

SPATIAL INTEGRATION AND SENSITIVITY CHANGES IN THE HUMAN ROD VISUAL SYSTEM

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(Received 3 February 1992)

SUMMARY

1. The factor by which increment threshold rises with increasing background intensity is less if the target is small than if it is large. The difference is usually attributed to a reduction in the area over which visual signals are integrated as the visual system light adapts. Recently, however, it has been argued that the difference in slope may instead be caused by an increase in the gain of the local response function with light adaptation.

2. To test this hypothesis in the rod-driven visual system, we compared monoptic, small and large target increment thresholds, and dichoptic, large target brightness matches, measured as a function of background intensity in a typical, complete achromat, who has no cone vision.

3. The dichoptic brightness matches were made using a large target of a similar intensity to the threshold intensity of the small target. If local intensity is important, the large target brightness matching curve should be more similar to the shallow, small target threshold curve. But, if changes in spatial integration are important, the brightness matching curve should be similar to the steeper, large target threshold curve.

4. The slope of the large (1.85 deg) target increment threshold functions measured with either 200 or 50 ms test flashes were steeper than those of the small (10 min of arc) target functions by 0.10 (on logarithmic co-ordinates) or about 15%.

5. The logarithmic slopes of the dichoptic brightness curves were also slightly steeper than the small target increment functions. This is contrary to the local response (only) hypothesis, which predicts that the brightness curve should have the same slope as the small target function because the luminance of the targets in the two cases is the same.

6. We conclude that there must be a change in spatial integration in the rod visual system during light adaptation, over and above that due to local gain changes.

INTRODUCTION

Information about rod sensitivity regulation can be derived from the gradient of the increment threshold curve. Rod increment threshold *versus* intensity (TVI)

curves measured with a small target rise less steeply than those measured with a large one (see, e.g. Barlow, 1958; Sharpe, Stockman, Fach & Marksthaler, 1992).

This change in gradient has been attributed to a decrease in the area over which the visual system integrates light with increasing background intensity (Barlow, 1958). As supporting evidence, it has often been cited that, in the cat, lateral inhibitory influences, which may cancel the direct excitatory effect of stimuli falling in the periphery of retinal receptive fields, become more prominent with background intensity (Barlow, Fitzhugh & Kuffler, 1957).

There is a problem with this explanation, however. The actual sizes of the centre and surround components of the receptive fields of rod-driven mammalian ganglion cells change very little, if at all, with adaptation (Cleland & Enroth-Cugell, 1968; Derrington & Lennie, 1982). It is true that the antagonism from the surround of the receptive fields decreases appreciably in latency at higher adaptation levels, making the surround relatively more effective in exerting an inhibitory influence on the centre; and that the stronger inhibitory influence may act to reduce the effective size of the central summing area of each cell (Enroth-Cugell & Lennie, 1975; Barlow & Levick, 1976; Derrington & Lennie, 1982). Nevertheless, the change in the effective integration is relatively small. In fact, Chen, MacLeod & Stockman (1987) have calculated that the reduction in integration area of (Gaussian-shaped) receptive field centres by surround inhibition is probably no more than 19% ($0.09 \log_{10}$ unit).

As well as arguing that spatial reorganization is not an important cause of the change in gradient of the *cone-detected* increment threshold curve, Chen *et al.* (1987) suggested an alternative explanation: that it is due to an increase in the slope of a strictly local adaptation-dependent non-linearity relating log stimulus intensity to response. The threshold intensity for detecting a small flash is (much) higher than that for detecting a large one. Hence, the local *response* required for threshold (at, say, some point on the retina underlying both small and large flashes) is correspondingly greater for the small flash (see Fig. 1A and B). If the function relating local response to log stimulus intensity steepens with light adaptation, the increase in intensity needed to produce a given increase in response falls. Thus, the increase in intensity needed to go from the local threshold response for a large flash to that for a small one will decrease, causing the small and large flash thresholds to converge (i.e. the small flash threshold curve is shallower than the large).

To decide between this local hypothesis and the reduction in spatial integration hypothesis, Chen *et al.* (1987) compared small and large flash thresholds and large flash suprathreshold dichoptic brightness matches, all measured as a function of background intensity. The large flash brightness matching was performed at the same stimulus intensities at which the small flash reaches threshold so as to produce the same high local response – but with a large flash. If there is (only) a change in the slope of the local response–intensity function with adaptation, the large flash brightness matching function should have the same shallow slope as the small flash threshold function, since both require the same high local response (Fig. 1C, local adaptation hypothesis). However, if there is (only) a reduction in spatial integration, the large flash response brightness matching function should have the same steep slope as the large flash threshold function, since a reduction in spatial integration will cause a decrease in sensitivity to all large flashes, whether threshold or suprathreshold, but not to small ones (Fig. 1C, spatial integration hypothesis).

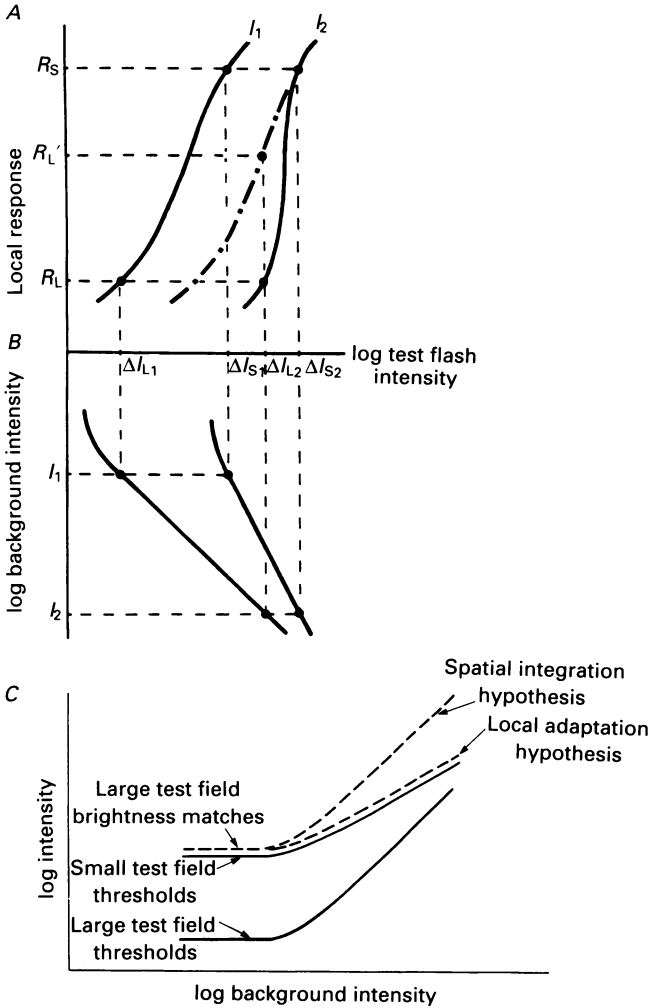


Fig. 1. The local adaptation (change in the response-intensity function) and spatial integration hypotheses for explaining the slopes of TVI curves measured with large and small diameter targets (after Chen, MacLeod & Stockman, 1987, Figs 1 and 2). *A*, functions relating the local test flash response to log test flash intensity for dim (I_1) and bright (I_2) backgrounds; *B*, TVI curves for large (left-hand curve) and small (right-hand curve) targets (rotated by 90 deg to allow comparison with the response-intensity curves) the dashed lines show how one is mapped onto the other. The detection of the small target requires a greater luminance and therefore a larger local incremental response (R_S on both hypotheses) than does the detection of the large target (local responses R_L or R'_L). In the local adaptation hypothesis, neither R_S nor R_L change with background luminance. The TVI curves converge because the gradient of the response-intensity curve increases. On the other hand, the hypothesis of greater spatial integration on the dimmer background implies that the large flash can be seen with a smaller local response level (R_L rather than R'_L) leading to the divergence of the TVI curves from I_2 to I_1 (and therefore their convergence from I_1 to I_2). R'_L is the local response required on the bright background I_2 assuming a reduction in spatial integration with adapting light. *C*, the brightness matches predicted by the spatial integration and by the adaptation-dependent non-linearity (local adaptation) hypotheses.

Chen *et al.* (1987) found that much of the difference between the slopes of large and small flash threshold curves could be accounted for by an increase in the steepness of the local response-intensity function. The asymptotic change in log integration area, after controlling for the effects of adaptation-dependent non-linearity, was between 0.02 and 0.14 \log_{10} unit. This amounts to a reduction in spatial integration of at most 28% in area or 15% in diameter.

Chen *et al.*'s findings only apply to cone-driven vision. They were unable to extend their findings to rod-driven vision because their rod measurements were obscured by the cones. This is unfortunate, since the light adaptation properties of the rod and cone visual systems may differ precisely in the extent to which local adaptation accounts for changes in the slope of increment threshold curves (cf. MacLeod, Chen & Crognale, 1989 with Cicerone, Hayhoe & MacLeod, 1990 and MacLeod, Williams & Makous, 1992).

Here we repeat the experiments of Chen *et al.* (1987) and circumvent the problem of cone intrusion by using as observer a typical, complete achromat who has no cone function. Our measurements suggest that neural spatial reorganization during light adaptation may play a relatively greater role in rod vision, with respect to that played by purely local changes, than it does in cone vision.

METHODS

Subject

K.N. is a typical, complete achromat (see Nordby & Sharpe, 1988; Sharpe & Nordby, 1990). During the experiments, he wore a +9.0 dioptre convex lens, which magnified the retinal image 1.22 times.

Stimuli

The display is shown in Fig. 2 (the reasons for favouring such a display are elaborated in Whittle & Challands, 1969; Whittle, 1973). For the increment threshold experiments (Fig. 2A), a green (Ilford 604; dominant wavelength approximately 518 nm for CIE illuminant A; see Wyszecki & Stiles 1982, p. 147) target was superimposed on an 11 deg diameter, red (Ilford 608; dominant wavelength approximately 660 nm) background. (The precise choice of target and field wavelengths is unimportant in the achromat.) The target's diameter was either 10 min of arc (Fig. 2A, left) or 1.85 deg (Fig. 2A, right). Both the target and the background were presented to the left eye of the observer, whose right eye was occluded with an eye-patch. The observer's alignment was aided by fixating the centre of four tiny orientation lights arranged in a square. The target appeared 4 deg below the lights, with its inner (i.e. right-most) edge aligned with the two left-most orientation lights (i.e. about 1 deg temporally in the visual field). This arrangement was necessary to make the increment threshold display compatible with the brightness matching display. The whole experiment was carried out twice, once with a flash duration of 50 ms and once with a duration of 200 ms.

For the dichoptic brightness matches (Fig. 2B), two simultaneously flashed monocular targets were superimposed on two monocular backgrounds, generally of different luminances. The two targets appeared to be on the same background, a binocular mixture of the separate monocular backgrounds, but on opposite sides of the orientation lights. The targets and backgrounds had the same wavelengths, durations and diameters as those used in the increment threshold experiments. To minimize spatial interactions, the targets in the binocular field were not juxtaposed but far enough apart to prevent binocular interaction between their contours (the apparent inter-target distance was about 1 deg). The inter-flash interval was 2 s.

Apparatus

The stimuli were seen in a binocular 6-channel Maxwellian view optical system, whose common source was a 50 W quartz-iodine projector bulb, run on stabilized direct current. This apparatus and its calibration have been fully described by Whittle & Challands (1969). Broad band Ilford

gelatine colour filters were used, to give maximum brightness. The luminances were controlled by neutral density filters and wedges. The transmittance characteristics of the neutral filters were calibrated with a PIN-10 photodiode with the appropriate Ilford colour filter in the beam.

Flash duration was controlled by electronic timers operating electromagnetic shutters cutting filament images in the target channels. A silicon photocell and an oscilloscope established that the time-to-peak rise and decay times of the flash were about 1 ms, and that the variability of the duration was negligible.

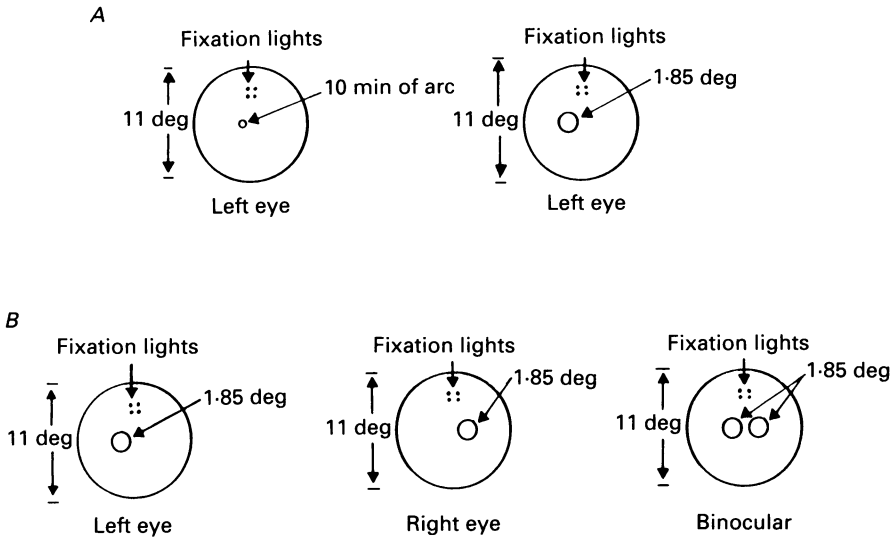


Fig. 2. The displays used for the increment threshold (A) and supra-threshold constant brightness matching (B) experiments. Not to scale.

All channels formed filament images at the plane of the observer's pupil 1.7 mm in diameter. The subject held his head steady by biting on a dental-wax impression of his teeth.

Luminances given in scotopic trolands were based on measurements of the maximum luminance in each channel, made with a photometer (EG&G Model 550), the detector head of which was equipped with a photopic luminosity filter. The photopic troland values were transformed to scotopic troland values on the basis of the conversion factors given by Wyszecki & Stiles (1982, p. 104).

Procedure

Increment thresholds and brightness matches were measured as a function of background intensity. The methods have been described before (Whittle, 1973), so only a summary will be given here.

Increment thresholds. Measurements of increment threshold were made by the method of adjustment. The subject set the incremental flash so that he saw it on almost every presentation (this corresponded to a ca 80% detection level). He did this three times on each background, each time setting the match by 'bracketing' the threshold value, and the average was taken. This procedure was repeated over an ascending series of background luminances. Each curve was measured at least twice for each combination of target duration (50 or 200 ms) and target size (10 min of arc or 1.85 deg); and all measurements were made with the observer's left eye, while the right eye was occluded. Before each run, the observer was fully dark-adapted for at least 30 min. At each new background level, he was given 3 min of pre-adaptation. These times ensured that all measurements were made in a steady state of adaptation.

Dichoptic brightness matching. For brightness matching, the basic procedure was to set a right-eye 'standard' display to a suitably chosen pair of flash and background luminances which were

then kept constant. The observer adjusted the luminance of the left-eye incremental flash, as a function of background luminance, to match the standard flash. As in the increment threshold experiments, settings were made three times at each level and averaged.

To rule out the possibility that adding a background to the right eye may have changed the adaptation level in the left eye, we measured the 50 ms large and small TVI curves both with and without a right eye background present. This made no difference to the slope or position of the TVI curves.

Curve fitting. The linear sloping parts of the increment threshold and brightness matching curves were selected with the help of a non-linear fitting routine (SYSTAT, Evanston IL, USA) using the logarithmic form of the following equation:

$$\Delta L = a(b + L_b)^n \quad (1)$$

In this equation, ΔL is the incremental luminance for threshold or brightness matching, L_b is the background field luminance, a and b are vertical and horizontal positioning constants, and n is the slope on logarithmic coordinates. This fitting routine gave no tolerance values for n . We obtained these as follows. We plotted each set of data points together with its best-fitting curve following eqn (1). From this graph it was possible to determine unambiguously which points lay on the linear part of slope n , excluding those ranges within which dark noise (at low luminances) or saturation (at high) were influencing ΔL . Regression lines were then fitted to just those data points on the linear part. For linear regression lines there are well-known procedures for calculating standard errors (S.E.M.) of the coefficients and the statistical significance of differences in slope (Student's two-tailed t tests).

RESULTS

Figures 3 and 4 display achromat K.N.'s small (10 min of arc) and large (1.85 deg) target increment threshold curves along with his large (1.85 deg) target supra-threshold (dichoptic) brightness matching curves. It will be seen for both the 200 ms (Fig. 3) and 50 ms (Fig. 4) target durations that the increment threshold curve is steeper for the large target than for the small one. The slopes of the curves (\pm S.E.M.), estimated on log-log co-ordinates according to eqn (1), are given in Table 1.

The standard errors in the table suggest which slope differences are statistically significant and which are not; t tests were also carried out. They reveal that the slopes for large and small target thresholds are significantly different at both durations (two-tailed, $P < 0.001$ at 200 ms; $P < 0.01$ at 50 ms). The slope values (0.581–0.720) fall within the ranges given in Sharpe *et al.* (1993) for rod-detected increment thresholds measured with various target durations and diameters. At high scotopic intensities, the threshold responses for the large and small flashes converge, both because of the differences in slope and because of the saturation of the rod response above $2.0 \log_{10}$ scotopic trolands (Aguilar & Stiles, 1954).

Comparisons between the slopes of the increment threshold and the brightness matching curves are critical for the testing of the alternative hypotheses. The intensity of the standard brightness matching field was chosen so that at low background levels the intensity of the large target required to match it was the same as the threshold intensity of the small target. According to a pure spatial integration hypothesis, the brightness matching function should have the same slope as the large target increment threshold function and, according to the pure response-intensity non-linearity, the brightness matching function should have the same slope as the small target increment threshold function (see above).

Student's t tests indicate that the brightness matching curves are significantly steeper than the small target threshold ones at both durations ($P < 0.01$ at 200 ms

and $P < 0.02$ at 50 ms), but that the large target brightness matching and threshold slopes are not significantly different at either duration. Since the large target brightness matching intensities rise more steeply than the small target threshold intensities, there must be some loss of rod sensitivity with increasing background

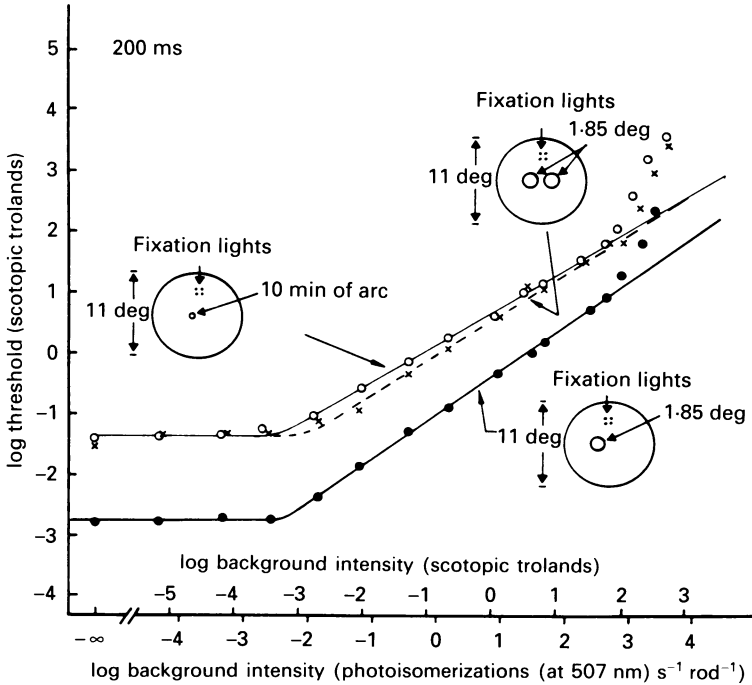


Fig. 3. The increment thresholds and constant brightness of matches of achromat K.N., for a green (Ilford 604; dominant wavelength approximately 518 nm), 200 ms target, plotted as a function of background intensity. All the measurements were made on a red (Ilford 608; dominant wavelength approximately 660 nm), 11 deg diameter background. The filled circles are 1.85 deg test field increment thresholds, the open circles are 10 min of arc (12 min of arc for K.N.) test field increment thresholds and the crosses are 1.85 deg (2.26 deg for K.N.) dichoptic brightness matches (see insets). For the brightness matches, the standard test field presented to the observer's right eye had an intensity approximately equal to that of the test field corresponding to the left-most data point of the 10 min of arc test field. Each curve is the mean of two separate experimental sessions in each of which every data point was measured three times and averaged. The linear rising lines drawn through the data points were generated by eqn (1). The scale of photoisomerizations per second per rod (abscissa) was calculated on the assumptions that for a wavelength of 507 nm (the peak of the scotopic luminosity function) one scotopic troland equals $5.66 \log_{10}$ quanta $s^{-1} \text{ deg}^{-2}$ (see Wyszecki & Stiles, 1982, p. 103), that 20% of the quanta incident at the cornea produce photoisomerizations, and that there are roughly 12500 to 15000 rods per square degree of external field in the retinal region where the targets were imaged.

intensity due to reduced spatial integration over and above that due to local adaptation.

In addition to diminishing the slope, reducing the target diameter from 1.85 deg to 10 min of arc causes a horizontal shift in the 50 ms TVI curves (the lateral shift in the 200 ms TVI curves is negligible). This can be determined by comparing for the

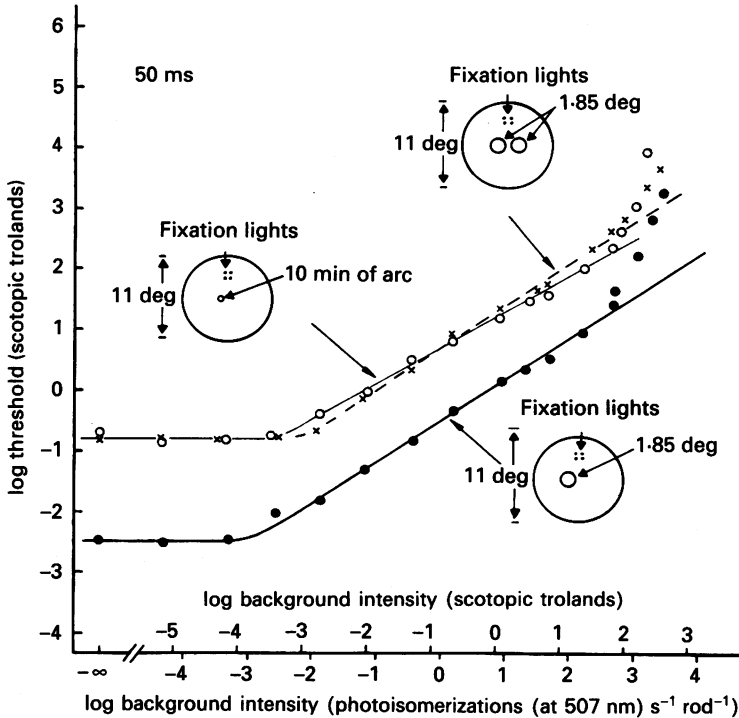


Fig. 4. The increment thresholds and constant brightness matches of achromat K.N., for a 50 ms target, plotted as a function of background intensity. Otherwise same conditions as in Fig. 3.

two curves the transition between the low-intensity (null slope) and high-intensity asymptote components. The transition roughly corresponds to the background intensity at which sensitivity begins to be reduced and has often been used as an estimate of the *Eigengrau* or dark light of the visual system (see, for example, Barlow, 1958).

TABLE 1. Slopes (eqn (1)) in logarithmic co-ordinates of the monocular (large and small diameter target) increment threshold and dichoptic (large target) brightness matching functions of achromat observer K.N.

Flash duration (ms)	Large target (1.85 deg diameter)	Small target (10 min of arc diameter)	Brightness match (1.85 deg diameter)
200	0.720 ± 0.0124*	0.618 ± 0.0124*	0.697 ± 0.0201*
50	0.694 ± 0.0184*	0.581 ± 0.0213*	0.697 ± 0.0350*

* Values are slopes ± s.e.m.

We find that the transition intensity for the small target 50 ms curve is displaced 0.5 log₁₀ unit rightward to that for the large target curve. A similar shift is reported by Chen *et al.* (1987; see their Fig. 8). Their data indicate a rightward shift in the transition or critical background of about 0.59 log₁₀ unit, produced by reducing the target diameter from 2.3 deg to 2.6 min of arc (the flash duration was 20 ms).

We also find that the transition intensity of the constant brightness (large target) curves are shifted to the right of those for the small target curves by about $0.4 \log_{10}$ unit, irrespective of target duration. Similar shifts were found by Chen *et al.* (1987; see their Fig. 8) in two of their four subjects and have been noted by Whittle & Challands (1969). This probably results from the fairly intense supra-threshold targets in the brightness matching experiment acting themselves as adapting lights. The effect would approximate the effect of adding an extra intensity adapting light, so that the transition between the low- and high-intensity asymptotes (dark light) of the curve moves to the right. The high-intensity asymptotic slope, however, should be unaffected.

DISCUSSION

The advantage of large over small flashes declines as background luminance increases. Traditionally, this is attributed to neural spatial reorganization somewhere in the retina; being most frequently related to the increasing prominence with light adaptation of the inhibitory surround in retinal ganglion cells (Barlow, 1958). However, Chen *et al.* (1987) have shown for cone vision, first that there is only a small change in TVI slope caused by changes in test flash size (the slopes of their small and large field increment threshold functions differ by not more than 20%; on average 0.97 *vs.* 0.8) – so that independent of any interpretation the change of spatial integration is less than is usually supposed – and second, that the change in slope can be mostly accounted for by local adaptation changes that involve no alteration in spatial organization with background intensity.

Is this also true for rod vision? Although Chen *et al.* (1987) did not provide rod measurements themselves, they established that even in the oft-cited rod-detected data of Barlow (1958) the differences in slope between small (0.01 deg^2) and large (23 deg^2) area test flashes of short (8.5 ms) or long (0.93 s) duration are only about 20 and 17%, respectively. This is similar to our data: with the 50 ms flash, the difference in slope between the thresholds measured with the small (0.022 deg^2) and large (2.69 deg^2) area targets is 14%; and with the 200 ms flash, the difference is 16%. Thus, the change in slope due to a change in target size is not large. In fact, Sharpe *et al.* (1993) report that the *maximum* difference in slope in rod-mediated increment threshold curves due to changes in target size, determined by comparing thresholds in achromat K.N. (the same achromat used in this study) for a 10 ms, 0.022 deg^2 test flash with those for a 10 ms, 28.27 deg^2 test flash (slopes of 0.76 ± 0.02 and 0.57 ± 0.04 , respectively), is only 25%.

Given that there is a small but significant change in the gradient of the increment threshold curve with target size, just how much of it is due to adjustments in integration in neural networks and how much to local adjustments? For rod vision, unlike for cone, we cannot explain all or most of the extra loss (over and above that due to photon fluctuations) by a local adaptation non-linearity in the function relating local response to test flash intensity (Chen *et al.* 1987). This is clear from the slopes in logarithmic co-ordinates summarized in Table 1. With the 200 ms test flash the slope of the brightness matching curve (measured with the small target) lies between that of the large and small target increment threshold curves. But, with the

50 ms test flash, the brightness matching curve is identical to that of the large target increment threshold curve. A local gain hypothesis, making no allowances for changes in spatial organization, would predict that in both cases the brightness matching curve should be identical with that of the small target increment threshold curve. Thus, there is an extra threshold elevation that cannot be explained by the local non-linearity.

We can determine the change in spatial integration over and above that due to a change in gradient of the response-intensity function by calculating the extra elevation of the large field brightness match above the small target increment threshold at the background luminance just before the onset of rod saturation (i.e. *ca* $2.0 \log_{10}$ scotopic trolands). The calculation is complicated by the fact that for both the 50 and 200 ms test flash conditions, the brightness matches are shifted about $0.4 \log_{10}$ unit rightwards to the small target increment thresholds (see above). However, if we ignore the lateral displacement by aligning the curves at their transition points, we find that for the 200 ms test flash condition this extra loss is less than $0.4 \log_{10}$ unit. On the assumption of complete spatial integration, this would correspond to a reduction in integration area by a factor of 2.5 or of diameter by 1.6. For the 50 ms test flash condition, the extra loss is $0.58 \log_{10}$ unit or a 3.8 times reduction in area or a 1.9 times reduction in diameter.

Why there should be a difference for the two flash exposure conditions is not clear. However, the results are consistent in suggesting that local adaptation alone cannot account for the change in gradient. We note others have reported that the upper limit of complete spatial summation is decreased by increasing the duration of the stimulus (Graham & Margaria, 1935; Barlow, 1958; Sharpe *et al.* 1993). This suggests that there may be some interaction between temporal and spatial reorganization which affects the slope of the curve.

Differences between rod and cone adaptation

Psychophysical (Rushton, 1965*a, b*; MacLeod *et al.* 1989) and electrophysiological (Baylor, Nunn & Schnapf, 1984) evidence supports the idea that the rise in rod-detected visual threshold produced by backgrounds is mainly due to an adjustment of sensitivity not at the rod photoreceptors themselves, but at a neural site where signals from many rods are pooled (Rushton, 1965*a, b*). In contrast, the evidence for cone-detected visual threshold is ambiguous: the psychophysics suggest that the rise is largely fixed by the size of the quantal responses of single cones (cf. Cicerone, Hayhoe & MacLeod, 1990; MacLeod *et al.* 1992); whereas membrane current recordings from monkey cone outer segments (Schnapf, Nunn, Meister & Baylor, 1990) and electroretinographic recordings of the human cone a-wave (Hood & Birch, 1991) suggest that background lights have little effect on the kinetics and the shape of the incremental response (however, see also Boynton & Whitten, 1970; Valeton & van Norren, 1983).

Given that there is no substantial local sensitivity regulation in human rod vision, you might expect that changes in integration area play a larger role than in cone vision. And, indeed, we show that since the large target brightness matching intensities rise more steeply than the small target increment threshold intensities, there must be some loss of rod sensitivity with increasing background intensity due

to spatial integration in addition to that due to local adaptation. But the extra loss we find here is surprisingly small.

On the basis of other psychophysical evidence, pertaining mostly to cone vision, MacLeod (1978) has speculated that adjustments of the integration area make only a small contribution to sensitivity regulation and that sensitivity is regulated entirely by adjustments of integration time. This may be roughly true for cone vision, but it cannot be true for rod vision. Not only do we show here that spatial reorganization in the visual system is driving the rod-increment threshold up with background intensity beyond what is predicted by local changes in the slope of the response-intensity function; but elsewhere we show (Sharpe *et al.* 1993) that, under conditions where only the rod system is active, the TVI curve slope hardly changes with target duration. This implies that rod temporal summation is practically independent of background intensity. (Table 1 indicates that reducing target duration from 200 to 50 ms decreases the slope by less than 6%).

The inferred adjustments in integration area are not large (a factor of at most 3.8). However, they are not insignificant. What is causing them? The physiological substrate most often invoked is that the reduced effectiveness of the antagonistic surround of retinal receptive fields during dark adaptation may significantly increase the optimal target size for the cell. However, as we point out in the introduction, the change in integration area resulting from the loss of the antagonistic surround may be less than $0.09 \log_{10}$ unit or 19% (Chen *et al.* 1987). This is much too small to account for the observed difference between small and large target TVI functions. Of course, it could be argued that the spatial integration constant of the visual system is not being determined at a single stage, but rather at many successive stages of lateral spreading (Chen *et al.* 1987).

The adaptation pool might be thought to be one of the stages at which lateral spreading reduces the integration area for the rods. However, recent psychophysical estimates suggest that it is too small for changes in its area to have any appreciable influence. In particular, MacLeod *et al.* (1989) estimated the diameter of the rod adaptation pool to be 10 min of arc at 10 deg retinal eccentricity; and Cicerone and Hayhoe (1990) estimated it to be between 5 and 7.5 min of arc at 5 deg nasal eccentricity (our smallest field size was 10 min of arc). Both of these values are much smaller than the original estimate made by Rushton & Westheimer (1962), 30 min of arc at 4.5 deg eccentricity, but they roughly correspond to the diameter of the dendritic fields of monkey rod bipolar cells (Grünert & Martin, 1991), which have been proposed as the anatomical substrate of the adaptation pool (Cicerone & Hayhoe, 1990).

This research was supported by a grant from the Medical Research Council, UK (awarded to P.W.). The visit of L. T. S. was made possible by funds received from the Deutsche Forschungsgemeinschaft, SFB 325, Teilprojekt B4, that of K. N. by funds received from Norwegian Telecom Research. We thank Drs A. Stockman and D. I. A. MacLeod for advice and comments.

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