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THE SPREAD OF ADAPTATION IN HUMAN FOVEAL AND PARAFOVEAL CONE VISION*

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Abstract—We investigated the spread of bleaching adaptation for human cone vision in the central fovea and at an eccentricity of 5 deg in the nasal retina. Cone thresholds measured after adaptation to a grating bleach were compared to those measured after a uniform bleach. We conclude that the foveal and parafoveal cone systems show excellent localization of the effects of adaptation. For areas 2.5–5 min removed from the bleach, our measurements show only small sensitivity losses amounting to between 0.10 and 0.25 log unit elevation in threshold, after taking account of optical scatter.

Adaptation Cones Fovea Parafovea

INTRODUCTION

Light adaptation in the human retina entails a number of different mechanisms (see Hood & Finkelstein, 1986, for a review). The mechanism most commonly identified with adaptation involves the loss of sensitivity, or gain, of retinal cells to incremental stimuli as a consequence of exposure to an adapting light. Although it is generally agreed that the gain changes associated with light adaptation occur early in retinal processing, there is still ambiguity about the anatomical sites of action. In the rod system the primary gain changes do not seem to occur in the receptors themselves (Baylor, Nunn & Schnapf, 1984), but at a site where signals from many rods converge (Rushton & Westheimer, 1962). Rushton (1965) pointed out that the scotopic increment threshold begins to rise at a level where individual rods receive, on the average, less than one quantum per second, suggesting that sensitivity is controlled by the pooled signals from many rods. This conclusion is supported by physiological evidence for spatial summation of the effects of adaptation as measured in the rod-driven activity of ganglion cells in the cat (e.g. Cleland & Enroth-Cugell, 1968; Enroth-Cugell & Shapley, 1973). Spatial summation is also observed in the loss of sensitivity associated with very bright bleaching

lights (Rushton & Westheimer, 1962; Andrews & Butcher, 1981; Barlow & Andrews, 1973; Bonds & Enroth-Cugell, 1979; MacLeod, Chen & Crognale, 1989; Cicerone & Hayhoe, 1990).

It is less clear whether there is a similar kind of spatial summation of adaptation in the cone system. Based on a number of lines of evidence, it has commonly been thought that the primary gain adjustment in response to light occurs in the cone photoreceptors themselves (e.g. Shapley & Enroth-Cugell, 1984). The π mechanisms isolated by Stiles' chromatic adaptation experiments closely resemble the photopigment spectral sensitivities (Pugh & Sigel, 1978), indicating, to a first approximation, that the different cone types adapt independently and much of adaptation occurs in the cones themselves. More clear cut evidence for receptor adaptation, at least for bleaching lights, is provided by Williams and MacLeod (1979), who found that bleaching exposures gave independent sensitivity losses in long- and middle-wavelength-sensitive cone systems. No clear picture has emerged from primate receptor physiology. Valeton and Van Norren (1983) found substantial gain changes in massed voltage recordings from monkey cones, conflicting with earlier evidence from Boynton and Whitten (1970). Recordings of outer segment membrane currents in single monkey cones, on the other hand, show receptor gain changes only at high light levels (Baylor, Nunn & Schnapf, unpublished

*The experiments reported here were performed while the authors were at the University of California, San Diego.

observations cited in Walraven, Enroth-Cugell, Hood, MacLeod & Schnapf, 1990).

The extent of the spread of sensitivity loss may help us to distinguish among the possible sites of adaptation in the retina. Spread of sensitivity loss beyond the area exposed to a bleach would rule out the possibility of adaptation confined solely to the bleached cones and would favor the existence of postreceptoral adapting sites. Some clues about the spread of sensitivity loss are provided by the appearance of afterimages. Brindley (1962) bleached the fovea with gratings of alternate light and dark bars and reported that the afterimages of fine gratings lost their initial crispness in the first minute or so, leaving a blurred uniform afterimage that lasted several more minutes. Brindley regarded these afterimages as a visible rendering of the distribution of sensitivity across the retina, and proposed the diffusion of desensitizing bleach products to account for the gradual encroachment of the afterimage into the unbleached strips. This interpretation was later challenged by Wooten and Makous (1973) and also Carpenter (1978). It was also shown by MacLeod and Hayhoe (1976) that a brief 50-msec bleach produced an afterimage which remained crisp and distinct until it finally vanished, indicating that Brindley's result could have been caused by smearing of the stimulus due to eye movements during the initial bleaching exposure. This result suggests that there is little or no spreading of the sensitivity loss to nearby cones. Additionally, MacLeod, Williams and Makous (1985) showed that the afterimage produced by a grating bleach can influence the appearance of stimuli presented upon the same foveal region. They measured aliasing when a grating of high spatial frequency is viewed by the fovea after bleaching by a grating of slightly different spatial frequency and concluded that their results are consistent with little or no spread of sensitivity loss after bleaching of foveal cones.

However, a strictly localized sensitivity loss does not necessarily indicate that the adapting effects of bleaches are confined to the cones themselves. In the primate retina, midget bipolars are observed to make one-to-one connections with the cones in fovea centralis and into the parafovea (Boycott & Dowling, 1969; Kolb, 1979), thus providing a means whereby cone signals can reach the inner plexiform layer without summation and thus without loss of spatial information. While this anatomical arrangement makes it difficult to pinpoint the

site of adaptation using foveal measurements alone, parafoveal measurements may be more amenable to interpretation for a number of reasons. First, the decline in cone density with eccentricity allows the possibility of selectively adapting a particular cone by exposing it to light, while sparing its near neighbors. Second, in parafoveal areas, in addition to the midget bipolars making one-to-one connections to cones, there is an increasing convergence of cones to flat bipolars. Third, psychophysical measures, for example measurements of the summation area for detection (e.g. Hallett, Marriott & Rodger, 1962; Limb & Rubinstein, 1977; Wilson & Bergen, 1979), point to greater convergence at parafoveal as compared to foveal locations.

To approach these issues, we extended the techniques of MacLeod and Hayhoe (1976) to assess the spread of adaptation among cones in parafoveal as well as foveal retina. Adaptation of selected areas of the retina was achieved by using a briefly exposed grating bleach (Rushton & Westheimer, 1962) which has the advantage of producing an immobile image on the retina, thus easing the task of measuring small sensitivity differences between regions directly exposed to light and those unexposed. After taking into account the effects of optical scatter, we find that there is little spread of adaptation for cone vision.

METHODS

Apparatus and procedures

Stimuli were presented by a two-channel, Maxwellian-view optical system. Illumination was provided by a 200 W quartz iodide bulb. An artificial pupil, 3.2 mm in diameter was placed in the plane of the Maxwellian image. The observer's head was held steady by a bite bar. A 30 cm focal length lens imaged the lamp filament at high magnification on the artificial pupil so that one coil of the filament filled the pupil. The bleaching stimulus was either uniformly white or composed of black and white square wave patterns produced by photographic slides. The test stimulus was also white. Accommodation and fixation were aided by a desaturated orange fixation grid. Lights were measured with an E.G.&G. silicon photodiode placed in the pupil plane. Estimates of the amount of pigment bleached were made using the results of Hollins and Alpern (1973).

The bleaching patterns of 3, 4, 6 and 12 c/deg (bar widths 10, 7.5, 5 and 2.5 min arc, respectively) were defined by field stops located between the observer and the lens and placed 72 cm away from the observer. A beam splitter was mounted in such a way that it could be removed during the bleach presentation and then quickly and precisely returned into position to bring in the test beam. The advantage of this procedure was that there were no optical components between the bleaching stimulus and the observer; thus, any degradation of the retinal image of the bleaching stimulus could be attributed solely to the optical components of the eye.

We used brief, 50 msec exposure durations for the bleach in order to minimize the effects of eye-movements which could also degrade the retinal image and lead to the spread of sensitivity loss. For such a brief exposure duration, even the largest estimate of 15 sec arc reported in previous studies (Ratliff & Riggs, 1950; Barlow, 1952; Ditchburn & Ginsborg, 1953; Riggs, Armington & Ratliff, 1954; Ditchburn, 1955) should not cause appreciable blur in the retinal image for the gratings we used. An eye-movement of 15 sec arc would reduce the contrast of a grating of 120 c/deg (bar width 15 sec) to zero. Our main conclusions rely on gratings bar widths of 5, 7.5 and 10 min arc, so that contrast, as determined by the relative intensities in the centers of the dark and light bars, should be unaffected by such eye-movements which are 1-2 orders of magnitude smaller than the width of the bars.

The observer's right eye was dark adapted for at least 10 min. When confident of good fixation, the observer pressed a button which immediately triggered a 50-msec presentation of either a grating bleach or a uniform bleach. For the grating bleach, the $7.7 \log \text{td}$ bleaching stimulus was estimated to bleach 51% of the cone pigments in the areas exposed to the bleach. To produce the uniform bleach, the field stop defining the grating was removed and the bleaching stimulus was attenuated by neutral density filters. (The consequence of any nonlinearities involved in the visual signal regulating adaptation is discussed later in the paper.) Test flashes (50 msec duration) were automatically presented at 2-sec intervals. The observer controlled a neutral density wedge to obtain a setting for which the test was just visible. When satisfied with a setting, the observer signalled the experimenter who recorded the time after

bleach and the neutral density setting. Using this procedure, the first measurement could be made as early as 5 sec following the bleach.

The results are based upon four sets of data, each collected on separate days. When results are presented in a single figure, all conditions which are compared were run in the same day's session. When results are presented as averages, error bars represent standard errors of the mean for these four separate measurements. Any standard error of the mean which was smaller than the sizes of the symbols is unmarked.

Estimating the amount of optical scatter

The amount of optical scatter was estimated by using the data of Campbell and Gubisch (1966, Fig. 7, p. 568) who reported contrast transmission as a function of the spatial frequency of sinusoidally varying stimuli for a range of pupil sizes. The average of the values reported for three observers was used. The results reported for 3.0 and 3.8 mm pupils were used to calculate, by linear interpolation, the values for the 3.2 mm pupil size used in our experiments. The Fourier expansion of a square wave provides an expression in terms of a sum of sinusoidal components whose fundamental is of the same frequency as the square wave and whose higher harmonics are odd multiples of the fundamental frequency. Thus, a square wave, such as that used in these experiments, with period χ can be considered as the infinite series:

$$\frac{4}{\pi} \left(\sin \frac{2\pi\chi}{\chi} + \frac{1}{3} \sin 3 \frac{2\pi\chi}{\chi} + \frac{1}{5} \sin 5 \frac{2\pi\chi}{\chi} + \dots \right)$$

Campbell and Gubisch report results for spatial frequencies up to 40 c/deg. The calculations for our square wave stimuli were carried out until this limit was reached. The solid curves in Figs 6 and 7 represent the relative illuminances in the centers of the dark regions calculated as described above.

Observers

The entire set of experiments was performed with two of the authors (CC and MH) as observers. A confirmatory set of experiments was performed on two other observers, one of whom was uninformed about the experimental aims and about the results. All observers had better than 20/20 acuity. For a task requiring the specification of orientation (45 deg to the left or to the right) of a grating at a level of 80% correct in a two-alternative, forced-choice procedure, visual acuity (inverse of grating bar

width expressed in min arc) was 1.6 for CC and 1.4 for MH. Gratings were presented at 5 deg eccentricity, for 50 msec, at a mean luminance of 11 cd m^{-2} , upon a dark field with the fixation target as described above.*

RESULTS

A lower limit on the size of the summation area for adaptation

Our first set of experiments was designed to provide a lower limit for the summation area of the adapting signals generated by bleached cones. We measured the recovery of sensitivity after grating bleaches of varying bar widths or after uniform bleaches matched to the grating bleaches in total flux. The bleaching stimulus covered 2 deg in visual angle. The test stimulus in all cases was uniform and was chosen so as to span several bar widths of even the coarsest grating bleaches. A test of diameter 0.5 deg was used after the bleaches with gratings having 2.5 and 5 min bars (12 and 6 c/deg, respectively); and a test of diameter 1 deg was used after the bleach with gratings having 10 min bars (3 c/deg). If, after a grating bleach of a particular spatial frequency, thresholds measured soon after the bleach show that the time course of recovery is more rapid than that measured after the uniform bleach of equal flux, then this implies that the desensitization produced by the grating bleach was spatially restricted, extending over less than half a bar width. On the other hand, a congruence of the results implies that desensitization after the grating bleach extended

into areas not directly exposed to the bleaching light.

Figures 1 and 2 show the results measured in the fovea for Observers CC and MH, respectively. For any given day's measurements, the uniform bleach was chosen as the first condition. Measurements during dark adaptation were recorded until thresholds stabilized, showing no more variation than 0.1 log unit from one measurement to the next. After each grating bleach, measurements were made until the threshold stabilized or differed by no more than 0.1 log unit from the last recorded threshold after the uniform bleach. In the fovea, for CC, the grating bleach of bar width 2.5 min arc gave a dark adaptation function for cone vision which was comparable to that for a uniform bleach matched for total flux. By comparison, the grating bleach with bar widths of 5 min resulted in a more rapid recovery of sensitivity than did the uniform bleach; and throughout the early course of dark adaptation, thresholds are lower after this bleach as compared to the uniform bleach. The same pattern of results were obtained for Observer MH, giving an estimate for a lower limit on the extent of the summation area for adaptation in the fovea of 2.5 min arc.

In the parafovea, for Observer CC (Fig. 3), the course of dark adaptation after a grating bleach of 5 min bar width is comparable to that measured after a uniform bleach matched for total flux. The results after bleaches having bar widths 7.5 and 10 min, by comparison, diverge from the results after a uniform bleach during the early course of dark adaptation. These results indicate that the lower limit for the size of the summation area for adaptation in the parafoveal cone system is 5 min arc for Observer CC. For Observer MH (Fig. 4) the results are consistent with spatial summation for adaptation in the parafovea over slightly less than 5 min arc, since measurements made in the first 25 sec during dark adaptation show a more rapid recovery after the grating bleach as compared to the uniform bleach.

A number of factors restrict the generality of these results. First, the extent of overlap in the cones contributing to neighboring receptive fields is unknown. Assuming there is no overlap, these estimates set an upper bound, as well as a lower bound for the size of the summation area for adaptation. On the other hand, if there is overlap in neighboring receptive fields, then these estimates can only set a lower limit, since

*These values indicate excellent acuity as compared against standard measures of grating acuity in this region of the retina (e.g. Westheimer, 1982; Virsu, Näsänen & Osmoviita, 1987). The classical literature on grating acuity reports large individual variability, as well as variability produced by the test stimulus and the exact conditions of measurement (Le Grand, 1967). Our two main observers had foveal acuities considerably better than the average when measured in various other contexts, so that parafoveal acuities which are correspondingly better than the norm are to be expected. Additionally, these were highly practiced observers, and as Le Grand (1967) reports, peripheral acuity can be increased up to a factor of 2 by practice. Also, the combination of pupil size (3.2 mm) and luminance level (11 cd m^{-2}) is near that which has been shown by Leibowitz (1952) to produce the highest measures of grating acuity. Finally, the test stimulus was a square subtending about 4 deg on a side, whereas most measures of acuity using grating stimuli restrict the extent of the target to one which allows viewing of only a fixed number of spatial cycles (*ca* 10).

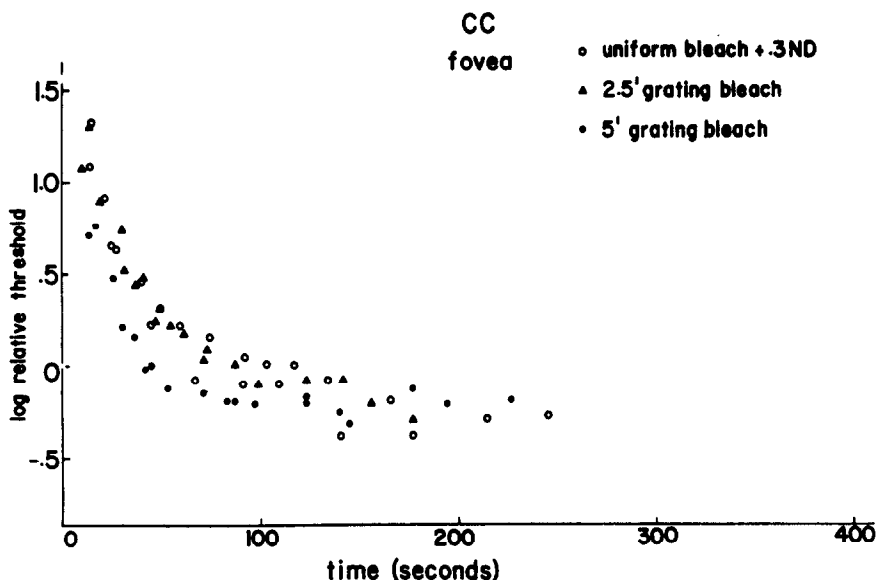


Fig. 1. Shown here are results of measurements made in the fovea for Observer CC. The course of dark adaptation for cone vision after a uniform bleach (○) is compared to that measured after grating bleaches of bar widths 2.5 min arc (▲) and 5 min arc (●). The bleaches have been equated for total flux. The grating bleach of bar width 2.5 min arc gave a dark adaptation function which was comparable to that for a uniform bleach matched in total flux, whereas there was a more rapid time course of recovery after the grating bleach of bar width 5 min arc. These results are consistent with a lower limit of 2.5 min arc for the extent of the summation area of adaptation.

in this case the summation area for adaptation could be larger and still allow the results we obtained. Second, optical scatter will inevitably cause a smearing of the retinal image of the grating bleach, reducing the relative contrast in the light and dark bars of the grating. This smearing has the effect of increasing the size of the summation area

as estimated by this procedure. Thus, the foregoing estimates should be regarded as setting a lower limit on the size of the pool, without taking into account optical scatter, whose effect would be to inflate this estimation of the lower limit.

It is worth noting here that after grating bleaches which produced faster time courses of

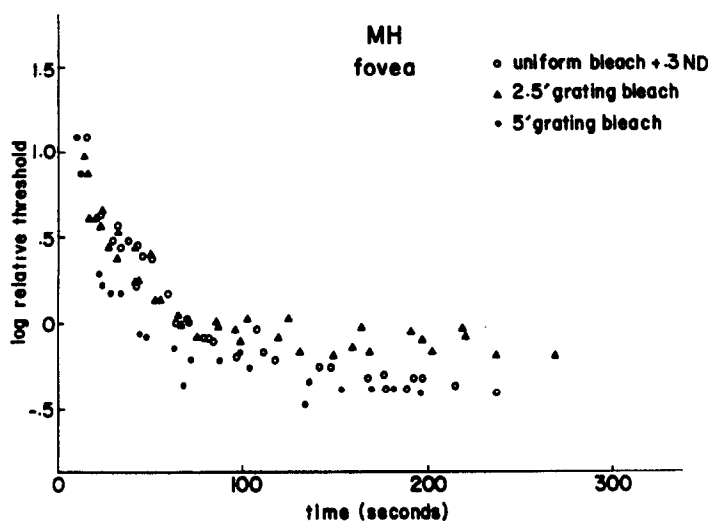


Fig. 2. Shown here are results of measurements made in the fovea for Observer MH. The grating bleach of bar width 2.5 min arc (▲) gave a dark adaptation function which was comparable to that for a uniform bleach (○) matched in total flux, whereas there was a more rapid time course of recovery after the grating bleach of bar width 5 min arc (●). The results are consistent with a lower limit of 2.5 min arc for the extent of the summation area of adaptation.

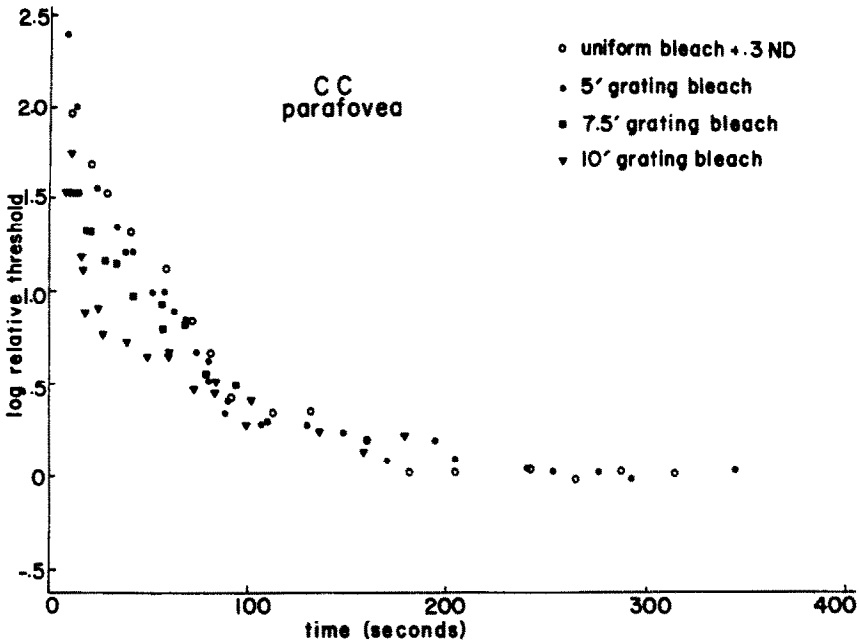


Fig. 3. In the parafovea, for Observer CC, the course of dark adaptation after a grating bleach of 5 min bar width (\bullet) is comparable to that after a uniform bleach (\circ) matched for total flux. The results after grating bleaches of 7.5 min bar widths (\blacksquare) and 10 min bar widths (\blacktriangledown), on the other hand, diverge from the results after a uniform bleach. These results indicate that the lower limit for the extent of the summation area of adaptation in the parafoveal cone system is 5 min arc for Observer CC.

dark adaptation than did the uniform bleach of equal flux, the observers reported a patterned afterimage.

Estimating the sensitivity loss in areas not directly bleached

The previous set of experiments has provided a lower limit for the extent of the summation

area for adaptation, but does not allow us to estimate the magnitude of desensitization due to the spread of adaptation. We designed the following experiments to gauge the reduction in sensitivity in the regions not directly exposed to the bleach. We used a modification of the method which Rushton and Westheimer (1962) had previously used to investigate the

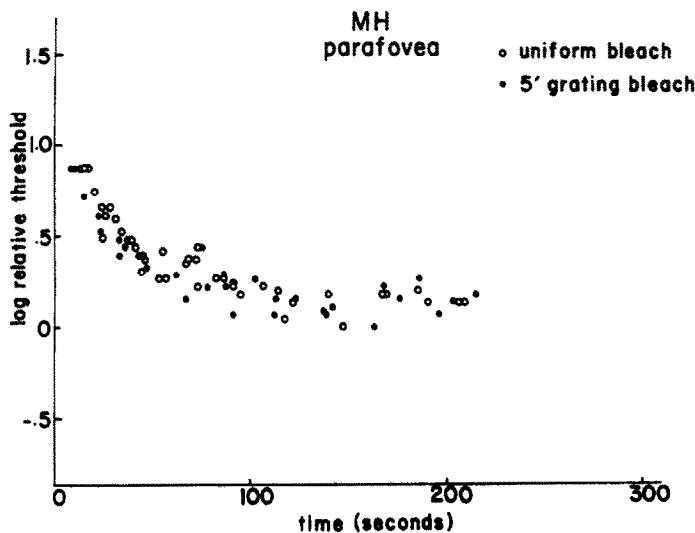


Fig. 4. For Observer MH the results are consistent with parafoveal summation of adaptation over slightly less than 5 min arc, since measurements made in the first 25 sec after the bleaches show a more rapid recovery after the grating bleach of 5 min arc bar widths (\bullet) as compared to the uniform bleach (\circ).

spread of adaptation in the rod system. A 2 deg region of retina was bleached with a pattern of alternating light and dark bars of 5, 7.5 and 10 min arc and of 50 msec duration. Recovery of sensitivity from these patterned bleaches was measured using a 50 msec presentations of a uniform, circular test spot which spanned a number of bars of the grating pattern (0.5 deg after the 5 and 7.5 min grating bleach and 1 deg test spot after the 10 min grating bleach). Under the assumption that the effect of the bleach is localized, then soon after the bleaching exposure, before appreciable recovery of sensitivity in the bleached strips, the uniform test spot will be visible only to the unbleached areas. Thus, early in dark adaptation the measured thresholds reflect the sensitivity of the *unexposed* areas. We matched this sensitivity by selecting an intensity of a uniform bleaching light which produces an identical time course of recovery

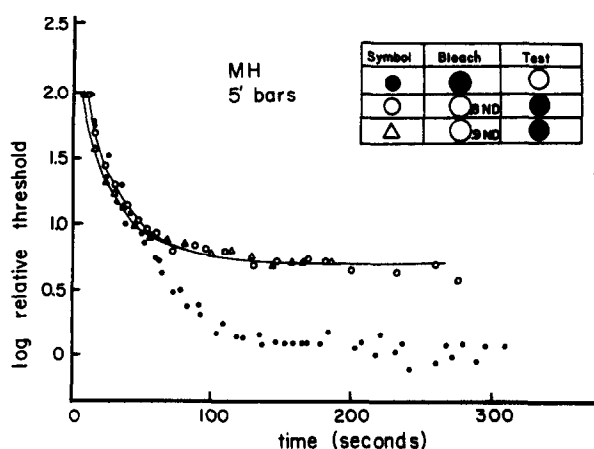


Fig. 5. A 2 deg region of retina was bleached with a pattern of alternating light and dark bars of 5, 7.5 or 10 min arc and of 50 msec duration. Recovery of sensitivity from these patterned bleaches was measured using a 50 msec presentation of a uniform, circular test spot which spanned a number of bars of the grating pattern (0.5 deg after the 5 and 7.5 min grating bleach and 1 deg test spot after the 10 min grating bleach). As shown in this example, we matched this sensitivity by selecting an intensity of a uniform bleaching light which produces an identical time course of recovery when measurements were made with a grating test composed of a pattern of light and dark bars matching the reverse of the retinal image profile for the bleaching stimulus. The return of sensitivity as measured with a uniform test after a grating bleach (●) was matched by the recovery of sensitivity measured with a grating test after a uniform bleach attenuated by 0.8 log unit (○). An intensity adjustment making the uniform bleach a mere 0.1 of log unit dimmer (△) now gave a distinctly different dark adaptation curve. In this way we identified for each grating bleach an equivalent uniform bleach which gave a dark adaptation curve matching the one measured after bleaching with the grating.

when measurements were made with a grating test which was composed of a pattern light and dark bars matching the reverse profile of the bleaching stimulus after taking into account optical scatter. We estimated the retinal image profile of the bleaching pattern by using the measurements of Campbell and Gubisch (1966) as outlined in the Methods section. We assumed that regions for which light scatter dropped to e^{-1} or less of the value of exposed strips contributed to detection, so that the test stimuli we used after uniform bleaches had a pattern, the reverse of the retinal image of the bleaches, of thin light bars (2.1, 3.1 and 4.2 min for the 5, 7.5 and 10 min stimuli, respectively) and thicker dark bars.

As an example of this matching procedure, a set of dark adaptation measurements are shown in Fig. 5. Early in dark adaptation, the return of sensitivity as measured with a uniform test after a grating bleach is shown to be matched by the recovery of sensitivity measured with a grating test after a uniform bleach attenuated by 0.8 log unit. As shown here, an intensity adjustment making the uniform bleach a mere 0.1 of log unit dimmer now gave a distinctly different dark adaptation curve. In this way we identified for each grating bleach an equivalent uniform bleach which gave a dark adaptation curve matching the one measured after bleaching with the grating. This experimentally defines an "effective intensity" in the dark-bar regions.

Figure 6 shows foveal estimates, made in this way, of the effective intensity in the regions not directly exposed to the grating bleach. Error bars are based on between-day variability in measurements made over four separate days. These estimates of the effective bleaching intensity in the regions underlying the dark bars as a function of bar width can be compared to the intensity of the retinal image at its local minimum in the center of the dark bars, estimated from the results of Campbell and Gubisch (1966) as outlined in the Methods section. The data points lie above this curve representing the estimated scattered light. This means either that our approximation of the amount of optical scatter as noted above was an underestimate or that there is a residual elevation of threshold in the dark bars which cannot be attributed to optical scatter. If the elevation is due to any residual optical scatter, then the results might be expected to parallel the optical scatter profile. Indeed, the displacement of the data points is approximately a constant value above the

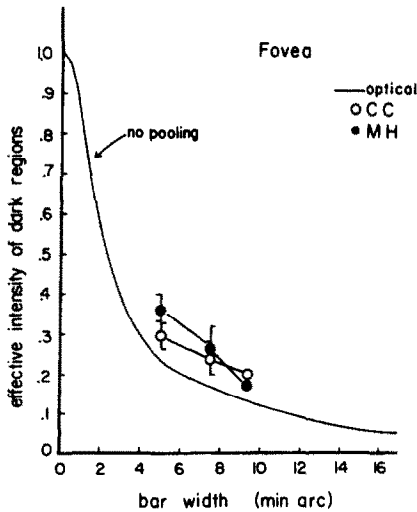


Fig. 6. Foveal estimates of the effective intensity in the regions underlying the dark bars as a function of bar width are compared to the intensity of the retinal image at its local minimum in the center of the dark bars, as estimated from the data of Campbell and Gubisch (1966) for Observers CC (○) and MH (●). The elevation above the curve representing optical scatter can be interpreted to represent 0.1 (for CC) and 0.2 (for MH) log unit loss in sensitivity due to the spread of adaptation, about a 10-fold reduction as compared to the loss of sensitivity at the bleaching locus.

estimated scatter profile, giving some indication that the results might be entirely attributable to optical scatter. Assuming, nonetheless, that our procedure accurately estimated the amount of optical scatter, we can use this displacement to assess the amount of desensitization in the center of the spared strips as that due to the spread of adaptation. Our measurements for bleaches of this magnitude showed that for each 0.1 log unit increase in bleach intensity there was a corresponding 0.17–0.20 log unit increase in threshold. The elevation of our measurements above the expected amount of optical scatter can therefore be interpreted to represent, for CC and MH, respectively, approx. 0.1 and 0.2 log unit loss in sensitivity due to the spread of adaptation, about a 10-fold reduction as compared to the loss of sensitivity at the bleaching locus.

Measurements made in the parafovea (Fig. 7) show that MH's results are elevated by only small amounts above what would be expected from optical scatter alone. Subject CC's results give, for every bar width, an estimated effective intensity in the center of the dark bars, more than would be predicted from optical scatter, corresponding to an additional sensitivity loss of approx. 0.25 log unit which may be due to neural adaptation. As in the fovea for this

observer, the elevation above the scatter estimate is constant for all bar widths, consistent with the interpretation that this elevation may be due to an underestimate of optical scatter in designing the appropriate test after the uniform bleach. Furthermore, since we estimated optical scatter in the parafovea by using measurements made in the fovea (Campbell & Gubisch, 1966), it is even more likely that scatter has been underestimated.

Summation areas for detection

In order to make a comparison between these estimates of the summation area for adaptation to the size of the summation area for detection, we measured the extent of Ricco's area for these two observers. Shown in Fig. 8 are the thresholds as a function of test diameter in the fovea and in the parafovea at 5 deg eccentricity for Observer CC. The results fall in line with Ricco's law for small dimensions, but the effectiveness of added light as a contribution to visual threshold diminishes beyond 4 min arc in the fovea and beyond 8 min arc in the parafovea. The results of this experiment for Observer MH are shown in Fig. 9. A divergence from Ricco's law behavior occurs for targets of diameters beyond 8 min arc for fovea as well as the parafovea for subject MH. The extent of summation for adaptation is one-third to one-half that for detection, according to this measure.

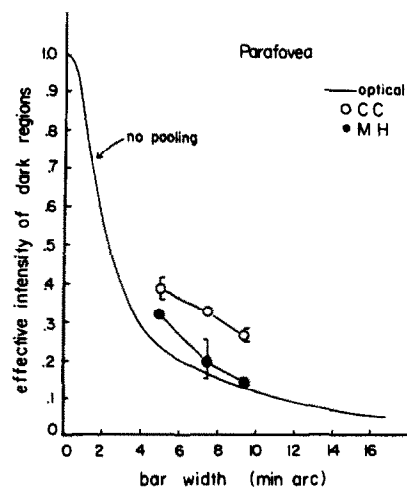


Fig. 7. Shown here are parafoveal estimates made in the same way as described in Figs 5 and 6 for the fovea. Observer CC's results (○) give an estimate of 0.25 log unit loss in sensitivity due to the spread of adaptation. MH's results (●) are not significantly elevated above what would be expected on the basis of optical scatter alone.

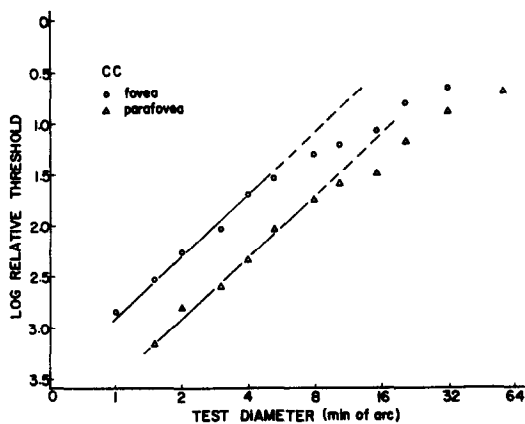


Fig. 8. The extent of spatial summation was gauged by measuring thresholds as a function of test diameter in the fovea (○) and the parafovea (△) for Observer CC. The results fall in line with Ricco's Law (—) for small dimensions, but the effectiveness of added light as a contribution to threshold diminishes beyond 4 min arc in the fovea and beyond 8 min arc in the parafovea.

Effects of nonlinearities

A possible difficulty with the logic leading to these estimates of a restricted spread of adaptation is that the visual signal regulating adaptation may involve a nonlinearity, which could on its own cause a divergence between the dark adaptation curves measured after the grating bleach and the uniform bleach, regardless of the nature of the spatial summation of adapting signals. A nonlinear relation between light intensity and bleached pigment would, on its own, lead to slightly less average bleached pigment after the grating bleach. We can rule out the confounding effects of nonlinearities on two grounds. First, one would expect that complete spatial summation after a grating bleach would lead to a uniform-appearing afterimage, whatever the preceding nonlinearity. This is not observed. Whenever measurements of the sensitivity loss after the grating bleach diverged from those after the uniform one, a patterned afterimage was observed. Second, we performed our experiments at two lower bleaching levels (0.6 and 0.9 log unit less than the original bleach), thereby changing the operating point on the putative nonlinear function. As compared to the original stimulus which bleached 51% of the cone pigments, these lower levels bleached 16% and 9%, respectively, of the cone pigments. If the divergence of uniform and grating dark adaptation curves had been due to a nonlinearity, then at these lower bleaching levels, estimates of the summation area for adaptation should change. This does not occur, instead we obtained the same estimates at all bleaching levels.

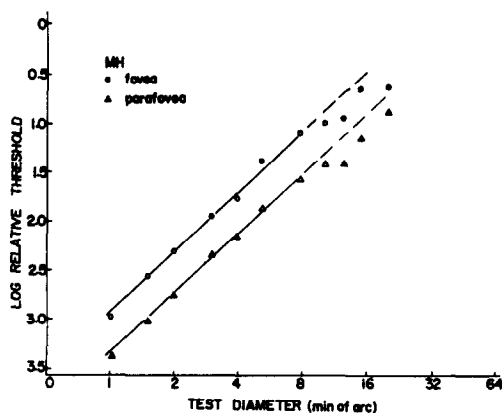


Fig. 9. For Observer MH, divergence from Ricco's Law behavior occurs for targets of diameters beyond 8 min arc for the fovea (○) and the parafovea (△).

DISCUSSION

We investigated the spread of bleaching adaptation in the human cone system by comparing thresholds measured after adaptation to a grating bleach to those measured after adaptation to a uniform bleach. We conclude that the foveal and parafoveal cone systems show excellent localization of adaptation. For areas 2.5–5 min removed from the bleach, only small sensitivity losses, amounting to no more than between 0.10 and 0.25 log unit elevation in threshold, could be attributed to the spread of adaptation, assuming that we had adequately taken into account the effects of optical scatter. This conclusion was based on a series of experiments which compared the loss of sensitivity after spatially uniform and grating bleaches of varying spatial frequencies. In our first set of experiments, a uniform test, large enough to span several grating bar widths, was used after both uniform and grating bleaches which were equated for total flux. We reasoned that the spatial frequency of the grating bleach which yielded a match to the uniform bleach in the time course of recovery of sensitivity after bleaching must define the lower limit of the size of the summation area for adaptation. This estimate was necessarily a lower limit, since an overlap in neighboring receptive fields would yield the same result, even if the summation areas were larger. Since optical scatter was not considered in this set, the estimates are inevitably inflated due to this factor.

A second set of experiments was aimed at estimating the sensitivity loss due to the spread of adaptation. Based on the observation that soon after the grating bleach, only the

unexposed areas can contribute to detection of a test we used a grating test after the uniform bleach and a uniform test after the grating bleach. In addition, we took into account the effects of optical scattering in the human eye which effectively broadens the bleached area and correspondingly narrows the spared areas. Using the estimates of Campbell and Gubisch (1966), we determined the relative widths of the dark and light bars which would be appropriate as the test stimulus to be used after the uniform bleach so as to match the areas contributing to detection after the grating bleach. In this set of experiments, the independent variable was the spatial frequency of the grating bleach and the dependent variable was the density in the uniform bleach required to match the time course of recovery after each grating bleach early in dark adaptation. In this way, we estimated an "effective intensity" in the unexposed area after the grating bleach. The extent to which this measure departed from that which could be expected on the basis of optical scatter alone was interpreted as a measure of the desensitization due to the spread of adaptation. Each of these two sets of experiments support the conclusion stated above: that the foveal and parafoveal cone systems show only very restricted spread of adaptation.

We can estimate the numbers of cones included within the summation area for adaptation in the following way. Anatomical estimates of cone density (d) can be converted to cone spacing (r) measured in min arc of visual angle by assuming triangular packing of the cones and LeGrand's (1957) theoretical eye:

$$r = (60/0.291)(\sqrt{3/2d})^{1/2}$$

Osterberg's (1935) measurements at fovea centralis and 5 deg nasal eccentricity yield cone center-to-center spacings of 0.50 min arc and 1.87 min arc, respectively. Curcio, Sloan, Packer, Hendrickson and Kalina's (1987) results yield center-to-center spacing for the cones of 0.48 min arc at the fovea centralis and 1.83 min arc at 5 deg nasal eccentricity. In addition, for Observer CC, results from previous psychophysical studies (Cicerone & Nerger, 1985, 1989; Nerger & Cicerone, 1991) provide individual estimates of cone spacing in the fovea centralis of 0.52 min arc and at 4 deg retinal eccentricity of 1.98 min arc. Consistent with these measurements of cone spacing, we can estimate that in each of our two observers in the parafovea, for regions roughly one cone (2.5 min arc) removed

from the bleach, the desensitization due to the spread of adaptation is small, amounting to no more than 0.14 (MH) to 0.25 (CC) log unit elevation in threshold, about a 10-fold reduction as compared to that produced at the bleaching site. In this same region of the retina, we estimate that the summation area for detection (8 min arc in dia.) extends over an area with a 5-cone dia., comprising approx. 21 cones. This allows the conclusion that there is virtually no spread of bleaching adaptation in the parafovea at 5 deg eccentricity. The same kind of argument is more difficult to make for the foveal cones since the foveal mosaic is so densely packed and the limitations of optical scatter preclude our use of gratings finer than the ones we have employed. In this regard, we can only make the observation that it would be unreasonable to expect, as compared to the parafovea, a greater spread of adaptation in the fovea which is populated exclusively by the one-to-one connections of midget systems.

The summation area for detection

In addition to Ricco's paradigm, a number of other means of assessing the area of summation for detection include bar detection with supra-threshold adapting stimuli (e.g. Thomas, 1968); subthreshold additivity contributing to bar detection (e.g. Kulikowsky & King-Smith, 1973; Wilson & Bergen, 1979); bar detection as a function of width of the bar (e.g. Limb & Rubinstein, 1977). These studies generally report a summation area for detection of 3–4 min in the fovea and, when parafoveal measurements are reported, 6–8 min in parafoveal regions near 5 deg eccentricity. These values are reasonably close to the estimates reported here.

The diameter of Ricco's area measured for CC was 4 min arc in the fovea and 8 min arc at 5 deg eccentricity. The sizes of MH's summation areas were 8 min arc for both fovea and parafovea. Since both observers had comparably excellent acuity (Methods section), blurring due to optical factors is not likely to be the reason for this difference between observers. Other studies have recently presented data on the size of the summation area for detection, as determined using Ricco's paradigm, at various retinal eccentricities (Wilson, 1970; Inui, Mimura & Kani, 1981). Our results for Observer CC closely match the results of Inui et al. (1981) who measured a foveal diameter of 4.2 min arc and a diameter of 7 min arc at 5 deg eccentricity, as well as Wilson's estimate at 5 deg eccentricity

of 8 min arc. The size of MH's summation area in the parafovea also corresponds well to the measurements of Wilson (1970) and Inui et al. (1981), but the foveal summation area is twice as large as compared to that obtained in these previous studies and as compared to CC's foveal summation area. The paradigm for measurements of Ricco's area uncovers the most sensitive of the multiple mechanisms for spatial vision (Wilson & Bergen, 1979). Thus, this result for MH does not necessarily imply that this is the smallest excitation pool in MH's fovea, only that it is the most sensitive. Overall, our results support the idea that in the parafovea as well as the fovea, the summation area for excitation is more extensive than that for adaptation.

The site of bleaching adaptation

These results contrast with the findings in rod vision showing that regulation of sensitivity involves the reduction in gain at a neural locus which recruits the responses of many photoreceptors. For bleaching adaptation, estimates of the size of the summation area for adaptation in rods have declined somewhat as compared to the earliest estimates provided by Rushton and Westheimer (e.g. Andrews & Butcher, 1971; MacLeod et al., 1989; Cicerone & Hayhoe, 1990). In addition, recent electrophysiological evidence consistent with localized effects of both bleaching and background adaptation have been demonstrated within the receptive fields of rod-driven ganglion cells of rat (Cicerone & Green, 1980a, b, 1981) and cat (Enroth-Cugell & Harding, 1980). Nonetheless, even the smallest estimate of the spread of adaptation in human rod vision involves about 50 receptors (Cicerone & Hayhoe, 1990).

In contrast, our results for the parafoveal cone system point to a 10-fold decline in the desensitizing effects of bleaching adaptation at locations a single cone's spacing away from the adapting site. We therefore conclude that there is virtually no spread of bleaching adaptation in the parafoveal cone system. In the midget system our result places the site of bleaching adaptation at the cones themselves or at the

midget bipolar cells, presumably making one-to-one contact with the cones. In the system of flat bipolars, each of which receives input from many cones, our result places the site of adaptation at the cones themselves. Furthermore, the restricted spread of adaptation as compared to the sizes of Ricco's area points to adaptation occurring prior to the site of summation in receptive field centers of ganglion cells. Our measurements do not provide as direct a conclusion for the foveal cone system. In order to reach the same kind of conclusion, the higher density of cones in the fovea would require measurements made with finer grating bleaches than those employed in this study. However, for stimuli generated with our apparatus, optical scatter would smear the retinal image of these finer grating stimuli, rendering them useless for this kind of analysis. Thus, we can only make the observation that it would be highly unlikely that, as compared to the parafovea, adaptation would be pooled more extensively in the primate foveal cone system with its characteristic one-to-one scheme of connectivity via the midget system (Boycott & Dowling, 1969; Kolb, 1979).

Although this experiment indicates that the gain changes associated with bleaching adaptation in the cone system are largely restricted to the bleached photoreceptors, we cannot conclude that this is true for all of the processes which govern sensitivity in photopic vision. There are at least two stages which affect sensitivity, a localized gain change, followed by response compression at a site with center/surround organization and a restricted operating range (e.g. Geisler, 1981 1983; Hayhoe, Benimoff & Hood, 1987; Hayhoe, 1990; Walraven et al., 1990).* One important mechanism which operates at this second site of adaptation is the lateral interactions demonstrated in Westheimer's sensitization paradigm. If increment threshold is measured in the center of a background of varying size, it is found to be low on very small backgrounds, reach a peak at some intermediate size, and then fall again on very large backgrounds (Westheimer, 1967). A similar dependence on bleach size is observed in cone dark adaptation (Hayhoe, 1979a). The peak threshold elevation has been interpreted as indicating the extent of the summation area for adaptation and has been identified with the dimensions of retinal receptive field centers of neurons which sum the signals from many cones (McKee & Westheimer, 1971; Enoch, 1978; Spillman, Ransom-Hogg & Oehler, 1987). The

*Some central adaptation may be involved with small, unstabilized backgrounds (Hayhoe, 1979b; Hayhoe & Smith, 1989), but this is a relatively small effect and unlikely to be present with bleaches (Hayhoe, 1979a). By using achromatic stimuli in these experiments we have probably avoided the so-called "second site" adaptation which acts at a chromatically opponent locus (e.g. Pugh & Mollon, 1979).

summation area for adaptation estimated in this way at 5 deg eccentricity is about 20 min, much larger than the spread of adaptation observed in the present experiments. Why is this extensive spatial pooling not observed here? It is likely that the threshold elevation observed in the sensitization paradigm results from response compression at a post-receptor nonlinear stage which sums the signals from many cones (Hayhoe, 1990). When the surround of a receptive field is sufficiently illuminated, however, responses can be kept in a linear range. Indeed, Ambrose and Hayhoe (1980) demonstrated that bleaching about 50% of the area of the receptive field surround was sufficient to eliminate the response-compressive threshold elevation produced by small bleaches which filled only the center, giving a dark adaptation curve identical to that after a uniform bleach of equal intensity. With the spatially extended grating stimuli used in the present experiment it is likely that receptive field surrounds received sufficient stimulation to prevent significant departures from linearity. However, it is possible that the small threshold elevation we observed in the dark bars does in fact reflect some response compression at this post-receptor site.

In conclusion, our results show that as little as one cone spacing removed from the bleaching locus, there is a sharp, 10-fold decline in the desensitization produced by bleaching adaptation. The severity of this decline is consistent with virtually no spread of adaptation in the human parafoveal cone system under the conditions of these experiments. This highly restricted spread of bleaching adaptation, in comparison with a much broader spatial summation as measured by Ricco's area, point to a site for bleaching adaptation located at the cones themselves or at the bipolars to which they make one-to-one contact. Furthermore, adaptation occurs prior to the pooling in the receptive field centers of ganglion cells, the site of summation of excitatory responses.

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