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Anisotropy in the chromatic channel: A horizontal–vertical effect*

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Abstract—We compared the chromatic contrast thresholds of drifting (2 Hz) red-green sine-wave gratings of horizontal, vertical, and two oblique orientations at three spatial frequencies (2, 4, 8 cpd). Luminance contrast thresholds for yellow-black gratings were also obtained. The classic oblique effect was found for high spatial frequency luminance and chromatic stimuli. For chromatic thresholds, a significant difference was found between the horizontal and vertical thresholds of all observers. One observer was retested with her head tilted 45 deg and demonstrated that the anisotropy was specific to retinal coordinates. These results give evidence for orientation selectivity in the chromatic channel which is at least partially independent of that in the luminance channel. We estimated the degree of lateral chromatic aberration in our observers' eyes and discuss the possible contribution of this aberration to the horizontal–vertical difference in the chromatic channel.

INTRODUCTION

On a variety of tasks involving the resolution of luminance contours humans are more sensitive to horizontal and vertical orientations than to oblique orientations (Howard, 1982); this orientational anisotropy is known as the 'oblique effect' (Appelle, 1972). The oblique effect in contrast sensitivity is most pronounced at the high spatial frequencies (Campbell *et al.*, 1966; Mitchell *et al.*, 1967) and low temporal frequencies (Nelson *et al.*, 1984) and is believed to be neural in origin since it remains after the optics have been bypassed with laser interference techniques (Campbell *et al.*, 1966). The phenomenon for luminance contours has been attributed to a greater proportion of orientation detectors tuned to horizontal and vertical lines than to oblique lines (Mansfield, 1974) and to differences in the breadth of tuning for various orientations (Rose and Blakemore, 1974). These differences appear to be induced by early visual experience (Hirsch and Spinelli, 1970).

For chromatic stimuli, however, Kelly (1975) reported that humans show equal sensitivity to flickering red-green gratings that are oriented along the cardinal and oblique axes. Kelly argued that this absence of the oblique effect would be expected if the color system does not have orientation selectivity. However, physiological evidence for chromatic simple cells in the striate cortex of the monkey (Poggio *et al.*, 1975; Michael, 1978) points to a possible mechanism for orientation selectivity in the chromatic channel. If the chromatic channel is orientation-selective and analyzes

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orientation independently of the luminance channel, then it may exhibit an anisotropy which differs from the standard oblique effect. The present experiment was designed to test this possibility. We compared the patterns of luminance and chromatic contrast thresholds for drifting gratings at four orientations and three spatial frequencies.

METHODS

Subjects

The authors and two others served as observers. They had normal or corrected-to-normal acuity and no measurable astigmatism or color vision defects. All were aware of the general purpose of the study and were experienced psychophysical observers of whom only one subject (AM) had not previously performed contrast threshold measurements.

Stimuli

The stimuli were sine-wave gratings modulated in color (red-green) or luminance (yellow-black). They were produced by a 512×480 resolution Grinnell Graphics System and displayed on a Conrac 5411 monitor. Red and green luminance gratings were generated by the phosphors of the monitor and added in antiphase to produce the red-green chromatic grating, and added in phase to produce the yellow-black luminance grating. The 1931 CIE chromaticity coordinates of the red and green phosphors were $x = 0.596$, $y = 0.346$ and $x = 0.293$, $y = 0.604$, respectively. The luminance contrast of the yellow-black grating was defined as the difference between the maximum and minimum luminances of the grating divided by their sum. Thus, a grating with 2% luminance contrast was the sum of a red and a green grating added in phase, each at 2% contrast. The red-green gratings were modulated symmetrically about the equiluminant yellow point (CIE coordinates $x = 0.485$, $y = 0.440$) between the red and green points specified above, and the chromatic contrast of these gratings was defined in terms of the percentage of the maximum chrominance modulation obtainable with the red and green phosphors. Hence, a 100% chromatic contrast grating was produced by modulating both the red and green phosphors at 100% contrast and adding them in antiphase, and similarly, a grating with 2% chromatic contrast was composed of red and green gratings added in antiphase, each modulated at 2% contrast.

All gratings appeared within a square aperture which subtended 2 deg^2 of visual angle at the 7.73 m viewing distance. The display, which was the only source of illumination in the room, had a mean luminance of 26 cd/m^2 and a dark surround. The gratings had spatial frequencies of 2, 4 or 8 cycles per degree (cpd) of visual angle. These relatively low spatial frequencies were not ideal for detecting an oblique effect in the luminance channel but we wished to obtain chromatic thresholds in the same frequency range and 8 cpd is near the acuity limit, 11–12 cpd, of the chromatic channel (Mullen, 1985). The gratings were presented at each of four orientations: vertical (90 deg), horizontal (0 deg), right oblique (135 deg) and left oblique (45 deg). The orientation of the stimulus was determined by the angular position of an optical system composed of three front-surface mirrors arranged to work like a dove prism. The oval-shaped fixation point at the center of the square display provided a cue to grating orientation, as well as a stimulus for accommodation. The gratings moved at a rate of 2 Hz in either of the two directions orthogonal to the grating axis.

Procedure

The testing was done monocularly using the natural pupil. The head was fixed with a dental impression bite bar. After adapting to the level of screen luminance the observer viewed the image of the stimulus reflected by the mirrors, through an achromatizing lens (Powell, 1981) which corrects axial chromatic aberrations of the eye. First luminance, then chromatic contrast thresholds were obtained for the four orientations at each of the three spatial frequencies. For both luminance and chromatic threshold measurements the four orientations were presented randomly to each subject, and the spatial frequencies were shown in ascending order. The psychophysical procedure was a revised ascending method of limits in which a computer-implemented algorithm allowed the contrast to increase more slowly through the anticipated threshold region (Brussel and Cavanagh, 1984). The observer's task was to initiate the trial and then to signal with a joystick when a grating was visible. The direction of grating motion was randomized on every trial.

Each luminance threshold was the mean of 12 measurements and a chromatic threshold was derived from 30 trials, six at each of five different red/green contrast ratios in the neighborhood of equiluminance. The chromatic threshold was defined as the highest threshold found within this range. The maximum threshold is assumed to occur at equiluminance since, in this spatiotemporal region, a chromatic grating is least visible when it contains no luminance contrast (Kelly, 1983; Mullen, 1985). The range of red/green ratios used in the experiment is shown in Fig. 1. The rise in threshold at equiluminance is shown in Fig. 1 where the five thresholds at the different red/green ratios have been combined across spatial frequencies, orientations and observers. The peak values were aligned and normalized to a contrast ratio of 1.0 and the red/green contrast values normalized to a maximum of 1.0. The red/green ratios of 0.87 and 1.14 represent values used only in some conditions by Observers PC and CM. The red/green ratio which produced the highest threshold, or the equiluminance point, did not vary

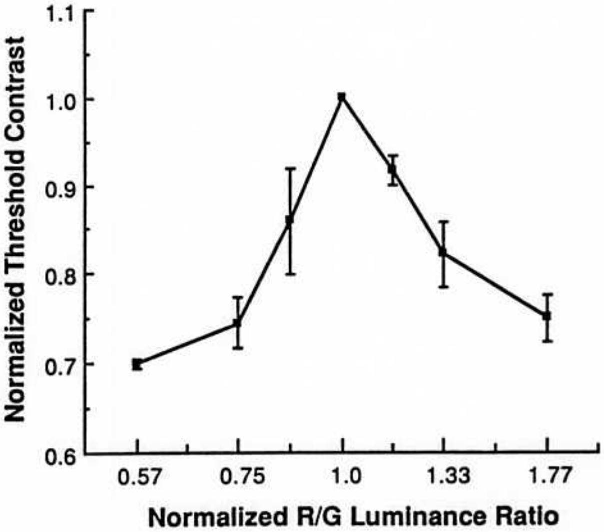

Figure 1. The range of red/green contrast ratios used to establish the equiluminance point. Chromatic contrast thresholds for all conditions and observers are aligned at the red/green contrast having the highest value and normalized to a maximum value of 1.0 before averaging. The means are plotted as a function of the normalized red/green contrast ratio of the stimulus. The vertical bars show standard errors of the mean (± 1 S.E.M). The peaks of the functions are defined as the chromatic thresholds at red/green equiluminance.

systematically with spatial frequency, confirming previously published results (Cavanagh *et al.*, 1987) or with orientation.

To examine the reliability of the threshold measurements and to check for apparatus artifacts, observer CM was retested one month later with her head tilted 45 deg to the right. The procedure was similar to that of the main experiment but only gratings of 2 cpd were used.

RESULTS

The luminance and chromatic thresholds of the four observers are shown in Fig. 2a and b, respectively. The thresholds are plotted against grating orientation for the three spatial frequencies. The chromatic values represent the mean of six measurements at red/green equiluminance and the luminance data are derived from 12 trials. In general, the luminance threshold functions were double-peaked at the higher spatial frequencies whereas a single-peaked anisotropy best described the chromatic data.

To investigate whether statistically significant differences between the luminance and chromatic anisotropies existed for each observer, a three-factor [Grating Type (2) × Spatial Frequency (3) × Orientation (4)] analysis of variance for unequal groups was performed on the individual thresholds. Since Orientation was the variable of interest, we will discuss only the effects of Orientation and its interactions. All four subjects showed a significant main effect of Orientation and a significant three-way interaction between Grating Type, Spatial Frequency and Orientation was present in the results of three of the observers [PC: $F(6, 192) = 4.7$, $P < 0.001$; AM: $F(6, 192) = 38.4$, $P < 0.001$; CM: $F(6, 192) = 5.9$, $P < 0.001$]. Observer DG exhibited a main effect of Orientation [$F(3, 192) = 10.8$, $P < 0.001$)] and an Orientation by Spatial Frequency interaction [$F(6, 192) = 6.5$, $P < 0.001$)]. These results confirm that for three observers, the effects of the four orientations were different for luminance and chromatic stimuli, at least at certain spatial frequencies.

The overall analysis of variance was designed to detect differences in thresholds between the four orientations, but we were more interested in describing the specific anisotropies present in the data. To do this, tests of orthogonal linear contrasts between group means were incorporated into the analysis of variance. One set of contrasts was used to determine whether the two oblique thresholds were significantly higher than the vertical and horizontal thresholds (Oblique Effect), and the other set examined whether there was a significant difference between the horizontal and vertical thresholds (H–V Effect). Interactions of each of these two sets of contrasts with Grating Type and/or Spatial Frequency could also be assessed.

Horizontal–vertical effect

Our main and unexpected finding was of a significant difference between the horizontal and vertical thresholds (H–V Effect) which was present only for chromatic thresholds. For three observers, the vertical thresholds were higher than the horizontal thresholds while the fourth observer (AM) exhibited the opposite pattern (See Fig. 2).

For Observers DG and CM the H–V Effect was present overall for chromatic gratings, as revealed by an interaction between the H–V Effect and Grating Type and by estimates of the linear contrast [DG: $F_{\mathrm{H-V \times GT}}(1, 192) = 4.2$, $P < 0.05$, $t_{\mathrm{Chrom}}(192) = -3.6$, $P < 0.001$; CM: $F_{\mathrm{H-V \times GT}}(1, 192) = 176.5$, $P < 0.001$, $t_{\mathrm{Chrom}}(192) = -15.9$, $P < 0.001$]. The other two observers displayed a significant three-way interaction between the H–V Effect, Grating Type and Spatial Frequency (PC: $F(1, 192) = 18.6$,

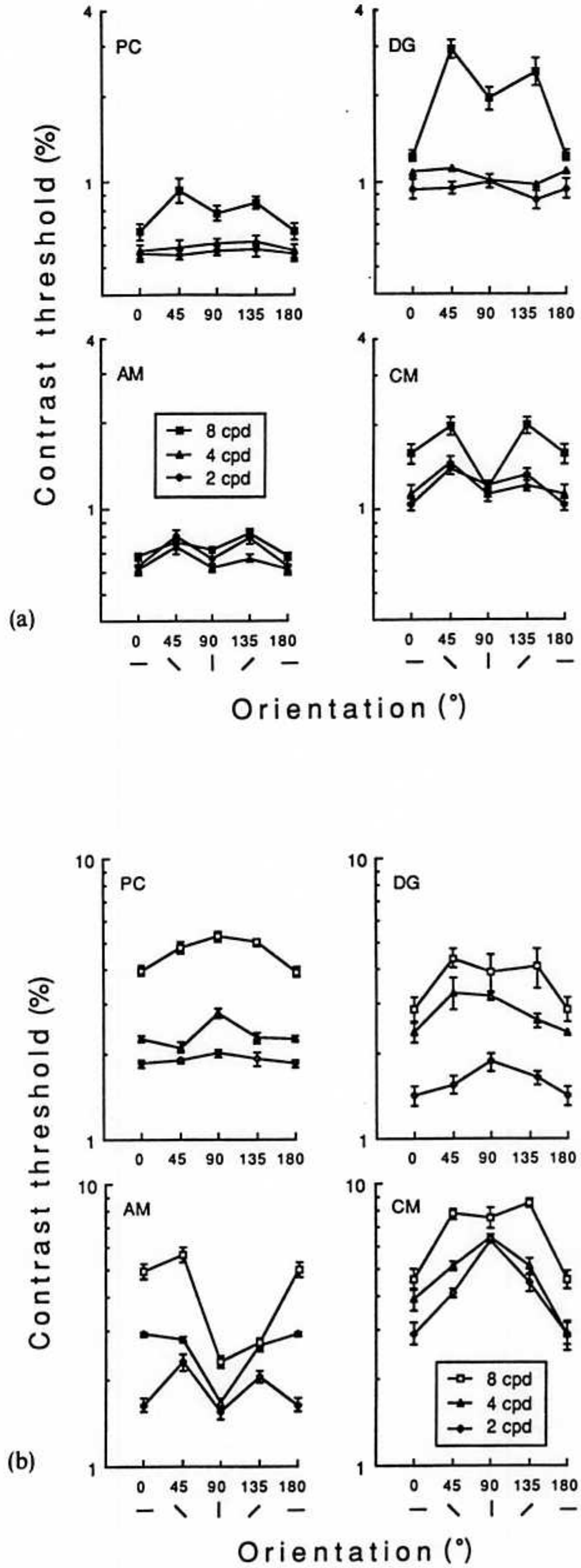

Figure 2. (a) The luminance contrast thresholds of the four subjects. The thresholds are plotted against grating orientation for each of the three spatial frequencies and each threshold is the mean of 12 measurements. Vertical bars show ± 1 S.E.M. (b) Individual chromatic contrast thresholds are plotted against grating orientation for each of the three spatial frequencies. A chromatic threshold was derived from six measurements at red/green equiluminance (see text for details). Standard errors bars are shown.

$P < 0.001$; AM:$F(1, 192) = 86.0$, $P < 0.001$] and subsequent estimates indicated that the H–V Effect occurred only for chromatic gratings at 4 and 8 cpd (PC:$t_4(192) = -3.8$, $P < 0.001$; $t_8(192) = -9.4$, $P < 0.001$; AM:$t_4(192) = 8.1$, $P < 0.001$; $t_8(192) = 16.6$, $P < 0.001$].

In summary, the four observers exhibited a significant H–V Effect for chromatic but not luminance gratings. The direction of the H–V difference, however, was not the same for all observers; three of them displayed higher vertical than horizontal thresholds and AM showed the opposite pattern.

Oblique effect

All observers exhibited an oblique effect for high spatial-frequency luminance and chromatic stimuli (see Fig. 2). A significant interaction between the Oblique Effect and Spatial Frequency was present in the data of two observers [PC:$F(1,192) = 8.0$, $P < 0.01$; DG:$F(1, 192) = 21.2$, $P < 0.001$) and subsequent estimates of this anisotropy at the three spatial frequencies revealed that it appeared only at 8 cpd (PC: $t(192) = -3.8$, $P < 0.001$; DG: $t(192) = -6.2$, $P < 0.001$]. Observer CM displayed an interaction between the Oblique Effect, Spatial Frequency and Grating Type [$F(1, 192) = 27.4$, $P < 0.001$) and according to subsequent estimates the Oblique Effect was greater for 8 cpd chromatic gratings than for luminance gratings of the same spatial frequency [$t_C(192) = -9.2$, $P < 0.001$; $t_L(192) = -3.8$, $P < 0.001$]. She did not show an Oblique Effect at spatial frequencies of 2 and 4 cpd. The fourth observer (AM) displayed a significant interaction between the Oblique Effect and Grating Type [$F(1, 192) = 29.4$, $P < 0.001$), with the anisotropy being greater for chromatic stimuli [$t_L(192) = -2.4$, $P < 0.05$; $t_C(192) = -8.3$, $P < 0.001$]. The Oblique Effect occurred at all spatial frequencies in this observer.

Thus, the oblique effect was found among both chromatic and luminance thresholds. However, the anisotropy was most prevalent at the highest spatial frequency tested.

Head tilt data

The results obtained from CM with her head tilted 45 deg were compared with the thresholds measured one month earlier with her head upright. These data are shown in Fig. 3. In the left-hand graph, luminance and chromatic thresholds for the head-upright and the head-tilted observer are plotted as a function of the grating's orientation on the retina. The same data are shown in the right-hand graph, but with orientation specified with respect to the ground. It is apparent from this figure that when orientation is described in retinal coordinates, the thresholds obtained with the head tilted closely match those derived with the head upright with the exception of one point (see Fig. 3 left). In contrast, there is very little correspondence between the two sets of data when orientation is specified with respect to the ground (see Fig. 3 right).

A three-factor analysis of variance (Head Position, Grating Type, Orientation) with incorporated tests of linear contrasts (H–V Effect, Oblique Effect) was performed on CM's thresholds. A main effect of Head Position was not found but significant three-way interactions were present for both anisotropies [$F_{\mathrm{HP \times GT \times Ob}}(1, 143) = 24.1$, $P < 0.001$; $F_{\mathrm{HP \times GT \times H-V}}(1, 143) = 23.2$, $P < 0.001$). According to the results of Scheffé's F-tests performed on the group means, only the vertical chromatic threshold (90 deg) varied significantly with head position [$F(15, 128) = 27.9$, $P < 0.05$].

The drop in the vertical chromatic threshold which occurred when the head was tilted had the expected consequences for the two chromatic anisotropies. The Oblique

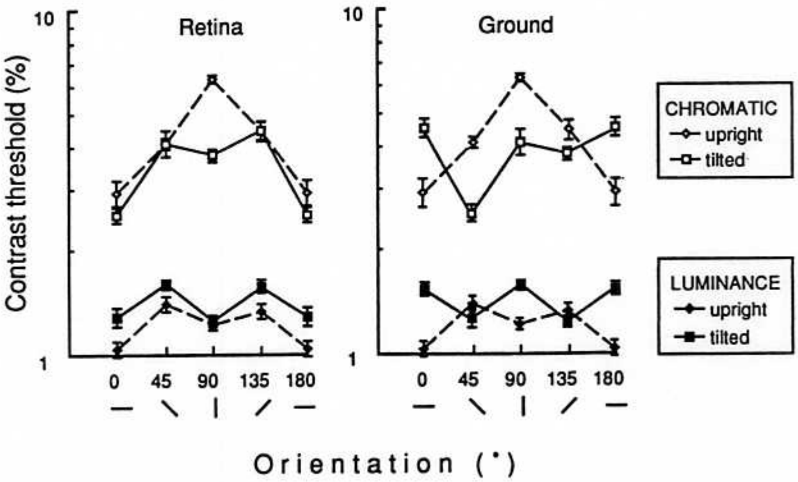

Figure 3. The thresholds obtained from observer CM with her head upright (broken lines) versus her head tilted 45 deg to the right. In the left-hand graph luminance and chromatic thresholds are plotted as a function of the retinal orientation of the grating. In the right-hand graph the same thresholds are plotted against the orientation of the grating with respect to the ground. The spatial frequency of the gratings was 2 cpd. Each luminance threshold is the mean of 12 measurements, and a chromatic threshold was derived from six measurements at red/green equiluminance. The vertical bars indicate ± 1 S.E.M.

Effect increased in magnitude when the head was tilted and the H–V Effect was attenuated. There was no Oblique Effect for chromatic gratings when the head was upright, but one appeared when the head was tilted [$t_U(143) = 2.1, P < 0.01$; $t_T(143) = -7.0, P < 0.001$; negative t values indicate an Oblique Effect]. In contrast, the Oblique Effect was always present for luminance gratings. The H–V effect in the chromatic thresholds existed for both head positions but the effect was attenuated when the head was tilted [$t_U(143) = -14.7, P < 0.001$; $t_T(143) = -5.5, P < 0.001$]. There was no H–V effect for luminance stimuli.

In summary, there was a significant change in one threshold when the observer was tested one month later with the head tilted 45 deg. The H–V Effect was present only for chromatic stimuli, however, whether the head was upright or tilted.

DISCUSSION

There is considerable intersubject variability in the present results but we believe that overall, the luminance and chromatic anisotropies are sufficiently different to merit attention. The chromatic channel is clearly anisotropic with the most pronounced differences in sensitivity occurring between the horizontal and vertical orientations. Within the spatiotemporal region tested, large and consistent differences between the two cardinal thresholds are present only in the chromatic channel. In contrast, the double-peaked oblique effect exists in both luminance and chromatic channels, and in accord with the reports of previous investigators (Campbell *et al.*, 1966) we find that the luminance oblique effect occurs only at high spatial frequencies. The presence of the horizontal–vertical effect in the chromatic channel suggests that there is orientation selectivity in the chromatic channel that is at least partially independent of that in the luminance channel.

The fact that the oblique effect was found for both types of threshold may be evidence for some overlap in the processing of orientation by the luminance and chromatic channels. This conclusion was reached by Flanagan *et al.* (1987) in their recent study of luminance and chromatic tilt aftereffects. In the present experiment, however, the presence of the oblique effect in the chromatic thresholds may be due to optical rather than neural factors. For instance, an oblique effect could appear in the chromatic thresholds if the red-green gratings contained some luminance modulation. Kelly (1975) found an oblique effect when 3 cpd chromatic gratings were flickered at frequencies below 10 Hz. Because the oblique effect was absent for stimuli of a lower spatial frequency to which the chromatic channel is relatively more sensitive, Kelly concluded that the subjects responded to a spurious luminance component in the red-green gratings. A similar explanation could be given for our results since the oblique effect appeared at the same spatial frequency (8 cpd) in both luminance and chromatic thresholds. At this relatively high spatial frequency the effects of chromatic aberration are the most severe, and the slightest deviation of the eye from the proper position in front of the achromatizing lens could result in a luminance modulation in the red-green display. Therefore at present we have not eliminated the possibility that a luminance artifact due to chromatic aberration is responsible for the oblique effect in the chromatic thresholds.

We propose that the horizontal–vertical anisotropy is evidence for orientation selectivity in the chromatic pathway. First, however, we will evaluate the likelihood that our results were caused by a physical difference between the horizontal and vertical stimuli arising from the apparatus or the optics of the eye. It is unlikely that some orientation-specific artifact in the apparatus produced the horizontal–vertical effect, for one subject showed the same effect but with opposite sign. Nonetheless, we checked for an apparatus artifact by re-testing one of the subjects with her head tilted and the difference between horizontal and vertical effect chromatic thresholds persisted. The dependence of the horizontal–vertical effect on the retinal orientations of the stimuli demonstrates that the effect has its origin in the visual system rather than in the apparatus. The most obvious optical source for a single-peaked anisotropy is astigmatism. However, none of the observers' eyes were astigmatic; an optometrist failed to find evidence for astigmatism in the three observers he examined at the beginning of the study and the fourth observer (PC) showed no signs of it in a laboratory test. Furthermore, the observers did not exhibit a significant horizontal–vertical difference in the luminance thresholds which would be expected if astigmatism were to explain this anisotropy.

One potential source of the horizontal–vertical effect in the chromatic channel which was not controlled in the study is lateral chromatic aberration. This type of chromatic aberration is not corrected for the Powell achromatizing lens. In most human eyes the optic axis intersects the retina about 4–5 deg nasally and 1.5 deg upwards from the fovea (Bennett and Francis, 1962) producing chromatic dispersion of the retinal image with the blue end of the spectrum on the nasal side (Vos, 1960). This wavelength-specific displacement of the image, known as lateral chromatic aberration, could be responsible for a luminance artifact at the orientation orthogonal to the direction of the shift and hence produce the chromatic anisotropy. Luminance thresholds would be similarly affected only if the lateral chromatic aberration is very large (Thibos, 1987). Since the lateral displacement of the image is usually larger than its vertical shift, typically the luminance artifact in the chromatic stimuli is more evident in vertical than horizontal gratings (Thibos, 1987) and this makes vertical gratings more visible. Three of our four observers, however, displayed *lower* sensitivity to vertical than horizontal gratings, the opposite to what would be predicted by a luminance artifact associated with lateral chromatic aberration.

Nevertheless, since lateral chromatic aberration is known to vary from individual to individual (Obgoso and Bedell, 1987) it was possible that our observers did not show a typical pattern of lateral chromatic aberration. To test this possibility we measured this aberration in our observers along both vertical and horizontal meridians using a vernier offset stimulus. The observers monocularly viewed two luminous lines, one red and one green, both oriented either vertically or horizontally and placed end-to-end with a vernier offset of 1 mm. The observers then varied their distance from the display until the lines appeared aligned and the size of the retinal shift of the green line relative to the red in terms of visual angle could then be calculated directly. Observers DG and CM displayed typical results in that the nasally directed shift of the green retinal image (1.12, 0.41 arcmin) was much larger than its upward displacement (0.29, 0.0 arcmin). In contrast, AM showed a larger upward (0.59 arcmin) than nasal (0.24 arcmin) shift, while PC's displacements were downward (0.35 arcmin) and temporal (0.29 arcmin). Such reversals have been previously reported (Ogboso and Bedell, 1987) and are attributed to eccentricities in the position of the pupil or in the pupil's point of maximum luminous efficiency as specified by the Stiles–Crawford effect (Vos, 1960; Thibos, 1987). According to our measurements, in three observers the grating axis most affected by lateral chromatic aberration corresponds to their orientation of *lowest* sensitivity, a result which is opposite to what would be produced by a luminance artifact. On the other hand, PC exhibited about equal shifts in the horizontal and vertical directions which suggests that a luminance artifact, if present, should be evident at the left oblique (45 deg) orientation. However, PC's peak sensitivity was at vertical, not left oblique. Overall then, it seems unlikely that lateral chromatic aberration contributes a luminance artifact but this aberration may well be related to the chromatic anisotropy, as we shall argue later. Since none of the alternative sources for the horizontal–vertical effect are consistent with our data, we conclude that this anisotropy has a neural source and, therefore, there is orientation selectivity in the chromatic channel which is at least partially independent of the orientation selectivity in the luminance channel.

Results of earlier psychophysical experiments have demonstrated the presence of orientation tuning in the chromatic channel, but the question of whether or not the chromatic and luminance systems share the same orientation-selective mechanism has been explored only very recently. Elsner (1978) found very similar tilt aftereffects in the luminance and chromatic channels and could only conclude that orientation tuning is similar in both systems. Likewise, Quick and Lucas (1979) reported the absence of subthreshold summation of the vertical and horizontal components of a chromatic checkerboard, thus showing that these two orientations are analyzed independently as they are in the luminance channel. On the other hand, Kelly (1975), upon finding no oblique effect in sensitivity to flickering chromatic gratings within a certain spatio-temporal range, suggested that there may not be orientation tuning in the chromatic system. Recently however, Flanagan *et al.* (1987) demonstrated independent tilt aftereffects for luminance and chromatic stimuli thereby providing compelling evidence for the existence of orientation processing by the chromatic channel. Our finding of different types of anisotropy for luminance and chromatic gratings further supports the view that the colour system analyses orientation and does so at least partially independently of the luminance channel. The double-opponent simple cells in the striate cortex of the monkey which are most responsive to chromatically modulated stimuli (Poggio *et al.*, 1975; Michael, 1978) may be the underlying mechanism for orientation tuning in the chromatic channel.

What source could lead to different anisotropies in the chromatic and luminance systems? It is known that simple cells in visual cortex are strongly influenced by early visual experience. For example, both meridional amblyopia (Mitchell *et al.*, 1973) and experimentally induced selective deprivation (Hirsch and Spinelli, 1970) lead to the underrepresentation of cortical cells tuned to the less stimulated orientations. It is possible that the oblique effect in the luminance channel arises from a greater exposure to horizontal and vertical contours compared with oblique contours in the early environment. Since lateral chromatic aberration degrades high spatial frequency chromatic contours of particular orientations, we speculate that this aberration, like meridional amblyopia, contributes to the development of fewer or less sensitive cortical cells tuned to chromatic contours at the affected orientations. Three of our subjects exhibited lowest sensitivity to chromatic contours at the orientation orthogonal to their axis of greatest chromatic aberration, or in other words, at the orientation most contaminated by the aberration. This result implies that the influence of lateral chromatic aberration on chromatic thresholds has a neural, rather than an optical basis. Although the lateral aberrations measured in our subjects were too small to significantly affect the appearance of chromatic contours, there is evidence that the displacement of the optic axis relative to the visual axis is much larger in newborn infants (Kestenbaum, 1963; Slater and Findlay, 1972) which suggests that lateral chromatic aberration and its effects on chromatic contours are greater early in life.

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