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SPATIAL AND TEMPORAL PROPERTIES OF HUMAN ROD VISION IN THE ACHROMAT

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SUMMARY

1. The spatial and temporal properties of rod vision were measured for stimuli at and above the detection threshold in an achromat whose spectral sensitivity, dark adaptation, spatial and temporal thresholds and Stiles–Crawford effect suggest the presence of only a normally functioning rod system. The properties of rod and cone vision were compared at illuminances where their respective sensitivities were optimum.

2. The threshold spatial sensitivity of the rod mechanism under optimum illumination (180 scotopic trolands) exhibits bandpass properties with a peak sensitivity of around 80 at 0·5 cycles/deg and a spatial acuity of 6–7 cycles/deg. The threshold temporal sensitivity also exhibits bandpass properties under these conditions with a peak sensitivity of around 80 at 5 Hz and a temporal acuity of 30 Hz. For stimuli of low spatial frequency ($<$ 0·3 cycles/deg) and low temporal frequency, the threshold sensitivities of rod- and cone-mediated vision are identical.

3. Rod- and cone-mediated vision display comparable spatial and temporal discrimination for targets of equal suprathreshold contrast over the low to mid spatial and temporal range that they share. Rod-mediated discriminations fall below those of cone vision above 1 cycle/deg for spatial judgements and above 15 Hz for temporal judgements.

4. The number of discriminable steps in spatial frequency and temporal frequency at threshold is similar for rod and cone vision over the spatio-temporal frequency range that they share. Over this range rod- and cone-mediated vision can discriminate four steps in spatial frequency and one step in temporal frequency.

5. These results suggest that rod vision shows comparable spatio-temporal discrimination performance to cone vision and that it is subserved by at least five spatial and two temporal labelled detectors. The response of the highest spatial frequency filter subserving rod vision extends from 0·5 to 6 cycles/deg.

INTRODUCTION

Over the past two decades a number of studies (Campbell & Green, 1965; Campbell & Robson, 1968; Campbell, Nachmias & Jukes, 1970; Pantle, 1978; Richards, 1979; Watson & Robson, 1981; Pelli, 1981; Thompson, 1983; Mandler, 1984; Mandler &

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Makous, 1984) have investigated the spatial and temporal limits of detection and discrimination for the normal visual system operating under photopic conditions. These results show that cone-mediated vision can detect spatio-temporal patterns with a peak sensitivity of 200 (0·5 % contrast) and can discriminate differences in spatial frequency to 3 % and differences in temporal frequency to 5 % for suprathreshold stimuli. As the stimulus contrast is reduced spatial and temporal discriminations worsen and reach a limiting case at the detection threshold. At threshold only six discriminable steps in spatial frequency can be made over a 6 octave spatial range and only one discriminable step in temporal frequency can be made over a similar temporal range. This finding led Watson & Robson (1981), and later Thompson (1983), to postulate that spatial vision is subserved by a limited number of labelled spatial (i.e. seven) and temporal (i.e. two) detectors. Hess & Plant (1985) have added to this by showing that at low spatial frequencies two, not one, discriminable steps in temporal frequency can be made at threshold. When interpreted along these lines the original proposal of Watson & Robson (1981) can be modified to include seven spatial detectors and *three* temporal detectors, one of which has restricted spatial acuity.

While our understanding of the spatial and temporal detection and discrimination ability of cone-mediated vision is well advanced, a similar understanding of these capabilities for rod-mediated vision is either completely lacking or limited to illuminance levels where the rod mechanism of normal vision is more adequately isolated from its cone counterpart and not where its sensitivity is maximal. This has constrained measurements in the upper mesopic region where rod-mediated contrast sensitivity is best (and where possibly discrimination is also best) but where cone-mediated sensitivity is superior. As an alternate approach we have investigated spatial and temporal detection and discrimination at and above detection threshold in a typical, complete achromat, who has been shown to exhibit only a rod mechanism of normal sensitivity. This has been verified by assessment of spectral sensitivity and dark adaptation (Nordby, Stabell & Stabell, 1984), the Stiles–Crawford effect (Sharpe & Nordby, 1984), spatial sensitivity and temporal sensitivity (Hess & Nordby, 1986).

Our results outline the spatial and temporal threshold detection and suprathreshold discrimination abilities of rod-mediated vision under mesopic illuminances where its contrast sensitivity is best. We show that the spatio-temporal threshold sensitivity of the rod mechanism can reach 100 (1 % contrast) at around 0·3 cycles/deg, a spatial acuity of 6 cycles/deg and a temporal acuity of 30 Hz. Furthermore, suprathreshold discrimination of rod- and cone-mediated vision is comparable over two-thirds of the spatial and temporal range that they share for stimuli of equal suprathreshold contrast. Discriminations at the detection threshold are also similar for rod- and cone-mediated vision over most of their shared spatio-temporal range. One interpretation of these results is that rod vision, like cone vision, is subserved by five spatial and two temporal detectors in the low to medium spatio-temporal range which is shared.

METHODS

General procedures

Stimuli were displayed on a Joyce raster screen with a large, evenly lit, luminance-matched surround (angular subtense 60 × 40 deg). The screen spatial frequency did not exceed 1 cycle/cm. Higher spatial frequencies were obtained by varying the viewing distance. At low spatial frequencies (0·1–1 cycles/deg) a field size of 20 × 30 deg was used. For the measurement of the contrast sensitivity function (Fig. 1) the field size varied in the following way. For spatial frequencies between 0·03 and 1 cycle/deg, a field size of 20 × 30 was used. Since higher spatial frequencies were obtained by changing the viewing distance, the field size reduced proportionally. This ensured that the display screen's frequency response did not limit measurements and that more than 5 cycles (in width and height) of the stimulus was displayed at all spatial frequencies (Howell & Hess, 1978). All stimuli were horizontally aligned to minimize image smear and image movement due to the slight horizontal nystagmus of the achromat's eye. A fixation point was provided to stabilize fixation, its luminance being set by the subject to be visible, but not dazzling.

The achromat only exhibits clinically observable nystagmoid eye movements under mid- to high-photopic conditions where receptoral saturation has occurred. Under the mesopic conditions of these experiments, only a slight nystagmus is present. This small-amplitude eye movement (less than 2 deg), has a horizontal direction, and its influence on the temporal discriminations reported here was minimal or non-existent, because we used one-dimensional stimuli whose axis was aligned parallel to the direction of the residual eye movements. The fact that it does not limit temporal discriminations is best seen in the close agreement between the subsequent temporal discrimination data of normal and achromat. For example, the achromat, like the normal, can successfully discriminate a stimulus of 0 Hz from one of 4 Hz at threshold. If the eye movements were limiting the lowest retinal temporal frequency such a discrimination would be impossible.

All of these experiments were done with natural pupils whose size was monitored photographically. The illuminance was set at 180 scotopic trolands for the achromat and at 2000 scotopic trolands for the normal trichromatic subject so that rod and cone performance could be compared each at their optimum illuminances. The subjects wore their full refractive correction under the goggles. All judgements were done monocularly with the left eye. The achromat is the author K.N.

Detection and discrimination experiments

The stimuli, which were sinusoidal gratings, sinusoidally reversing in contrast (or drifting) at various rates, were generated digitally by a PDP 11/20 and displayed on a Joyce raster screen. The contrast of each stimulus was weighted with Gaussian functions of space (x, y) and time (t), thus the luminance distribution of the stimulus was

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

where L_0 indicates the space-averaged luminance, C is the contrast variable and f_x and f_t are the spatial and temporal frequencies. The window function is given by:

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

The over-all window function is the product of the horizontal, vertical and time Gaussians of spreads S_x, S_y and S_t. (The term spread signifies the distance in time or space that the Gaussian falls from 1 to 1/e). The stimuli were presented with a Gaussian time spread of 250 ms and space spread of 1·5 periods for the lower spatial frequency. The task was either to just detect in which interval the stimulus was presented (two-alternate forced-choice method; 2 a.f.c.) or to detect as well as discriminate (two-by-two-alternate forced-choice method; 2 × 2 a.f.c.) which of two spatial frequency or temporal frequency stimuli were presented (i.e. the higher or lower spatial or temporal frequency). The spatial phase of the stimulus relative to the envelope was moved randomly from trial to trial to eliminate positional cues. For detection, the 2 a.f.c. method was used in conjunction with a staircase procedure whereas for detection and discrimination a 2 × 2 a.f.c method was used in conjunction with the method of constant stimuli. For detection both methods produced similar results. A number (usually four to six) of different contrast levels (each presented eighty times) were used in the detection/discrimination task (2 × 2 a.f.c) for each (higher and lower) spatial frequency stimulus, gauged to straddle the detection threshold. Prior threshold measurements for each stimulus, separately using an identical (2 a.f.c) procedure, guided the choice of these contrast levels. The detection and discrimination data obtained concurrently were fitted with Wiebull psychometric functions (Watson, 1979) and the 82% threshold derived. The slope parameter was unconstrained and its value varied between 3 and 4·5. Our criterion for discrimination at threshold was similar to that of previous workers (Watson & Robson, 1981; Thompson, 1983). If the averaged threshold difference between the two sets of psychometric data (low and high spatial (or temporal) frequency) did not exceed 1 dB, each having an acceptable chi square for goodness of fit ($P = 0{\cdot}05$), correct discrimination was said to occur at the detection threshold.

We verified that this criterion was acceptable for our experimental results in the following way. The log likelihood ($\log L^{\mathrm{a}}_{\mathrm{H}}$) was computed separately from the fitted detection psychometric function and for the discrimination psychometric function ($\log L^{\mathrm{b}}_{\mathrm{H}}$). Each having two parameters and I stimulus levels. Then the log likelihood was compared for a single psychometric function fitted to the combined results ($\log L^{\mathrm{a}}_{\mathrm{H}}{}^{\mathrm{b}}$) having two parameters and $2I$ levels. Twice the log likelihood ratio of hypothesis ($2 \log L^{\mathrm{a}}_{\mathrm{H}} + \log L^{\mathrm{b}}_{\mathrm{H}} - \log L^{\mathrm{a}}_{\mathrm{H}}{}^{\mathrm{b}}$) with two degrees of freedom gives an estimate of the chi square for the comparison of whether two curves are required to fit the data: that is the detection and discrimination data are fitted by different curves. The null hypothesis (i.e. data adequately fitted by one curve) was rejected at the 2% level and this was satisfied, in all cases, by adopting a criterion of less than 1 dB in the contrasts corresponding to the 82% correct level for detection and discrimination. Similar results were obtained for psychometric fits of data where the slope was constrained ($\beta = 3{\cdot}5$).

Noise-masking experiments

In these experiments contrast thresholds were determined for stimuli embedded in low pass filtered noise, having an approximate Gaussian amplitude probability distribution. The slope of the roll-off was 48 dB/octave. The noise was produced from a white noise generator. The notch filtering was achieved by two parallel channels of kemo filters (each of two filters in series of 24 dB/octave). The stimuli were presented in a Gaussian time envelope (time sigma = 250 ms) using a 2 a.f.c. paradigm. The test signals were contrast reversing at 1 Hz and the noise was dynamic (flat temporal spectrum).

Suprathreshold discrimination experiments

The stimuli, which were stationary or contrast-reversing sine-wave gratings, were generated digitally and presented within a Gaussian time envelope (sigma = 250 ms) using a PDP 11/34 computer. A staircase method was used with random interlacing of all stimuli. The task consisted of identifying the interval containing the higher spatial or temporal frequency grating. In a typical run ten reversals were averaged for each stimulus condition. In order to ensure that the number of bars did not give a secondary clue to spatial frequency discrimination at low base frequencies a fixed display of approximately 20 cycles was used for the base frequency. Higher and lower base frequencies were obtained by changing viewing distance. In this case each run consisted of a single staircase. The spatial phase was randomized between trials.

In a series of preliminary experiments on the spatial and temporal discrimination of normal subjects, we found that perceived contrast was sometimes used as a strong cue to spatial or temporal differences, especially at high frequencies. We eliminated this cue by randomizing the contrast of the two stimuli whose spatial or temporal frequency differed. Informal testing of experienced normal subjects indicated that contrast was not used as a cue to spatial or temporal judgements in the high frequency range when as little as 1 dB contrast-jitter was randomly added to either stimulus. That is, if the subjects chose a perceived contrast criterion instead of a spatial or temporal one, performance fell to chance levels. This was also found to be the case for the achromat who is also an experienced psychophysical observer.

RESULTS

Spatial detection threshold

The results displayed in Fig. 1 compare the spatial threshold sensitivity functions for rod- and cone-mediated vision operating at their respective, optimum illuminances (see Hess & Nordby, 1986). For rod-mediated vision the spatial sensitivity function is seen to have a bandpass characteristic with a peak sensitivity of around 80 at 0·5 cycles/deg and a spatial acuity of 6–7 cycles/deg. The cone mechanism displays similar spatial contrast sensitivity at low spatial frequencies, but a higher peak sensitivity (around 200) at 2 cycles/deg and a higher acuity (around 50 cycles/deg). The stimuli were sinusoidal gratings, sinusoidally modulated at 1 Hz. Similar results have been obtained for temporal rates between 0 and 5 Hz. For large field sizes (20 × 30 deg), the rod peak sensitivity asymptotes to around 100 at 0·3 cycles/deg (see Hess & Nordby, 1986).

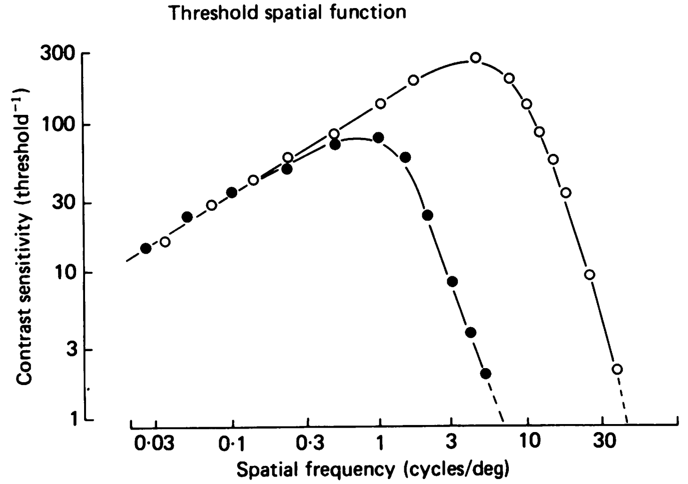

Fig. 1. Threshold contrast sensitivity (threshold^{-1}) is plotted against the spatial frequency for a 1 Hz, contrast-reversing sine-wave grating. The results for the rod (●; K.N.) and cone mechanisms (○; R.F.H.) are compared at their optimum illuminances of 180 and 2000 scotopic trolands, respectively. The standard deviations were never larger than twice the symbol size. All stimuli were horizontally aligned.

Spatial discrimination above threshold

Figs. 2 and 3 display results for spatial frequency discrimination (±1 S.D.) for stimuli temporally modulated at 0 and 16 Hz, respectively. All stimuli were presented at 16 dB (a factor of 6) above their pre-determined thresholds. In each Figure the achromat's results (filled symbols) under optimum conditions of illuminance (i.e. mesopic) are compared with those of a normal observer operating under photopic conditions (open symbols). The results of the normal observer represent the capabilities of the cone system. The percentage increment in spatial frequency for which reliable

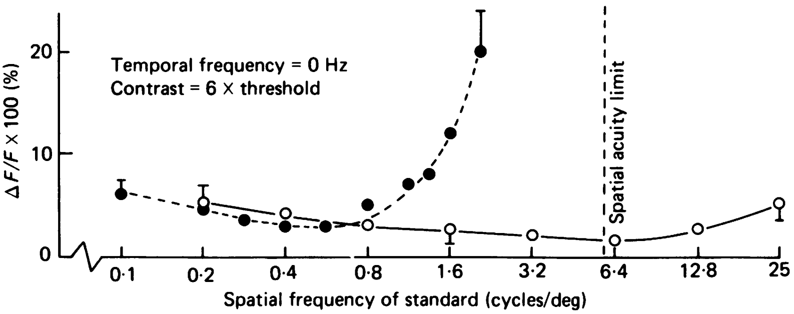

Fig. 2. The discriminable increment of spatial frequency, expressed as a percentage of the comparison frequency, is plotted against the spatial frequency of the comparison for the cone mechanism of normal vision (○; 2000 scotopic trolands) and the rod mechanism of the achromat (●; 180 scotopic trolands). The stimuli are stationary sine-wave gratings presented 16 dB (i.e. a factor of 6) above their detection thresholds. The spatial discriminations of cone vision, under photopic conditions, are similar to those of rod vision, under mesopic conditions, for stimuli between 0·2 and 0·8 cycles/deg. Above 0·8 cycles/deg spatial discrimination for stationary stimuli falls off more rapidly for the rod mechanism.

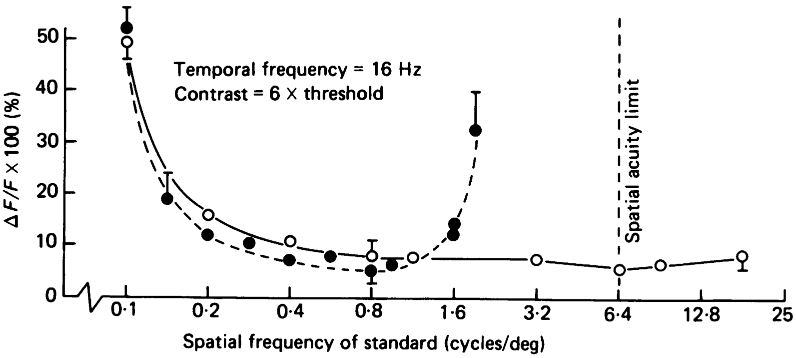

Fig. 3. The discriminable increment of spatial frequency, expressed as a percentage of the comparison frequency, is plotted against the spatial frequency of the comparison stimulus for the cone mechanism of normal vision (○; 2000 scotopic trolands) and the rod mechanism of the achromat (●; 180 scotopic trolands). The stimuli are sine-wave gratings, temporally modulated at 16 Hz and presented at 16 dB (i.e. a factor of 6) above their detection thresholds. The spatial discriminations of cone vision, under photopic conditions, and that of rod vision, under mesopic conditions, are similar in the 0·1–1 cycles/deg range. Above 1 cycle/deg spatial discrimination for a rapidly moving stimulus falls off more rapidly for the rod mechanism.

discriminations could be made are plotted against the spatial frequency of the standard, comparison stimulus.

For normal cone vision, spatial discrimination is best at intermediate spatial frequencies (around 3–6 cycles/deg) and at low (0 Hz) rather than high (16 Hz) temporal frequencies. The results for spatial stimuli, temporally modulated at 16 Hz (Fig. 3), show less acute (5 % compared with 2 %) discrimination for intermediate spatial frequencies, and a more marked loss in discriminability at low spatial frequencies. The results of previous studies (Campbell *et al.* 1971; Hirsch & Hilton,

1982) are similar to these. The spatial discriminations of rod vision, represented by the achromat's results, are seen to exhibit similar absolute sensitivity as well as a similar dependence on the spatial and temporal frequency of the stimuli used. This similarity of spatial discriminations, for normal and achromat, exists over a large part of their shared spatial range (0·1–1 cycles/deg). Above 1 cycle/deg, however, rod-mediated spatial discriminations fall below that of their cone counterparts.

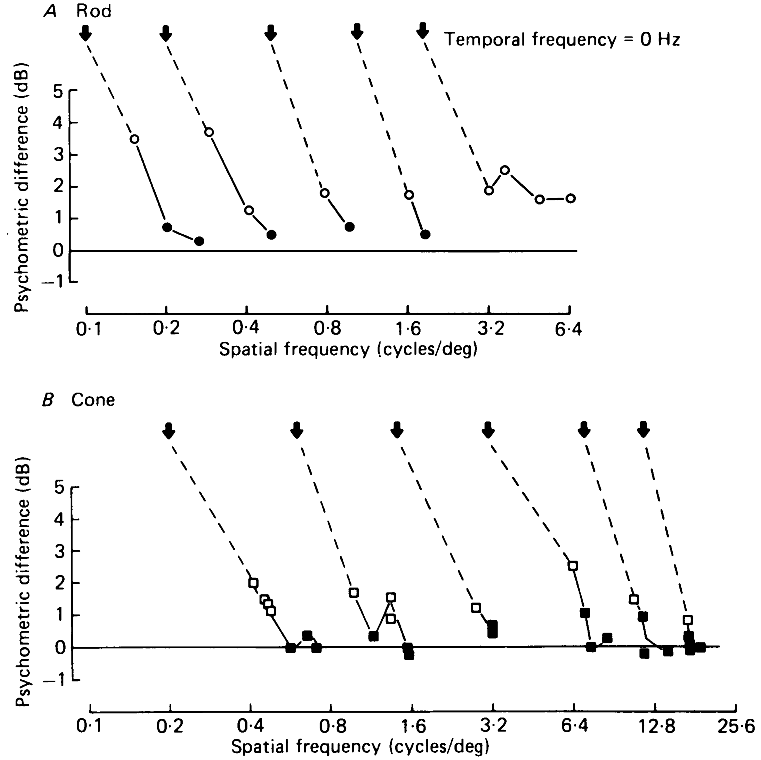

Fig. 4. Detection-to-discrimination ratios for *A* the rod (○,●), and *B* cone (□,■) mechanisms of the achromat and normal observer are plotted against the spatial frequency of the standard (higher frequency of the pair). The lower, comparison, spatial frequency of each pair is indicated by an arrow. The stimuli are stationary sine-wave gratings presented in a gaussian time window (sigma = 250 ms). A difference of less than 1 dB in the thresholds for detection and identification (●,■) satisfies the criterion (see Methods) for perfect discrimination at threshold as opposed to when the criterion is not met (○,□). Four discriminable steps can be made in spatial frequency for stationary stimuli of between 0·1 and 2 cycles/deg for rod (*A*) and cone mechanisms (*B*). The cone results have been re-plotted from Watson & Robson (1981).

Spatial discrimination at threshold

In Figs. 4 and 5 the detection-to-discrimination ratios are compared for (a) the achromat (circles), and (b) normal (squares) in a simultaneous detection/discrimination experiment. In each Figure the difference in the contrast (in decibels) corresponding to the 82% correct response for detection and discrimination is plotted against the higher spatial frequency of the stimulus pair. The spatial frequency of the other stimulus is denoted by the arrow. A contrast difference in thresholds of less than 1 dB was taken to satisfy the criterion (see Methods) for successful discrimination at threshold (i.e. psychometric functions for detection and discrimination are identical). Only data whose goodness of fit produced a chi square of less than 5% were analysed.

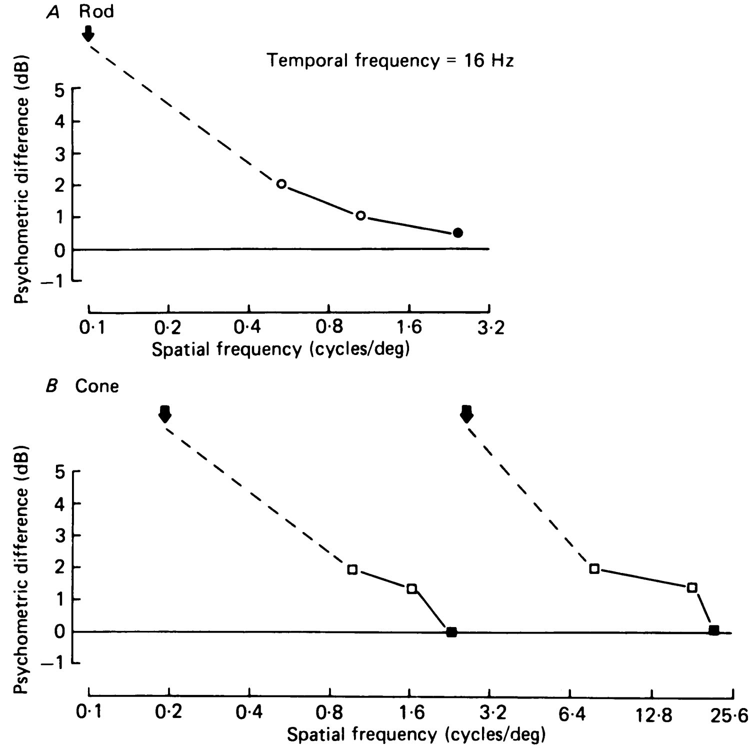

Fig. 5. Detection-to-discrimination ratios for *A* the rod (○,●) and *B* cone (□,■) mechanisms of the achromat and normal observer are plotted against the spatial frequency of the standard (higher frequency of the pair). The lower, comparison, spatial frequency of each pair is indicated by an arrow. The stimuli are sine-wave gratings, temporally modulated at 16 Hz and presented in a gaussian time window (sigma = 250 ms). One discriminable step in spatial frequency can be made for these rapidly moving stimuli in the 0·1–2 cycles/deg spatial range (●,■) for both the rod (*A*) and cone mechanisms (*B*). The cone results have been re-plotted from Watson & Robson (1981). Stimulus pairs which could be perfectly discriminated at threshold are indicated by filled symbols.

The normal results in Figs. 4*B* and 5*B* are those of Watson & Robson (1981), using an identical method under mid-photopic conditions. Since they did not attempt spatial discriminations for stimulus as low in frequency as 0·1 cycles/deg, we have subsequently verified that a normal subject can discriminate between a 0·1 and 0·2 cycles/deg stimulus at threshold (data not displayed).

For stationary stimuli (Fig. 4*A*) a spatial stimulus of 0·1 cycles/deg could be successfully discriminated at threshold from a spatial stimulus of 0·2 and 0·25 cycles/deg, but not from one of 0·15 cycles/deg. Similarly, 0·2 cycles/deg could be discriminated from 0·5 cycles/deg when presented at their respective contrast thresholds. In all, four discriminable steps (each an octave in size) could be made in spatial frequency for stationary stimuli between 0·1 and 6·4 cycles/deg, at threshold, for rod-mediated vision. Similar results are found for cone-mediated vision as depicted in Fig. 4*B* (Watson & Robson, 1981; Thompson, 1983). Hence, over a large part of the spatial range (0·2–2 cycles/deg) that is common to both rod- and cone-mediated vision, similar spatial discriminations can be made for stationary stimuli at threshold.

Compare these results for stationary stimuli (Fig. 4*A* and *B*) with those displayed in Fig. 5*A* and *B* for spatial stimuli, temporally modulated at 16 Hz. Results for the normal (Fig. 5*B*, re-plotted from Watson & Robson, 1981) and achromat (Fig. 5*A*, circles) are compared. As for the supra-threshold experiment, the spatial discrimination at threshold is much coarser for rapidly moving stimuli. Only one discriminable step can be made (of size 4 octaves) by the achromat over this same spatial frequency range. For cone vision (Fig. 5*B*), two discriminable steps can be made between 0·2 and 32 cycles/deg. This consisted of one discriminable step between 0·2 and 3 cycles/deg and one between 3 and 32 cycles/deg (Watson & Robson, 1981; Thompson, 1983).

Hence within the low to medium spatial frequency range (from 0·1 up to an octave from the acuity limit of the rod system) rod- and cone-mediated vision display similar spatial discriminations for stimuli of low and high temporal frequency at, and above, their respective thresholds.

Temporal detection threshold

The results in Fig. 6 compare the temporal threshold sensitivity functions for rod- and cone-mediated vision operating at their respective optimum illuminances (see Hess & Nordby, 1986). The stimuli are sine-wave gratings of 0·3 cycles/deg, although the conclusions are similar for targets of between 0·1 and 1 cycles/deg. For rod-mediated vision, the temporal sensitivity function is seen to have a bandpass characteristic with peak sensitivity of 80 occurring at 5 Hz and a temporal acuity limit of 30 Hz. The cone mechanism displays similar temporal contrast sensitivity at low temporal frequencies, a higher peak sensitivity (around 200) at 10 Hz and a higher temporal acuity at 60 Hz.

Temporal discrimination above threshold

The results concerning temporal frequency discrimination for low and medium spatial frequency gratings of equal suprathreshold contrast are displayed in Figs. 7 and 8. The contrast of all stimuli was set to be 16 dB (a factor of 6) above their pre-determined thresholds. The achromat and the normal observer performed this task under mesopic and photopic illuminances respectively, where temporal sensitivity was optimum for rod and cone vision. In Fig. 7 temporal discrimination (discriminable increment expressed as a percentage of the temporal frequency of the standard) is plotted against the temporal frequency of the standard for normal (open symbols) and achromat (filled symbols). The stimulus is a 0·2 cycles/deg spatial frequency sine-wave grating. For both normal and achromat temporal discrimination improves from 1 to 6 Hz, reaching discrimination levels of around 5 % and thereafter (6–12 Hz) abruptly falls off. Although the responses of the normal and the achromat are similar

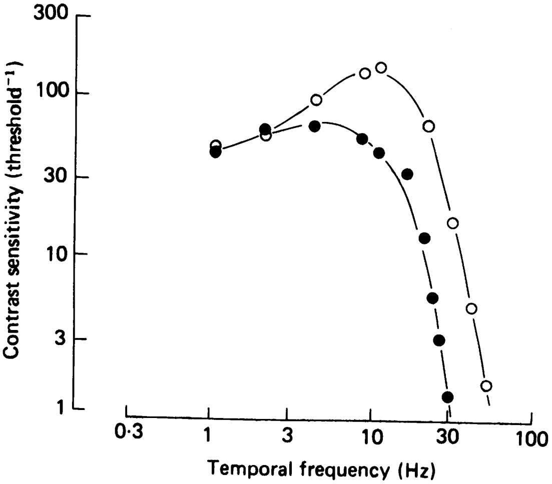

Fig. 6. Threshold contrast sensitivity (threshold^{-1}) is plotted against the temporal frequency for a 0·2 cycles/deg sine-wave grating. The results for the cone mechanism of normal vision (○) are compared with those of the rod mechanism of the achromat (●) each working under their optimum illuminance: 2000 and 180 scotopic trolands, respectively. The field size was 20 × 30 deg and the standard deviations were never larger than twice the symbol size.

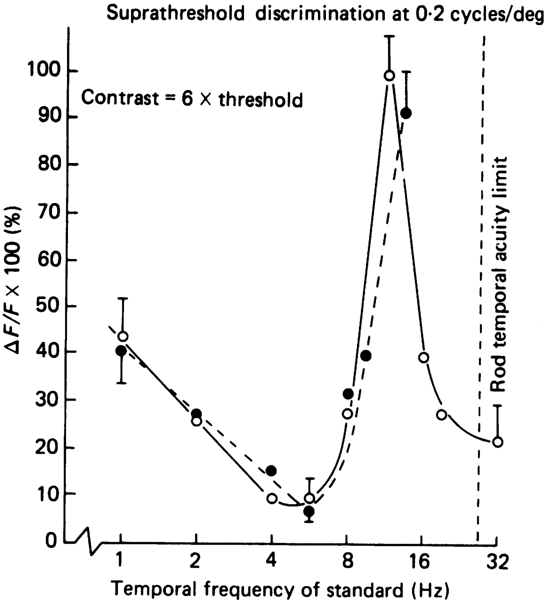

Fig. 7. The discriminable increment of temporal frequency (expressed as a percentage of the comparison temporal frequency) is plotted against the temporal frequency of the comparison stimulus for the cone mechanism of normal vision (○) and the rod mechanism of the achromat (●). The stimuli are sine-wave gratings of 0·2 cycles/deg presented at 16 dB (i.e. a factor of 6) above their detection thresholds. The temporal discriminations of cone vision under photopic conditions are similar to those of rod vision under mesopic conditions in the temporal range 0–16 Hz. For stimuli above 16 Hz, discrimination improves for cone vision and cannot be measured for rod vision.

in form and absolute sensitivity within this low to medium temporal range, marked differences are shown in their respective behaviours above 16 Hz. Between 16 Hz and the achromat's temporal acuity limit (around 28 Hz) discrimination cannot be measured using this technique. In contrast, within this temporal region discrimination improves for the cone mechanism achieving a second discrimination minimum of around 22% at 32 Hz. The finding of this second minimum in discrimination for normal cone vision was one reason that prompted Hess & Plant (1985) to postulate the existence of a third, higher temporal frequency mechanism or mechanisms. A number of other recent studies have independently argued for the existence of a higher temporal mechanism (Pantle, 1978; Richards, 1979; Pelli, 1981; Mandler, 1984; Mandler & Makous, 1984). The present results which suggest the absence of such a mechanism in the achromat are not so surprising because for normal vision this postulated higher temporal mechanism (or mechanisms) is located around 30 Hz which is at, or just beyond, the temporal acuity limit of the achromat.

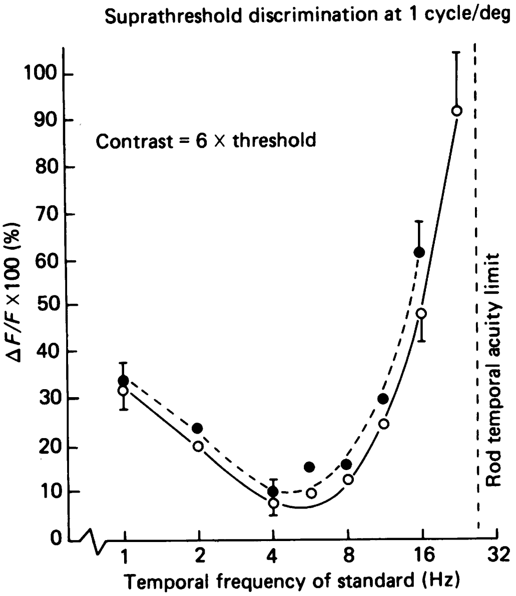

Fig. 8. The discriminable increment of temporal frequency (expressed as a percentage of the comparison frequency) is plotted against the comparison frequency for the cone mechanisms of normal vision (○) and the rod mechanism of the achromat (●). The stimuli are sine-wave gratings of 1 cycle/deg presented 16 dB above their detection thresholds. The temporal discriminations of cone vision under photopic conditions are similar to those of rod vision under mesopic conditions in the temporal range 0–16 Hz.

In Fig. 8 the results of a similar comparison of temporal frequency discrimination is displayed for normal (open symbols) and achromat (filled symbols) but this time for a sine-wave grating of medium spatial frequency (1 cycle/deg). Normal and achromat exhibit very similar temporal discriminations for suprathreshold stimuli between 1 and 16 Hz, the discrimination of the achromat being only slightly worse

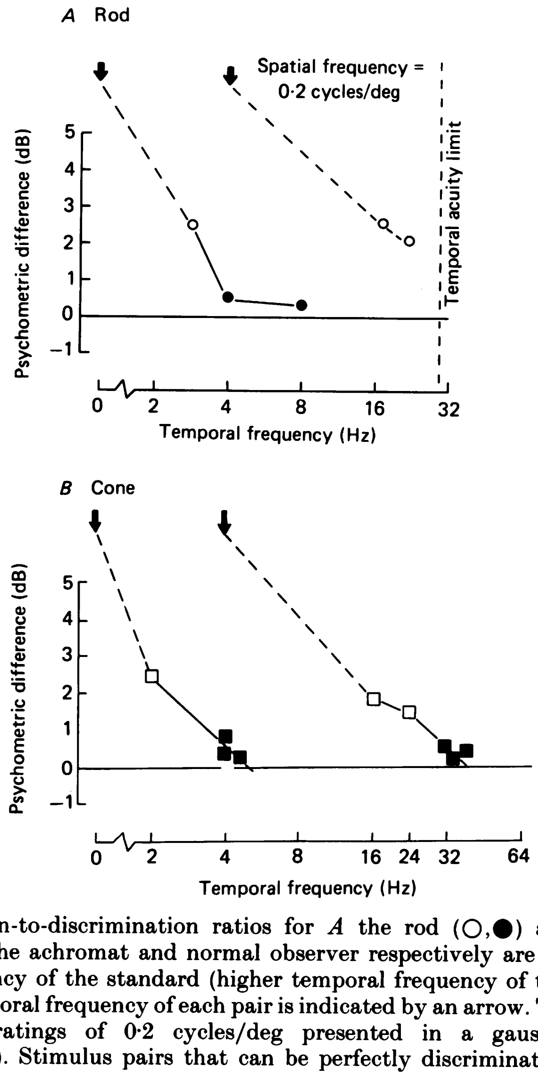

Fig. 9. Detection-to-discrimination ratios for *A* the rod (○,●) and *B* cone (□,■) mechanisms of the achromat and normal observer respectively are plotted against the temporal frequency of the standard (higher temporal frequency of the pair). The lower comparison temporal frequency of each pair is indicated by an arrow. The stimuli are pairs of sine-wave gratings of 0·2 cycles/deg presented in a gaussian time window (sigma = 250 ms). Stimulus pairs that can be perfectly discriminated at threshold are indicated by filled symbols. A difference of less than 1 dB in the thresholds for detection and discrimination (●,■) satisfies the criterion for perfect discrimination at threshold. One discriminable step in temporal frequency can be made in the temporal range from 0 to 24 Hz for rod (*A*) and cone (*B*) mechanisms. The cone results are re-plotted from Hess & Plant (1985).

at all temporal frequencies. In both cases a single minimum in discrimination around 6 Hz is seen (6–8 %) with a more gradual (as compared with that for 0·2 cycles/deg in Fig. 7) fall-off in discrimination as temporal frequency is increased. Thus, for both low and high spatial frequency stimuli (i.e. high relative to rod acuity) of similar suprathreshold contrast, the temporal discriminations of normal (under photopic conditions) and achromat (under mesopic conditions) are similiar in form and absolute sensitivity in the temporal range from 1 to 16 Hz (an octave from the temporal limit of the achromat).

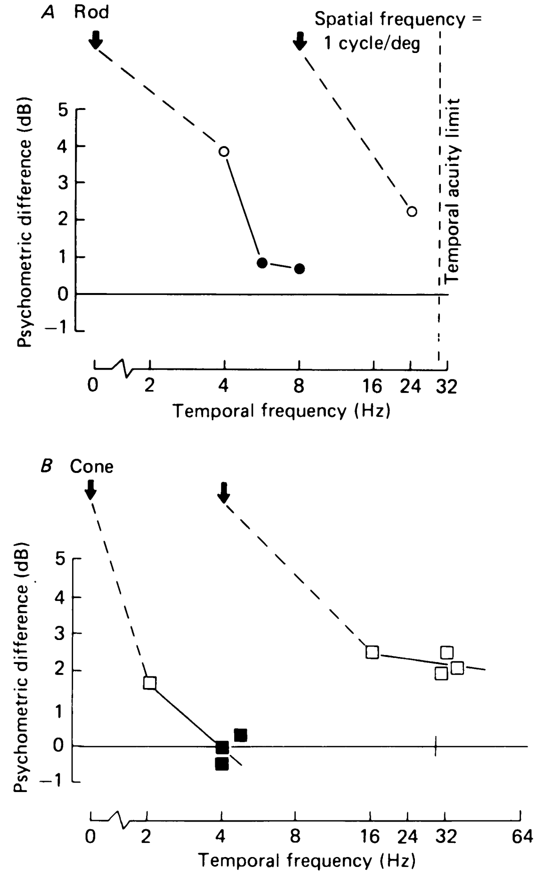

Fig. 10. Detection-to-discrimination ratios for *A* the rod (○,●) and *B* cone (□,■) mechanisms of the achromat and normal observer respectively, are plotted against the temporal frequency of the standard (higher temporal frequency) stimulus. The lower temporal frequency of each pair is indicated by an arrow. The stimuli are pairs of sine-wave gratings of 1 cycle/deg presented in a gaussian time window (sigma = 250 ms). Stimulus pairs that can be perfectly discriminated at threshold are indicated by filled symbols. A difference of less than 1 dB in the thresholds for detection and discrimination (●,■) satisfies the criterion (see Methods) for perfect discrimination at threshold. One discriminable step in temporal frequency can be made in the temporal range 0–24 Hz for both rod (*A*) and cone (*B*) mechanisms. The cone results are re-plotted from Hess & Plant (1985).

Temporal discrimination at threshold

In Figs. 9 and 10 the detection-to-discrimination ratios are compared for (a) the achromat (circles), and (b) normal (squares) in a simultaneous detection/discrimination experiment. In each Figure the difference in the contrast (in decibels) corresponding to the 82 % correct response for detection and discrimination is plotted against the temporal frequency of one of the stimulus pair. The temporal frequency of the other stimulus is indicated by the arrow. A contrast difference in thresholds of less than 1 dB was taken to satisfy the criterion (see Methods) of successful discrimination at threshold (filled symbols). The normal results (Fig. 9*B* and 10*B*) are taken from Hess & Plant (1985) and were measured under identical conditions but at photopic levels of illumination.

For stimuli of low spatial frequency, a stationary stimulus can be successfully discriminated from one that is temporally modulated at 4–8 Hz at their respective thresholds. However, a 4 Hz stimulus cannot be successfully discriminated from one of any higher temporal frequency (up to 24 Hz) by the achromat (Fig. 9*A*). Thus, only one discriminable step in temporal frequency can be made by the achromat between 0 and 24 Hz. The normal photopic results suggest that the cone-mediated system (Fig. 9*B*) can make two discriminable steps in temporal frequency for stimuli of low spatial frequency (Hess & Plant, 1985). For cone vision 0 and 4 Hz can be discriminated at threshold as can 4 and 32 Hz. The achromat performs only the first of these two discriminable steps because the second falls outside the achromat's temporal range (acuity = 30 Hz).

For spatial stimuli of high spatial frequency (1 cycle/deg) the results of Fig. 10*A* show that the achromat is also capable of only one discriminable step in temporal frequency between 0 and 24 Hz. A stationary stimulus can be successfully discriminated from one temporally modulated at 6–8 Hz. However, an 8 Hz stimulus cannot be discriminated from any higher temporal rate (threshold difference exceeds 1 dB). For a 1 cycle/deg stimulus, normal cone vision (Fig. 10*B*) is also only capable of one discriminable step in temporal frequency over the temporal range 0–44 Hz (Watson & Robson, 1981; Thompson, 1983; Hess & Plant, 1985). Thus, the achromat (under mesopic conditions) and the normal subject (operating under photopic conditions) are capable of the same number of discriminable steps in temporal frequency discrimination for threshold stimuli over their shared spatio-temporal frequency range.

DISCUSSION

Our understanding of the capabilities of spatial and temporal visual processing by the rod-mediated mechanism of normal vision is very rudimentary. Such knowledge that we have is limited to threshold detection and to scotopic illuminances where it is easier to isolate the rod-mediated response from its cone-mediated counterpart. It is of obvious importance to extend this view by undertaking measurements at mesopic illuminances where the rod-mediated contrast sensitivity is highest, and to suprathreshold, as well as threshold, signal levels. While it may be possible to extend observations in the normal to mesopic conditions by assuming that rod isolation procedures are adequate, it is especially hazardous to apply this approach to a suprathreshold investigation of the normal rod mechanism. As an alternative approach to that of isolating the rod-mediated response of normal vision, we have investigated threshold and suprathreshold processing of information in the typical, complete achromat under illuminances where sensitivity is optimum (i.e. the mesopic). In previous studies we have sought to prove that the typical, complete achromat exhibits threshold sensitivity which suggests the presence of a normally sensitive, rod-driven, post-receptoral system working in isolation. Other studies have assessed the visual function of this achromat in terms of spectral sensitivity, dark adaptation (Nordby *et al.* 1984), and Stiles–Crawford function (Sharpe & Nordby,

1984) and arrived at a similar conclusion. Thus we look upon our achromat as a suitable model for normal rod vision.

Spatial sensitivity

A number of studies, using isolation techniques for normal vision, have contributed to our present understanding of detection capabilities of rod vision. For spatial vision we know that rod acuity is around 7 cycles/deg (Green, 1972; D'Zmura & Lennie, 1984) and that contrast sensitivity is around 10 (or incremental sensitivity of 0·1: Aguiler & Stiles, 1954; Green, 1972; Conner, 1982), and that the illuminance range extends up to 2–3000 trolands after which saturation is complete. In the present study, using contrast sensitivity measurements for sine-wave grating stimuli we find that the best sensitivity attainable by the rod- and cone-mediated mechanism is identical at low spatial frequencies (0·03–0·2 cycles/deg). Both rod and cone vision exhibit bandpass responses at illuminances in the upper part of their range. The peak contrast sensitivity occurs at 0·3 cycles/deg for the rod mechanism, as opposed to 2 cycles/deg for the cone mechanism. Rod-mediated contrast sensitivity can reach 80–100 under optimum spatio-temporal conditions, compared with 500 for cone vision. Rod-mediated spatial acuity is around 6 cycles/deg, a factor of 10 reduced from that of cone vision.

Two findings are of special interest. First, the sensitivity of rod- and cone-mediated vision is identical for stimuli of low spatial frequency. This follows from the finding of Van Nes & Bouman (1967) for normal vision, that for low spatial frequency stimuli, contrast thresholds remain invariant with illuminances over the mesopic to photopic range. Secondly, the maximum spatial sensitivity exhibited by the rod mechanism is around 80–100, a factor of 8–10 higher than the previous estimates of contrast sensitivity (Van Nes & Bouman, 1967; Daitch & Green, 1969; Smith, 1973; Conner, 1982). Recently, D'Zmura & Lennie (1984) have reported rod-mediated contrast sensitivities of 50 in normal subjects using a spectral isolation technique. The most likely reason for the previous, low estimates of rod sensitivity is that the isolation procedures have not been adequate, requiring lower than optimum mesopic illuminance for the rod mechanism. The much smaller difference between D'Zmura & Lennies' results using a superior isolation technique on normals and those of the achromat, is probably due to the larger field sizes used in the present investigation. Since the rod response is restricted to lower spatial frequencies, it is expected that the larger absolute stimulus areas would benefit threshold sensitivity (Howell & Hess, 1978).

Suprathreshold, spatial discriminations are also similar for rod and cone mechanisms in the low to medium spatial frequency range (0·1–1 cycle/deg), when tested at their optimum illuminances. This is true of spatial discriminations for stationary stimuli (peak discrimination sensitivity of 2%) or for rapidly moving (16 Hz) stimuli (peak discrimination sensitivity of 6%). For stationary stimuli, the rod mechanism can make just four discriminable jumps at threshold over its entire spatial range (0·1–6 cycles/deg). In the spatial range 0·2–1·6 cycles/deg the cone mechanism displays similar performance. For rapidly moving (16 Hz) stimuli, only one discriminable jump in spatial frequency discrimination can be made by the rod mechanism between 0·1 and 6 cycles/deg. Likewise, in this range (0·2–1·6 cycles/deg) the cone system displays similar performance.

These results, concerning spatial discrimination at threshold, have been used to estimate the number of labelled detectors subserving spatial vision in normal, cone-mediated vision (Watson & Robson, 1981; Thompson, 1983). It has been argued that, at threshold, for stimuli to be correctly discriminated more than one mechanism, or labelled detector, needs to be active. The minimum number of discriminable steps in spatial or temporal frequency can, then, be used to estimate the number of detectors across the spatial or temporal range. The results of these previous studies of normal cone vision are consistent with there being seven labelled spatial detectors in the low temporal frequency range (six steps can be made between 0·2 and 30 cycles/deg) and two labelled spatial detectors operating in the high temporal frequency range. The results of the present study when interpreted in this way suggest that rod-mediated spatial vision is subserved by four labelled detectors operating at high temporal frequencies. Thus, within the low to medium spatial range, contrast sensitivity and suprathreshold discrimination are similar for rod and cone vision. Furthermore, threshold discrimination results suggest that a similar number and band width of underlying detectors subserve rod and cone vision in this range.

Another way of looking at these results is to suppose that there are a very large number of spatial and temporal detectors with different characteristic frequencies subserving these discriminations, but that two stimuli can only be discriminated at threshold when the envelope of their neural activity is statistically separable. The limiting number of discriminable steps at threshold would then reflect the accuracy of this more central process, rather than the actual number of peripheral detectors. Although the present results cannot choose between these two possible explanations, they do indicate that multiple spatial and temporal peripheral mechanisms must be subserving rod vision, and that these mechanisms must exist in the same regions (to the extent to which these stimuli have been spatially localized).

The smallest rod receptive field

Although the acuity of rod vision is around 6 cycles/deg the suprathreshold and threshold spatial discrimination results suggest that the peak location of the highest spatial frequency filter may be much lower. The finding that, at threshold, a 2 cycles/deg grating cannot be discriminated from one of any higher spatial frequency, suggests an upper limit of around 2 cycles/deg. Suprathreshold spatial discrimination is also impossible after 2·4 cycles/deg. Since, for suprathreshold discrimination, the standard was of lower spatial frequency, the spatial location where discrimination falls off rapidly, and can no longer be measured should correspond to the acuity limit of the second highest spatial frequency mechanism. This corresponds to around 2·4–3 cycles/deg.

The location of the low spatial frequency limit of the highest spatial frequency mechanism can be estimated in the following way: if the position of the 3 dB roll-off of low pass spatial noise is advanced to high frequencies, when it falls within the response range of the highest spatial frequency mechanism, then the contrast sensitivity of the high spatial frequency limb of the spatial sensitivity function (for which this mechanism is solely responsible) should fall in a unitary fashion. Thus, the location of the low spatial frequency limb of the highest spatial frequency mechanism can be estimated by noting the spatial location where low pass noise initiates a parallel displacement of high spatial frequency thresholds. The results for such an experiment are shown in Fig. 11. In this Figure contrast sensitivity is plotted for the achromat for low pass noise, whose high frequency cut-off occupies different spatial positions. The filled symbols represent sensitivity without noise and the open symbols represent sensitivity measurements in the presence of noise. A parallel fall in the high spatial frequency limb is seen to occur when the noise cut-off is higher than 0·5 cycles/deg. This suggests that the highest spatial frequency mechanism subserving rod vision has a low spatial frequency cut-off around 0·5 cycles/deg. Thus the highest spatial frequency mechanism subserving rod vision must extend from 0·5 to 6 cycles/deg, with at least a 2 octave overlap with the second highest mechanism.

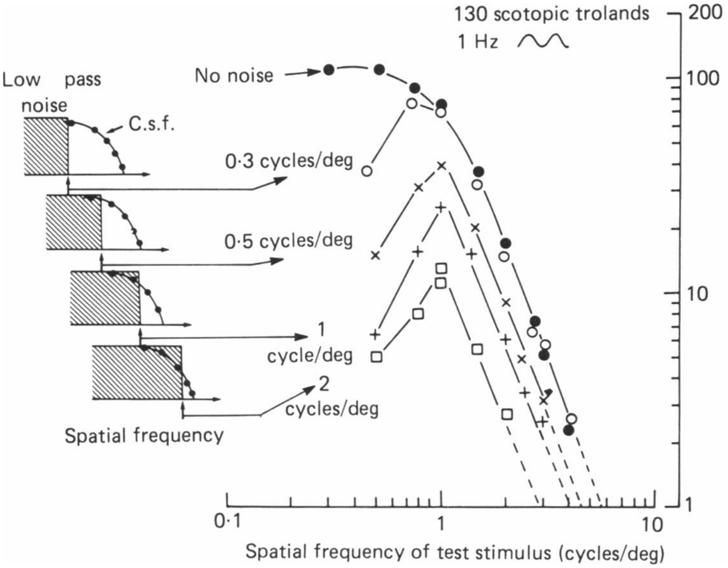

Fig. 11. Threshold contrast sensitivity (threshold^{-1}) is plotted against spatial frequency for the achromat. The stimuli are sine-wave gratings sinusoidally reversing at 1 Hz in spatial noise (○, □, × +) and without spatial noise (●). The spatial noise is low pass with its 3 dB point at 0·3 cycles/deg (○), 0·5 cycles/deg (×), 1 cycle/deg (+) and 2 cycles/deg (□). Note the parallel displacement of all high spatial frequency thresholds for noise whose cut-off is at 0·5 cycles/deg or greater. The insets to the left of the Figure represent the relative positions of the noise cut-off and the high spatial frequency limits of the achromat's contrast sensitivity function (c.s.f.).

Temporal sensitivity

A number of studies using isolation techniques for normal vision have investigated aspects of the temporal sensitivity of the normal rod mechanism. It was once thought that the temporal acuity of rod vision was around 12 Hz on the basis of the double-branched temporal acuity *versus* illuminance response (Hecht & Shlaer, 1936). More recently, the results of Conner & MacLeod (1977) and Conner (1982) have convincingly shown that the rod mechanism has an acuity around 28 Hz. The discontinuity, at around 12 Hz in this function, is attributed to either two rod mechanisms or a reorganization of the temporal properties of one rod mechanism.

Conner (1982) has shown that for temporally modulated fields of light, the isolated rod response can exhibit an acuity of 28 Hz, a peak modulation sensitivity of 10 (Michelson contrast) and an illuminance limit of 1000 scotopic trolands. The temporal transfer function, when measured under mesopic conditions, is bandpass in shape with a peak at around 6–9 Hz.

In the present study, using contrast sensitivity measurements for patterned and unpatterned stimuli, we find that the best sensitivities obtainable by the rod- and cone-mediated mechanisms are similar at low temporal frequencies (0–3 Hz). The peak contrast sensitivity occurs around 8 Hz for the rod mechanism, as compared with 10–12 Hz for the cone mechanism. Rod-mediated contrast sensitivity had a bandpass characteristic under mesopic conditions and can reach 80–100 (equivalent Weber sensitivity of 40–50) under optimum conditions, as compared with 500 for the cone mechanism. Rod-mediated temporal acuity is around 28 Hz, a factor of two below that of the cone mechanism.

The eye movements of the achromat did not interfere with these measurements because first, under mesopic conditions the nystagmus is of small amplitude, and secondly, the stimuli were modulated along an axis orthogonal to the eye movements (see Methods).

Suprathreshold temporal discriminations are also comparable for the rod and cone mechanisms, when compared at their respective optimum illuminances in the low to medium temporal frequency range (0–16 Hz). This is true for stimuli of low (discriminable limit of 6 %) and high (discriminable limit of 6–8 %) spatial frequencies (relative to rod-mediated acuity). For threshold stimuli, the rod mechanism can only make one discriminable jump within its entire temporal range. This is true irrespective of the spatial frequency of the stimulus. For stimuli of low spatial frequency (0·2 cycles/deg) Hess & Plant (1985) have shown that the cone mechanism is capable of two such discriminable jumps; 0 Hz to 4 Hz and 4 Hz to 32 Hz. Since the second discriminable jump falls outside the rod temporal range of 0–30 Hz, the organization underlying these temporal discriminations appears to be similar for rod and cone mechanisms over their shared temporal range. For stimuli of high spatial frequency the cone mechanism, like the rod mechanism, is capable of only one discriminable jump in temporal frequency; 0 Hz can be discriminated from 4–8 Hz, but 4–8 Hz cannot be discriminated from any higher temporal frequency (Watson & Robson, 1981; Thompson, 1983). Again, similar threshold discrimination performance is seen for rod and cone mechanisms over their shared temporal frequency range up to 30 Hz.

These results for cone vision have been used to estimate the possible number of labelled detectors for temporal frequency. The results of Watson & Robson (1981) and Thompson (1983) suggest a minimum of two labelled detectors for temporal frequency within the mid to high spatial frequency range, whereas those of Hess & Plant (1985) have extended this scheme and suggested a minimum of three temporal detectors subserving the low spatial frequency range. This third detector responds to high temporal and low spatial frequencies. If we subject comparable data from the rod mechanism to this interpretation, we conclude that there are the same number, band width and distribution of labelled, temporal detectors subserving rod and cone temporal vision over their shared range. The high temporal frequency detector that the data of Hess & Plant (1985) suggest is located beyond rod acuity and must be driven solely by cones.

Our previous understanding of the rod mechanism has come largely from experiments performed at scotopic illuminances where only the rod mechanism operates. While this is understandable, on the argument that the rod response should be best isolated under these conditions, it has led to the general impression that rod vision, unlike that of cone vision, is severely limited in sensitivity and acuity. For example, the rod-mediated contrast sensitivity has been estimated from a number of previous studies to be 10 (see Shapley & Enroth-Cugell, 1984) and rod temporal acuity around 12 Hz (Hecht & Shlaer, 1936). While these conclusions may be true of a scotopic/photopic comparison they are not true of a comparison of rod/cone mechanisms *per se*, when each is operating at an optimum. The achromat used in these investigations has been shown to be functionally a rod monochromat and, hence, allows an examination of detection and discrimination sensitivity of the rod mechanism for a wide variety of spatio-temporal stimuli at, and above, their detection thresholds under mesopic conditions.

The results suggest that the rod and cone mechanisms are more disparate in their detection sensitivity (i.e. beyond 0·3 cycles/deg and 2 Hz) than they are in their discrimination sensitivity (i.e. beyond 2 cycles/deg and 15 Hz). The peak spatio-temporal detection sensitivity of the rod mechanism is between 80 and 100 for large field sizes (a factor of 5 below that of the cone system) and spatial and temporal acuities are around 6 cycles/deg and 30 Hz respectively (a factor of 10 and 2 below that of the cone system). However, threshold discrimination and suprathreshold discrimination of spatial and temporal stimuli are matched for the rod and cone mechanisms over a large part of their shared (low to medium) spatio-temporal range (up to a factor of two from the rod acuity) for stimuli of constant suprathreshold contrast. Thus, it is likely that within this range the neural machinery that subserves their respective discrimination sensitivities is similar, if not the same, being composed of multiple spatial and temporal neural filters within the same region of the visual field. Hence, the rod mechanism and cone mechanism are capable of very similar suprathreshold performance over most of the spatio-temporal range, and we are left with the intriguing question as to how these two mechanisms of equal suprathreshold sensitivity co-exist under mesopic conditions.

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