Pergamon

0042-6989(95)00159-X

Vision Res., Vol. 36, No. 5, pp. 645–653, 1996

0042-6989/96 $15.00 + 0.00

Color and Luminance Vision in Human Amblyopia: Shifts in Isoluminance, Contrast Sensitivity Losses, and Positional Deficits

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Received 16 November 1994; in revised form 21 March 1995; in final form 12 May 1995

The deficits for contrast detection and positional accuracy were compared for chromatic and luminance mechanisms within a group of strabismic and anisometropic amblyopes. We found that the isoluminant point was shifted towards red in the amblyopic compared to the fellow normal eye. This was not accounted for by eccentric fixation by the amblyopic eye. Contrast sensitivity deficits were similar for luminance and color stimuli in normal and amblyopic visual systems. In the majority of our amblyopic subjects, however, the deficits in positional acuity were greater for the chromatic than the luminance stimuli.

Amblyopia Color Isoluminance Position Contrast

INTRODUCTION

Evidence suggests that the earliest site of the neural dysfunction in amblyopia is in area V1 of the visual cortex. There is also a growing body of psychophysical evidence suggesting that the processing of color and luminance contrast occurs in separate cortical pathways. Evidence for a substantial degree of independence of the chromatic and luminance mechanisms comes from studies involving adaptation (Krauskopf, Williams & Heeley, 1982; Bradley, Switkes & De Valois, 1988), subthreshold summation (Cole, Stromeyer & Kronauer, 1990), and spatial noise masking (Gegenfurtner & Kiper, 1992; Losada & Mullen, 1995). Although, sinewave masking studies indicate color–luminance interactions, it has been argued that these effects are still compatible with an underlying independence of color and luminance transduction (Switkes, Bradley & De Valois, 1988; Cole *et al.*, 1990; Mullen & Losada, 1994). The existence of specific cortical pathways for color and luminance processing is also suggested for higher order tasks such as contour integration (McIlhagga & Mullen, 1996) and reading (Legge, Parish, Luebker & Wurm, 1990). A more complete understanding of the extent of the cortical deficit in amblyopia must involve an assessment of the relative dysfunction of these two pathways. This can be achieved by comparing functions for luminance and chromatically-defined stimuli.

One previous report (Bradley, Dahlman, Switkes & De Valois, 1986) has shown that the magnitudes of the color and luminance contrast sensitivity deficits are similar in both anisometropic and strabismic amblyopia. The amblyopic anomaly, however, is not only characterized by reduced contrast sensitivity (Gstalder & Green, 1971; Levi & Harwerth, 1977; Hess & Howell, 1977), but also by reduced spatial localization (Rentschler & Hilz, 1985; Levi & Klein, 1983; Hess & Holliday, 1992). Recently it has been shown that there are independent deficits which differentially affect strabismic and anisometropic forms of the condition (Levi & Klein, 1983; Hess & Pointer, 1985; Hess & Holliday, 1992).

To gain a better understanding of the nature of the cortical dysfunction in amblyopia we have assessed the relative losses of both contrast sensitivity and spatial localization for luminance and chromatically defined stimuli. Our results for contrast sensitivity agree with, and extend, the previous results of Bradley *et al.* (1986) as we find similar contrast sensitivity losses for chromatic and luminance stimuli. We find, however, significant differences in the isoluminant points for normal and amblyopic eyes, which have not been previously reported. To assess spatial localization, we use suprathreshold spatially narrowband stimuli in a three gabor alignment task. Color and luminance contrasts of the stimuli were matched in multiples of detection threshold to allow performance on the task to be compared between the two. We find a small but significantly greater loss for

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the localization of chromatically-defined stimuli compared with their luminance-defined counterparts.

METHODS

Apparatus and calibration

All stimuli were displayed on a Barco Calibrator (7651) RGB monitor with a frame rate of 75 Hz and a line rate of 60 kHz. Only the red and green guns were used (the blue was at zero). The CIE chromaticity coordinates were calibrated using a spectroradiometer (Photo Research, PR 700–PC) and were $x = 0.610$, $y = 0.342$ for the red gun, and $x = 0.298$, $y = 0.588$ for the green gun. The gamma functions of each phosphor were measured using a UDT Optometer (model S370) fitted with a 265 photometric head. The phosphors were linearized in software using look-up tables and a gamma fit (Pelli & Zhang, 1991). Stimuli were generated using a combined framestore and waveform generator VSG2/1 (Cambridge Research Systems). One dimensional stimuli (color and luminance gratings) were generated using the waveform generator, which has 14 bit output DACs, and the two dimensional stimuli (gabor patches) were generated using the framestore with 8 bit output DACs. The computation of the gabor stimuli in the frame store allowed a sub-pixel resolution of their relative displacements to be achieved. Chromatic spatial frequencies higher than 4 c/deg were not used because of the risk of introducing luminance artefacts from chromatic aberrations (Bradley, Zhang & Thibos, 1992).

Stimuli

(a) Sine wave gratings. Sinewave gratings were displayed horizontally, and Gaussian enveloped along the axis of modulation. Each gun (r, g) was modulated using the function:

$$F(x) = r_{\text{mean}}\,(1 + c \cdot \sin(2\pi f x) \cdot \exp(-x^2/2\sigma^2))$$

$$F(x) = g_{\text{mean}}\,(1 + c \cdot \sin(2\pi f x) \cdot \exp(-x^2/2\sigma^2))$$

These component gratings were combined in antiphase to form a red–green chromatic stimulus, and in phase to form a yellow–black luminance stimulus. The spatial extent of the grating in the vertical (enveloped) dimension was set at $\sigma = 1.4$ cycles. The grating was sharply truncated in the horizontal direction, extending the full width of the screen, giving a horizontal bar length of 10 deg for viewing at 150 cm, and 30 deg for viewing at 50 cm. The contrast of the gratings (c) was defined by the usual Michelson formula. The overall mean luminance ($r_{\text{mean}} + g_{\text{mean}}$) of the grating stimuli was held constant at 20 cd m^{-2}, where r_{mean}, g_{mean} are the mean gun luminances measured with the UDT 265 photometric sensor. All stimuli were viewed monocularly and with a natural pupil.

(b) Alignment stimuli. For the alignment task three Gabor patches were generated, and were presented one above the other with a separation of 7 deg. The central gabor element was viewed foveally. Each gabor element had the following function:

$$g(x, y) = L_p\left(1 + c \cdot \sin(2\pi f x) \cdot \exp\left(-\frac{x^2 + y^2}{2\sigma^2}\right)\right)$$

where (x, y) is the distance in degrees from the element centre, c is the Michelson contrast, and L_p is the mean luminance of the red or green phosphor. The sinusoidal frequency f is 1 c/deg, and the space constant (σ) is 1.1 cycles. The axis of sinusoidal modulation was horizontal and thus the bars appeared vertically oriented. Displays were composed of either luminance or chromatic gabor element patches: a luminance element was produced by combining the modulations of the red and green guns of the display in-phase, whereas the color element had counter-phase red and green gun modulations. The mean luminance of the gabor stimuli was 10 cd m^{-2}.

Determination of isoluminance

Isoluminance was determined for each eye of each observer, and for each of the spatial conditions used. A similar method was used both for the sinewave grating stimuli and for the gabor elements. For the grating stimuli isoluminance was determined at 0.25–2 c/deg in 1 octave steps. Additional stimuli of 4 c/deg were used in the contrast sensitivity experiments, but because subjects found it difficult to make an isoluminance setting at this frequency, we used the $r/(r + g)$ value obtained at 2 c/deg. Isoluminance was determined using a minimum motion technique. The chromatic stimulus was set to drift or flicker at a fixed rate and was continuously displayed (for some subjects we used a stimulus drifting at 1 Hz and for others one flickering at 2 Hz). Using a method of adjustment with a step size used of 1% $r/(r + g)$, subjects varied the relative red and green mean luminances (r_{mean} and g_{mean}) to select a point of minimum drift/flicker. The summed r_{mean} and g_{mean} was held constant. At isoluminance the image appears stationary or to drift/flicker very slowly compared to the non-isoluminant stimuli (Moreland, 1982; Cavanagh, Tyler & Favreau, 1984), and at this point r_{mean} and g_{mean} are of equal 'sensation luminance' for that observer (Kaiser, 1988). The procedure was repeated at least four times, each with a new randomly selected starting value of $r/(r + g)$. Isoluminance was taken as the average of the settings.

For the alignment stimuli, isoluminance was determined individually for the central and the peripheral gabors. An average of the two values was used because we could not display two stimuli with different isoluminant points on the screen at the same time. However, the average difference in the isoluminant point between the central and peripheral gabor elements was 3.0% $r/(r + g)$, and thus the gabor stimuli were within 1.5% of the actual isoluminant point, averaged across our subject group. Given the contrasts we used for the experiment, the average luminance contrast present in the chromatic gabor stimuli is less than 1% and is below detection thresholds.

Psychophysical methods

(a) Contrast sensitivity. Thresholds for the chromatic and luminance gratings were obtained using a two alternate forced choice staircase procedure. The temporal presentation was Gaussian modulated with a σ of 88 msec. Two intervals of 500 msec were presented, each preceded by a tone. The subject indicated by means of a button press in which interval the stimulus appeared. For the first four reversals, two consecutive correct responses caused the contrast to be reduced by 0.15 log units, and one incorrect response produced a contrast increase of 0.15 log units. For the remaining reversals, two consecutive correct responses caused the contrast to be reduced by 0.05 log units, and one incorrect response produced a contrast increase of 0.10 log units. The staircase was terminated after 12 reversals. The threshold was calculated as the average in logunits of the last seven reversals. This corresponds to a threshold value of 82% correct on the psychometric function. Each plotted data point represents three threshold measurements.

(b) Positional accuracy. Positional accuracy is defined as the accuracy of the subject at making a perceptual alignment of the central gabor element with respect to the upper and lower ones. It was measured using a method of constant stimuli. The middle gabor element was presented in one of 11 possible displacements, aligned with, or to the left, or the right of the two peripheral elements. The contrast envelope and the carrier of the gabor were displaced in unison. The whole stimulus (the three gabors) was randomly shifted in its position on the screen from trial to trial within a 16 min range. The subject's task was to indicate the position of the middle element with respect to the upper and lower ones (i.e. to the left or right). At least 60 trials were performed at each displacement for all subjects. The stimulus was presented in a temporal gaussian envelope with a σ of 88 msec. A psychometric function describing the probability of seeing the gabor element to the right as a function of the displacement was obtained and fitted with a cumulative gaussian. The mid-point (0.5, chance performance) indicates the alignment bias and the slope indicates the alignment acuity. This task is similar to the one used by Hess and Holliday (1992).

Clinical details

The clinical details for the amblyopic subjects are summarized in Table 1. Our group comprised four strabismic amblyopes, three anisometropic amblyopes and one mixed amblyope. For some of the measurements of isoluminance an additional mixed amblyope (OA) was used. All subjects had normal color vision. All had been recently refracted and wore their optical corrections.

Determination of fixation

The degree of eccentric fixation, if any, was determined using a measurement of Maxwell's spot, an entoptic phenomenon centered on the fovea and which is thought to depend on the foveal macular pigmentation. The monitor was set to white and a radial 'grid' of thin lines spaced at 1 deg displayed on it, resembling a dart board. Subjects were asked to fixate the center carefully. While maintaining fixation, the screen was viewed through a neutral density filter, and a deep blue gelatine filter (Wratten No. 34) in alternating sequence. The two filters were approximately matched in their

TABLE 1. Clinical details of the subjects

Subject	Age (year)/sex (M/F)	Amblyopic eye/type	Age (year) at patching/ surgery	Acuity	Correction	Fixation (deg) T = temporal N = nasal I = inferior S = superior
CT	40/F	0S	6/None	6/6	PL	Central
		/STRAB		6/60	PL + 3.25 × 90	3.0 S
SB	35/M	OS	None/None	6/6	−0.5	Central
		/STRAB		3/60	+1.5	1.0–2.0 NS
MJS	24/M	OS	7/8	6/6	PL	Central
		/STRAB		6/18	PL − 0.25 × 100	3.0 NI
MXS	22/F	OS	9/None	6/18	+0.75	Central
		/STRAB		6/6	+1.00	Central
CP	40/F	OD	5/None	6/18	−5.25–2.25 × 180	2.0 T
		/STRAB				
		ANISO		6/6	−3.00–1.75 × 170	Central
CS	20/F	OS	6/None	6/6	+0.5	Central
		/ANISO		6/90	+6.0 + 2.0 × 100	4.5 NS
VS	22/F	OS	8/8	6/4.5	−1.25	Central
		/ANISO		6/9	+4.00–2.50 × 70	0.5–1.0 S
TK	30/F	OD	None/None	6/12 + 3	+4.00–5.00 × 180	1.0–1.5 N
		/ANISO		6/5 − 3	−0.50–0.25 × 180	Central
OA	17/M	OD	Not available	6.24	+4.50–5.00 × 30	4.0 NS
		/STRAB-				
		ANISO		6/9	−1.75–1.75 × 150	Central

STRAB = strabismic amblyopia; ANISO = anisometropic amblyopia. Entries for 'Acuity', 'Correction', and 'Fixation' columns are quoted for OD and OS respectively.

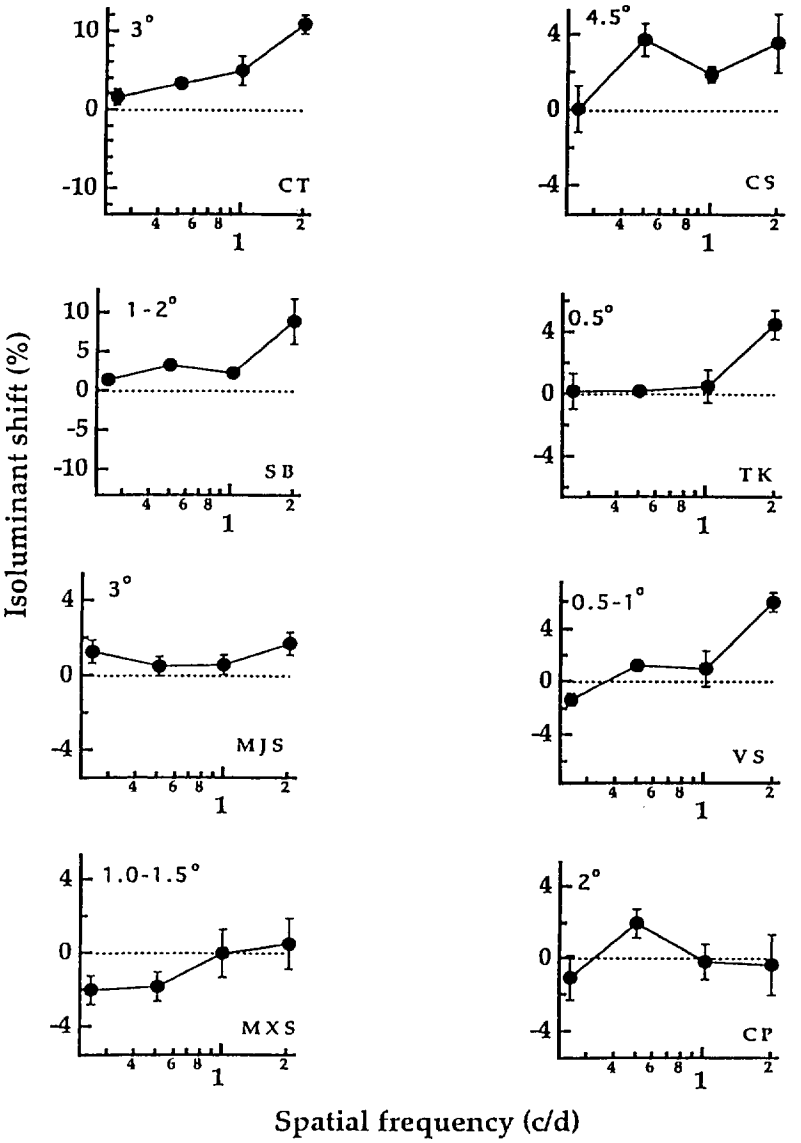

FIGURE 1. Isoluminant shifts in percentage points [% $r/(r+g)$] between the normal and fellow amblyopic eyes of eight amblyopes are plotted as a function of spatial frequency. The eccentric fixation (degrees) is indicated for each amblyope. Note the changes in scale used for subjects CT & SB. (Mean ± 1 SE.)

transmissions. This reveals the dark Maxwell's spot to the subject who could indicate the position with respect to their fixation on the center of the grid. This method was found to be a reliable means of measuring fixation.

RESULTS

Isoluminance

The accurate measurement of chromatic thresholds requires the determination of the isoluminant point. Using the grating stimuli, we measured the isoluminant point for each eye of each subject for four spatial frequencies (0.25–2 c/deg in 1 octave steps). In Fig. 1, each frame represents the difference of the isoluminant points between the normal and fellow amblyopic eye, plotted as a function of spatial frequency. The frames on the left of the figure are for the four strabismic amblyopes, those on the right are for the anisometropic amblyopes, with the exception of the bottom right frame which is for the mixed amblyope (CP). The degree of eccentric fixation is indicated for each subject. Across our group of amblyopes the results show a trend in which the isoluminant point shifts towards red between the amblyopic and normal eye. This effect also appears to increase with spatial frequency. In order to test whether these effects are significant we performed a two-way analysis of variance on the data (ANOVA, two-way repeated measured analysis of variance, balanced design). The results confirm that there is a significant shift in isoluminant point towards red in our group of amblyopes ($P = 0.02$) and that this effect is significantly greater as spatial frequency increases. Thus, on average, more red relative to green is required by the amblyopic eye to achieve isoluminance, indicating that a perceived dimming of the red (or brightening of the green) occurs in these affected eyes.

It is known in normal vision that the isoluminant point shifts towards red for stimuli imaged eccentrically

TABLE 2. The shift in isoluminant point of the amblyopic eye with respect to the fellow normal eye, in percentage points of $r/(r+g)$

Subject/ spatial frequency (c/deg)	Natural	Foveal	Eccentric
CT 1.0	3.75 ± 0.25	5.75 ± 0.66	3.0 ± 0.0
2.0	10.75 ± 0.66	9.0 ± 0.50	9.75 ± 0.89
MJS 1.0	0.61 ± 0.52	2.82 ± 0.54	−0.87 ± 0.58
2.0	1.75 ± 0.74	1.69 ± 0.36	0.42 ± 0.66
CP 1.0	−0.11 ± 1.06	−3.7 ± 1.04	1.89 ± 1.17
2.0	−0.25 ± 2.16	−3.3 ± 2.30	3.05 ± 1.56
VS 1.0	0.9 ± 1.29	3.5 ± 1.31	−0.1 ± 1.07
2.0	6.0 ± 0.73	6.25 ± 1.17	2.45 ± 0.71
OA 2.0	3.75 ± 1.26	2.0 ± 1.22	4.75 ± 1.26

A positive value indicates an increase of red light relative to green. 'Natural': using the subject's natural fixation point for the normal and amblyopic eye; 'Foveal': using foveal retinal locations for the normal and amblyopic eyes; 'Eccentric': using retinal locations for the normal and amblyopic eye matched for the eccentric fixation point of the amblyopic eye. Results for two spatial frequencies of grating (1 and 2 c/deg). (Mean ± 1 SE).

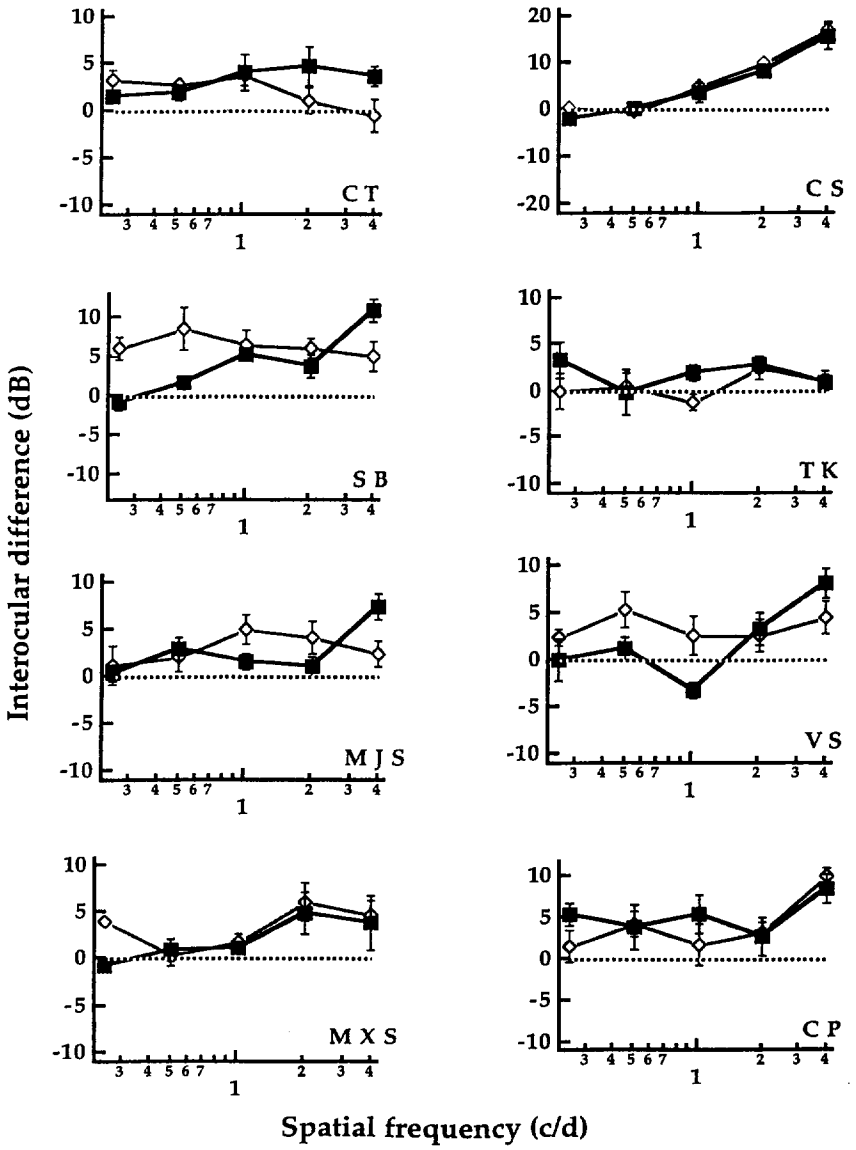

FIGURE 2. The interocular ratio of contrast sensitivities (in decibels) of the normal to the fellow amblyopic eyes is plotted against spatial frequency for chromatic (open diamonds) and luminance (solid squares) sinusoidal stimuli. 20 dB = 1 log unit. Note the change in scale used for subject CS. (Mean ± 1 SE.)

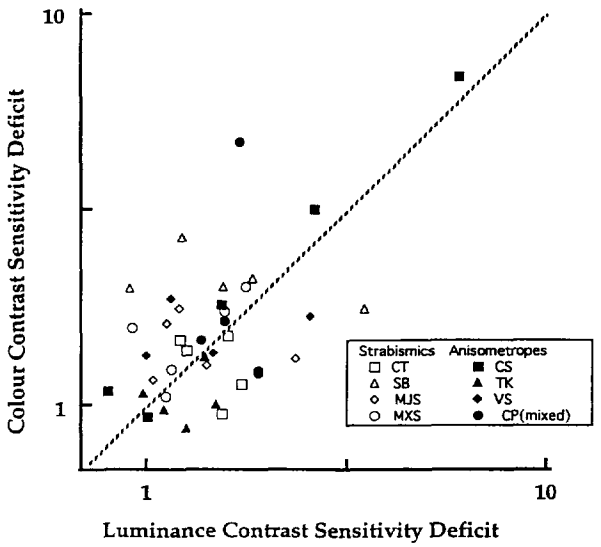

FIGURE 3. The deficit for color contrast sensitivity plotted against the luminance contrast sensitivity deficit for all measured spatial frequencies in our amblyopic population. The deficit is the ratio of contrast sensitivity for the normal to amblyopic eye. The dashed rule has a slope of unity.

(Mullen, 1991). [Data from the normal eyes of our amblyopes obtained using the more localized gabor stimuli, indicate that this shift is in the order of 0.5% $r/(r+g)$/deg.] Although the grating stimuli of Fig. 1 are of greater spatial extent than the gabor stimuli, it remains possible that shifted isoluminant points in the amblyopic eye are produced by an eccentric fixation of the eye. To evaluate this, we measured the natural point of fixation in each eye of our subjects using the Maxwell spot (see Methods). For spatial frequencies of 0.25, 0.5, 1 and 2 c/deg, the correlation coefficients (r^2) were 0.1, 0.1, 0.05 and 0.001, respectively. Thus there is no correlation between the degree of eccentric fixation of the subjects and the shift in the isoluminant point. Despite these negative findings we have evaluated this possible explanation more fully by measuring the isoluminant points for the normal and amblyopic eyes at comparable retinal loci. This was performed on four amblyopes that showed a shift in isoluminant point between their normal and affected eyes (CT, MJS, VS, and OA). The retinal locations were matched in one of two ways and the isoluminant points remeasured for grating stimuli of 1 and 2 c/deg (with the exception of OA, for whom only 2 c/deg was measured). In the first case, the normal fellow eye fixated eccentrically in order to match the natural, eccentric fixation of the amblyopic eye. In the second case, stimuli were imaged on the anatomical fovea of each eye. Results are given in Table 2. Also included in the table are the data for the isoluminant shift shown in Fig. 1 for the natural fixation of both eyes at these spatial frequencies. Inspection of the data show that a shift in the isoluminant point remains for the stimuli matched in retinal location, whether the match is for foveal or eccentric retina. We pooled the data across the retinal location because this improves the power of the statistics and applied a two-way ANOVA. The results show that at matched retinal loci there remains a significant shift in isoluminant point towards red in the amblyopic eye ($P = 0.01$). Thus the data suggest that this shift is not solely a consequence of eccentric fixation.

Color and luminance contrast thresholds

We have compared luminance (solid squares) and chromatic (open triangles) contrast sensitivity over a range of spatial frequencies (0.25–4 c/deg) for each subject. These results are displayed in Fig. 2, in which the ratio of sensitivity between the normal and fellow amblyopic eye is plotted against spatial frequency for color and luminance stimuli. Over this low to mid frequency range, luminance contrast sensitivity deficits occur which either increase with spatial frequency or are invariant with spatial frequency. The deficits in chromatic and luminance contrast sensitivity are compared in Fig. 3 in which the inter-ocular sensitivity ratios for color and luminance contrast are plotted with a different symbol for each subject. The diagonal line has a slope of unity and represents equal deficits for color and luminance contrast sensitivity. Although the data are scattered they are approximately equally distributed about this line. The scatter results from the variation in the inter-ocular sensitivity ratio for color and luminance across spatial frequency in individual amblyopes. An ANOVA confirmed that across our group of amblyopes, while there are significant losses in contrast sensitivity in the amblyopic eye at all spatial frequencies ($P < 0.05$), there are no significant differences between the losses for chromatic and luminance stimuli.

Positional accuracy

We compared positional accuracy for alignment of the gabor stimuli defined by either luminance or color contrast. For each eye, detection thresholds were measured for the peripheral gabor element (superior), and its contrast was set to a fixed value of 2.5 times threshold. This controls for any differential losses in color and luminance contrast sensitivity in the subject, and hence allows performance for color and luminance stimuli to be compared. Within each eye, the subject then matched the perceived contrast of the foveal gabor to that of the peripheral gabor using a method of adjustment. The subject fixated the central gabor and adjusted its contrast to achieve a match. The stimuli were presented in a temporal envelope with the same parameters as used for the alignment experiment. The match was made three to five times and an average taken. This removes the differences in perceived contrast that occur when central and peripheral stimuli are each at equivalent multiples of detection threshold.

Data for all subjects are shown in Fig. 4. The color deficit (the ratio of positional accuracy for the amblyopic eye to that of the normal fellow eye) is plotted against the luminance deficit expressed in the same way. The results show that there is a significant loss in positional accuracy for both the luminance and color stimuli. There are two features of these data that are noteworthy. First,

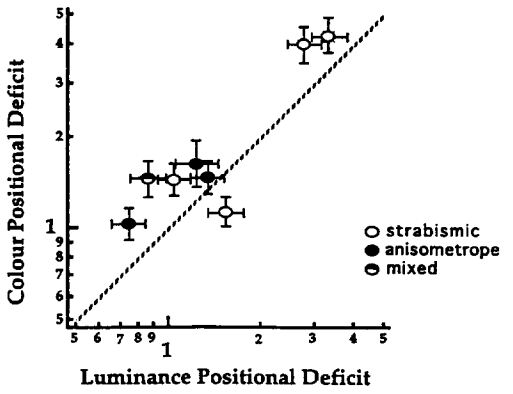

FIGURE 4. Comparison of the deficits in positional accuracy for luminance and chromatic stimuli in our amblyopic population. The deficit is the ratio of positional accuracy for the normal to amblyopic eye. The dashed rule has a slope of unity. (Mean ± 1 SE.)

positional deficits for color and luminance contrast in our subject group extend over a range of ratios from close to one to greater than four. Second, the data for all subjects except one fall above the dashed line of slope of unity, demonstrating that deficits in positional accuracy for chromatic stimuli are greater than for luminance stimuli in the amblyopic group as a whole. An ANOVA confirms that these results are significant ($P = 0.04$).

Previous results indicate that the positional deficit is greater in strabismic amblyopes (Hess & Holliday, 1992). Although the strabismic amblyopes in our group have on average a greater positional deficit than the anisometropic amblyopes, our sample size is too small to provide an effective test of the significance of this effect. The selectivity of the deficit for chromatic stimuli appears to occur equally in both amblyopic types, but a considerably larger sample size would be required to test this effectively.

In Fig. 5, the biases or points of subjective equality are compared for the luminance and chromatic stimuli for the normal (open symbols) and fellow amblyopic eye (solid symbols) of each observer. In our group overall there is no significant bias for either luminance or chromatic stimuli. The largest biases observed were of the order of 15 and 20 min and were comparable for luminance and chromatic stimuli. Overall the offsets for the amblyopic eyes are significantly larger than for the normal eyes; such an effect has been reported previously for luminance stimuli (Hess & Holliday, 1992).

DISCUSSION

The shift in isoluminant point found in five out of eight of our subjects was unexpected since there are no previous reports in the literature of alterations in the photopic spectral sensitivity of amblyopic eyes. Harwerth and Levi (1978) used 25 Hz flicker on two amblyopes to measure luminosity functions which were found to be normal. Other reports in the literature also suggest that the amblyopic photopic luminosity function is normal (see also Alpern & Fitman, 1960). Bradley *et al.* (1986) reported no differences in the isoluminant point between the eyes of their subjects, although no data were shown. One possible explanation is that the effect has been previously overlooked since relatively few subjects have been tested. Indeed, in our sample not all amblyopes show the effect and it appears to have some spatial frequency dependence. Furthermore, the effect is relatively small, representing a few percent change in sensitivity to one of the chromatic components, and to be revealed in a luminosity function would require detailed spectral sensitivity measurements. Lastly, for unknown reasons the effect may be greater at the lower temporal frequencies that we have used, than at the higher ones commonly used for photopic luminosity measurements.

Since the isoluminant point is known to shift with eccentricity such that more red is required in the red-green balance (Mullen, 1991; Livingstone & Hubel, 1987), one potential cause of the shift in isoluminant point is that the amblyopic eye is fixating eccentrically. However, we find that the degree of eccentric fixation shows no correlation with the shift in isoluminance across our population. Furthermore, experiments four of our affected subjects show that the difference in isoluminant point cannot be removed by matching the retinal locations of the stimuli in each eye. The shift in isoluminant point is generally larger than would be predicted from eccentric fixation. In the normal eye changes in the isoluminant point with eccentricity for the gabor stimuli of approx. 0.5% $r/(r + g)$/deg occurred. The eccentric fixations of our amblyopes would produce smaller changes in the isoluminant points than we actually find, especially given that the measurements are made with the grating stimuli that are not well localized.

There is evidence that within the central visual field in strabismic amblyopia the loss in visual sensitivity is greatest at high spatial frequencies (Gstalder & Green, 1971; Levi & Harwerth, 1977; Hess & Howell, 1977; Hess & Pointer, 1985). This may correspond to a loss of the cone-only projection subserved by the midget retinal

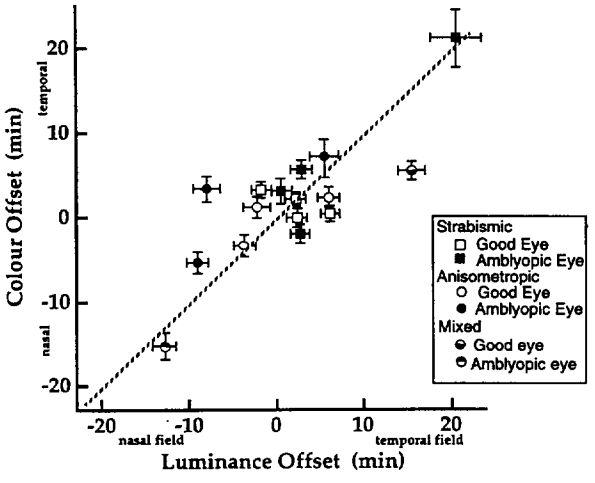

FIGURE 5. Comparison of the positional offset deficits for luminance and chromatic stimuli in our amblyopic population. The dashed rule has a slope of unity. (Mean ± 1 SE.)

ganglion cells, or an expansion of the cone-only input to include mixed receptoral inputs. Thus, we speculate that in amblyopia the central visual field may be more biased towards a mixed rod–cone projection, which is likely to alter the spectral sensitivity function in the direction found. This still remains consistent with the site of the amblyopic deficit being cortical.

Our subjects were selected because their amblyopia was severe enough to show deficits in contrast sensitivity in the low to mid spatial frequency range (0.125–4 c/deg). On average over the eight subjects tested, however, there was no evidence for a selective loss of color contrast sensitivity over luminance contrast sensitivity, or *vice versa*. While some individuals appeared to have a greater color loss or greater luminance contrast sensitivity loss, no significant trend emerged across the population for either the strabismic or the anisometropic amblyopes. This confirms the previous results of Bradley *et al.* (1986) who used a similar number of subjects. It is potentially less compatible with previous reports of changes in the chromatic spectral sensitivities of amblyopes. For example, Harwerth and Levi (1977, 1978) reported that subjects tended to show a loss of color opponency in spectral sensitivity functions obtained on a white background. In particular there is a loss of the normal 'Sloan's notch' in sensitivity in the yellow spectral region, which suggests a greater loss of color over luminance sensitivity (Sperling & Harwerth, 1971; King-Smith & Carden, 1976; Mullen, 1987). In stimulus deprived (lid sutured) monkeys results were mixed. Only in some monkeys were the changes in the spectral sensitivity function suggestive of a greater color sensitivity loss (Smith, Harwerth, Duncan & Crawford, 1986; Harwerth, Smith, Crawford & von Norden, 1990). Thus the spectral sensitivity measures suggest that there tends to be a selectively greater, although inconsistent, loss in color sensitivity. The differences between these and the present study may arise because a relatively small number of subjects/animals were tested, and our data suggest that there is considerable variability between individuals in the size of the color deficit relative to the luminance deficit.

In order to measure deficits in positional accuracy independently from any differential loss in color or luminance thresholds in the individual subject, all peripheral gabor elements in the alignment stimulus were equated in multiples of detection threshold. (Foveal stimuli were then matched in perceived contrast to the peripheral ones.) This method of equating stimuli between the two eyes is supported by the results of Hess and Holliday (1992) who have shown using an identical task that alignment performance has a similar dependence on contrast for the amblyopic and normal eye. A similar result has also been reported for vernier acuity measured with sinusoidal patterns (Bradley & Freeman, 1985). The method adopted of matching the contrasts, however, is unlikely to affect the color and luminance comparison, providing the same method is applied to both color and luminance stimuli. Our results show that seven of our eight subjects showed a greater chromatic than luminance deficit in positional accuracy. This deficit becomes highly significant when averaged across the subject population.

There is psychophysical evidence from masking and adaptation studies that color and luminance detection thresholds are mediated by separate mechanisms which retain their independence up to relatively high suprathreshold contrasts (Bradley, Switkes & De Valois, 1988; Cole *et al.*, 1990; Mullen & Losada, 1994; Losada & Mullen, 1995). Furthermore there is evidence for separate color and luminance mechanisms involved in higher order tasks such as contour detection (McIlhagga & Mullen, 1996) and reading speed (Legge *et al.*, 1990). This evidence suggests that there are separate pathways mediating color and luminance detection at the level of the cortex. These results, of course, do not exclude the existence of additional cortical pathways sensitive to both color and luminance contrast. Our results suggest that in amblyopia both the chromatic and luminance representations of space are affected but that the fidelity of the chromatic representation of space is more degraded.

If the primary deficit for luminance contrast in Amblyopia arises from a lack of binocular competition during development, the existence of binocularity in chromatic neurones allows for a similar etiology in the case of the color loss. There is physiological evidence for the existence of binocular chromatic neurons in primate striate cortex. The presence of binocularity in chromatic cells appears to follow a similar pattern to that of luminance cells, being dependent on the cortical layer and the cell's receptive field classification (Lennie, Krauskopf & Sclar, 1990; Michael, 1978a, b). There is some suggestion that chromatic cells located in the 'blobs' of layers two and three tend to be more monocular than inter-blob cells (Livingstone & Hubel, 1984; Ts'o & Gilbert, 1988). Extra striate cells, however, are binocular and there is nothing to indicate that chromatically tuned neurones are different. Why the chromatic representation should be more affected remains unexplained.

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Acknowledgements—We are very grateful to our amblyopic subjects for the time and effort they contributed to this work. The work was supported by Canadian MRC grants MT-10819 and MT-10818.