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COLOUR VISION AS A POST-RECEPTORAL SPECIALIZATION OF THE CENTRAL VISUAL FIELD

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Abstract—The experiments address the question whether there is evidence that the central visual field is any more specialized for colour than it is for luminance contrast detection. The decline in contrast sensitivity across the visual field for colour-only (red–green) gratings is compared to that for monochromatic luminance gratings at a range of spatial frequencies in the nasal and temporal fields. Measurements are made of the chromatic spatial summation area and the relevant parts of the chromatic temporal contrast sensitivity function at different eccentricities in order to control for their influence on the decline in contrast sensitivity. Results show that at each spatial frequency colour contrast sensitivity declines with eccentricity approximately twice as steeply as luminance contrast sensitivity. The more rapid decline in colour contrast sensitivity than luminance contrast sensitivity across the visual field reveals that chromatic mechanisms are more confined than luminance mechanisms to the central field.

INTRODUCTION

It is well established and can be readily demonstrated that there is a loss of colour sensation in the peripheral visual field. Chromatic stimuli appear more desaturated and hue discrimination deteriorates with eccentricity (Ferree & Rand, 1919; Gordon & Abramov, 1977; Noorlander, Koenderink, den Ouden & Edens, 1983). There are also changes in colour matching resembling protan; deutan and tritan-like defects (Moreland & Cruz, 1958; Gordon & Abramov, 1977; Alpern, 1979). These deficits are dependent on the spatial parameters of the stimulus and are much reduced or eliminated if the stimulus size is increased with eccentricity. For example, the same range of hues and saturations seen in a small (5′) target in the fovea are also seen at 45° for a larger (6.5°) target (Gordon & Abramov, 1977). Hue discrimination across space or time as good as that in the fovea can be achieved at eccentricities as great as 50° by increasing the stimulus size or decreasing its spatial frequency (Noorlander et al., 1983). This and other studies show that with sufficiently large stimuli some colour sensation can be achieved out to eccentricities of 80–90° in the nasal retina (e.g. Wooten & Wald, 1973; Wooten, Fuld & Spillman, 1975).

Some deterioration of colour sensation in the periphery is not surprising, however, because performance on most visual tasks declines with eccentricity. Since aspects of both colour and luminance vision deteriorate with eccentricity, it becomes interesting to ask whether the central visual field can be considered to be any more specialized for colour vision than it is for luminance vision. One approach to this question is to compare, using a common metric, the deterioration with eccentricity of equivalent aspects of colour and luminance vision.

In this paper, the variation across eccentricity of contrast sensitivity to chromatic (colour-only) and luminance gratings is compared. This could have various possible forms, reflecting the extent and type of any specialization for colour processing in the central visual field. Firstly, I was interested to know whether there is any evidence for a region of relatively uniform colour sensitivity followed by a decline, since this could indicate the presence of a discrete physiological or anatomical specialization for colour confined to the central field. There is some anatomical evidence, described in the Discussion, to support this expectation. Other forms of contrast sensitivity loss may also suggest a central field specialization for colour of a different type. For example, a steeper decline in colour contrast sensitivity than luminance contrast sensitivity across the visual field would suggest a relative confinement of colour processing to the central region. This might be expected if, for example, the proportion of neurons exhibiting chromatic sensitivity in the retina or cortex declines with eccentricity.

On the other hand, if colour and luminance contrast sensitivity decline in parallel it would suggest that the central visual field is no more specialized for colour processing than for luminance processing. Thus, the form of this psychophysical relationship may reveal whether colour vision can be considered as a particular specialization of the central visual field and provide a basis for the interpretation of physiological and anatomical data.

METHODS

A more detailed description of the stimulus and a figure of the apparatus can be found in Mullen (1985). A red/green sinusoidal chromatic grating was produced by displaying two luminance modulated gratings, each on Joyce (DM1) display screens with white P4 phosphors. These are each viewed through narrow band interference filters with peak transmissions at 526 and 602 nm respectively. The two monochromatic gratings, presented 180° out of phase, are combined optically to produce a chromatic grating. A bite bar is used to align the subject's head. Viewing is monocular and with a natural pupil. The grating patch is circular and sharp edged. The fixation target is a small light and eccentricity is measured from the centre of the grating patch. Four spatial cycles are displayed horizontally at each spatial frequency and the stimulus is sinusoidally phase reversed at 0.4 Hz unless stated otherwise. The effects of spatial cycle number and the frequency of temporal modulation on contrast sensitivity at different eccentricities are both measured in the investigation.

The contrast of each component luminance grating is defined by the usual formula:

$$C = \frac{I_{max} - I_{min}}{I_{max} + I_{min}}$$

where I_{max} and I_{min} are the peak and trough luminance values respectively. The contrasts of the two component gratings are always equal to each other although their respective mean luminances may differ. Hence the contrast of these component gratings is used to refer to the contrast of the chromatic stimulus. Output contrast was calibrated using a UDT (united Detector Technology) lightmeter and mean luminances were measured with a calibrated SEI spot photometer. The mean luminance of the stimulus is 15 cd/m^2. For the results of Fig. 10 two more recent Joyce screens (DM2) were used and both the mean luminances and contrasts of these were calibrated using a UDT lightmeter. The mean retinal illuminance of the stimulus produced with these screens is 42 cd/m^2. The two component wavelengths in the colour-only chromatic stimulus selectivity stimulate the medium and long wavelength cone-opponent pathways and produce very little modulation in short wavelength cones (see MacLeod & Boynton, 1979).

The chromatic differences of magnification of the eye was corrected at all spatial frequencies by adjusting the spatial frequency of one of the component gratings for foveally-viewed, fully-modulated square-wave stimuli. Further details of the method of correction are given in Mullen (1985) and Mullen and Baker (1985). The gratings are displayed horizontally in the nasal and temporal fields which will eliminate the effects of any residual chromatic difference of magnification. These corrections are important since transverse aberrations produce a wavelength-dependent difference of position on the retina which increases with eccentricity. The chromatic difference of focus of the eye was not corrected because there is a likelihood of introducing further aberrations arising from the misalignment of the optic axis of the correcting lens and the eye for the eccentrically viewed stimuli, but will be small for these wavelengths.

A method of adjustment was used to measure contrast thresholds. Stimuli are displayed continuously and their contrast adjusted by the subject in 0.05 log unit (1 dB) steps until the bar pattern can just be detected. Data points show the means of at least four threshold settings measured in separate experimental runs within one session. Contrast sensitivity to the chromatic stimuli refers to the reciprocal contrast of the component gratings at threshold.

Two subjects were used in the experiments, one of whom is the author. Both have normal colour vision measured using standard tests, including the Farnsworth–Munsell 100-hue test.

RESULTS

Defining colour-only stimuli

The intensity ratio between the two colours in the stimulus required to produce a threshold stimulus detected only by chromatic mechanisms is likely to vary with eccentricity or field size. Variation in the isoluminant point with spatial frequency has been reported to occur for blue–yellow stimuli (Cavanagh, MacLeod &

Anstis, 1987; Mullen, 1985). Variation in the isoluminant match with eccentricity for red–green stimuli has also been reported (Livingstone & Hubel, 1987).

The colour-only point was measured using the method described by Mullen (1985) over the full range of spatial frequencies (0.2–4 c/deg) and at each field size and eccentricity used in the experiments. Contrast sensitivity to the stimulus is measured at different red/green ratios of mean luminances, expressed as the percentage of red light in the overall red–green mixture. Some results are shown in Fig. 1 and further results can be seen in Mullen (1990).

The results shown are for a spatial frequency of 2 c/deg for stimuli viewed foveally and at two eccentricities (10 and 18 deg) in the nasal and temporal fields. In each case a minimum in contrast sensitivity occurs and the colour-only point is defined from the red/green luminance ratio at the minimum. At this point in all of the measurements, two colours can be seen at threshold. This is often called the isoluminant point although since here it does not necessarily correspond to an equation of luminosities it is termed the colour-only point. The results of Fig. 1 show that the position of the minimum changes with eccentricity, notably in this case for the stimulus presented at 18 deg in the nasal field. This result is supported by the measurements made at other spatial frequencies and eccentricities, which are summarized in the next figure (Fig. 2).

In Fig. 2 the ratio at which minimum contrast sensitivity occurs is plotted as a function of eccentricity for all the colour-only points measured. Different symbols indicate results for nasal and temporal fields, and results for all spatial frequencies have been included. These results show that the red/green ratio is constant over a radius of 7 or 8 deg from the fovea, and thereafter a shift occurs towards red indicating that more red is needed in the red/green ratio to obtain the colour-only point. After this shift the ratio is again relatively constant with eccentricity out to the greatest eccentricities measured of 30–36°. The size of the shift is approximately 11 percentage points for KTM (from 50 to 61%) and 7 percentage points for EO'S (from 51 to 58%). There was no evidence for any change in the colour-only point of these stimuli with either field size or spatial frequency. However, it can be seen from Fig. 2 that if a stimulus is presented in a retinal region where the red/green ratio is changing then field size will be likely to have an influence. The measured colour-only

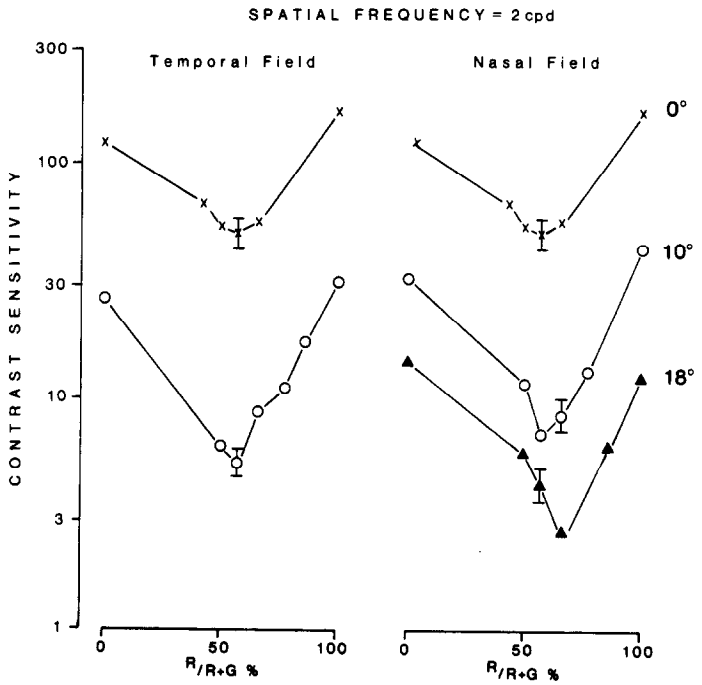

Fig. 1. The stimulus is a red monochromatic luminance grating (602 nm) added in antiphase with a green monochromatic luminance grating (526 nm). Contrast sensitivity is plotted as a function of the ratio of red to green mean luminances in the stimulus expressed as a percentage (see text). Results for three different eccentricities are shown for the nasal field (0, 10 and 18 deg) and two eccentricities for the temporal field (0 and 10 deg). Spatial frequency = 2 c/deg. Subject: KTM.

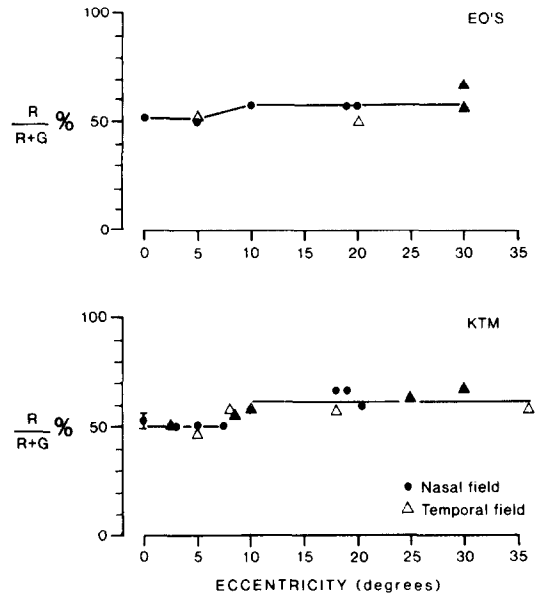

Fig. 2. The ratio of red to green mean luminances (in %) required at the colour-only point for different eccentricities. The colour-only point is defined from a minimum in contrast sensitivity, as described in Fig. 1 and the text. Results for all spatial frequencies are included. Filled circles and hollow triangles indicate nasal and temporal visual field, respectively. (The coincidence of these two symbols appears as a filled triangle.) Upper panel: EO'S; straight lines indicate the average percentage from 0 to 7 deg (51%) and from 12 to 35 deg (58%). Lower panel: KTM; straight lines indicate the average percentage from 0 to 8 deg (50%) and 12 to 36 deg (61%).

points were used for the stimuli in all the following experiments.

A shift in the colour-only point is to be expected since spectral sensitivity changes with eccentricity in the short and medium wavelength regions of the spectrum (e.g. Wooten et al., 1975; Abramov & Gordon, 1977; Stabell & Stabell, 1981a, b). There is no evidence for variation with eccentricity in the relative sensitivities of medium and long wavelength cone types (Stabell & Stabell, 1981a). Factors which cause the change in the short wavelength region of the spectrum, however, include variation with eccentricity in macular pigmentation, the sensitivity of short-wavelength mechanisms and rod sensitivity. The results summarized by Wooten et al. (1975) suggest that the change in sensitivity arising from macular pigmentation is about 0.1 log units which would alter the colour-only point by 6 percentage points. It is also likely, however, that there is some rod contribution to spectral sensitivity for the eccentrically viewed stimuli. Hence, some of the variation in the colour-only point may arise from the cancellation of luminosity arising from combined rod and cone outputs, especially since the mean retinal illuminance of the stimuli (at about 200 td, with a 4 mm natural pupil diameter) is not above rod saturation.

Although rods may influence the intensities in the colour-only point, the fact that two colours can always be seen in the stimulus at threshold indicates that they are not determining detection threshold. The absence of a rod contribution to detection is supported by measurements made at a brighter mean luminance (42 cd/m^2) which produced similar contrast sensitivities (Fig. 10).

Colour contrast sensitivity as a function of eccentricity

The contrast sensitivity to chromatic gratings presented at their colour-only points as a function of eccentricity in the nasal and temporal fields is shown for five spatial frequencies in Fig. 3 for KTM and in Fig. 4 for EO'S. Results show that there is a continuous decline in colour contrast sensitivity across the visual field at each spatial frequency. Colour contrast sensitivity is maintained to greater eccentricities for the lower spatial frequencies. There is no evidence in these results for a region of maintained colour contrast sensitivity in the central visual field.

Some nasal/temporal asymmetries are evident; the most marked occurs after the blind spot at 20–30 deg where chromatic sensitivity is greater in the temporal field than in the nasal field. The asymmetry is more pronounced for chromatic than for luminance thresholds.

The next experiments compare the declines in colour and luminance contrast sensitivity across the visual field in order to test whether there is evidence for a *relative* sparing of colour contrast

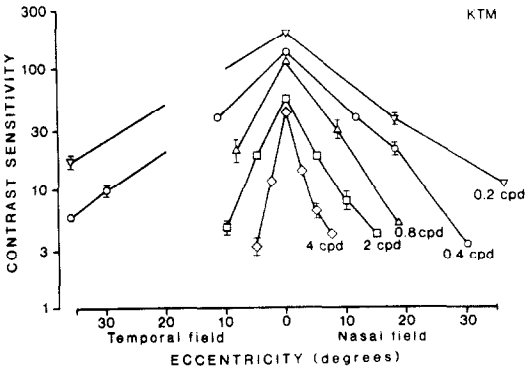

Fig. 3. Contrast sensitivity to colour-only chromatic gratings as a function of eccentricity in the nasal and temporal fields. The colour-only point has been individually assessed for each retinal location and spatial frequency. Results are shown for 5 spatial frequencies: 0.2, 0.4, 0.8, 2 and 4 c/deg. Subject: KTM.

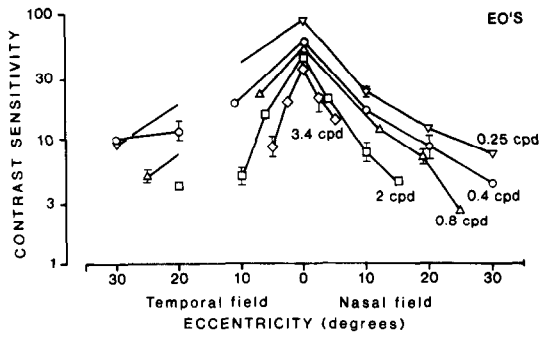

Fig. 4. Contrast sensitivity to colour-only chromatic gratings as a function of eccentricity for 5 spatial frequencies: 0.25, 0.4, 0.8, 2 and 3.4 c/deg. Subject: EO'S. The results for 0.25 and 0.4 c/deg have each been displaced upwards by 0.25 log units to avoid overlap of functions.

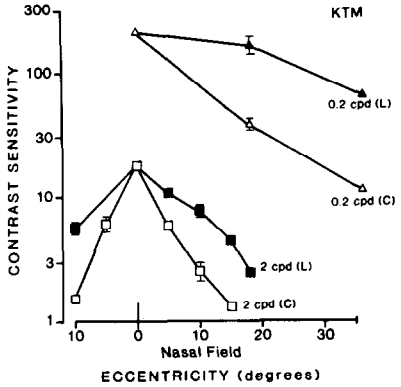

Fig. 5. Contrast sensitivity as a function of eccentricity in the nasal field and the first 10 deg of the temporal field is compared for luminance (L) gratings (filled symbols) and colour-only chromatic (C) gratings (hollow symbols). Results are shown for two spatial frequencies: 2 c/deg (squares) and 0.2 c/deg (triangles). Each spatial frequency has been normalized at the fovea to the contrast sensitivity for the chromatic grating. To avoid overlap of functions all the 2 c/deg results have been displaced downwards by 0.5 log units. Subject: KTM. (Note: for normalization the 0.2 c/deg luminance results have been displaced upwards by 0.375 log units and the 2 c/deg ones downwards by 0.4 log units.)

sensitivity over luminance contrast sensitivity. Luminance contrast sensitivity was measured using the green monochromatic component grating of the chromatic stimulus (0% R/(R + G)) presented at the same spatial and temporal frequencies and mean luminance as the chromatic stimulus. The choice of luminance grating is not important, since contrast sensitivity is the same for the red and green monochromatic gratings. This was confirmed by measuring contrast sensitivities for both red (602 nm) and green (526 nm) monochromatic gratings as part of the procedure for establishing the colour-only point (see Fig. 1). For KTM, contrast sensitivity averaged over all eccentricities and spatial frequencies is 0.07 log units greater to the red than the green gratings (SD = 0.09), and for EO'S the difference is 0.06 (SD = 0.09). Neither of these values is significantly different from zero. No significant difference in contrast sensitivity to the red and green luminance gratings emerges with either eccentricity or spatial frequency.

Results are shown in Fig. 5 for KTM and Fig. 6 for EO'S. The declines were measured for each spatial frequency, but only two are given in each figure to allow for clarity. At each spatial frequency luminance contrast sensitivity has been normalized to the colour contrast sensitivity at the fovea. Some further comparisons can be seen in Mullen and O'Sullivan (1988). For each spatial frequency colour contrast sensitivity declines more steeply than luminance contrast sensitivity across the visual field, indicating that the difference between colour and luminance contrast sensitivity increases with eccentricity.

In Fig. 7, colour and luminance contrast sensitivities are compared at each eccentricity for all spatial frequencies. The ratio of colour contrast sensitivity to luminance contrast sensitivity is plotted as a function of eccentricity. Different symbols show results for different spatial frequencies. Colour and luminance contrast sensitivities have been normalized at the fovea for each spatial frequency in the manner of Figs 5 and 6.

The results demonstrate the decrease in colour contrast sensitivity relative to luminance contrast sensitivity as eccentricity increases. The results for each spatial frequency can be adequately fitted by a linear regression although only the average regression is given in the figure. For KTM the averaged slope is 0.61 ± 0.13 and

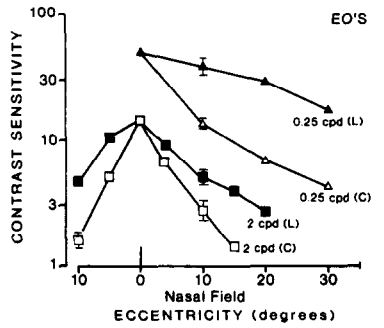

Fig. 6. Contrast sensitivity as a function of eccentricity is compared for luminance and colour-only chromatic gratings; details and symbols as for Fig. 5 legend. The two spatial frequencies are 0.25 (triangles) and 2 c/deg (squares). Subject: EO'S. (For normalization the 0.25 c/deg luminance results have been displaced upwards by 0.15 log units and the 2 c/deg results downwards by 0.31 log units.)

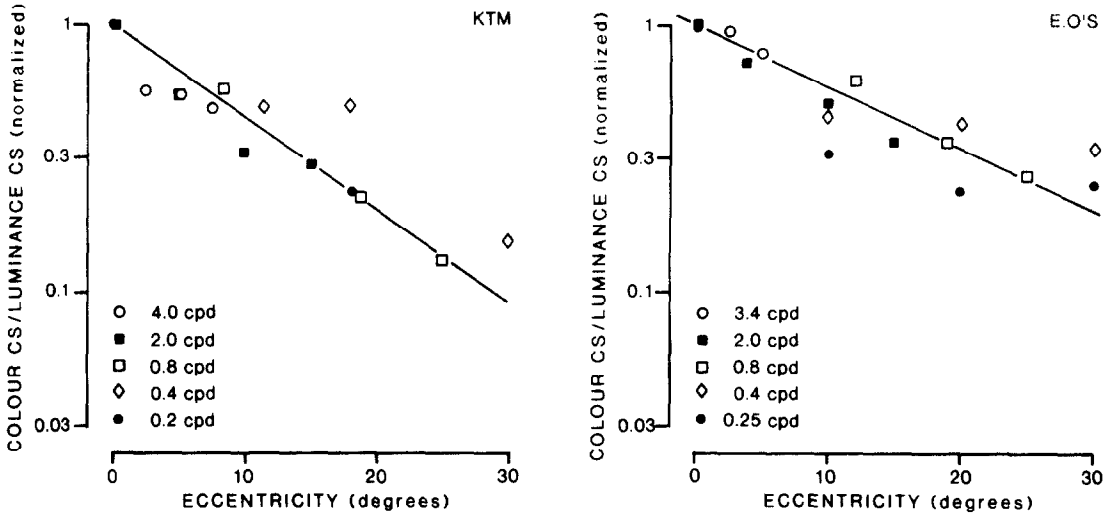

Fig. 7. Colour contrast sensitivity as a proportion of luminance contrast sensitivity is plotted at each eccentricity. This ratio represents the separation between the colour and luminance contrast sensitivities in Figs 5 and 6 and, as in these figures, luminance contrast sensitivity has been normalized to colour contrast sensitivity at the fovea for each spatial frequency. Different symbols show results for different spatial frequencies as marked. Subjects: KTM (left panel) and EO'S (right panel).

for EO'S it is 0.46 ± 0.10. An interesting feature of these results is that the decline in colour contrast sensitivity as a proportion of luminance contrast sensitivity is very similar for each spatial frequency.

In Fig. 8 (upper panels), the slope of the decline in contrast sensitivity with eccentricity is plotted as a function of spatial frequency for colour (squares) and luminance (circles) gratings. The declines in contrast sensitivity with eccentricity, shown in Figs 3–6, were measured by fitting the data with a linear regression. The results show that the form of the function is very similar for both colour and luminance thresholds, however, the vertical displacement between the two functions indicates an overall difference in the value of the slope.

The difference in slope (ratio of the slope of the colour and luminance contrast sensitivity declines) is plotted in the lower panels of the figure for each spatial frequency. Solid curves and circles indicate the results for the nasal field, and broken curves with squares for those for the temporal field. In the temporal field, only contrast sensitivity losses prior to the blind spot could be calculated (i.e. for the two highest spatial frequencies). The results show that, overall, colour contrast sensitivity declines across the nasal field visual field approximately twice as steeply as luminance contrast sensitivity.

The dotted curve and triangles on the lower panel show the ratio which would occur if the loss in colour contrast sensitivity as a proportion of luminance contrast sensitivity is the same for each spatial frequency; i.e. if all the data on Fig. 7 were to fall along the same slope. This assumption accounts for the shallow decline in the ratio of colour slope to luminance slope which occurs across spatial frequency.

Temporal contrast sensitivity as a function of eccentricity

One factor which may influence measurements of colour contrast sensitivity across the visual field is the temporal frequency of the stimulus. Chromatic contrast sensitivity depends on the frequency of temporal modulation of the stimulus and has low pass characteristics; examples of temporal contrast sensitivity functions have been reported by Kelly (1983). If the form of this function were to change with eccentricity, measurements of chromatic contrast sensitivity across the visual field may be affected. In order to ascertain whether such an effect has influenced the results reported here, chromatic contrast sensitivity for a range of temporal frequencies was measured at different eccentricities. The colour-only point was established for each temporal frequency used. No evidence was found for an influence of temporal frequency on these colour-only point within the range investigated and in keeping with other measurements made for these particular stimuli (Mullen & Boulton, 1989).

Results are given in Fig. 9. For KTM (left panel), chromatic contrast sensitivity is measured

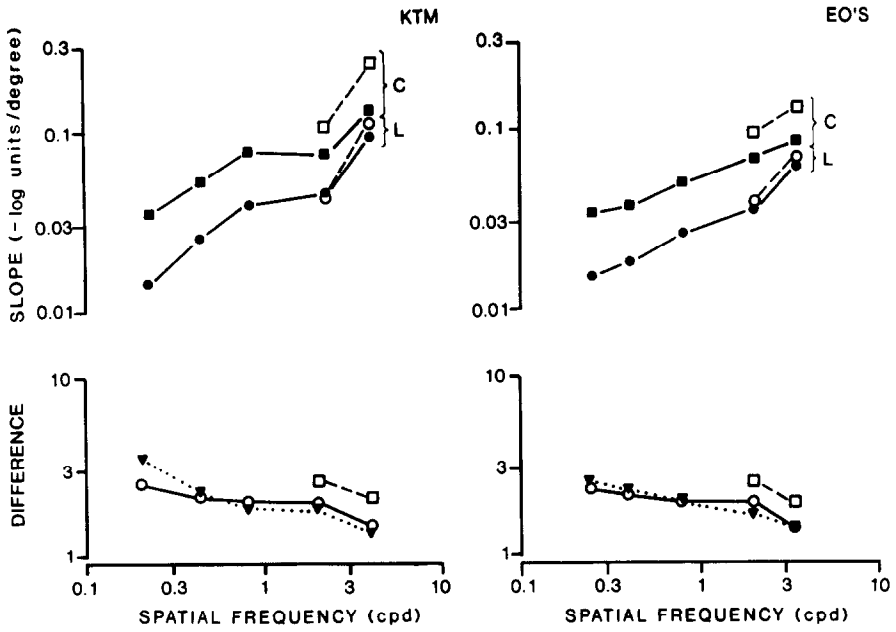

Fig. 8. The upper panels show the gradient of the declines in colour (C; squares) and luminance (L; circles) contrast sensitivity, in log units per degree, at each spatial frequency. Filled symbols give results for the nasal field and open symbols for the temporal field. Gradients for only the two highest spatial frequencies in the temporal field could be calculated, due to the blind spot. The two lower panels show the difference between the colour and luminance gradients, expressed as the ratio of the colour contrast sensitivity gradient to the luminance contrast sensitivity gradient. The open circles give results for the nasal field and open squares give results for the temporal field. The filled triangles and dotted line give the ratio which would be obtained if the decline in colour contrast sensitivity as a proportion of luminance contrast sensitivity was the same each spatial frequency: i.e. if all the results of Fig. 7 are fitted by the same line. Subjects: KTM (left) and EO'S (right).

as a function of temporal frequency for two spatial frequencies (0.4 and 4 c/deg), at the fovea and at an eccentricity of twelve spatial cycles of each stimulus (30 and 3 deg). For EO'S, measurements are also made for two spatial frequencies (0.4 and 4 c/deg) at the fovea and at the two eccentricities given in the legend. The results show no significant change in the shape of these temporal contrast sensitivity functions with eccentricity within the range measured. These results confirm that the temporal frequency used (0.4 Hz) is within the range of optimum chromatic contrast sensitivity at all eccentricities measured and has not affected the rate of decline in contrast sensitivity with eccentricity shown in Figs 3 and 4.

The chromatic summation area as a function of eccentricity

The spatial extent of the grating stimulus may also influence the rate of decline in chromatic contrast sensitivity with eccentricity. For luminance contrast sensitivity, it has been shown that both the number of spatial cycles and their length affects contrast thresholds (Savoy & McCann, 1975; Howell & Hess, 1978; Robson & Graham, 1981). An initial improvement in sensitivity with increasing number of cycles, thought to reflect summation within the receptive fields of the detectors involved, is followed by a much more gradual improvement due to probability summation between detectors (e.g. Savoy & McCann, 1975; Howell & Hess, 1978; Robson & Graham, 1981; Anderson & Burr, 1987). For luminance gratings, the four spatial cycles displayed in the stimulus is sufficient to be within the range of probability summation. However, the dependence of chromatic contrast sensitivity on the spatial extent of the stimulus both foveally and eccentricially is unknown. If, for example, four spatial cycles in the chromatic stimulus is insufficient to produce a near-optimum contrast sensitivity at all eccentricities, the rate of decline of colour contrast sensitivity with eccentricity may be affected.

The dependence of colour contrast sensitivity on the spatial extent of the stimulus was measured at a range of eccentricities. The stimulus was displayed within a circular sharp edged aperture, thus both the number of spatial cycles and the length of the bars are varied simultaneously. Results are given in Fig. 10 for colour-

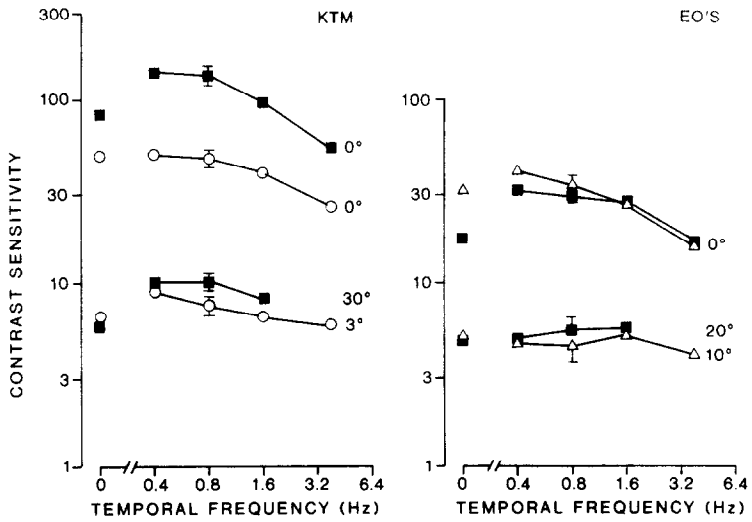

Fig. 9. Contrast sensitivity is plotted as a function of temporal frequency of contrast reversal for colour-only chromatic gratings presented foveally and at various eccentricities in the temporal visual field. For KTM (left panel) results are for a spatial frequency of 0.4 c/deg (squares) presented foveally and at 30 deg eccentricity, and for a spatial frequency of 4 c/deg (circles) presented foveally and at 3 deg. For EO'S (right panel), a 0.4 c/deg stimulus (squares) is presented foveally and at 20 deg and a 2 c/deg stimulus (triangles) is presented foveally and at 10 deg.

only stimuli and show a steep increase in contrast sensitivity as the number of spatial cycles increases, followed by a region of constant or gradually increasing contrast sensitivity.

Both the spatial frequency and eccentricity of the stimulus influence the number of cycles at which the steep increase in contrast sensitivity levels off. For foveal stimuli (left panel of Fig. 10), as spatial frequency increases more spatial cycles are required to obtain constant or nearly constant contrast sensitivity: from approximately one spatial cycle for at 0.24 c/deg to 3.5 cycles at 3.2 c/deg. As eccentricity increases from 10 to 20 deg (middle and right panels of Fig. 10), a greater number of cycles is required at each spatial frequency to obtain constant contrast senstivity: at 20°, approximately 2 cycles for 0.24 c/deg and 6 cycles at 3.2 c/deg are required.

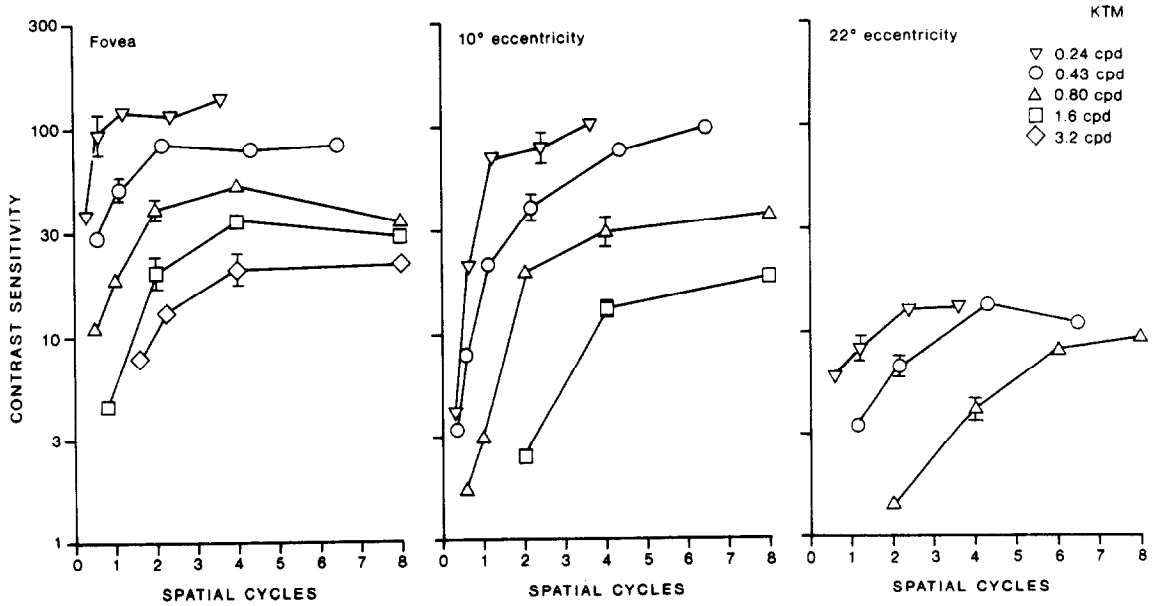

Fig. 10. The three panels show contrast sensitivity to colour-only chromatic gratings plotted as a function of the number of spatial cycles in the stimulus. Each panel shows the results obtained at different eccentricity in the nasal field: 0, 10 and 20 deg from left to right. Different symbols show results obtained for different spatial frequencies as marked. Mean luminance is 42 cd/m^2.

The chromatic contrast sensitivity measurements of Figs 3 and 4 will not be significantly affected by the use of 4 spatial cycles in the stimulus up to an eccentricity of 10 deg. At 20 deg however, chromatic contrast sensitivity to the highest spatial frequency (0.8 c/deg) is affected, since approximately 6 cycles are required to achieve near-optimum sensitivity. The use of 4 cycles has reduced sensitivity by about 0.2 log units and this has increased the calculated slope of decline in contrast sensitivity by 9.5%. Lower spatial frequencies are unaffected at this eccentricity. This small change in slope has not been incorporated in the results since it does not influence the conclusions reached. Also, many of the results require a comparison between colour and luminance effects and it is not known whether the spatial summation for luminance stimuli also varies with eccentricity.

DISCUSSION

Similarities in the processing of colour and luminance contrast across the visual field

An interesting feature of the results is that the *form* of the variation in contrast sensitivity across the visual field is very similar for both colour and luminance stimuli. Sensitivity to both colour and luminance contrast declines smoothly across the visual field at each spatial frequency, approximating a linear function on semi-logarithmic coordinates. The absence of any discontinuities in colour contrast sensitivity within the visual field suggest that there is no *discrete* clustering of post-receptoral chromatic mechanisms within the central visual field. For example, it has been observed that the dendritic field size of the primate retinal P-cells is invariant over the central radius of approx. 8 deg before increasing, whereas that of the M-cells increases continuously (Shapley & Perry, 1986). This has led to speculation that the colour opponent P-cells of the primate central retina might provide the basis for a specialization for colour which is discretely localized to the central field.

Another similarity in the form of the results for colour and luminance contrast lies in the variation in the slope of the contrast sensitivity decline at different spatial frequencies. This is demonstrated in Fig. 11 in which colour and luminance results taken from Fig. 8 (upper panels) are averaged, replotted and compared with the form of previous results obtained for luminance gratings. Eccentricity is expressed in terms of the periods of the stimulus and the decline in contrast sensitivity is plotted in log units per period. The scaling of eccentricity for the size of the stimulus, and so for the putative size of the luminance-detecting mechanisms, has been used in previous studies to show that the slope of the decline in contrast sensitivity is constant above approximately 1.5 c/deg (Pointer & Hess, 1989; Robson & Graham, 1981) but becomes shallower at lower spatial frequencies (Pointer & Hess, 1989).

For present results for luminance gratings follow the same form as these previous results. Furthermore, colour contrast sensitivity displays a similar variation with spatial frequency although with an overall difference in slope. This similarity of form suggests that the factors which govern the variation in luminance contrast sensitivity with eccentricity similarly affect chromatic mechanisms.

What are "equivalent" spatial frequencies for colour and luminance vision?

Is it relevant to make the comparison between the declines in colour and luminance contrast sensitivity at the same spatial frequency? This question arises because single opponent neurones have different spatial tuning for colour and luminance contrast (Ingling & Martinez, 1983, 1985; Thorell, DeValois & Albrecht, 1984). Hence a colour and luminance grating of the same spatial frequency will produce an optimum response in groups of single opponent neurones with different average receptive field sizes. On the other hand, if the chromatic-detecting mechanisms have band-pass spatial

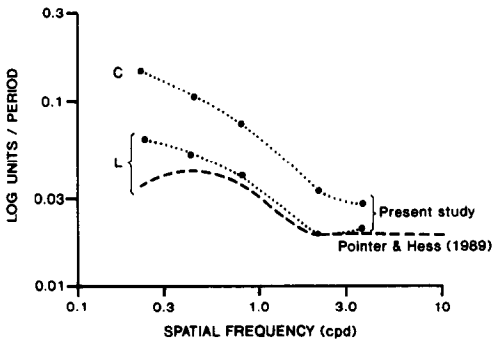

Fig. 11. The gradient of the decline in contrast sensitivity in log units per period of the stimulus is plotted as a function of spatial frequency. The dashed curve gives the form of the results for luminance gratings taken from Pointer and Hess (1989). The dotted curves give the present results (from Fig. 8, averaged across subjects) for luminance gratings (lower curve) and colour-only chromatic gratings (upper curve). (Note: results of Pointer & Hess have been matched on the vertical axis to the present luminance results.)

characteristics, as have the dual opponent neurones of the primate cortex (Thorell et al., 1984; Michael, 1978), comparisons between colour and luminance contrast at the same spatial frequency would represent a comparison at a neuronal level between filters of the same average size.

Psychophysical studies of adaptation and masking suggest that chromatic detection is by band pass mechanisms (DeValois & Switkes, 1983; Switkes, Bradley & DeValois, 1988; Bradley, Switkes & DeValois, 1988). Furthermore, when the effects of masking transfer (from chromatic masks to luminance test gratings) the peak effect on the test stimulus occurs at the same spatial frequency as the masking stimulus (DeValois & Switkes, 1983; Switkes et al., 1988). These results suggest that luminance and chromatic-detecting mechanisms have a peak responses at the same spatial frequency. Thus the comparisons in this study between contrast sensitivity to colour and luminance gratings of the same spatial frequency are likely to be between neural detection mechanisms of similar average receptive field size.

Further evidence to support this conclusion comes from the comparisons of the declines in colour and luminance contrast sensitivity with eccentricity at different spatial frequencies summarized in Fig. 11. A horizontal translation of the colour function on the figure does not provide a good fit to the luminance results. In other words, the results for the chromatic stimuli cannot be simply matched to the results for luminance gratings of a lower spatial frequency. Hence, the suggestion that similar neural mechanisms are detecting both colour and luminance contrast but with a shift in optimum spatial frequency is not supported by the results.

Differences in the processing of colour and luminance contrast across the visual field: evidence for specialization

The results have shown that there is a steeper decline in colour contrast sensitivity than luminance contrast sensitivity across the visual field at each spatial frequency, resulting in a continuous decline in colour contrast sensitivity relative to luminance contrast sensitivity. This suggests that there is a greater confinement of post-receptoral chromatic mechanisms than luminance sensitive mechanisms to the central visual field and that the central visual field has a greater degree of specialization for colour contrast detection.

What might be the physiological origin of this result? There are many possible factors which could influence the decline in the colour sensitivity relative to luminance contrast sensitivity across the visual field. Firstly, the relative sensitivity to colour and luminance contrast may be affected by the degree, or strength of opponency of individual cone-opponent mechanisms and this may change with eccentricity. Secondly, the relative numbers of individual opponent and non-opponent neural mechanisms may vary with eccentricity. Other factors may also have an influence, such as a variation in the contrast gains of chromatic and achromatic units with eccentricity. Furthermore, since contrast thresholds are being measured in this study, the variation of these factors may only be important within the neural population which determines threshold.

It is interesting that Derrington, Krauskopf and Lennie (1984) find no change in the degree of opponency of primate parvocellular neurones within a central radius of 10 deg. De Monasterio and Gouras (1975) report a decline in the proportion of colour opponent ganglion cells in the primate retina with eccentricity, although this effect may be reduced if concealed colour opponent units are counted with the opponent units, since these are reported to increase eccentrically (De Monasterio, Gouras & Tolhurst, 1975).

There is no evidence for any change with eccentricity in the proportion of M- and P-cells projecting from the primate retina to the LGN, although only eccentricities greater than 10 deg could be measured (Perry, Oehler & Cowey, 1984). There are, however, reports of differential projections from the LGN to the recipient cortical layers of primate P-cells and M-cells with eccentricity such that the relative projection of M-cells become more dominant with eccentricity (Connolly & van Essen, 1984; Schein and De Monasterio, 1987). However more direct measurements of the M- and P-cell innervation of the striate cortex have not supported these results (Livingstone & Hubel, 1988). Furthermore, there is evidence that the neural density within the M- and P-cell recipient cortical layers is constant with eccentricity (Livingstone & Hubel, 1988). A direct interpretation of psychophysical results from these anatomical data, however, is not possible since P- and M-cells are not the exclusive or unique sub-cortical substrate for, respectively, colour and luminance contrast detection. For example, P-cells are

sensitive to both colour and luminance contrast and M-cells can have some degree of colour opponency (Derrington et al., 1984). Furthermore, the psychophysical evidence outlined above suggests that the contrast detection mechanisms are more likely to be cortical in origin than sub-cortical.

An interesting aspect of these results is that the decline in the colour contrast sensitivity as a proportion of luminance contrast sensitivity with eccentricity is very similar for each spatial frequency. Although there is some scatter in this result, particularly for the two lowest spatial frequencies measured, it suggests that the decline in colour contrast sensitivity relative to luminance contrast sensitivity depends on the retinal or cortical location of the stimulus regardless of its spatial frequency.

Naso–temporal asymmetries

The most noticeable naso–temporal asymmetry occurs beyond the blind spot where contrast sensitivity is greatest in the temporal field. There are too few data points to allow functions for the decline in contrast sensitivity to be fitted in this field, however the effect has been confirmed by further measurements, and is more pronounced for colour than luminance contrast sensitivity (Anderson, Mullen & Hess, 1989). Naso–temporal asymmetries in performance on various visual tasks have been reported before including for incremental sensitivity (Ferree & Rand, 1919) colour contrast sensitivity (Noorlander et al., 1983) and luminance contrast resolution and vernier acuity (Fahle & Schmidt, 1988), although other tasks show no asymmetry (e.g. Blake & Mills, 1979). These effects may be related to the asymmetric distribution in the density of cones and ganglion cells in the nasal and temporal retina, which show a more rapid decline in cell density on the nasal retina (Perry et al., 1984; Perry & Cowey, 1985). The observation that the effect is more pronounced for the chromatic than luminance stimuli at the same spatial frequency is probably accounted for by the generally steeper decline in colour contrast sensitivity than luminance contrast sensitivity with eccentricity, since the steeper the overall decline in performance of a task across the visual field the greater the absolute magnitude of any asymmetry at a particular eccentricity.

A less marked asymmetry but in the opposite direction also occurs before the blind spot since here contrast sensitivity is less, and the rate of decline steeper, in the temporal than the nasal field. The effect is small and appears to be confined to the chromatic stimuli, but may be too small to detect for the luminance gratings.

The chromatic summation area

These results show that the use of four spatial cycles in the stimulus is sufficient to produce near optimum contrast sensitivity for most spatial frequencies out to an eccentricity of 20 deg. However, as a study of chromatic spatial summation they have to be interpreted within the limitations of the experimental procedure used. The presentation of stimuli within a sharp-edged surround means that they are not well localized in spatial frequency and the variation in size will affect their overall spatial frequency content. The height and the number of cycles in the stimuli covary and both of these may have an influence on the change in contrast sensitivity. The change in contrast sensitivity for increasing stimulus size may also be affected by the variation in contrast sensitivity within the stimulus area. The foveal results resemble those of Anderson and Burr (1987) although these were obtained for luminance contrast using a motion discrimination task. Despite their limitations the present results suggest that the chromatic spatial summation area depends on spatial frequency and that this dependence changes with eccentricity. One possible interpretation of these results is that the size of the chromatic receptive field selective for each spatial frequency increases with eccentricity.

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