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# HUMAN PHOTOPIC VISION WITH ONLY SHORT WAVELENGTH CONES: POST-RECEPTORAL PROPERTIES

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## SUMMARY

1. Spatial and temporal contrast sensitivities were investigated in two subjects whose photopic vision has been previously shown to be subserved by only short wavelength cones.

2. Spatial contrast sensitivity was uniformly reduced compared with that of the normal trichromatic observer. Peak contrast sensitivity reached 40 which is a factor of 2–3 better than previous estimates and extrapolated acuity was around 15 cycles $deg^{-1}$. Central, non-aliased grating acuity was between 6–9 cycles $deg^{-1}$. This declined with eccentricity such that at 20 deg it was around 1 cycle $deg^{-1}$.

3. The variation in contrast sensitivity across the visual field was measured for a range of different spatial frequencies. It was found to be of the same form as that for the normal trichromat but reduced in overall sensitivity.

4. Temporal contrast sensitivity was measured for two different spatial frequencies and found to exhibit the spatio-temporal covariation which is typical of normal trichromatic vision. Temporal acuity exhibited a strong dependence on illuminance and reached asymptotic values of around 40–45 Hz. While this is more than a factor of two above most previous estimates for the short wavelength receptors of normal vision it agrees with some more recent estimates obtained using a different technique. Temporal resolution was found to be evenly distributed across the visual field.

5. Similarities were found between the post-receptoral properties of these achromats and the properties of the isolated blue mechanism of normal vision and also the properties of normal luminance contrast processing in general. The present results provide an upper bound on the contribution of the short wavelength mechanism to normal vision and also provide a suitable model of its possible contribution to the processing of luminance contrast in the normal visual system.

## INTRODUCTION

Photopic vision in primates is subserved by three different classes of receptors with different peak absorptions in the short, middle and long wavelength regions of the spectrum. Their post-receptoral connections form the basis of at least two

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functionally distinct and possibly anatomically separate pathways which process luminance and colour information. The post-receptoral contribution of the short wavelength-absorbing cones has been singled out for special attention: their distribution is very different from that of the other two classes of cones (Marc & Sperling, 1977; De Monasterio, Schein & McCraine, 1981) and there is debate as to whether they contribute to luminance contrast processing. There is little doubt that short wavelength cones contribute very little if at all to tasks which are associated with a luminous efficiency function ($V\lambda$) such as flicker photometry or judgments of a minimally distinct border (see Boynton, 1979; Mollon, 1982 for further discussion). However, their contribution to other tasks which involve intensity detections or discriminations but do not have a characteristic $V\lambda$ luminous efficiency function is open to question (Guth, Alexander, Chumbly, Gillam & Patterson, 1968; Mollon & Krauskopf, 1973; Foster & Snelgar, 1983; Whittle, 1974; Tansley & Boynton, 1978; Eisner & MacLeod, 1980; Cavanagh, MacLeod & Anstis, 1987; and for a counterview see Marks, 1974; Drum, 1983; Blythe, Bromley, Holliday & Ruddock, 1986).

This issue is complicated by the likelihood, explored in the discussion, that there is more than one type of pathway able to process luminance contrast, namely, achromatic cone-additive pathways and cone-opponent pathways which also respond to luminance contrast. Physiological evidence suggests that at the retinal level short wavelength cones may not provide an input to the achromatic, non-opponent neurones but only to opponent ones (Gouras, 1968; De Monasterio, 1975; Gouras & Zrenner, 1983). Accurate knowledge of the spatial and temporal properties and limitations of the short wavelength mechanism would allow a more comprehensive understanding of its contribution to normal visual function.

The short wavelength (or blue) mechanism refers to psychophysical responses which are mediated by signals originating from short wavelength cones. Although Stiles isolated three different short wavelength mechanisms ($\Pi_1$, $\Pi_2$ and $\Pi_3$) there is evidence to suggest that these are not independent (Pugh & Mollon, 1979).

The post-receptoral properties of the short wavelength mchanism have been investigated in normal vision by various psychophysical isolated procedures along the lines proposed by either Stiles (1939, 1959, 1978) or Rushton, Powell & White (1973). The general picture which has emerged is one of a system with a high degree of spatial summation (Brindley, 1954), low spatial acuity (Brindley, 1954; Green, 1968; Kelly, 1973; Cavonius & Estevez, 1975; Williams & Collier, 1983), low temporal resolution (Green, 1969; Kelly, 1974; Wisowaty & Boynton, 1980) and low overall sensitivity (Green, 1968; Cavonius & Estevez, 1975). Results of a similar kind (Green, 1972; Daw & Enoch, 1973) have been obtained by studying the visual properties of a group of achromats (of the complete and atypical variety) in which it is thought that only short wavelength cones subserve photopic function (Blackwell & Blackwell, 1957; Daw & Enoch, 1973; Smith, Pokorny, Delleman, Cozijnsen, Houtman & Went, 1983).

In this study we continue this approach by investigating the spatial and temporal properties of two atypical achromats of the complete variety whose receptoral properties suggest that they are functionally blue mono-cone monochromats (Hess, Mullen, Sharp & Zrenner, 1989). We address three questions concerning the properties of the short wavelength mechanism which remain unresolved by the

psychophysical isolation procedures applied to normal vision. Firstly, what is the absolute spatio-temporal contrast sensitivity of the isolated blue mechanism? This cannot be obtained by the two-colour threshold technique of Stiles or its variants because the contrast of the stimulus to the short wavelength-detecting mechanisms is not accurately known (see Green, 1968). Secondly, what is the temporal resolution of the blue mechanism? Recent findings for normal vision have suggested that the temporal acuity of the short wavelength receptors is similar to that of the middle and long wavelength receptors (Stockman, MacLeod & De Priest, 1987). Thirdly, how does spatio-temporal sensitivity vary across the visual field? There is little information available on this from studies of normal vision yet it directly bears on how the connections from short wavelength cones, whose distribution is now known (Marc & Sperling, 1977; De Monasterio *et al.* 1981), converge on post-receptoral neurones.

The results suggest that the short wavelength mechanism can obtain contrast sensitivities as high as 40 and temporal resolution as high as 43 Hz and that its regional spatio-temporal variation in contrast sensitivity is similar to that of normal luminance contrast sensitivity. These results set an upper limit on the contribution of the short wavelength mechanism to normal visual processes and provide a suitable model of its potential contribution to luminance contrast processing in normal vision.

## METHODS

*Central field contrast sensitivity.* All stimuli were digitally generated and responses collected by a PDP11/34A laboratory computer connected to a Joyce display screen via a CED 502 interface. The Joyce screen had a P36 phosphor, a frame refresh rate of 100 Hz for spatial measurements and 200 Hz for temporal measurements, a screen size of $20 \times 30$ cm and a mean photopic luminance of 420 cd $m^{-2}$. The luminance distribution of the stimulus is given 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 $L_0$ is the mean luminance, $C$ is the contrast variable, G is the spread function and $F_x$ and $F_t$ are the spatial and temporal frequencies. The window function is given by:

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

where $S_x$, $S_y$ and $S_t$ are the spread parameters of horizontal, vertical and time Gaussians. The spread parameter $S$ is the distance or time over which the Gaussian falls to 1/e of its peak value. From all central field measurements $S_x = S_y = 4$ deg. The time spread ($S_t$) was 250 ms, with a total stimulus duration of $4\,S_t$. The spatial contrast sensitivity measurements were done with 1 Hz sinusoidally contrast-reversing stimuli. Contrast was changed in steps of 1/4 dB using digital attenuators.

*Peripheral field contrast sensitivity.* In order to compare the decline in sensitivity for a range of different spatial frequencies, all stimuli had a horizontal and vertical spread of a fixed number of periods: $S_x = S_y = 3$ periods (Howell & Hess, 1978; Robson & Graham, 1981). The temporal spread remained at 250 ms. Eccentricity is plotted in degrees relative to fixation. For subject S. B. fixation was central whereas for P.S. it was vertically misaligned by 2 deg (see Fig. 1 of Hess *et al.* 1989).

*Spatial acuity.* Spacial acuity was measured in two different ways. In the first method the task was to detect which of two temporal intervals contained a high frequency grating (98% contrast). The other interval contained a mean luminance. The stimulus was either oriented 10 deg to the right or 10 deg to the left of the vertical. The stimulus was a sinewave grating contained within a

circular field with a diameter of 2·2 deg. This gave two measures of *detection acuity* one for each orientation. In the second method each temporal interval contained the same high frequency, high contrast grating but in one it was oriented 10 deg to the right of vertical whereas in the other interval it was oriented 10 deg to the left of vertical. The subjects' task was to identify which interval contained the stimulus of a particular orientation. This gave a measure of *discrimination acuity*. In all other ways the stimulus parameters and methods used were identical for both measurements.

*Temporal acuity versus illuminance.* In these measurements we were keen to extend both the temporal resolution and illuminance ranges. A Joyce screen with a P4 phosphor was used and the frame rate was increased to 254 Hz. The pupil was fixed and dilated by prior instillation of 1 or 2 drops of 1% tropacamide and measured using the pupil measurement attachment of a Goldman perimeter before and after each experimental session. The modulation depth was 70% and the stimulus was a 2-D Gaussian envelope of spread parameter 2·25 deg contained within the central region of the screen. The surrounding region was lit to approximately half that of the mean luminance of the screen. Illuminance was changed by means of neutral density filters fitted into light-tight goggles which contained a light-tight air inlet to stop 'fogging' of the goggles. Two methods were used: a two-temporal-alternative force-choice procedure and a method of adjustment. Both methods gave essentially similar results. The results obtained with the two-alternative forced-choice procedure using a staircase method are displayed.

*General procedures.* Thresholds were measured using a two-temporal forced-choice procedure driven by an interleaved staircase procedure from which the 83% threshold was derived. The subjects responded via the appropriate button and feedback was given to indicate an incorrect response. Thresholds were obtained from the mean of ten reversals once the staircase had stabilized.

For all the measurements of spatial contrast sensitivity and measurements of temporal contrast sensitivity in the central field natural pupils were used and their size measured under the relevant experimental condition. For the measurement of temporal acuity at different illuminances and eccentricities, the pupil was dilated and measured before and after each experimental run. The subjects viewed the stimulus monocularly with their right eye at a distance which varied between 57 cm and 4 m. The room was artificially lit and a fixation mark was provided. Each subject received enough practice to ensure that all of the subsequent results correspond to asymptotic levels of performance.

*Calibration.* The linearity and contrast of the two different Joyce screens (P4 and P36 phosphors) were calibrated regularly throughout these experiments using a United Detector Technology photometer. The spectral emission of the screen with the P4 phosphor was measured using a scanning spectroradiometer which had been previously calibrated against a standard light from the National Physical Laboratory. To obtain a comparison of the luminance of this screen to the normal trichromat and the blue-cone monochromats its spectrum was multiplied by the photopic $V\lambda$ curve obtained by adding the L- and M-cone fundamentals of Smith & Pokorny (1975) and then integrating this response. The 'luminance' to the S cones was obtained by multiplying the screen's emission spectrum by the S-cone fundamental with the relative sensitivity adjusted to equal that of the summed L- and M-cone sensitivities adjusted to equal that of the summed L- and M-cone sensitivities at 400 nm (Smith & Pokorny, 1975) and was found to be 1·5 log units lower. For the photopic, trichromatic system this measurement provided values which matched others that we had obtained using the UDT photometer. The luminance of the P36 screen was measured with the UDT photometer. To obtain the 'luminance' of the green (P36) screen to the S cones we asked the two achromats to match it to the white P4 screen, and it was judged to be 0·25 log units dimmer than the white screen.

*Subjects.* Two achromats of the typical and complete variety were used. The results in the preceding paper show that for a variety of retinal loci the vision of these subjects at photopic levels is mediated by only short wavelength-absorbing photoreceptors whose spectral response is similar to that of the normal eye. Thus they are functionally blue mono-cone monochromats. Their fixation is steady, and central for S.B. whereas for P.S. there is a vertical misalignment of 2 deg (see Fig. 1 of Hess *et al.* 1989).

The normal trichromatic results were obtained on laboratory personnel whose history showed no previous ocular or cortical pathology. All subjects were optimally corrected for the viewing distances using both objective and subjective means.

## RESULTS

### *Spatial sensitivity*

The spatial sensitivities of the central retina of the two blue mono-cone monochromats are displayed in Fig. 1. The stimulus is a Gabor function with a 4 deg

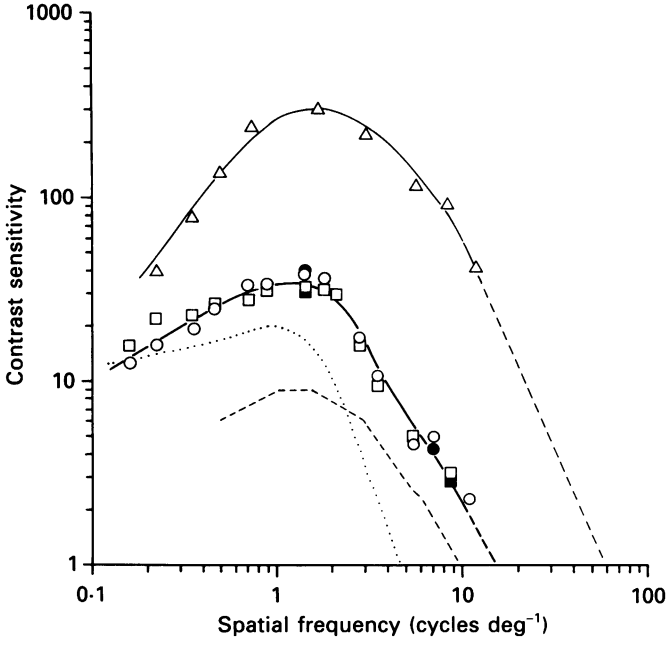


Fig. 1. Spatial contrast sensitivity functions are displayed for the two monochromats and for a normal trichromat. Contrast sensitivity is plotted against spatial frequency for 1 Hz contrast-reversing sinewave grating. The filled symbols represent sensitivity measured at a higher mean luminance (see text). The dashed and dotted curves represent similar measurements by Green (1972) and Daw & Enoch (1973) respectively. △, trichromat; ○, S.B.; □, P.S.

spread parameter (see Methods). It is sinusoidally phase reversed in contrast at 1 Hz and modulated about a mean luminance of 418 cd $m^{-2}$. The mean retinal illuminance is within the range of rod saturation measured under comparable conditions (Hess & Nordby, 1986) hence these results do not contain a contribution from rod photoreceptors at any spatial frequency. Contrast sensitivity is plotted as a function of spatial frequency and the sensitivity of the monochromats (○, □) is compared with that of a normal trichromat (△).

The results for the two monochromats are very similar and can be adequately described by one curve. This curve has typical bandpass characteristics: its peak is located at 1–2 cycles $deg^{-1}$ with a maximum contrast sensitivity of between 30–40. Spatial acuity obtained from extrapolation of the high frequency limb is around 15 cycles $deg^{-1}$. This sensitivity curve differs from that found in the normal trichromat in two main ways. Contrast sensitivity is reduced by an order of magnitude and the low spatial frequency decline in sensitivity appears to be

shallower since its slope is close to unity for the normal trichromat (see Howell & Hess, 1978) and close to 0·5 for the monochromats.

Previous estimates of the spatial sensitivity of the blue mono-cone monochromats are illustrated by the dashed (Green, 1972) and dotted curves (Daw & Enoch, 1973). They are similar to the present results in that the spatial position of optimum contrast sensitivity is the same and so is the rather shallow low spatial frequency decline. However they differ from the present results in their absolute contrast sensitivity. This is likely to be explained by individual differences in experimental conditions rather than by differences in the sensitivity of blue mono-cone monochromats: Green's (1972) measurements were for a stimulus of smaller angular extent and lower luminance whereas Daw & Enoch (1973) measured sensitivity at a 5 deg eccentric locus.

We calculate that the luminance of the P36 display screen was a factor of 1·50 log units less intense to the short wavelength receptors alone (see Methods) and so it is possible that these contrast sensitivities (Fig. 1) were limited by the mean luminance at which they were measured. We assessed this in two different ways. Firstly, we made measurements of sensitivity for each monochromat for a mid-spatial frequency and a high frequency (a factor of 2 within the resolution limit) at a mean luminance almost a factor of 2 higher. This was achieved by using a Joyce screen with a P4 phosphor which provided a greater quantum catch to the short wavelength receptors (see Methods). These measurements are plotted as filled symbols in Fig. 1 and it is clear that contrast sensitivity for either spatial frequency is not significantly improved.

Our second approach was to measure the relationship between contrast sensitivity and mean retinal illuminance. Natural pupils were used so as to optimize optical quality and their diameter was 2 mm for P.S. and 2·5 mm for S.B. Their size did not significantly alter over the photopic range investigated. A high spatial frequency was used since luminance-dependent effects should be best revealed in this range under photopic conditions (Van Nes & Bouman, 1967). The results are displayed in Fig. 2. The vertical dashed line represents the illuminance of the screen with the P36 phosphor with which the initial measurements reported in Fig. 1 (open symbols) were obtained. These results show that contrast sensitivity even at this high spatial frequency is in the Weber region and remains constant with illuminance to a level a log unit lower than that used to obtain the results displayed in Fig. 1 and all subsequent spatial results. Thus none of the spatial measurements to be reported in this section are limited by the mean luminance of our stimulus.

In order to understand how spatial sensitivity varies across the visual field for the blue mono-cone monochromat we measured contrast sensitivity for a range of different spatial frequencies and at a number of retinal eccentricities along the horizontal meridian of the nasal field. Each stimulus was well localized within a 2-D Gaussian patch and in order to compare the results of different stimuli their spatial and orientational bandwidth was held constant with a spread parameter of three periods. Thus the absolute size of the stimulus patch varied inversely with its peak frequency (see Howell & Hess, 1978 for justification). The results for a normal trichromat (*A*) and for the two monochromats (*B* and *C*) are displayed in Fig. 3. Contrast sensitivity is plotted against eccentricity in degrees for different spatial

frequencies. The stimulus was sinusoidally reversing in contrast at 1 Hz and presented within a Gaussian time envelope whose spread parameter was 250 ms. Zero on the abscissa refers to natural fixation which was central for S.B. but vertically misaligned by 2 deg for P.S. (Hess *et al.* 1989). The mean illuminance corresponds to

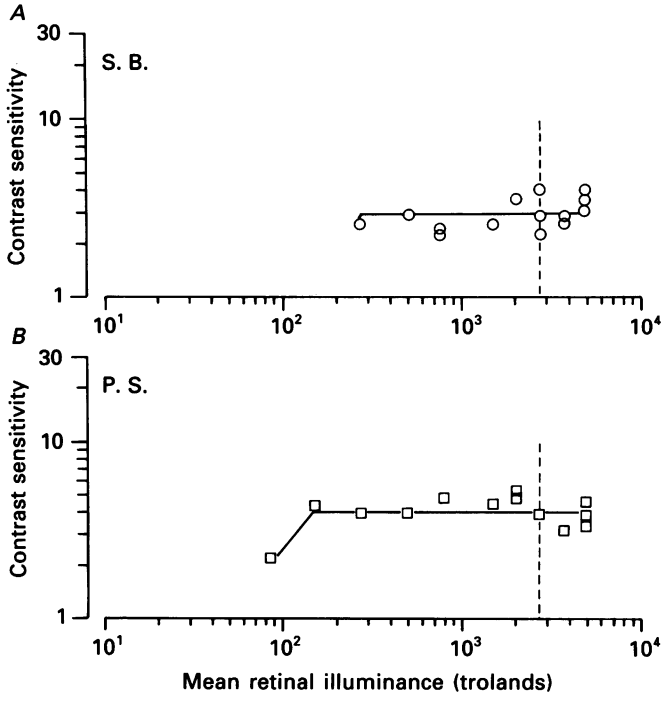


Fig. 2. The relationship between contrast sensitivity and mean retinal illumination is displayed for the two monochromats for a relatively high spatial frequency of 7·6 cycles $deg^{-1}$. The vertical dashed line represents the mean illuminance at which the measurements of Fig. 1 (open symbols) were made.

the vertical dashed line of Fig. 2 and is well above rod saturation. The rate of decline in contrast sensitivity across the visual field depends on the spatial frequency for both the trichromat and achromat, but the main difference between them is the higher absolute sensitivity of the trichromat for all spatial frequencies which extends to all eccentric locations. Thus, contrast sensitivity at any spatial frequency declines at the same rate with retinal eccentricity for both the trichromat and monochromat.

This relationship is more clearly shown in Fig. 4 where the ratio of the contrast sensitivity decline of the trichromat and monochromat, from the results of Fig. 3, is plotted against test spatial frequency. This ratio does not change significantly from unity over the spatial frequency range investigated. The slopes for P.S. have been derived without taking into account the sensitivity measurement at zero eccentricity on this figure owing to the finding that sensitivity is reduced here. Since this observation in itself is interesting we further explored the regional distribution of this small but consistent loss of sensitivity by measuring sensitivity in a horizontal and vertical transection through the anatomical fovea. We were especially interested to

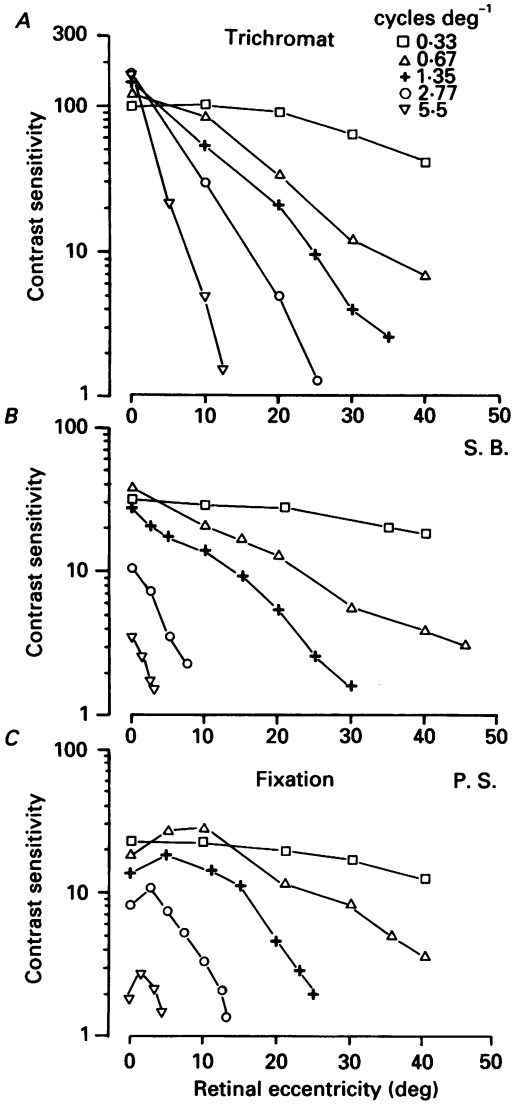


Fig. 3. The regional distribution of spatial contrast sensitivity is shown for trichromat (*A*) and monochromats (*B* and *C*). Contrast sensitivity is plotted against eccentricity (deg) with spatial frequency as a parameter.

know whether sensitivity at the anatomical fovea, which was not tested in the results of Fig. 3, was better than that of the eccentric region (2 deg vertical eccentric fixation) used for his natural fixation.

These results are displayed in Fig. 5 where sensitivity is measured for P.S. for a 2·7 cycle deg$^{-1}$ stimulus along the vertical (*A*) and horizontal (*B*) meridian (see inset for their relationship to the eccentric fixation of this monochromat). Contrast sensitivity was slightly better at the eccentric fixation point than at the anatomical

fovea. Best sensitivity was obtained in an oval region extending obliquely through the natural fixation point.

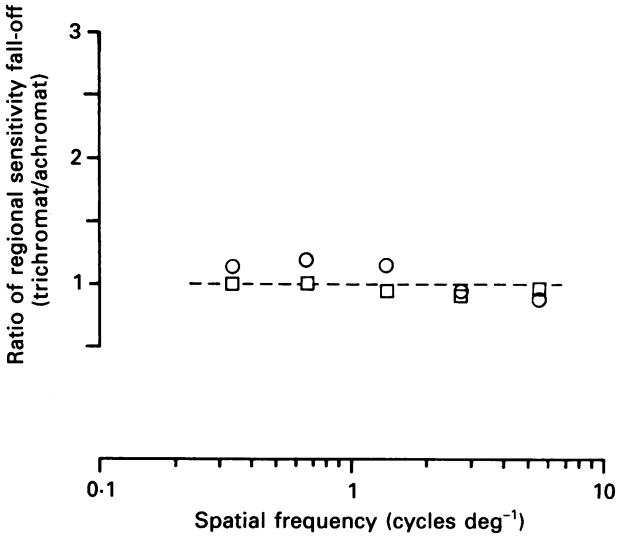


Fig. 4. The ratio of the regional sensitivity fall-off of trichromat and monochromat is compared across spatial frequency for the results of Fig. 3. The ratio is close to unity across the spatial frequency range investigated, indicating that apart from a sensitivity scaling parameter the results in Fig. 3 are similar for trichromat and monochromat. ○, S.B.; □, P.S.

*Spatial acuity*

Two different methods were used to measure spatial acuity. In the first experiment, termed detection acuity, the subject was forced to choose which of two temporal presentations contained a stimulus. The stimulus was a high spatial frequency sinewave grating of 98% contrast oriented either 10 deg to the right of vertical or 10 deg to the left of vertical. The other presentation of the pair was a uniform field of the same space-averaged luminance. This corresponds to the vertical arrow in Fig. 2 which is well above rod saturation. Detection acuity was measured for each of these stimulus orientations using a standard staircase procedure. In the second experiment, termed discrimination acuity, both orientations of grating were presented, one occurring in each interval. The subject chose which temporal interval contained the grating of a particular orientation. For both methods the spatial frequency of the stimulus (or stimuli) was varied between trials. The field was circular and 2·2 deg in diameter. These two methods were used so that any artificial elevation of acuity by spatial aliasing could be measured (see Williams & Collier, 1983). This follows from the fact that only the detection acuity measurement are elevated by aliasing.

The results are displayed in Fig. 6. In this figure spatial acuity (cycles deg$^{-1}$) is plotted against retinal eccentricity (deg) for each acuity measure. Detection acuity is given by open symbols and discrimination acuity by filled symbols. Zero retinal

eccentricity refers to the point of natural fixation. Since monochromat S.B. had central fixation and monochromat P.S. had a 2 deg vertical eccentric fixation we first investigated whether the region of natural fixation exhibited best acuity. These results are shown in the figure inset. For both P.S. and S.B. the region of natural fixation corresponded to the region of best acuity.

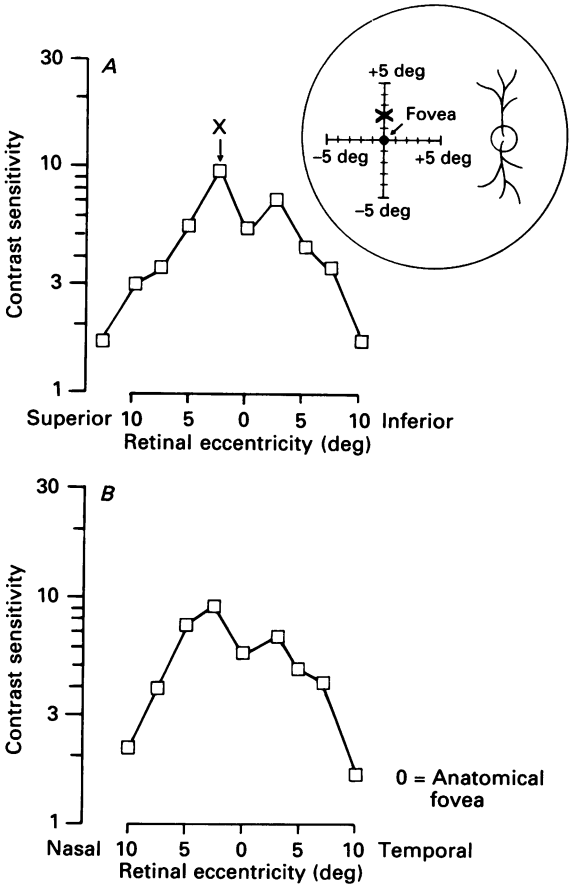


Fig. 5. The regional depression of spatial sensitivity for monochromat P.S. in Fig. 3*C* is further investigated by measuring sensitivity profiles along the vertical (*A*) and horizontal (*B*) meridian centred on the anatomical fovea. Monochromat P.S. has a 2 deg vertical misalignment of fixation. Sensitivity is reduced at the anatomical fovea. ×, natural fixation; 0, anatomical fovea.

For the main experiment the more expected result was obtained from monochromat P.S. (*B*) since his detection acuity for central vision was higher, by about a factor of 2, than his discrimination acuity. This difference can be explained by spatial aliasing occurring because of the sparse distribution of the short wavelength receptors (Marc & Sperling, 1977; De Monasterio *et al.* 1981). At these spatial frequencies the target was only seen as a 'bright shimmer' which enabled performance on the detection task to be elevated. This difference between the two acuity measures decreases with eccentricity since detection acuity shows a more

rapid decline over the central 15 deg than does discrimination acuity. The perception of shimmer was not seen beyond 15 deg eccentricity.

The results of monochromat S.B. show only a small effect of aliasing for central vision and this corresponded to only a very narrow spatial range over which the high

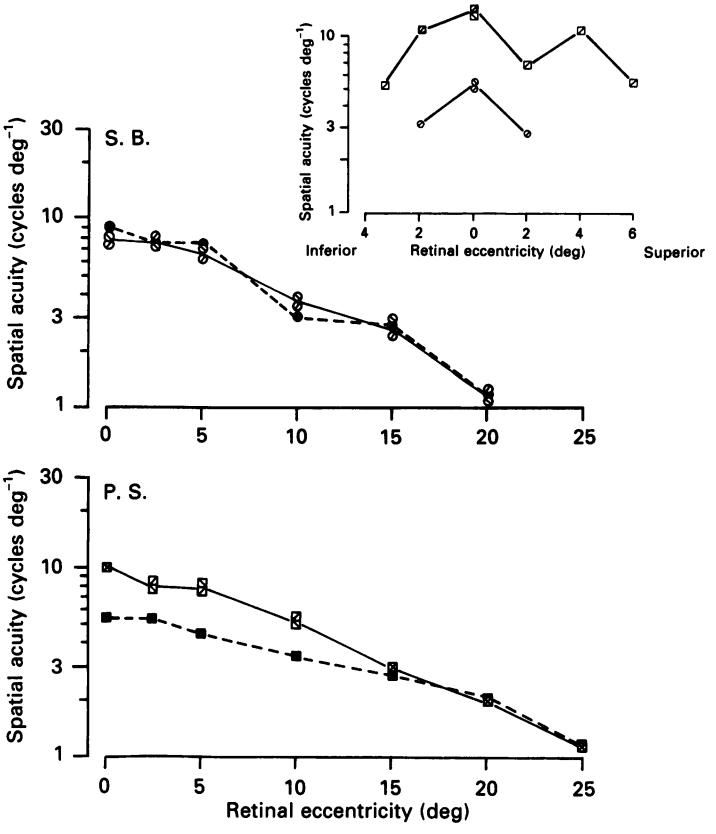


Fig. 6. Grating acuity is measured across retinal eccentricity for the two monochromats. Aliased acuities were estimated using a two-alternative forced-choice detection task (open symbols with the bar indicating the orientation of the detected grating, 10 deg to the left or right of vertical) whereas true unaliased or resolution acuities were measured using a two-alternative forced-choice discrimination task (filled symbols). Monochromat P.S. exhibited spatial aliasing out to 10 deg of eccentricity. The field size was 2·2 deg in diameter. The results in the inset show that best spatial acuity was obtained at the region of natural fixation (0 degrees) for both monochromats. ○, S.B.; □, P.S.

frequency grating was seen as a 'bright shimmer'. Compared with the results of P.S. the central discrimination acuity for S.B. was elevated. It should be noted that the presentation of two stimuli per trial (for the discrimination measure) as compared with one stimulus per trial (for the detection measure) affords a probabilistic advantage to the discrimination measure. We calculated that this is producing 15% higher acuities for the discrimination task. This difference is acting to diminish the reported separation between the aliased and non-aliased acuities.

There is likely to be a differential effect on field size on these two acuity measures.

Since spatial summation is larger for the aliased lower frequency components, detection acuity is more likely to increase with field size (see, for example, Howell & Hess, 1978). We investigated the effect of field size on central acuity using these two methods and results are shown in Fig. 7.

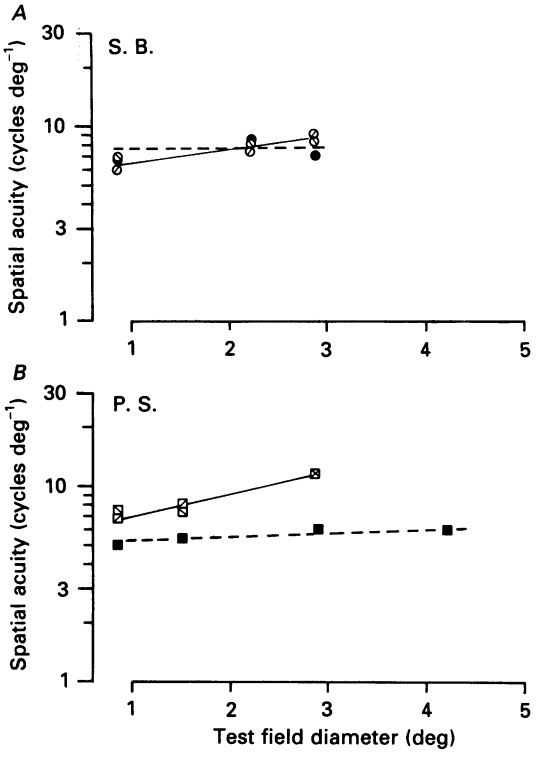


Fig. 7. The effect of the diameter of the stimulus field on the two acuity measures is shown (symbols as for Fig. 6). The aliased acuity depends on the field size whereas the resolution acuity does not. The results for the two monochromats are shown. Only monochromat P.S. exhibited a clear aliasing effect (see text).

Again monochromat P.S. whose results showed the effects of aliasing for the small field size also shows a rise in detection acuity as a function of field size. Detection acuity rose to around 12 cycles deg$^{-1}$ for a 3 deg diameter field whereas discrimination acuity remained constant at 5–6 cycles deg$^{-1}$. The results for monochromat S.B. show a similar function for discrimination acuity but a much flatter detection function. For example, for a 3 deg diameter field size discrimination acuity was around 7 cycles deg$^{-1}$ and detection acuity was 9 cycles deg$^{-1}$. All spatial frequencies between these two values were seen to 'shimmer' but the effect was much smaller than that seen in the results of P.S. From these results we conclude that the best *resolution* acuity (discrimination acuity) of the blue mono-cone monochromat is between 6–9 cycles deg$^{-1}$ and that aliasing effects can artificially elevate this acuity to an extent which depends on the field size under which it is measured.

*Temporal sensitivity*

Measurements of temporal sensitivity for a low spatial frequency Gabor function (peak at 0·16 cycles deg$^{-1}$, spread = 4 deg) are given in Fig. 8. In this figure, contrast sensitivity is plotted against temporal frequency of sinusoidal contrast reversal for

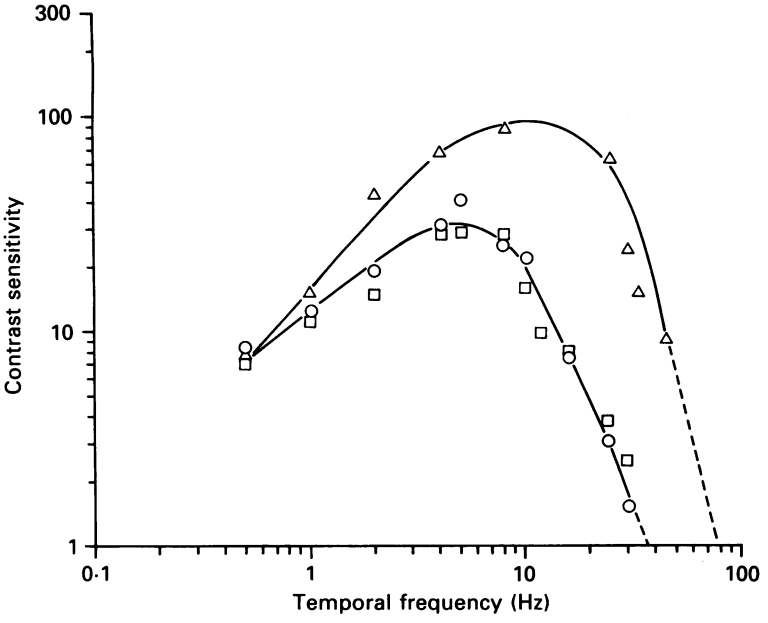


Fig. 8. Temporal contrast sensitivity function for a normal trichromat and two monochromats for a low spatial frequency stimulus. Contrast sensitivity is plotted against the temporal frequency of sinusoidal modulation. Trichromat and monochromat exhibit bandpass functions. △, trichromat; ○, S.B.; □, P.S.

the trichromat and the two monochromats. These results were obtained using a screen (P36 phosphor) with a photopic luminance of 595 cd m$^{-1}$ which is above rod saturation. The results for the two monochromats are similar and adequately described by a single function with a bandpass characteristic. This differs from that found for the normal trichromat in that the absolute sensitivity is reduced, the peak is displaced to lower temporal frequencies, and the decline in sensitivity to low temporal frequencies is shallower. Temporal acuity, obtained from extrapolation, is around 35 Hz and peak contrast sensitivity is round 40.

Measurements obtained for stimuli with a Gabor function and a peak spatial frequency of 1·46 cycles deg$^{-1}$ are shown in Fig. 9. For both monochromats and trichromat the temporal contrast sensitivity function at this spatial frequency is of a low-pass form. The results for both monochromats are essentially the same with a peak sensitivity of around 40 and an extrapolated acuity of 30 Hz. These results for the monochromat cannot be described simply in terms of a change in sensitivity because the curve which best fits the trichromats' results when displaced vertically is not an adequate fit to the monochromats' data.

In order to ascertain whether these temporal acuities were limited by the reduced brightness of the stimulus to the monochromats we measured temporal acuity as a function of mean illuminance for a stimulus with a 2-D Gaussian envelope of spread parameter 2·25 deg (see Methods). The results are displayed in Fig. 10 where

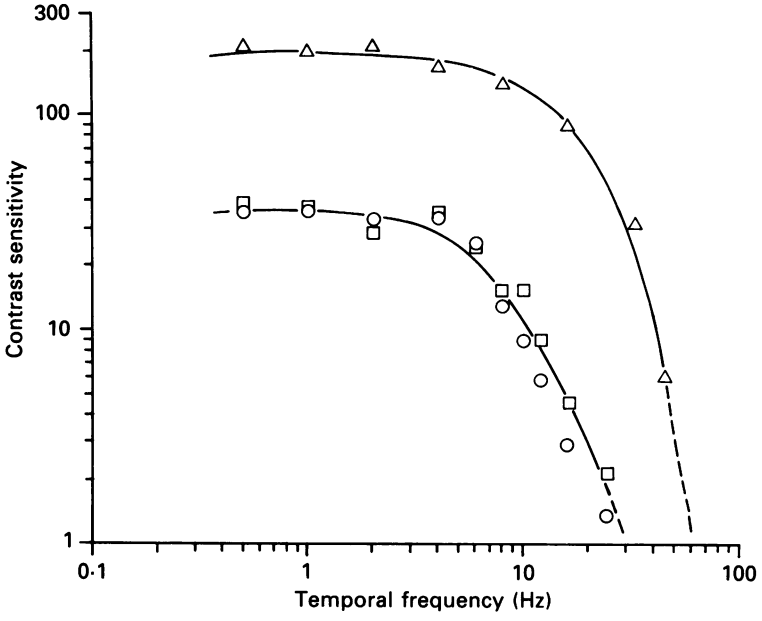


Fig. 9. Temporal contrast sensitivity functions for a normal trichromat and two monochromats for a mid-spatial frequency stimulus. Contrast sensitivity is plotted against the temporal frequency of sinusoidal modulation. Trichromat and monochromats exhibit a low-pass function. Symbols as for Fig. 8.

temporal acuity is plotted against the mean illuminance of the stimulus (photopic trolands) for monochromat P.S. and a normal trichromat. The data for the normal trichromat show the expected biphasic curve. This was originally thought to reflect a division between rod and cone function (Hecht & Schlaer, 1936) but is now thought to be solely a property of the normal rod mechanism (Hecht, Schlaer, Smith, Haig & Peskin, 1948; Conner, 1982; Hess & Nordby, 1986). The transition from rod-mediated to cone-mediated function occurs at around 30 Hz in normal vision (Conner, 1982).

The data for the blue mono-cone monochromat are best described by a triphasic curve. At scotopic illuminances, temporal resolution is similar to that of the trichromat and remains so up to mesopic illuminances where resolution reaches a temporal plateau at around 29 Hz. Thereafter a second plateau is exhibited at around 43 Hz. These results are consistent with the idea that the two plateaux in the mesopic and scotopic regions are due to normal rod function and the photopic plateau is a property of the short wavelength mechanism. For comparison, the response of the rod monochromat is shown by the dotted curve. These latter results were obtained under similar, but not identical, conditions since a larger stimulus field

size was used (Hess & Nordby, 1986). The results suggest that the short wavelength cones and their post-receptoral pathways are at least capable of transmitting temporal frequencies of between 40 and 45 Hz at photopic mean illuminances.

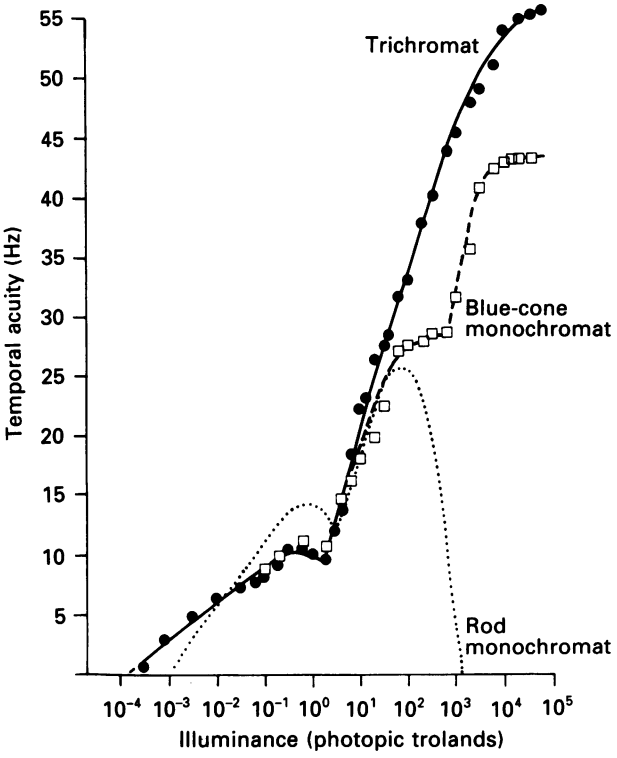


Fig. 10. The relationship between temporal acuity and mean retinal illuminance for normal trichromat (●) and blue mono-cone monochromat (□). The dashed curves represent the results for the rod monochromat from Hess & Nordby (1986) replotted in terms of photopic trolands.

In Fig. 11, the variation of temporal acuity across the visual field is shown for a trichromat and the two blue mono-cone monochromats. Temporal acuity (Hz) is plotted against retinal eccentricity along the horizontal meridian (temporal retina) for the same stimulus as was used to obtain the results of Fig. 10. Data for the trichromat were obtained for illuminances a log unit lower in order to control for the fact that the illuminance to the monochromats was reduced by around 1·5 log units (see Methods). At high photopic illuminances which are above rod saturation, temporal acuity for the trichromat increases gradually with eccentricity around 50 Hz at the fovea to 65 Hz at 40 deg of eccentricity. At lower photopic illuminances temporal acuity is independent or slightly decreases with eccentricity. The temporal acuity profiles for the two monochromats (one of which extends through the anatomical fovea) show an essentially similar result. Temporal acuity is relatively independent of eccentricity for this stimulus. The slightly greater decline in temporal acuity with increasing eccentricity in the monochromat may be attributable to the

fact that the illuminance was still 0·5 log units less to the monochromats than to the trichromats.

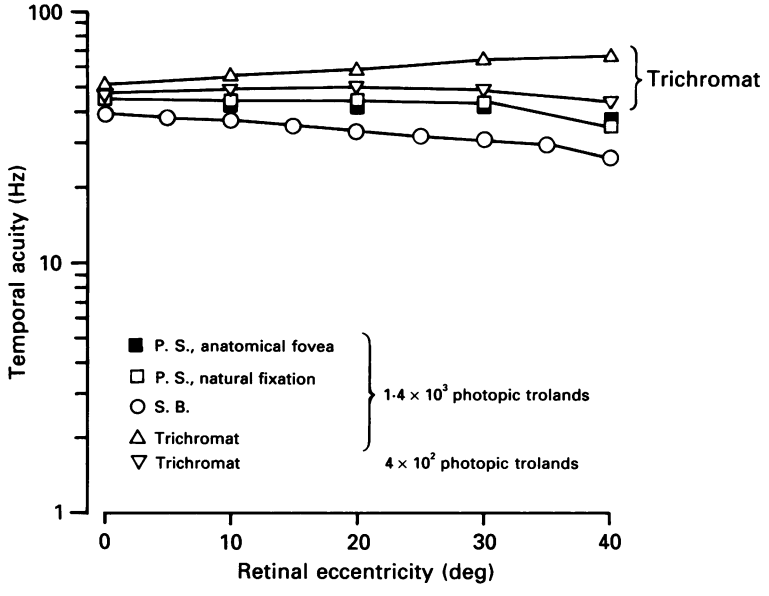


Fig. 11. The regional distribution of temporal resolution is displayed for the normal trichromat and two monochromats. Temporal acuity (Hz) is plotted against eccentricity (deg) across the horizontal retinal meridian. Results are given for the trichromat for two different retinal illuminances to gauge how the reduced retinal illuminances to the short wavelength receptors might affect the results. Under conditions of comparable retinal illumination the temporal acuity distribution is similar for trichromat and monochromat.

## DISCUSSION

The present results have outlined how spatial and temporal contrast sensitivity varies across the retina of the blue mono-cone monochromat for a stimulus whose mean luminance is above rod saturation, and as such they supply upper estimates for some of the key properties of the short wavelength cones and bear directly on the post-receptoral connections made by these receptors in the eyes of these rare individuals. However, can these results help our understanding of the post-receptoral connections made by the short wavelength receptors in the eyes of normal individuals? In other words, can the blue mono-cone monochromat serve as a model for the contribution of the short wavelength cones to normal vision? In the main the answer has to be no, because the short wavelength cones are known to contribute to cone-opponent pathways in the normal retina which are not present in the monochromat. Nevertheless, there is still the question raised in the Introduction as to whether short wavelength cones in the normal retina can contribute to the detection of luminance contrast.

The evidence suggests that short wavelength cones do not contribute to achromatic, cone-additive pathways in the normal retina but only to cone-opponent, chromatic pathways (see Introduction). However, this in itself does not exclude the contribution of short wavelength cones to the detection of luminance contrast, since the cone-opponent pathways are also potentially able to mediate its detection. Firstly, under conditions of strong chromatic adaptation to medium and long wavelength light the cone-opponent mode of the response of the short wavelength chromatic pathways is diminished (Pugh & Mollon, 1979; Polden & Mollon, 1980). Adaptation within the opponent, or second site, means that the psychophysical response becomes dominated solely by the activity of short wavelength cones and so will have non-opponent characteristics. It is likely that the strong adapting fields typically used to isolate the blue mechanism in normal subjects are eliciting just such a non-opponent mode of response from the short wavelength chromatic pathways and in this mode the detection of luminance contrast in the stimulus will be favoured.

Secondly, it has been described how cone-opponent pathways in general are able to perform a 'double duty' since their response is governed by both the luminance and the colour contrast in a stimulus (Ingling & Drum, 1973; Ingling & Martinez, 1983). Thus, any arrangement of the short wavelength chromatic mechanisms into spectrally and spatially opponent pathways is likely to provide both a cone-additive (non-opponent) and a cone-subtractive (opponent) component to their response.

For both of these reasons, the short wavelength chromatic mechanisms, by acting in a non-opponent mode, are likely to contribute to the detection of luminance contrast in normal subjects, especially when the blue mechanism is in a state of isolation. In these cases the monochromats might serve as an excellent model of the properties of non-opponent modes of processing mediated by short wavelength cones in the normal subject. To explore this possibility further we ask two related questions: 'How similar are the properties of the blue mono-cone monochromat and the isolated blue mechanism of normal vision?' and 'How similar are the post-receptoral properties of the monochromat and the properties of the normal processing of luminance contrast in general?'

*Properties of monochromat and isolated blue mechanism of normal vision*

Although the information which is available on the properties of the isolated short wavelength mechanism of normal vision is not as extensive as one would like there is generally good agreement between these and the present results. Firstly, the spatial contrast sensitivity function of the isolated short wavelength mechanism using an exchange method (Cavonius & Estevez, 1975) or a two-colour incremental threshold technique (Green, 1968) is identical in its shape and its spatial position to that reported here for the blue mono-cone monochromat. This comparison is shown in Fig. 12.

Secondly, it is known that the central acuity of the short wavelength mechanism can be artifically elevated by aliasing at the level of the receptor mosaic. Williams & Collier (1983) report unaliased acuities of the central field for the normal short wavelength mechanism to be around 10–15 cycles $deg^{-1}$ and aliased acuities to extent up to 25–30 cycles $deg^{-1}$. Our results suggest that the unaliased acuity of the central

field for the blue mono-cone monochromat is around 6–9 cycles deg$^{-1}$ whereas aliased acuities reach 12 cycles deg$^{-1}$. This latter estimate was shown to depend on the field size and if we extrapolate our estimates to the larger field size used by Williams & Collier (1983) in their study of normal vision we would predict similar values, namely around 30 cycles deg$^{-1}$.

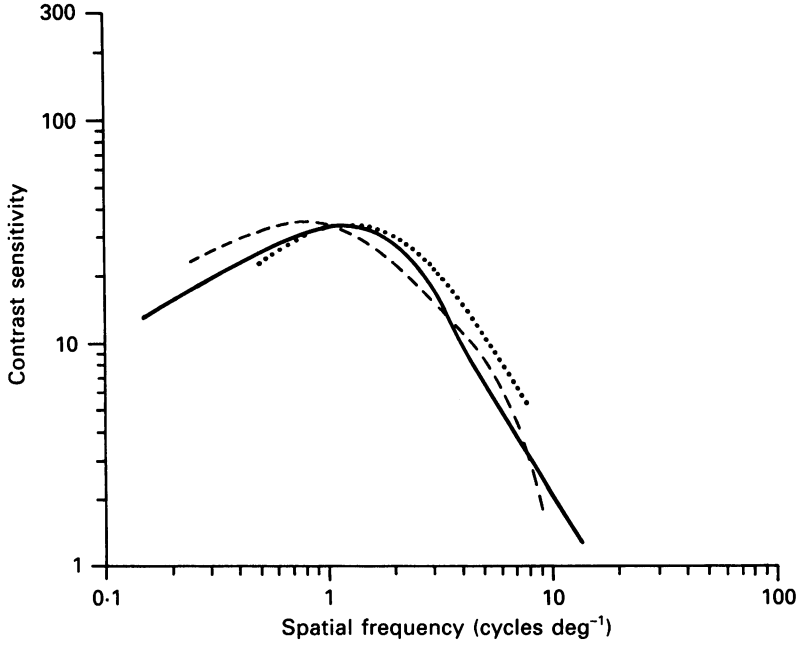


Fig. 12. The averaged spatial contrast sensitivity results from the present study for the blue mono-cone monochromats (continuous curve) is compared with that of the isolated blue mechanism of normal vision. The dotted curve is from Green (1972), who used strong chromatic backgrounds, whereas the dashed curve is from Cavonius & Estevez (1975), who used an exchange method combined with weak chromatic adaptation. All curves are for low rates of temporal modulation (stationary or 1 Hz) and for central vision. The results of Green and Cavonius & Estevez have been adjusted vertically so as to coincide in peak sensitivity to the present results.

Thirdly, the temporal resolution of the short wavelength mechanism of normal vision, once thought to be around 18 Hz (Brindley, Du Croz & Rushton, 1966), is now thought to be as high as 40–50 Hz (Stockman & MacLeod, 1986; Stockman *et al.* 1987). This is in good agreement with the present results which suggest that the blue mono-cone monochromat can resolve temporal frequencies as high as 43 Hz. The only result from the present study that is not in agreement with results from the isolated short wavelength mechanism of normal vision is the shape of the temporal sensitivity function (Green, 1968; Kelly, 1974; Wisowaty & Boynton, 1980). This may be due to the fact that the spatial properties of the stimulus which are important (compare Figs 8 and 9, and see Robson, 1966) have not been controlled in previous studies (i.e. spatially broad band stimuli have been used). Furthermore, different methods of isolation (see Wisowaty & Boynton, 1980) have also been used which may

selectively isolate either cone-opponent or non-opponent processing modes (Polden & Mollon, 1980). Until these two issues have been addressed it is difficult to know whether this discrepancy is physiologically important.

Thus on the basis of the above comparisons it seems that the properties of the blue mechanism are similar in the achromat and normal. Most methods of isolation of the blue mechanism in normal subjects, except that of Wisowaty & Boynton (1980), have involved the use of strong background adaptation which would strongly polarize any cone-opponent site (Pugh & Mollon, 1979) thereby isolating non-opponent modes of processing. Thus the monochromats may provide a good model for the contribution of the blue mechanism to non-opponent modes of processing in the normal visual system.

*Properties of the monochromat and luminance detection of normal vision*

A comparison of the post-receptoral properties of the blue mono-cone monochromat with those of normal luminance contrast sensitivity also reveals a number of similarities. Firstly, the spatial contrast sensitivity functions for central vision are very similar in their shape and in their spatial position. The main difference between these functions is one of sensitivity, notwithstanding the slight difference in the rate of low frequency attentuation which may be accounted for by eye movements. Secondly, a similar type of spatio-temporal covariation is seen in the threshold response of monochromat and for the detection of luminance contrast targets by the normal visual system; a bandpass temporal response at low spatial frequencies and a low-pass temporal response at high spatial frequencies. Apart from the slightly reduced dynamics exhibited by the monochromat, the main difference between the temporal responses of the monochromat and normal subject is also one of sensitivity. Lastly, spatial and temporal sensitivity is distributed across the retina in the same manner in the monochromat as it is for the achromatic pathways(s) of normal vision, again the only difference being one of sensitivity. In short, the main difference between spatio-temporal sensitivity of the monochromat and the properties of luminance contrast sensitivity of normal vision could be simply explained by assuming that the contribution of the other two cone types in the normal retina result in greatly enhanced overall sensitivity and a modest increase in dynamics.

In summary, the results for these blue-cone monochromats provide an upper bound on the contribution of short wavelength cones to normal luminance contrast processing whether by chromatic pathways operating in a non-opponent mode or by achromatic pathways. Such information may be valuable for assessing the relative importance of receptoral and post-receptoral limitations on short wavelength cone opponent processing. The results also provide an estimate for the potential contributions of short wavelength cones to normal luminance processing over a wide range of spatial and temporal conditions both foveally and eccentrically.

*Convergence within the blue-cone pathway*

If we assume that the short wavelength receptoral distribution and post-receptoral connections are similar in the pathway or pathways responsible for non-opponent processing in the normal and blue mono-cone monochromat then one can derive a

prediction for how the average minimum convergence for the short wavelength cones of normal vision changes with retinal eccentricity. In Fig. 13 the acuity fall-off with eccentricity (continuous curve) has been estimated from the normal short-wavelength cone distribution (Marc & Sperling, 1977) and compared with the

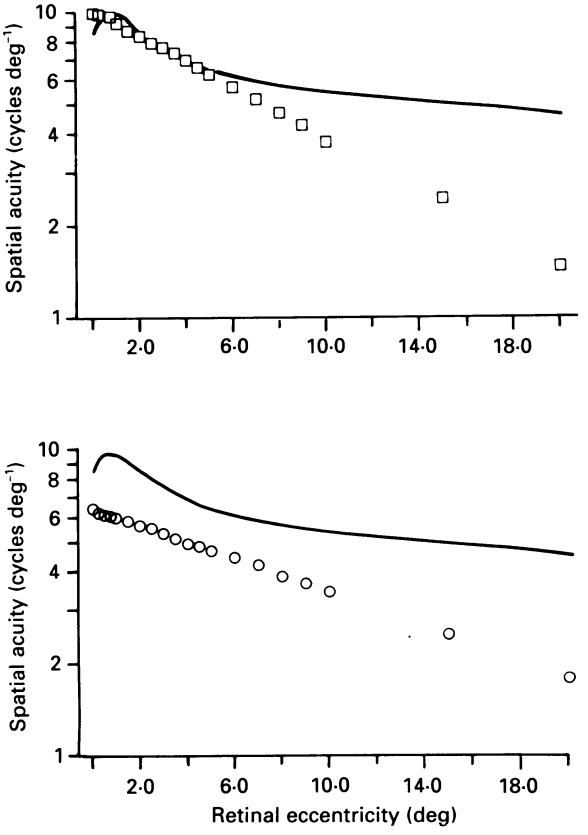


Fig. 13. The spatial resolution acuity is plotted as a function of eccentricity for the two monochromats from the results of Fig. 6. These are compared with the predicted acuities (continuous curve) based on receptor spacing of the short wavelength receptors (Marc & Sperling, 1977). The difference in the slopes of the measured and predicted acuity functions suggest that minimal receptoral convergence increases beyond 5 deg eccentricity. Upper panel, S.B.; lower panel, P.S.

*unaliased* resolution acuities of the two blue mono-cone monochromats (symbols). Although there is a difference in the absolute acuities of these two subjects their acuity fall-off with eccentricity is very similar. When the slope of the fall-off of the measured acuity function is compared with that predicted from the average receptor spacing one can see that the average minimum convergence for short wavelength receptors increases only very gradually with retinal eccentricity and there is virtually no change up to 5 deg eccentricity. At 20 deg it has increased by only a factor of 3.

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