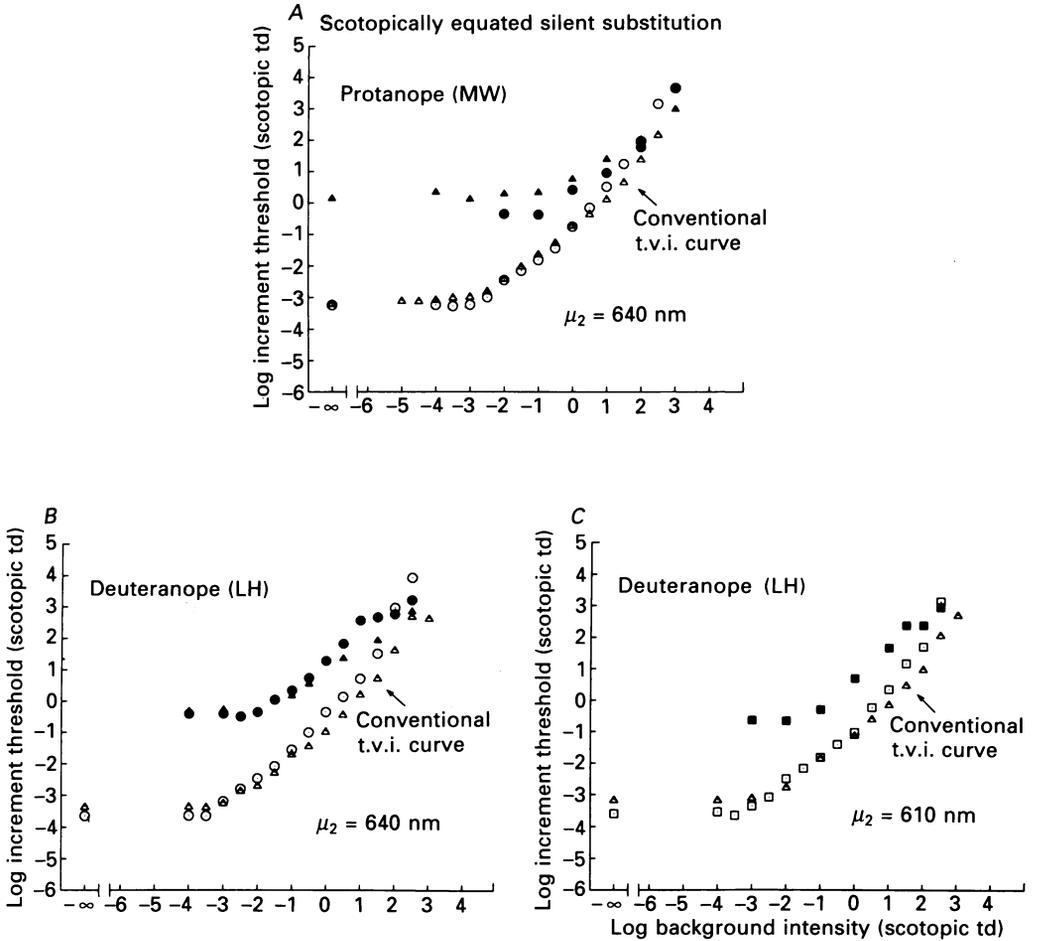


Fig. 8. Field-substitution experiments (scotopically equated silent substitution) for protanope M. W. and deuteranope L. H. In *A* (M. W.) and *B* (L. H.), incremental thresholds (○) were measured following the substitution for 400 ms of a 640 nm (μ_2) background for a 506 nm background (μ_1), both of which were equated for their effects on the rods (see Fig. 7*B* and *D* and legend for more details). For comparison, rod thresholds measured on a single steady 640 nm field are shown as △ (▲ are cone thresholds for the same conditions). Also shown are cone thresholds (●) measured following the background substitution. *C*, similar rod and cone thresholds are shown for the deuteranope L. H., but the substitution is between 610 nm (μ_2) and 506 nm (μ_1) backgrounds equated for their effects on the rods (the cone plateau thresholds for the steady 610 nm field were not measured).

increase in background intensity seen *mainly* by rods (*A* and *C*) or *only* by cones (*B* and *D*). Adjacent to each curve are the slopes estimated by fitting eqn (1) to the threshold data. The effect is more pronounced for the transition seen mainly by the rods, as might be expected from the transient rod saturation experiments of Adelson (1982). Nevertheless, a transition that is invisible to the rods, and thus seen only by the cones, also causes an elevation of rod threshold, as was first shown in the elegant

Stiles-Crawford background substitution experiment of Makous & Boothe (1974) and the masking experiments of Ingling *et al.* (1977).

Colour-deficient observers. In the normal, the transient cone stimulation produced in the rod silent substitution experiments causes a larger elevation of rod threshold than does the sustained stimulation in steady field experiments. By using this method, we may be able to demonstrate a cone influence in our protanope observer M.W., for whom, with steady-state adaptation, the slope of the single field 640 nm t.v.i. curve is not much steeper than the slopes at shorter field wavelengths.

When scotopically equated, however, the 640 nm field is only about 40 times more effective in stimulating the M-cones of the protanope (and the normal) than is the 506 nm field (see above). This is a large difference, yet it is much smaller than the effect of the transition on the L-cones of the deuteranope and the normal (approximately 470 times). Consequently, if there is an extra elevation of rod threshold in the protanope following the substitution it should be less, and, given the relative insensitivity of M-cones to 640 nm, it should occur at a higher background intensity than in the deuteranope and normal.

Figure 8 shows the results of the rod silent substitution experiment for protanope M.W. (A) and for deuteranope L.H. (B). In both panels, the open and filled circles indicate, respectively, rod and cone thresholds measured immediately following the background substitution (i.e. on the 400 ms duration, 640 nm background); and the open and filled triangles, rod and cone thresholds obtained on the 400 ms component background presented as a single steady field.

The background substitution in the protanope, which is seen only by M-cones, does cause an elevation of rod threshold above that found on a steady field, but as expected the elevation is smaller (by nearly $0.5 \log_{10}$ unit) and occurs at a much higher background intensity (about $1.5 \log_{10}$ unit higher) than the elevation caused by the L-cones in the deuteranope (or by the combined L- and M-cones in the normal; see Fig. 7). These results clearly implicate M-cones, in addition to L-cones, in failures of rod-adaptive independence. A further indication of the influence of cones is that in both panels rod thresholds begin to deviate from their steady-state levels only when cone thresholds begin to rise.

Figure 8C shows rod silent substitution results for the same deuteranope L.H., when a scotopically equated 610 nm field is substituted for the 506 nm field. The 610 nm field is approximately 40 times more effective than the 506 nm field in stimulating the L-cones, which is equivalent to the difference in effectiveness between scotopically equated 640 and 506 nm fields in stimulating the M-cones. Thus, if M- and L-cones are equally effective on a quantum basis in raising rod threshold, the extra elevation of rod threshold in the deuteranope for the 506 to 610 nm substitution should be roughly similar in magnitude to that found for the protanope when the substitution is between the 506 and 640 nm fields (relative to their peak sensitivities λ_{\max} , the M-cones of the protanope are about $0.2 \log_{10}$ unit more sensitive to the two scotopically equated fields than are the L-cones of the deuteranope). The elevation in threshold found following the 506 to 610 nm substitution in the deuteranope is indeed comparable to that found following the 506 and 640 nm substitution in the protanope (compare A and C). This result again suggests that M-cones as well as L-cones are involved in the elevation of rod

threshold on long-wavelength backgrounds. And, it further suggests that the greater effectiveness of the L-cones over the M-cones in raising rod threshold is because they are more strongly excited by long-wavelength backgrounds, not because they have a special relationship with the rods.

DISCUSSION

The experiments described here indicate that the sensitivity of the rods to an incremental target is not determined solely by quantal absorptions in the rods alone but by quantal absorptions in both the rods and cones. This finding accords with other psychophysical observations of rod and cone interactions and with physiological and anatomical reports of common rod and cone pathways.

Other psychophysical results

Stiles (1939) and Aguilar and Stiles (1954) assumed that rod adaptation alone controlled the sensitivity to an incremental flash detected by rods, even at relatively high background intensities. This parsimonious assumption accorded with the spectral and field sensitivity investigations of Flamant and Stiles (1948), but those measurements were made at only moderate background intensities where cones remain relatively unadapted. We find, under similar conditions to those of Aguilar and Stiles (1954), when a long-wavelength background is used to suppress the cones, failures of rod-adaptive independence.

Our findings are consistent with many other observations that rod incremental thresholds are higher against long-wavelength backgrounds than against short- and middle-wavelength ones of equal scotopic intensity (e.g. Makous & Boothe, 1974; Sternheim & Glass, 1975; Ingling *et al.* 1977; Latch & Lennie, 1977; Makous & Peeples, 1979; Alexander & Kelly, 1984; Alexander, Kelly & Morris, 1986; Stabell, Nordby & Stabell, 1987; Sharpe *et al.* 1989). Some reports suggest that the influence of the cones can be larger against small backgrounds than against large ones (e.g. Lennie & MacLeod, 1973; Frumkes & Temme, 1977; Latch & Lennie, 1977; Blick & MacLeod, 1978; Buck, Peeples & Makous, 1979; Buck & Makous, 1981). Nevertheless, cone elevations of rod threshold are preserved with large backgrounds and in stabilized vision (Hayhoe & Smith, 1989).

Rod thresholds and the three cone types

By using colour-blind individuals we have been able to demonstrate a large elevation of rod threshold caused by L-cone stimulation, a smaller elevation caused by M-cone stimulation, but no clear effect of S-cones. Our findings for red-green dichromats are preceded by those of Alexander and his colleagues, who measured in normal and dichromat observers the influence of cones on rod saturation using flashed backgrounds (Alexander & Kelly, 1984) and backgrounds of differing size (Alexander *et al.* 1986) and found less cone influence in protanopes than in deuteranopes or normals.

Their and our apparent differences in efficacy between deuteranopes and protanopes may depend more on the differences in spectral sensitivity between each cone type and the rods than on any underlying differences in post-receptoral

organization. To demonstrate experimentally an effect of cone adaptation on rod threshold requires the use of a field that will adapt the cones, yet still allow the threshold sensitivity of the rods to be measured. For the S-cones, fields that only begin to adapt the cones have already driven rod thresholds to near saturating levels (see Fig. 2*B*, blue-cone monochromat). Thus, although we can conclude that on large adapting fields the S-cones have little or no effect on rod threshold below rod saturating levels, we cannot conclude that the S-cones are not potentially capable of elevating rod threshold. It is only on long-wavelength fields that we can strongly adapt the cones; and then only the M- and L-cones; and at the same time measure rod threshold for an incremental target. On short- and middle-wavelength fields, rod thresholds can only be measured on fields that hardly elevate cone threshold at all (see Figs 1–3). This dependence on the use of long-wavelength fields to demonstrate the effect of cone adaptation on rod sensitivity means that the effect of the M-cones (which are less sensitive to long-wave light than L-cones) is always likely to seem less than the effect of L-cones, even though the two could be equally effective (in quantal terms) in elevating rod threshold.

The site of the common adaptation pool

Our results imply that the cones must have access to post-receptoral sites where rod sensitivity is regulated. That such sensitivity regulation does not take place within the rod photoreceptors themselves, but is preceded by substantial interaction between signals from many rods is suggested by much psychophysical evidence (e.g., Rushton & Westheimer, 1962; Rushton, 1965*a, b*; MacLeod, Chen & Crognale, 1989). Moreover, direct photoreceptor recordings show that macaque rods, unlike those in lower vertebrates, do not show significant gain control (Bayler, Nunn & Schnapf, 1984), though rods in other mammals, such as cat, rabbit, cattle, rat and some primate species, do show light adaptation (Tamura, Nakatani & Yau, 1989).

The common post-receptoral adaptation pool could occur at several retinal sites where signals for neighbouring rods and cones converge before exiting the eye. Rods and cones are electrically coupled by gap junctions (Raviola & Gilula, 1973; Kolb, 1977) and AII amacrine cells connect rod bipolars with 'on' cone bipolars by way of gap junctions to 'off' ganglion cells via inhibitory synapses (see Daw, Jensen & Brunken, 1990 for a review). Other opportunities for the merging of rod and cone signals exist in the horizontal cells. Which of these sites is primarily responsible for the psychophysical rod-cone interactions observed here is unclear.

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