J. Physiol. (1987), **388**, *pp.* 101–119
With 10 *text-figures*
Printed in Great Britain

REGIONAL VARIATION OF CONTRAST SENSITIVITY ACROSS THE RETINA OF THE ACHROMAT: SENSITIVITY OF HUMAN ROD VISION

BY R. F. HESS†*, K. NORDBY AND J. S. POINTER*

*From * The Physiological Laboratory, Cambridge CB2 3EG and The Institute of Psychology, University of Oslo, N-0317, Norway.*

(*Received 5 September 1986*)

SUMMARY

1. Detection thresholds for two-dimensional Gabor functions of varying spatial and temporal frequency were used to investigate the post-receptoral sensitivity across the retina of the typical and complete achromat.

2. Under photopic conditions there is no evidence for post-receptoral cone function at any retinal eccentricity investigated. Sensitivity saturates in a way consistent with known psychophysical and electrophysiological measures of rod saturation. This occurs in a unitary fashion across the retina.

3. Under scotopic conditions the regional fall-off in spatio-temporal sensitivity is similar for the achromat and duplex retina. This suggests that the rods in the achromat make normal neural connections.

4. Taken together this supports the contention that the typical and complete achromat is a functional rod monochromat and hence can be used to explore the sensitivity of the isolated rod post-receptoral mechanism under mesopic conditions where its sensitivity is optimal. This is where its contribution is most difficult to isolate in the duplex retina.

5. For the human rod mechanism, mesopic post-receptoral sensitivity for all spatio-temporal stimuli is optimal in the central region of the retina and falls off as a function of eccentricity.

6. For localized stimuli, peripheral spatial sensitivity is reduced evenly at all spatial frequencies compared with that of the central retina. A similar displacement of the spatial sensitivity function of the rod mechanism occurs as illuminance is reduced.

7. For localized stimuli, temporal acuity of the rod mechanism is around 20–25 Hz irrespective of retinal position. As the illuminance is further lowered dynamics of the rod pathway are reduced irrespective of retinal position and the sensitivity function maintains a bandpass shape.

8. The regional distribution sensitivity of the rod mechanism changes as illuminance is reduced from mesopic to scotopic levels.

† Address for correspondence.

INTRODUCTION

Our understanding of the physiology of typical and complete achromatopsia has been in a state of continual flux ever since it was first recognised by Huddart over 200 years ago (Huddart, 1777). Towards the end of the last century it was believed to be the result of a congenital absence of cone photoreceptors (Galezowski, 1868), but this view was overturned in the first half of this century by the histological findings of cone receptors in the achromat retina (Larsen, 1921 *a*, *b*; Harrison, Hoffnagel & Hayward, 1960; Falls, Wolter & Alpern, 1965; Glickstein & Heath, 1975). These cones were much reduced in number and anomalously distributed across the retina. Subsequent psychophysical investigation produced evidence of high-intensity receptor function in the complete achromat (Sloan, 1954; Walls & Heath, 1954; Alpern, Falls & Lee, 1960), thereby establishing the view that, at least to some degree, the achromat possessed a functional, although impoverished, duplex retina. However, recently an investigation into post-receptoral sensitivity in the achromat found no evidence for anything other than normal rod receptoral function (Hess & Nordby, 1986*a*,*b*). Independent but complementary investigations of the type that had previously found evidence for cone function, namely measurement of the Stiles–Crawford effect, spectral sensitivity and dark adaptation, all support the conclusion that cone function is absent in this achromat (Nordby, Stabell & Stabell, 1984; Sharpe & Nordby, 1984). Other investigations have suggested that some of the previous evidence may have been contaminated by an artifact due to inadequate retinal adaptation (Sakitt, 1976). This led Hess & Nordby (1986*a*,*b*) to propose a modification of Dr Galezowski's original explanation of the physiology of total and complete achromatopsia, namely that while the retina may be to some extent duplex from the histological perspective, these cones do not communicate with the visual areas of the achromat's brain.

The evidence upon which this proposal is based came from experiments involving only the central region of the achromat's retina (i.e. mainly within 5 deg of the fovea), because it is here that one of the more detailed histological studies (Falls *et al.* 1965) suggested that the cone distribution was maximal. Since so much rests on this recent finding it is important that it encompasses peripheral as well as central regions of the achromat's retina. This will not only lead to a more complete picture of retinal function in achromatopsia but it is essential for other reasons. First, there is disagreement among the four histological studies as to where the cones are distributed. Some say they are sparse in the periphery but present in substantial numbers in the foveal region (Falls *et al.* 1965), whereas others say the opposite (Larsen, 1921*a*,*b*; Glickstein & Heath, 1975). Secondly, at least some of the previous psychophysical evidence for cone function has involved the use of stimuli located in the more peripheral parts of the visual field (Alpern *et al.* 1960). Finally, the resolution of this issue in general could be of much greater physiological importance than resolving an historical debate about a clinical curiosity. For, if it is the case that there are human eyes with a normal population of rod receptors which in turn make normal post-receptoral connections, but lacking all cone post-receptoral function, then we have the luxury of being able to study the performance of the rod mechanism in complete isolation. This is particularly important under mesopic conditions where rod

contrast sensitivity is optimal, yet where the rod response is most difficult to isolate in the duplex retina from its more sensitive cone counterpart.

In the present study we assess whether there are peripheral cones in the achromat retina relaying information to post-receptoral sites. The results suggest that if peripheral cones are present they do not relay visual information to post-receptoral sites. Furthermore, the peripheral rods make normal post-receptoral connections. Having established this, the post-receptoral sensitivity of the human rod pathway is compared as a function of both illuminance and retinal eccentricity using the achromat as a functional rod-monochromat.

METHODS

General procedures

Monocular detection thresholds were measured for sinusoidal grating stimuli varying in spatial and temporal frequency using a temporal, two-alternative forced-choice technique (Levitt, 1971). A staircase procedure driven by the subject's responses and controlled by a computer determined the detection threshold. Each trial consisted of two presentations (denoted by auditory tones) one of which contained the stimulus while the other was a blank field of the same space-averaged luminance. The average of six to eight reversals of the staircase constituted one mean. This method was used for the determination of contrast sensitivity as well as spatial and temporal acuity. In the former case the contrast was the variable whereas in the latter the spatial or temporal frequency was the variable (contrast = 90 %). Each datum consisted of the average of at least two means.

Stimuli were presented in the centre of a Joyce Electronics (Cambridge, U.K.) raster display (P4 phosphor) at a frame rate of 200 Hz. The display screen was surrounded by a large luminance-matched field (40 deg vertically × 60 deg horizontally). This was crucial for the photopic experiments. The room was artificially illuminated. The display screen's contrast linearity was measured, and found to be linear with input voltage to 98 % contrast (accuracy of ±1 %). A fixation light of adjustable intensity was used to direct the subject's fixation so that eccentric regions could be tested. The viewing distance was 3·7 m. The subject's refractive error was fully corrected prior to testing. Under mesopic to scotopic conditions fixation was 1·5 deg eccentric on the temporal retina (see Hess & Nordby, 1986*a*). This was taken into account in all subsequent experiments so that the results in all Figures refer to retinal coordinates relative to the anatomical fovea.

Stimulus

Horizontally orientated sinusoidal grating patterns were used to measure contrast detection thresholds. This orientation ensured that any functional unsteadiness of the subject's eye (predominantly in the horizontal plane and at mesopic light levels) did not interfere with our measurements by introducing retinal image smear (Volkmann, Riggs, White & Moore, 1978). These patterns were digitally generated using a PDP 11/34A laboratory computer. The contrast of each stimulus was weighted with Gaussian functions of space and time (x, y, t). This ensured that the stimuli were well localized spatially and temporally and that eccentric detection was not differentially biased to the edge of the stimulus proximal to the fovea.

The luminance distribution of each stimulus is specified by

$$L(x, y, t) = L_0[1 + CG(x, y, t) \sin(2\pi F_x x) \cos(2\pi F_t t)], \quad (1)$$

where L_0 indicates the space-averaged luminance, C the contrast variable, G the spread function and F_x and F_t the spatial and temporal frequencies. Contrast is defined as $L_{max} - L_{min}/L_{max} + L_{min}$ where L_{max} and L_{min} are the maximum and minimum luminances of the luminance profile of the stimulus. Contrast sensitivity is the reciprocal of the contrast needed for threshold detection. The spread function, G, is given by

$$G(x, y, t) = \exp[-(x/S_x)^2 - (y/S_y)^2 - (t/S_t)^2]. \quad (2)$$

The term spread signifies the distance in time or space that the Gaussian falls from 1 to 1/e. The over-all spread function is the product of the horizontal, vertical and time Gaussians having spreads S_x, S_y and S_t. The spread was varied within the range 0·2 to 3 deg.

Flicker for an unstructured field and eight spatial frequencies (their spectrum was positioned at 0·27, 0·8, 1·2, 2, 2·4, 4·8, 8 and 16 cycles/deg) were used in conjunction with two temporal frequencies (spectrum positioned at 1 and 5 Hz). A list of the stimuli and their corresponding spatial Gaussian spreads (circularly symmetrical, $S_x = S_y$) and band widths is given (Tables 1 and 2).

Subjects

Co-author K.N., a total and complete achromat, was the subject in these experiments. The normal results were obtained from one of the co-authors (J.S.P.) and verified on one other subject. Pupils were dilated by 1% cyclopentolate hydrochloride instilled 3 h prior to testing. Pupil size was monitored photographically before and after each experimental run.

TABLE 1. Contrast sensitivity measurements

Spatial frequency (cycles/deg)	Spatial spreads* (deg)	Spatial band widths (octaves)
0·2	3	0·61
0·8	2	0·23
1·2	1	0·28
2	1	0·17
2·4	1	0·14
4·8	0·7	0·10
8	0·4	0·11
16	0·2	0·11

Two temporal conditions were employed, 1 Hz (band width = 1·6 octaves) and 5 Hz (band width = 0·3 octaves), each within a Gaussian time-window whose spread was 250 ms and whose total duration was 1 s. * $S_x = S_y$.

TABLE 2. Acuity measurements

Stimulus	Spread (deg)
Temporal (flicker)	3
Spatial (0 Hz)	3

Temporal spread S_t was 250 ms for all experiments; the total duration of presentation was 1 s. At 1 Hz the temporal band width was 1·6 octaves while at 5 Hz the temporal band width was 0·3 octaves.

RESULTS

The results in Fig. 1 show how contrast sensitivity in different regions of the visual field depends upon the retinal illumination within the upper mesopic to lower photopic range. Results are shown for two spatial frequencies, 0·8 and 2 cycles/deg, which span the achromat's spatial sensitivity function (see Fig. 1*B*, inset). The temporal frequency is 5 Hz contrast reversal which represents the optimum of the achromat's temporal frequency function (see Fig. 1*A*, inset). The stimulus was windowed by a two-dimensional Gaussian whose spread (see Methods for definition) was either 2 deg (0·8 cycles/deg) or 1 deg (2 cycles/deg) (see Table 1) within a large 40 × 60 deg luminance matched surround field. Under optimal conditions of retinal illuminance (i.e. at 620 scotopic trolands) notice that for both spatial stimuli the peak sensitivity occurs in the central region of the visual field. As the retinal illuminance is increased into the lower photopic range, sensitivity is evenly reduced at all eccentricities out to 25 deg on either side of fixation. Above 1530 scotopic trolands (T_s), neither spatial stimulus can be detected even at unit contrast sensitivity

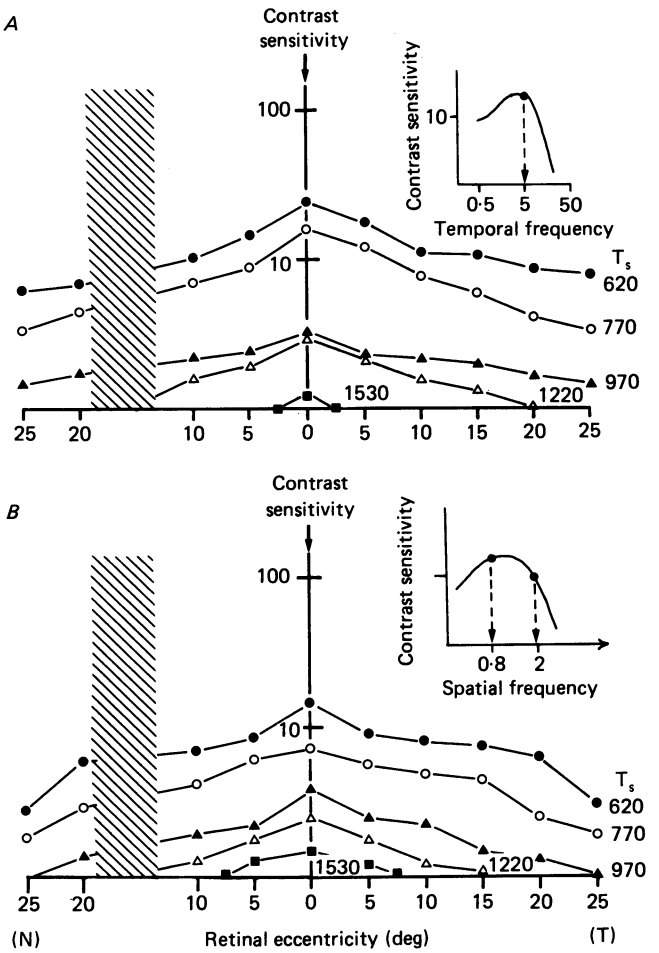

Fig. 1. Contrast sensitivity is plotted against retinal eccentricity in degrees for the achromat. Results are shown for 5 Hz stimulus of spatial frequency 0·8 cycles/deg (*A*) and 2 cycles/deg (*B*) for a range of retinal illuminances from upper mesopic to lower photopic. 'N' indicates nasal retina, 'T' temporal retina. The insets depict the spatio-temporal stimulus parameters relative to the achromat sensitivity function. The standard deviation was never greater than twice the symbol size. As illuminance increases, sensitivity reduces evenly across the visual field.

regardless of its eccentricity. This finding does not depend upon the temporal frequency of stimulation (data not displayed). The absolute retinal illuminance at which sensitivity begins to fall, as well as its time constant (with respect to retinal illuminance), is in good agreement with previous results for central vision in the achromat (Hess & Nordby, 1986*a*). This is better seen in Fig. 2 in which the data from different retinal eccentricities (from Fig. 1) have been normalized and plotted against retinal illuminance for the 0·8 cycles/deg (*A*) and 2 cycles/deg (*B*) condition. The continuous curve is an exponential whose decay constant is 0·0024 (note double logarithmic coordinates). This was found to describe the photopic saturation in the achromat for a wide range of spatial and temporal stimuli (Hess & Nordby, 1986*a*).

The horizontal bar represents the range of retinal illuminances which was found by Aguilar & Stiles (1954) to correspond to absolute saturation in a group of normal subjects.

This result suggests that neither central nor peripheral regions of the visual field show any evidence of post-receptoral signals from the 'high-intensity receptors' postulated by Alpern *et al.* (1960). The fall-off in sensitivity follows a similar course for different spatial frequencies, temporal frequencies (Hess & Nordby, 1986*a*) and eccentricities, and can be modelled by rod saturation. This also suggests that

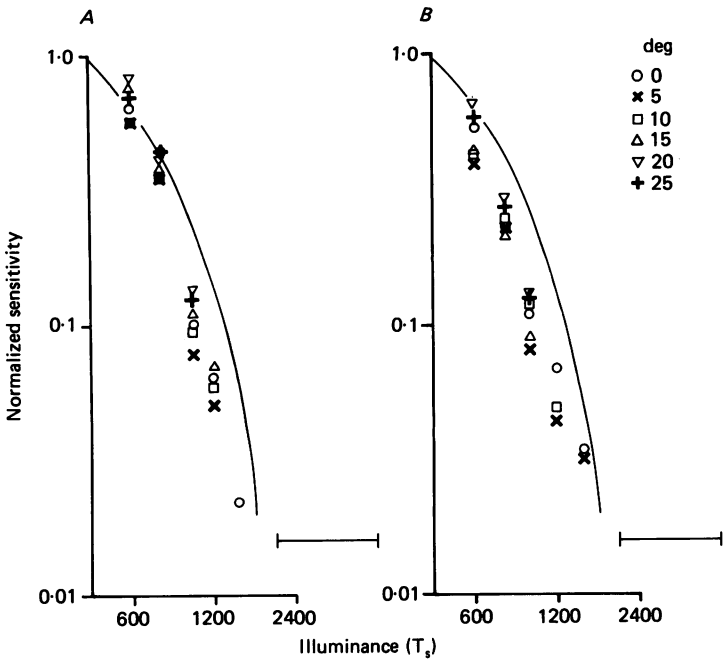

Fig. 2. Normalized contrast sensitivity is plotted against retinal illuminance for 5 Hz stimulus of spatial frequency 0·8 cycles/deg (*A*) or 2 cycles/deg (*B*). Results are displayed for a number of retinal eccentricities. The continuous curve is an exponential whose decay constant is 0·0024 (see Hess & Nordby, 1986*a*). The horizontal bar represents the range of absolute saturation illuminances found by Aguilar & Stiles (1954) for normal subjects.

peripheral rods saturate at a similar illuminance to that of central rods. Since at higher retinal illuminances post-receptoral sensitivity across the achromat's visual field is explicable solely in terms of the known properties of rod receptors, it is important to ask now whether the neural connections that these receptors make with post-receptoral neurones is the same as for a duplex retina. This can best be assessed by comparing the spatio-temporal contrast sensitivity of an achromat and normal observer as a function of eccentricity for illuminances below these mesopic values. If the neural connections across the achromat's retina are the same as for the normal duplex retina, the normal and achromat should exhibit exactly the same sensitivity under scotopic conditions where only the rod pathway of the duplex retina is functional. In Figs. 3–6 results are displayed for such a comparison for a wide range of spatio-temporal stimuli imaged at central and peripheral retinal loci.

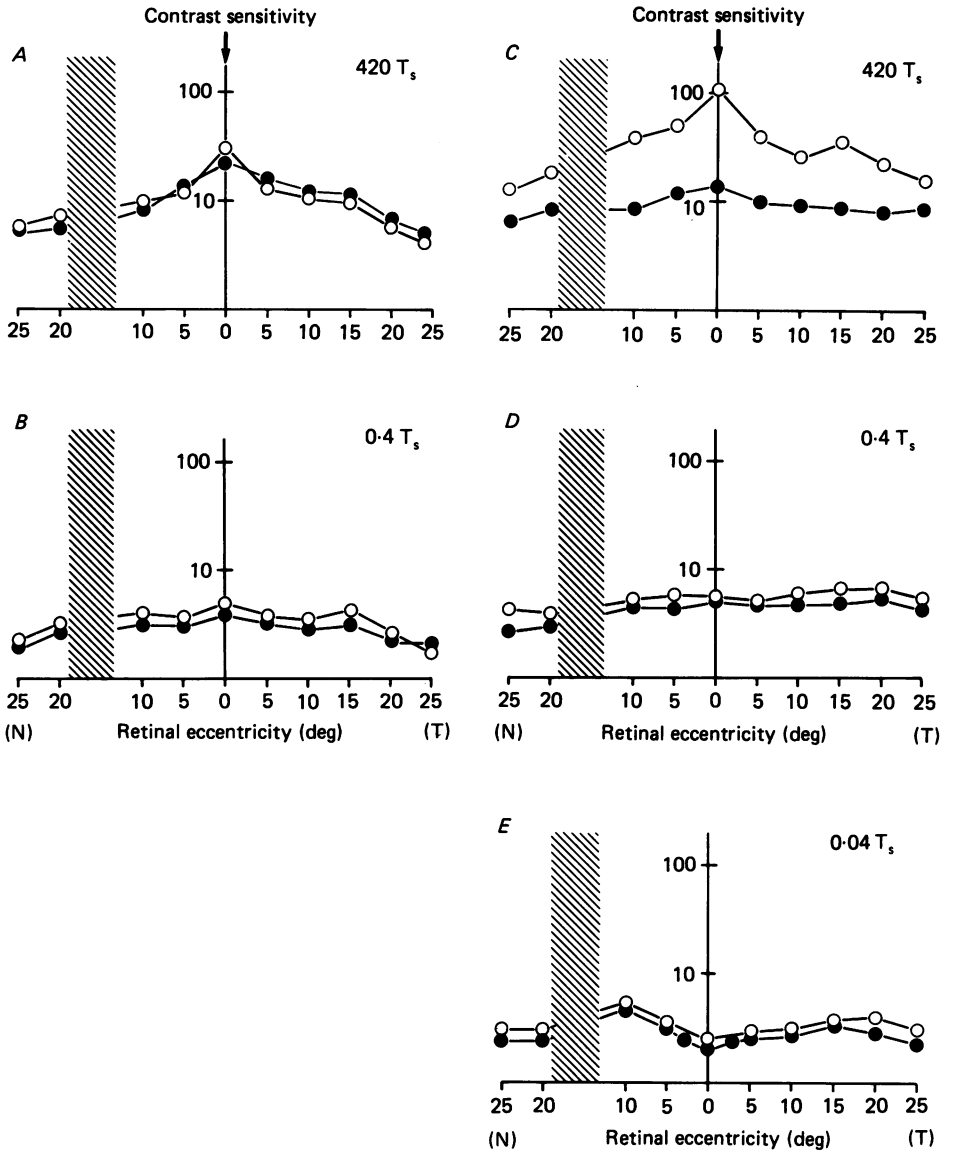

Fig. 3. Contrast sensitivity is plotted against retinal eccentricity in degrees for the achromat (●) and normal trichromat (○). Results are shown for a spatial frequency of 0·2 cycles/deg over a range of illuminances ranging from upper mesopic to lower scotopic. The temporal frequency of stimulation is either 1 Hz (*A* and *B*) or 5 Hz (*C*, *D* and *E*). 'N' indicates nasal retina, 'T' temporal retina. The standard deviation was never greater than twice the symbol size. Under scotopic conditions (0·4–0·04 T_s) spatio-temporal sensitivity of achromat and normal trichromat are equivalent across the retina.

In Fig. 3 *A–E*, spatio-temporal sensitivity as a function of retinal eccentricity is displayed at one mesopic and two scotopic illuminances. The open symbols represent results for a normal observer and the filled symbols are for the achromat. The spatial frequency is 0·2 cycles/deg and the temporal frequency is either 1 or 5 Hz. At the

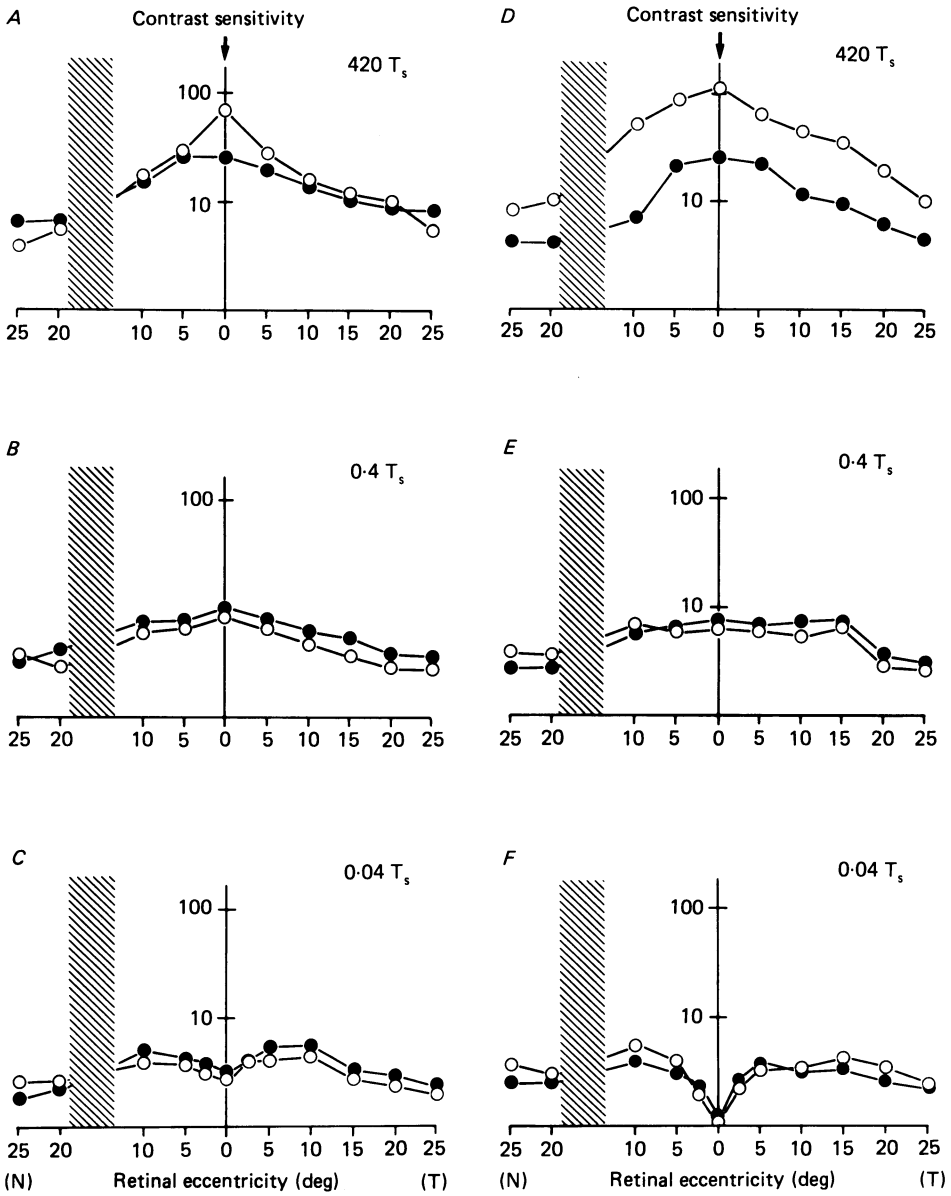

Fig. 4. Contrast sensitivity is plotted against retinal eccentricity in degrees for the achromat (●) and normal trichromat (○). Results are shown for a spatial frequency of 0·8 cycles/deg over a range of illuminances ranging from upper mesopic to lower scotopic. The temporal frequency is either 1 Hz (*A*, *B* and *C*) or 5 Hz (*D*, *E* and *F*). Standard deviations were never greater than twice the symbol size. Under scotopic conditions (0·4 T_s and lower) spatio-temporal sensitivity of achromat and trichromat are equivalent across the retina.

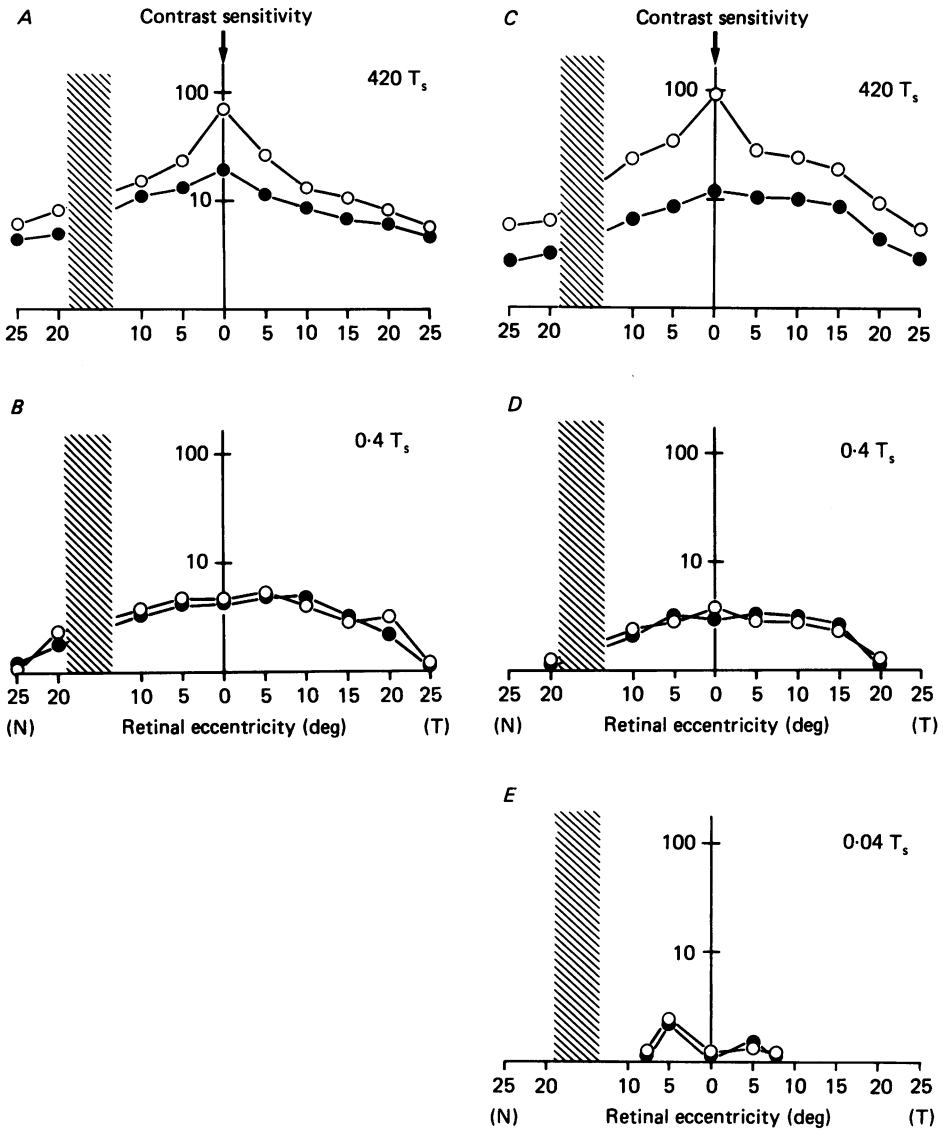

Fig. 5. Contrast sensitivity is plotted against retinal eccentricity in degrees for the achromat (●) and normal trichromat (○). Results are shown for a spatial frequency of 2 cycles/deg over a range of illuminances ranging from upper mesopic to mid-scotopic. The temporal frequency is either 1 Hz (*A* and *B*) or 5 Hz (*C*, *D* and *E*). The standard deviation was never greater than twice the symbol size. Under scotopic conditions the spatio-temporal sensitivity of achromat and trichromat are matched at all eccentricities.

lower temporal frequency, sensitivities of normal and achromat are comparable at all eccentricities and illuminances, although the absolute sensitivity and the rate of fall-off of sensitivity with eccentricity vary with illuminance for both subjects. At the higher temporal rate there is a substantial difference between the sensitivities of normal and achromat at the mesopic illuminance. This difference, which is greater for central than for peripheral vision, results from an elevation of the trichromat's

sensitivity for this stimulus presented at the higher temporal rate. No such effect is evident at the two scotopic illuminances where the sensitivity of trichromat and achromat are matched across both retinal eccentricity and retinal illuminance.

When the spatial frequency of the stimulus is raised from 0·2 to 0·8 cycles/deg (Fig. 4), there is a greater departure in the mesopic contrast sensitivity of trichromat and achromat. Now a difference is seen for the 1 Hz temporal rate (Fig. 4 *A*) but is restricted to the foveal region. A greater difference is seen at 5 Hz (Fig. 4 *D*), one which

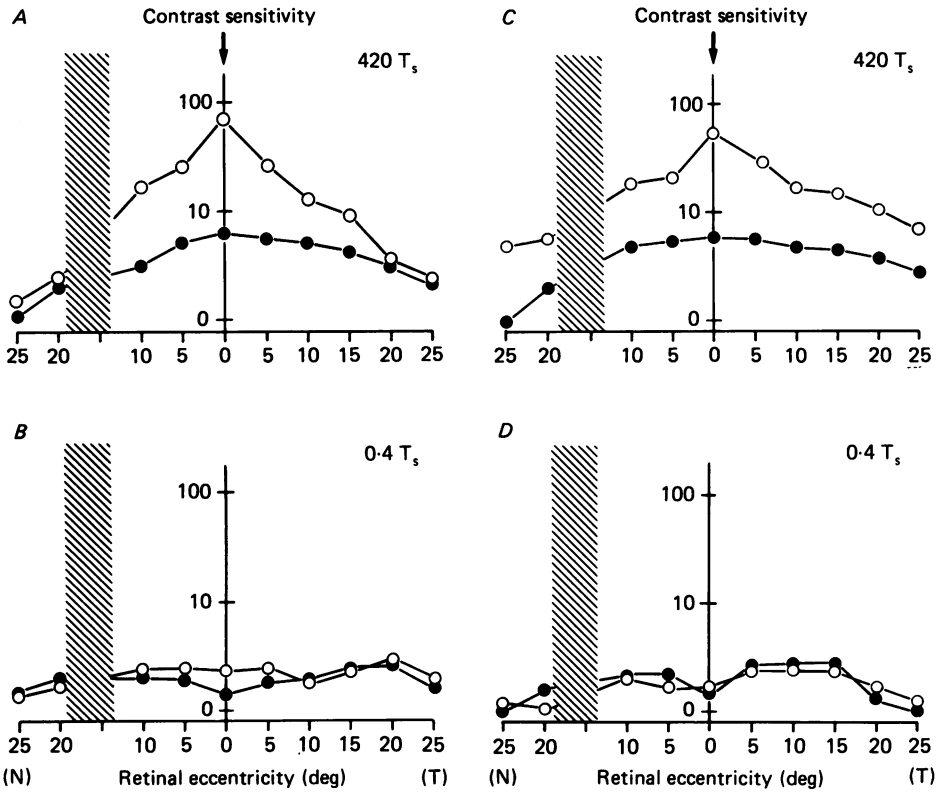

Fig. 6. Contrast sensitivity is plotted against retinal eccentricity in degrees for the achromat (●) and normal trichromat (○). Results are shown for a spatial frequency of 2·4 cycles/deg at mesopic and upper scotopic illuminances. The temporal frequency is either 1 Hz (*A* and *B*) or 5 Hz (*C* and *D*). The standard deviation was never larger than twice the symbol size. Under scotopic conditions, spatio-temporal sensitivity is very similar for achromat and trichromat at all retinal eccentricities.

extends across all retinal eccentricities. Again, although the shape of the fall-off in sensitivity with eccentricity changes for the scotopic conditions (Fig. 3 *B*, *C*, *E* and *F*), the sensitivity for trichromat and achromat remain in register.

At a higher spatial frequency, namely 2 cycles/deg (Fig. 5), similar results are seen. Under mesopic conditions (Fig. 5 *A* and *C*), sensitivity of the trichromatic observer is higher than that of the achromat and this extends to all eccentricities measured, even for the 1 Hz temporal rate (Fig. 5 *A*). However, the elevation is greater for central vision. Under scotopic conditions which can be followed to lower levels for 5 Hz

stimulation, the sensitivity of trichromat and achromat are coincident at all eccentricities out to 25 deg.

The highest spatial frequency for which reliable results can be obtained for the achromat and where sensitivity can be followed to scotopic levels is 2·4 cycles/deg (Fig. 6). At this spatial frequency one sees the largest deviations in the sensitivities of normal and achromat under the mesopic conditions (420 T_s). As before, this is greatest at the fovea, and diminishes at increasing eccentricities. Under scotopic conditions, sensitivity of normal and achromat are matched. When taken together,

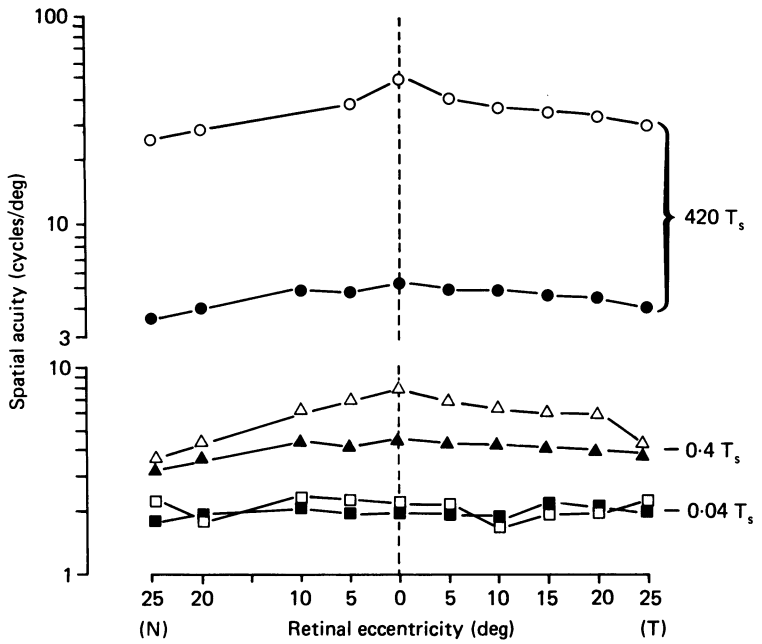

Fig. 7. Spatial acuity in cycles/deg is plotted against retinal eccentricity in degrees for achromat (●, ▲, ■) and normal trichromat (○, △, □). Results are shown for a mesopic, an upper scotopic and a lower scotopic illuminance. Temporal frequency, 0 Hz. Standard deviations were never greater than twice the symbol size. Notice that under upper scotopic conditions (0·4 T_s) the trichromat's acuity is superior to that of the achromat over the central 10 deg. At the lower scotopic illuminance the spatial acuity of achromat and trichromat are equal at all eccentricities.

all of these results suggest that the post-receptoral sensitivity of the duplex and achromat retina are identical under scotopic conditions. The only departures occur in mesopic conditions where the cones of the duplex retina are functioning.

Finally, spatial (90 % contrast; 0 Hz; 3 deg spread) and temporal (90 % contrast; 0·05 cycles/deg; 3 deg spread) acuity at different retinal eccentricities in the duplex and achromat's retina are compared at one mesopic and two scotopic illuminances in Figs. 7 and 8. In the comparison of spatial acuity at the lower mesopic illuminance (420 T_s), there is a constant factor (0·8 log unit) between the spatial acuity of the duplex and achromat retina as a function of retinal eccentricity. In both cases the acuity fall-off with eccentricity is gradual. At the upper scotopic illuminance (0·4 T_s), the spatial acuity of the duplex and achromat retina are still not identical.

The difference is now 0·25 log units in the central retina and this reduces as a function of retinal eccentricity until the difference falls to within experimental error at 25 deg. At the lower scotopic illuminance (0·04 T_s), spatial acuity is matched for normal and achromat at all retinal eccentricities.

Temporal acuity is relatively independent of eccentricity for both trichromat and achromat. At the lower mesopic level (420 T_s) there is a difference of a factor of 2 between normal and achromat at all but one eccentricity whereas the results are in register at the two scotopic illuminances (0·4 and 0·04 T_s). Apart from the 0·25 log unit differences between spatial acuity of trichromat and achromat under the upper scotopic luminance, these results confirm that post-receptoral sensitivity of normal and achromat are matched under scotopic conditions.

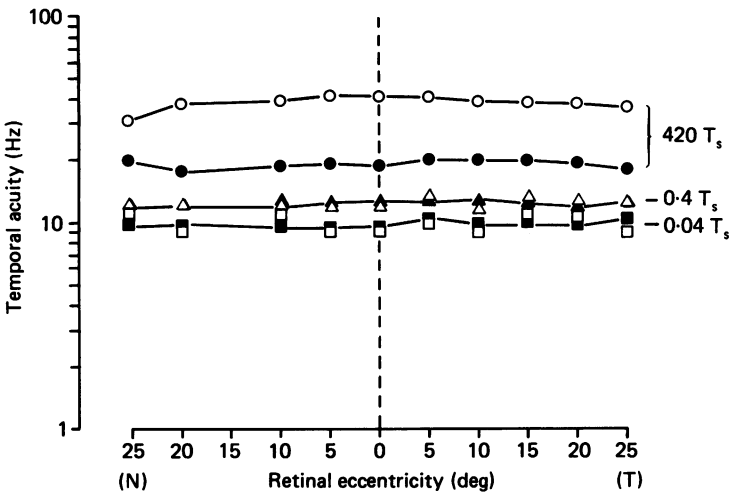

Fig. 8. Temporal acuity in Hz is plotted against retinal eccentricity in degrees for achromat (●, ▲, ■) and normal trichromat (○, △, □). Results are shown for a spatial frequency of 0·05 cycles/deg for mesopic, upper scotopic and a lower scotopic illuminance. Standard deviations were never greater than twice the symbol size. Under the two scotopic conditions temporal acuity for achromat and trichromat are matched at all retinal eccentricities.

A complementary way of examining the spatio-temporal sensitivity of the achromat, and hence indirectly of the rod mechanism itself, is to compare spatial and temporal sensitivity functions at representative retinal locations (e.g. central and 20 deg) and illuminances (e.g. mesopic and scotopic). The results of such a comparison are seen in Figs. 9 and 10. In these Figures the open symbols represent central sensitivities and filled symbols represent peripheral sensitivities. The achromat's spatial sensitivity function at mesopic illuminances (Fig. 9*A*) for these spatially confined stimuli peaks at around 1 cycle/deg for central vision and reaches a sensitivity of 30. These sensitivities are a factor of 2–3 lower than those found using larger field sizes (Green, 1972; Daw & Enoch, 1973; Hess & Nordby, 1986*a*; D'Zmura & Lennie, 1986). The spatial acuity is around 6–7 cycles/deg for central vision. Notice that at this mesopic illuminance the peak sensitivity for the trichromat is a factor of 2 higher, peaks around 3 cycles/deg and extends to much higher spatial

frequencies. Two points are worth noting about the peripheral spatial transfer function of the rod mechanism of the achromat. First, at this same illuminance cone-mediated sensitivity of the trichromat is no better than rod-mediated sensitivity of the achromat over most of the spatial range. It is only above 2 cycles/deg that cone-mediated sensitivity of the trichromat is better. Secondly, the rod-mediated

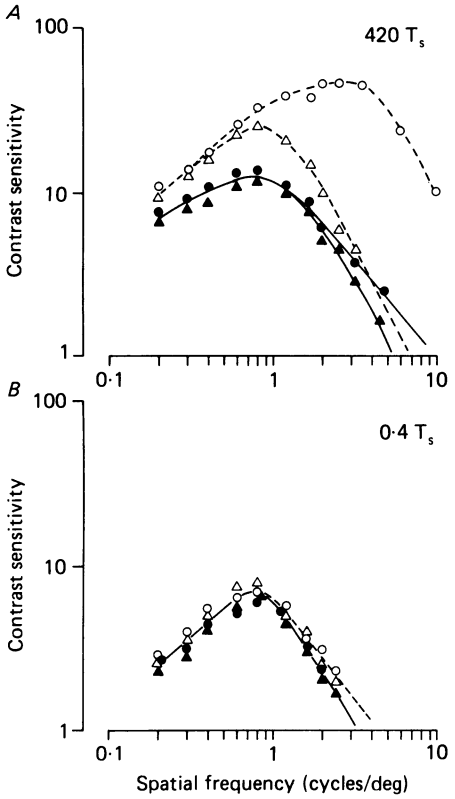

Fig. 9. Contrast sensitivity is plotted against spatial frequency in cycles/deg for achromat (△, ▲) and trichromat (○, ●). At each of two retinal illuminances, namely 420 T_s (*A*) and 0·4 T_s (*B*), spatial contrast sensitivity functions are compared for achromat and trichromat for central and peripheral (20 deg) retina. △, ○, central sensitivities; ▲, ●, peripheral sensitivities (20 deg). The temporal frequency is 1 Hz. Under scotopic conditions central and peripheral contrast sensitivity are similar and matched for achromat and trichromat.

sensitivity of the achromat for the peripheral retina is reduced in a similar way for all spatial frequencies compared with central vision. The scotopic spatial sensitivity function for rod vision for these stimuli is seen in Fig. 9*B*. Peak sensitivity is now 15 at 0·8 cycles/deg. It is essentially a parallel displaced version of the mesopic function (Fig. 9*A*). Central and peripheral retinal sensitivity is now comparable over the whole spatial range, indicating a flat sensitivity profile across the retina.

A similar comparison of the temporal transfer function under mesopic conditions (Fig. 10*A*) for central vision shows that a peak sensitivity of around 30 is obtained

at 5 Hz. The temporal acuity is around 25 Hz for central vision. The sensitivity of the central retinal projection of the trichromat is a factor of 1·7 higher, peaks around 10 Hz and exhibits greater sensitivity at higher temporal frequencies. The rod-mediated temporal sensitivity function of the achromat for the peripheral retina

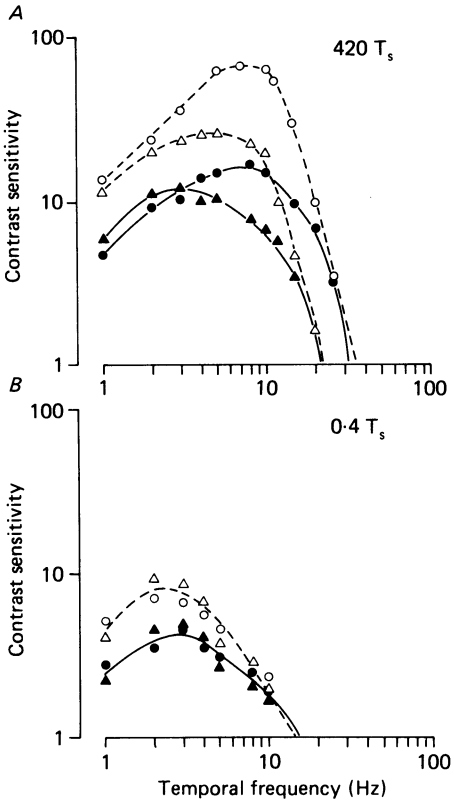

Fig. 10. Contrast sensitivity is plotted against temporal frequency in Hz for achromat (△, ▲) and trichromat (○, ●). At each of two retinal illuminances, namely 420 T_s (*A*) and 0·4 T_s (*B*), temporal contrast sensitivity functions are compared for the central and peripheral retina. △, ○, central sensitivity; ▲, ●, peripheral sensitivity (20 deg). The spatial frequency is 0·05 cycles/deg (3 deg spread) and the standard deviation is less than twice the symbol size. Under scotopic conditions central and peripheral sensitivity functions differ, but the sensitivity of achromat and trichromat are in register.

is reduced below that for central vision for all temporal frequencies except at the very highest (above 15 Hz). Hence rod temporal acuity (achromat's results) does not significantly vary across the visual field (see also Fig. 8). Temporal sensitivity of the cone-mediated function (trichromat's result) of the peripheral retina is a factor of 2 better than that for rod vision above 5 Hz. This also means that the peripheral cone temporal sensitivity of the trichromat is reduced below that for central vision at all temporal frequencies except at the very highest (above 20 Hz). This also results in cone temporal acuity being invariant with retinal eccentricity (see also Fig. 8). Under

scotopic conditions (Fig. 10*B*) the peak of the temporal sensitivity function has been displaced to around 2 Hz and thus it is not a parallel displaced version of the mesopic function (Fig. 10*A*). For this low spatial frequency target, rod sensitivity of the central retina is still almost a factor of 2 better below 5 Hz than that for the peripheral retina. Temporal acuity, which is now around 15 Hz, is again similar for central and peripheral retinal regions. The transfer function still exhibits a bandpass shape under scotopic conditions.

DISCUSSION

The two main conclusions of this study of the spatio-temporal sensitivity of the achromat's retina, are first, that only rod receptors are functioning, and secondly, that the neural connections made by these receptors are identical to those of the normal duplex retina. The first conclusion follows from the finding that sensitivity saturates in a unitary manner across the retina in a way that parallels normal rod saturation (Aguilar & Stiles, 1954; Blakemore & Rushton, 1965; Conner, 1982; Nunn & Baylor, 1982; Baylor, Nunn & Schnapf, 1984). The data of Aguilar & Stiles (1954) suggest an upper limit for rod saturation of between 2000 and 5000 T_s. This is in accord with previous results from the achromat for central vision (Hess & Nordby, 1986*a*), namely 1800 T_s, as well as those presented here for the peripheral retina. This finding is sufficient to reject the hypothesis put forward by Alpern *et al.* (1960) of there being 'high-intensity receptors' present in the retina of this achromat. This conclusion also receives support from measurements of peripheral dark adaptation and spectral sensitivity (Nordby *et al.* 1984), and the Stiles–Crawford effect (Sharpe & Nordby, 1984) in this achromat.

The second conclusion follows from the finding that spatio-temporal sensitivity across the retina is matched for normal and achromat within the scotopic region. This suggests that the post-receptoral neural connections made by rods in the achromat's retina are similar to those in the duplex retina. Both these conclusions support and extend an earlier study on the sensitivity of the central retina of the achromat (Hess & Nordby, 1986*a*). Hence, this achromat is, as far as all the available data is concerned, a rod monochromat in the functional sense of the word. On the available histological evidence one supposes that cone receptors are present in this achromat's retina, be they few in number and anomalous in distribution, but that they contribute no measureable or useful signal to post-receptoral sites. The only finding which appears to run contrary to this involves the lack of coincidence of the spatial acuity of achromat and normal observer at the upper scotopic illuminance. As can be seen in the contrast sensitivity results of Fig. 9, this is in fact not a violation but a consequence of the fact that cones in the normal duplex retina still exert a small influence in this spatial region (around 3–5 cycles/deg) at this upper scotopic illuminance (0·4 T_s). This is because these spatial frequencies correspond to the peak of the spatial sensitivity function for cone-mediated vision. Because sensitivity is best at these frequencies, they are more resistant to reduction in illumination, and a cone-mediated influence can still be seen at the upper scotopic illuminance of 0·4 T_s. This feature of normal duplex function has also been demonstrated using spectral stimuli designed to isolate rod and cone function in the normal retina (D'Zmura &

Lennie, 1984, 1986). It highlights the fact that the changeover from cone to rod vision is spatial frequency as well as illuminance dependent.

Sensitivity of the normal rod pathway

One of the main motivations for wanting to know whether the achromat is a functional rod monochromat is to use this subject to investigate rod sensitivity under mesopic conditions where contrast sensitivity is optimal but where it is most difficult to isolate in the normal duplex retina. These results suggest that when comparing the differential sensitivity of rod and cone mechanisms under mesopic conditions, factors such as the spatial and temporal frequency of the stimulus and retinal eccentricity should be taken into account. The cone mechanism is pre-eminent in sensitivity for stimuli of high spatial and temporal frequencies presented in the centre of the visual field. Until we have comparable results for the cone mechanism alone it is impossible to know whether the coincidence of sensitivities for the achromat and normal observer for peripheral stimuli of low spatial and temporal frequencies is due to equal sensitivities of rod and cone mechanism or to the rod mechanism alone.

The achromat's data allows an estimate of the sensitivity of the rod mechanism of the normal duplex retina under mesopic conditions where it exhibits optimal contrast sensitivity. Mesopic sensitivity of the rod mechanism exhibits a broad peak in the central region of the retina for all spatial and temporal frequencies of stimulation. The slope of the fall-off in sensitivity with retinal eccentricity, which is independent of the spatial or temporal frequency of the stimulus, is approximately 6 dB/10 deg of eccentricity. This dependence differs from that of the cone mechanism under photopic conditions where the fall-off for all spatial frequencies above 1 cycle/deg is comparable only when plotted in terms of relative eccentricity (i.e. in periods of eccentricity). This sensitivity fall-off is approximately 20 dB/60 periods (Robson & Graham, 1981).

The finding that optimal rod sensitivity under mesopic conditions occurs in the centre of the visual field is not at odds with the well-established anatomical finding of at least a 1 deg rod-free area in the centre of the visual field, because the resolution of these measurements across the dimension of eccentricity is not sufficient to detect such a small absolute scotoma. One finding that can be stated with some certainty is that as illuminance is reduced the distribution of sensitivity across the retina changes dramatically for the rod mechanisms. The fall-off in sensitivity initially flattens, and at the lower illuminances there is a significant loss of central sensitivity. In some cases a similar loss can be seen in the far periphery resulting in optimal scotopic sensitivity at the mid-peripheral location (around 10–15 deg).

The spatial and temporal contrast sensitivity results (Figs. 9 and 10) highlight two interesting aspects about the sensitivity of the rod pathway. First, it is commonly believed that under mesopic conditions rod sensitivity is maximal away from the centre of the retina, although this is only seen to be the case under extreme scotopic illumination. Under mesopic conditions rod-mediated sensitivity for all spatio-temporal stimulation is optimal over the central 10 deg of the visual field. Secondly, it is believed that the spatial contrast sensitivity functions for both foveal and peripheral vision changes from a photopic bandpass characteristic to a low-pass characteristic under scotopic conditions (Van Nes & Bouman, 1967; Daitch & Green,

1969). Indeed, a recent study has shown that this changeover occurs within the rod mechanism and is not strictly a rod–cone difference (Hess & Nordby, 1986*a*; see their Fig. 4). In the present study much smaller stimulus fields were used and these results suggest that locally the spatial sensitivity function maintains a bandpass shape and is only reduced in its over-all sensitivity as if determined by a unitary mechanism. This is as true for central as it is for peripheral retinal regions. A similar picture emerges in terms of temporal contrast sensitivity. The results of Conner (1982) suggest that the temporal transfer characteristic changes from bandpass to low pass as illuminance is changed from mesopic to scotopic for the rod mechanism. His results were for large (9 deg), peripheral (16 deg) targets. Similar results have also been obtained for larger fields, centrally fixated (Hess & Nordy, 1986*a*). The present results suggest a different picture for more localized stimuli. The results also show that under both mesopic and scotopic conditions the temporal sensitivity of the peripheral retina is a high-pass version of that of the central retina. The slower dynamics of rod vision at lower light levels is not seen in the receptoral response (B. J. Nunn, personal communication) and must therefore be post-receptoral.

Neural connections subserving rod vision

The primate retina contains ganglion cells which either receive a pure cone input or a mixed rod–cone input. The ganglion cells receiving cone-only input are restricted to the central region of the visual field, and are likely to underlie the larger difference in spatial contrast sensitivity between rod and cone mechanisms for central vision as the spatial frequency is increased. The temporal resolution of rod and cone pathways does not vary as a function of eccentricity and is likely to depend on explanations other than the dynamics of ganglion cells receiving only cone input.

The finding that rod mesopic sensitivity is better in the central region of the retina and falls off monotonically with eccentricity is surprising when one considers how receptor convergence ratio changes with eccentricity. A consideration of the combined data of Österberg (1935) on the distribution of primate rod receptors and that of Perry, Oehler & Cowey (1984) and Perry & Cowey (1984) on the distribution of primate ganglion cells, shows that the combined receptor-to-ganglion cell convergence ratio changes monotonically from around 2 at 1 deg eccentricity to around 40 at 40 deg eccentricity. This feature, combined with the fact that peripheral rods are fatter and may thereby have a more favourable signal-to-noise ratio (larger catchment area per unit synaptic noise), might lead one to expect that rod sensitivity would increase monotonically with retinal eccentricity. Even under mesopic conditions this is not seen as there is a peak in sensitivity at around 10 deg on either side of which sensitivity falls off. Can we understand the mesopic results by considering what happens under scotopic conditions? The most dramatic change that occurs at scotopic illuminances involves sensitivity changes for the rod mechanism in different retinal regions. These changes in sensitivity are largely independent of the spatial and temporal aspects of the stimulus. Previously, owing to the fact that rod and cone vision were compared via a photopic–scotopic comparison, this type of retinal sensitivity profile was thought to be an invariant property of the rod mechanism. The present results suggest that this is a property of the rod mechanism only under scotopic conditions. The fact that these sensitivity gains at parafoveal sites have not

been at the expense of losses in acuity in these regions suggests that a neural reorganization in the extent of receptor convergence has not taken place for the rod mechanism.

This work was supported by an European Science Foundation Twinning Grant. We also acknowledge support from the U.K. Medical Research Council and The Wellcome Trust. R.F.H. is a Wellcome Lecturer.

REFERENCES

AGUILAR, M. & STILES, W. S. (1954). Saturation of the rod mechanism of the retina at high levels of stimulation. *Optica acta* **1**, 59–65.

ALPERN, M., FALLS, H. & LEE, G. (1960). The enigma of typical total monochromacy. *American Journal of Ophthalmology* **50**, 996–1012.

BAYLOR, D. A., NUNN, B. J. & SCHNAPF, J. L. (1984). The photocurrent, noise and spatial sensitivity of rods of the monkey *Macaca fascicularis*. *Journal of Physiology* **357**, 575–607.

BLAKEMORE, C. B. & RUSHTON, W. A. H. (1965). Dark adaptation and increment threshold in a rod monochromat. *Journal of Physiology* **181**, 612–628.

CONNER, J. (1982). The temporal properties of rod vision. *Journal of Physiology* **332**, 139–155.

DAITCH, J. M. & GREEN, D. G. (1969). Contrast sensitivity of the human peripheral retina. *Vision Research* **9**, 947–952.

DAW, N. W. & ENOCH, J. M. (1973). Contrast sensitivity, Westheimer function and Stiles–Crawford effect in a blue cone monochromat. *Vision Research* **13**, 1669–1680.

D'ZMURA, M. & LENNIE, P. (1984). Spatial contrast sensitivities of rods and cones measured concurrently. *Investigative Ophthalmology and Visual Science* **25**, suppl., 53.

D'ZMURA, M. & LENNIE, P. (1986). Shared pathways for rod and cone vision. *Vision Research* **26**, 1273–1280.

FALLS, H. F., WOLTER, J. R. & ALPERN, M. (1965). Typical total monochromacy. *Archives of Ophthalmology* **74**, 610–616.

GALEZOWSKI, X. (1868). *Du Diagnostic des Maladies des Yeux per la Chromatoscopie Retinienne Procede d'une Etude sur Lois Physices et Physiologiques des Coleurs*. Paris: J.-B. Baillière.

GLICKSTEIN, M. & HEATH, G. G. (1975). Receptors in the monochromat eye. *Vision Research* **15**, 633–636.

GREEN, D. G. (1972). Visual acuity in the blue cone monochromat. *Journal of Physiology* **222**, 419–426.

HARRISON, R., HOGGNAGEL, D. & HAYWARD, J. N. (1960). Congenital total color blindness. *Archives of Ophthalmology* **64**, 685–692.

HESS, R. F. & NORDBY, K. (1986*a*). Spatial and temporal limits of vision in the achromat. *Journal of Physiology* **371**, 365–385.

HESS, R. F. & NORDBY, K. (1986*b*). Spatial and temporal properties of human rod vision in the achromat. *Journal of Physiology* **371**, 387–406.

HUDDART, J. (1777). An account of persons who could not distinguish colours. *Philosophical Transactions of the Royal Society B* **67**, 260–265.

LARSEN, H. (1921*a*). Demonstration mikroskopischer Praparate von einem monochromatische Auge. *Klinische Monatsblatter für Augenheilkunde* **67**, 301–302.

LARSEN, H. (1921*b*). Demonstration mikroskopischer Praparate von einem monochromatische Auge. *Ophthalmologica* **46**, 228–229.

LEVITT, H. (1971). Transformed up–down methods in psychophysics. *Journal of the Acoustical Society of America* **49**, 467–477.

NORDBY, K., STABELL, B. & STABELL, U. (1984). Dark-adaptation of the human rod system. *Vision Research* **24**, 841–849.

NUNN, B. J. & BAYLOR, D. A. (1982). Visual transduction in retinal rods of the monkey *Macaca fascicularis*. *Nature* **299**, 726–728.

ÖSTERBERG, G. (1935). Topography of the layer of rods and cones in the human retina. *Acta ophthalmologica*, suppl. **6**, 1–102.

PERRY, V. H. & COWEY, A. (1984). Retinal ganglion cells that project to the superior colliculus and pretectum in the macaque monkey. *Neuroscience* **12**, 1125–1137.

PERRY, V. H., OEHLER, R. & COWEY, A. (1984). Retinal ganglion cells that project to the dorsal lateral geniculate nucleus in the macaque monkey. *Neuroscience* **12**, 1101–1123.

ROBSON, J. G. & GRAHAM, N. (1981). Probability summation and regional variation in contrast sensitivity across the visual field. *Vision Research* **21**, 409–418.

SAKITT, B. (1976). Psychophysical correlates of photoreceptor activity. *Vision Research* **16**, 129–140.

SHARPE, L. T., COLLEWIJN, H. & NORDBY, K. (1986). Fixation, pursuit and optokinetic nystagmus in a complete achromat. *Clinical Vision Sciences* **1**, 39–50.

SHARPE, L. T. & NORDBY, K. (1984). Receptor function and interaction in a rod monochromat. *Perception* **13**, A7–8.

SLOAN, L. L. (1954). Congenital achromatopsia: a report of 19 cases. *Journal of the Optical Society of America* **44**, 117–128.

VAN NES, F. L. & BOUMAN, M. (1967). Spatial modulation transfer in the human eye. *Journal of the Optical Society of America* **57**, 401–406.

VOLKMANN, F. C., RIGGS, L. A., WHITE, K. A. & MOORE, R. K. (1978). Contrast sensitivity during saccadic eye movements. *Vision Research* **8**, 1195–1199.

WALLS, G. L. & HEATH, G. G. (1954). Typical total color blindness reinterpreted. *Acta ophthalmologica* **32** 253–297.