On the Binocular Summation of Chromatic Contrast

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The binocular summation of chromatic contrast was investigated under a variety of stimulus conditions. Binocular and monocular contrast detection thresholds were measured using 0.5 cpd Gabor patches. It was found that, using stimuli which contained combinations of chromatic and luminance contrast, binocular detection could take place independently in luminance-contrast- and chromatic-contrast-sensitive mechanisms. It was also found that, with chromatic stimuli, levels of binocular summation were above those expected from probability summation between the eyes, and thus showed evidence for binocular *neural* summation within chromatic detection mechanisms. The implications of these results for (a) the binocularity of chromatic detection mechanisms, and (b) the suggested link between stereopsis and binocular neural summation, are discussed. © 1998 Elsevier Science Ltd. All rights reserved.

Colour   Binocular summation   Contrast sensitivity   Isoluminance

INTRODUCTION

Having two eyes rather than one provides a number of benefits to a visual system. The superiority of binocular performance over monocular performance in a given visual task is usually termed "binocular summation", and has been studied extensively (see Blake & Fox, 1973; Blake, Sloane & Fox, 1981; Howard & Rogers, 1995 for reviews). One particular area of interest has been the reduced contrast threshold for binocular detection as compared with monocular detection, and it is with this subject that this study is concerned.

In his seminal study, Pirenne (1943) suggested that the lower luminance detection thresholds that were obtainable under binocular viewing conditions were attributable to "probability summation", whereby the two eyes

were acting as independent detectors whose outputs were pooled only just prior to the decision stage. More-recent studies have, however, firmly established that binocular detection performance exceeds monocular detection performance by a greater margin than that expected from probability summation (e.g. Campbell & Green, 1965; Thorn & Boynton, 1974; Legge, 1984a). The consensus from these and other studies is that binocular contrast detection thresholds under ideal conditions are generally a factor of 1.4–1.6-times lower than monocular detection thresholds, compared with the factor of approximately 1.2 expected from probability summation§. This finding has been taken as evidence for "neural summation" between the left and right eyes, meaning that some sort of interocular facilitation enhances binocular performance in detection tasks. A number of models of this facilitatory interaction have been proposed (e.g. Campbell & Green, 1965; Legge, 1984a,b; Anderson & Movshon, 1989; Anzai, Bearse, Freeman & Cai, 1995).

The parallel-processing theory of Livingstone and Hubel (1988) put forward that chromatic mechanisms had no involvement in stereoscopic depth perception, largely based on the evidence that stereopsis is impaired at isoluminance. Simmons and Kingdom (1997) have shown, however, that stereoscopic performance with compound stimuli consisting of a combination of colour and luminance contrast is better explained by the existence of at least two stereopsis mechanisms, one sensitive to luminance contrast and the other sensitive to chromatic contrast. This evidence, combined with the knowledge that some colour aftereffects, colour contrast adaptation, and colour contrast induction show intero-

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§Note that the precise size of this factor is related to the slopes of the psychometric functions for monocular detection. In this study we have followed the convention employed in previous studies (e.g. Rose, Blake, & Halpern, 1988), where the fixed ratio of 1.2 was used as the baseline for neural summation calculations rather than the more accurate $2^{1/\beta}$ (β being the slope parameter of the psychometric function). This assumption was justified by the range of β values obtained in this study and makes no difference to the overall conclusions.
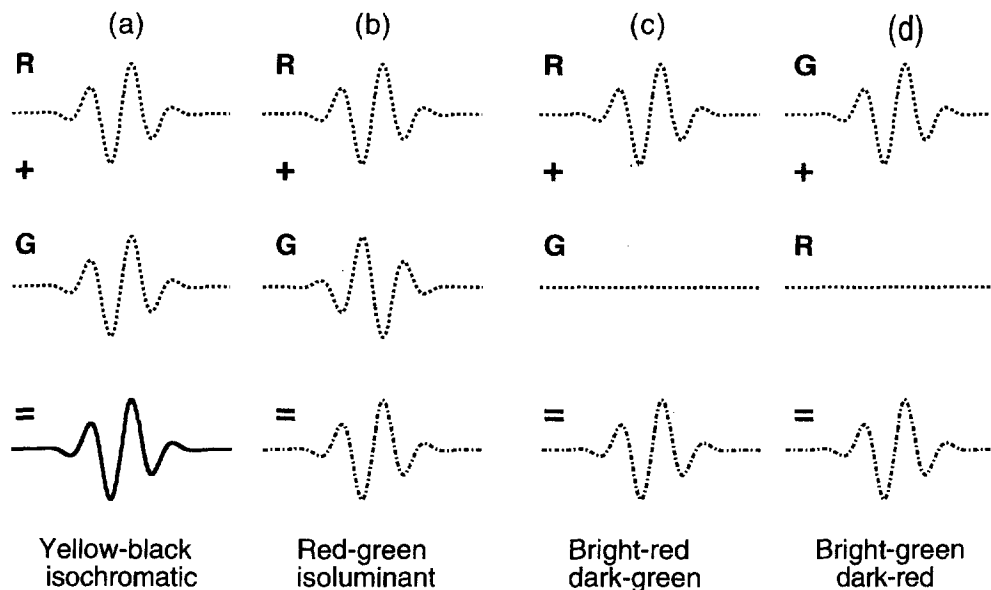
FIGURE 1. Schematic diagram to illustrate the construction of colour/luminance compound stimuli. Columns (a) and (b) show how the in-phase and anti-phase modulations of the red (R) and green (G) monitor guns produced the nominally isochromatic (bright and dark yellow bars) and isoluminant (red and green bars) stimuli, respectively. The chromatic contrast of the isoluminant stimuli was defined as the luminance contrast (see text) on the red (or green) gun required to produce a given chromaticity modulation. Compound stimuli were generated by asymmetric modulation of the red and green guns. The two cases illustrated in columns (c) and (d) correspond to the chromatic and luminance contrasts (by our definition) being equal, and therefore the CLC ratio was 1.0. Note that for the compound stimuli, the chromatic and luminance contrasts were specified in terms of contrasts of the putative chromatic and achromatic components, rather than the explicit gun modulations.

cular transfer (Beauchemin, Faubert, Delorme & Bérubé, 1993; Webster & Mollon, 1994; Singer & D'Zmura, 1994) indicate that mechanisms sensitive to chromatic contrast should show some degree of binocularity.

What levels of binocular summation would be expected with chromatic stimuli? This question is an interesting one, given the suggestion of Rose *et al.* (1988) that the mechanisms of stereopsis and binocular *neural* summation are intimately linked. In their study, binocular summation levels were measured at a range of disparities using stimuli with a range of peak spatial frequencies. It was found that the disparity range over which binocular summation levels exceeded the levels expected from probability summation (i.e., the range over which neural summation was obtained) coincided with the range over which stereoscopic depth perception was obtained. They were at pains to point out that this disparity range was greater than that over which binocular fusion was obtainable. They concluded that neural summation occurs in the mechanisms which subserve stereopsis, as well as those which subserve fusion.

Simmons and Kingdom (1994) showed that, with vertically oriented isoluminant red–green Gabor patches, stereopsis was obtainable at a range of disparities, but that, unlike with isochromatic patterns, stereoscopic depth identification was not possible at the appropriate contrast detection threshold. Furthermore, with horizontally oriented patterns, stereoscopic performance at isoluminance was even worse, particularly when compared with the relatively high levels of performance obtainable with horizontally oriented isochromatic patterns. Hence we have a situation where a stimulus does

not support stereopsis when at detection threshold. What, then, is the level of binocular summation?

To investigate these questions further, a series of measurements of monocular and binocular detection thresholds were made. The stimuli were always 0.5 cpd Gabor patches and were isoluminant red–green, isochromatic yellow–black, or some combination of the two. The results reveal that "neural" binocular summation is obtained with isoluminant stimuli. The implications of these results for models of colour vision and the mechanisms of binocular summation are discussed.

METHODS

The methods used in this study have been reported previously in other studies (Simmons & Kingdom, 1994, 1995, 1997; Kingdom & Simmons, 1996). The data collated in this study were all obtained during the course of these previous investigations of stereopsis at isoluminance, where monocular detection thresholds were measured in order to determine the contrast thresholds for "simultaneous monocular detection" of various stimuli (Simmons & Kingdom, 1994). In footnotes to the Methods sections of each of these previous studies, it was noted that a concurrent study of binocular summation was being performed. Consequently, only a brief summary of the methods employed will be provided here.

Stimuli

The stimuli used were "Gabor" patches, consisting of a sinusoidal variation in luminance and/or colour (the "carrier") modulated by a gaussian (the "envelope"). The

spatial frequency of the carrier was 0.5 cpd and the standard deviation of the envelope was 1 deg, resulting in a spatial bandwidth of approximately 1.1 octaves (full-width at half maximum). The spatial parameters of the stimuli were designed to minimize luminance artifacts due to chromatic aberration (Scharff & Geisler, 1992). The stimuli were either vertically or horizontally oriented and the carrier was always in sine phase relative to the envelope. The stimuli appeared in a high-contrast white fixation circle of radius 3 deg which was present throughout the experiment. In most experiments, a pair of high-contrast vertical nonius lines, each 36 arcmin long and 1.8 arcmin (1 pixel) wide, was present both before, between, and immediately after stimulus presentation. The exceptions were the data collected during the course of the study reported in Kingdom and Simmons (1996). When used, the nonius lines ensured that subjects' eyes were correctly positioned. The ensemble of fixation stimuli used in the detection experiments was intended to be identical to those used for the investigation of stereopsis. An illustration of a typical stimulus with fixation markers is presented in Fig. 1 of Simmons and Kingdom (1994).

Luminance contrast was generated by modulating the red and green guns of the monitor in spatial phase, whereas chromatic contrast was generated by modulating these guns in spatial antiphase. Compound stimuli were generated by specifying the luminance and chromatic contrasts separately (as a ratio of one to the other) and then calculating the appropriate gun modulations. Additionally, the experimenter also set a polarity parameter that specified the relationship of the red and green chromatic phases to the bright and dark luminance phases. Thus, for example, a colour/luminance contrast (CLC) ratio of 1.0 with polarity set to "red bright" resulted in modulation of only the red gun of the monitor relative to the yellow background field. The resultant percept was of a stimulus with bright red and dark green bars (see Fig. 1).

The luminance and chromatic contrasts reported are the Michelson contrasts (i.e., $(L_{max} - L_{min})/(L_{max} + L_{min})$) of the Gabor carrier before multiplication by the gaussian envelope. This measure of contrast is directly proportional to one based on the Gabor stimulus itself, such as $(L_{max} - L_{mean})/L_{mean}$. The luminances, L, were those measured with a photometer.

The ratio of red to overall mean luminance (the R/(R + G) ratio) was determined by the isoluminance setting (see below). Variations in R/(R + G) ratio from low to high values resulted in the colour of the background field varying from greenish through yellow to reddish. The mean luminance of the background field and stimulus at the eye was approx. 2 cd/m^2. The luminance of the fixation stimuli at the eye was approximately 10 cd/m^2. The chromaticity coordinates of the red and green phosphors were ($x = 0.623$, $y = 0.340$) and ($x = 0.278$, $y = 0.584$) respectively before passage through the shutter glasses and ($x = 0.614$, $y = 0.347$) and ($x = 0.270$, $y = 0.594$), respectively, after

passage through the shutter glasses (i.e., at the eye of the subject).

Dichoptic presentation method

Dichoptic separation was obtained using a pair of liquid-crystal shutters (Displaytech Inc.) synchronized to the monitor frame rate of 160 Hz, resulting in a refresh rate of 80 Hz in each eye. It is well known that interocular "cross-talk" can occur when using liquid crystal shutters to separate stereo half-images in a set-up such as this one. In a previous study (Simmons & Kingdom, 1994) it was shown that at low stimulus contrasts (i.e., close to detection threshold) this cross-talk was undetectable.

Subjects

Subjects were the two authors. Both are colour normal and have good stereopsis. One (FK) is emmetropic and the other (DS) wore his prescribed optical correction.

Procedure—contrast detection

The stimulus was presented at random in one of two temporal intervals, each 200 msec long, separated by a 1 sec gap. The other interval was blank. Stimulus onset and offset were abrupt. The subject was asked to decide whether the stimulus had appeared in the first or second interval. During the course of a single experimental run, binocular and monocular presentations were randomly interleaved. The stimulus configuration, stimulus duration and number of trials were exactly the same as in the stereopsis experiments in the appropriate study. Where parameters such as stimulus eccentricity are relevant they will be reported in the Results section.

Procedure—isoluminance setting

Two different methods were used to determine the isoluminant point. In those detection data obtained during the course of Simmons and Kingdom (1994) and Simmons and Kingdom (1995), the method of minimum motion was used, although additional experiments were performed at a range of R/(R + G) ratios. In both Kingdom and Simmons (1996) and Simmons and Kingdom (1997), the method of worst performance was used, where the R/(R + G) ratio at which either the disparity threshold or the contrast threshold for depth identification was highest was taken to be the isoluminant point. In none of these cases was the isoluminant point specifically designed to be the appropriate one for either monocular or binocular detection. However, the examination of detection performance at a range of ratios of colour to luminance contrast presented in this study, together with the important observation that stereopsis was impaired at quite a broad range of R/(R + G) ratios (Simmons & Kingdom, 1994, 1995; Kingdom & Simmons, 1996) suggests that this study did not require an overly precise determination of the isoluminant point for detection mechanisms.

Data analysis

A maximum-likelihood procedure, similar to that

employed by Watson (1979), was used to fit the detection psychometric functions with Weibull–Quick functions. A "bootstrap" procedure (Maloney, 1990; Foster & Bischof, 1991) was used to determine confidence limits on the estimates of the threshold (α) and slope (β) parameters of the fitted functions.

ASSESSMENT OF THE INDEPENDENCE OF CHROMATIC AND ACHROMATIC BINOCULAR DETECTION MECHANISMS

Before considering the nature of summation *between* the eyes, it was first necessary to consider separately the nature of the summation between chromatic and achromatic detection mechanisms when stimuli consisting of compounds of colour and luminance contrast are presented binocularly. The aim was to establish whether or not chromatic and achromatic detection mechanisms were independent since, without this knowledge, any subsequent analysis of the nature of summation between the eyes would be difficult to interpret.

Predictions were made under two hypotheses, namely that detection performance at a range of CLC ratios was due to activity in a single luminance-contrast-sensitive pathway or in a combination of colour-contrast- and luminance-contrast-sensitive pathways. The prediction method is outlined in detail in Simmons and Kingdom (1997), so only a summary will be provided here.

Single-pathway hypothesis

If a single luminance-contrast-sensitive pathway were responsible for detection at all CLC ratios, then changes to the CLC ratio would simply result in changes in the effective luminance contrast of the stimulus. This situation was modelled by calculating an equivalent luminance contrast of the nominally isoluminant stimulus by finding the luminance contrast, c_{eq}, required to obtain the same detection performance level using the expression:

$$c_{eq} = \alpha_{col} \left(\frac{c_{lum}}{\alpha_{lum}} \right)^{\beta_{lum}/\beta_{col}}, \qquad (1)$$

where α_{lum} and β_{lum} are the threshold and slope parameters, respectively, of the psychometric function for detection of the isochromatic stimulus, α_{col} and β_{col} are those same parameters taken from the detection psychometric function of the nominally isoluminant stimulus, and c_{lum} is the contrast of the isochromatic stimulus that allows the same performance level (i.e., probability of detection). This equivalent contrast of the chromatic stimulus component was then added to the luminance contrast component of the stimulus to calculate the "effective" luminance contrast, c_{mod}, of the compound stimulus:

$$c_{mod} = c_{lum} + c_{eq}. \qquad (2)$$

The insertion of c_{mod} into the psychometric function for detection of the isochromatic stimulus allowed the prediction of contrast thresholds for the different compound stimuli to be calculated in terms of the luminance and chromatic stimulus components.

This modelling method differs from the conventional method for predicting "linear" summation, which involves simply drawing a straight line in the appropriate coordinate space joining the thresholds on the axes (see Graham, 1989). This modified method is necessary in this situation because (a) it takes into account the possibility that the slopes of the psychometric functions for detection of the isoluminant and isochromatic stimuli are different; and (b) it incorporates the information that a luminance signal would be "signed"*. Consequently, the predictions show two behaviours which are unusual in analyses of this type. First, the predictions do not necessarily lie on a straight line joining thresholds on the two axes, although they do if the psychometric functions obtained with isoluminant and isochromatic stimuli share the same or similar slope parameters. Second, the predictions exhibit a "null" region, where the luminance contrast provided by the chromatic component of the compound stimuli destructively interferes with the *bona fide* luminance component of the stimulus.

Dual-pathway hypothesis

An alternative to the single-pathway hypothesis is that detection takes place "independently" in separate chromatic- and luminance-contrast detection mechanisms. Such a hypothesis suggests that detection performance at different CLC ratios can be predicted via probability summation (Graham, 1989) between the two mechanisms. Again the methods for generating these predictions are outlined in Simmons and Kingdom (1997). The principle is that the probabilities of detection, P_D, of the compound stimulus are given by the complement of the probability of not detecting the stimulus in either the chromatic- or luminance-contrast-sensitive pathway. After correction for guessing, the resultant expression is:

$$P(c_{lum}, c_{col}) = 1 - 0.5\left\{ \exp\left[-(c_{lum}/\alpha_{lum})^{\beta_{lum}} \right] \right\}$$

$$\left\{ \exp\left[-(c_{col}/\alpha_{col})^{\beta_{col}} \right] \right\}, \qquad (3)$$

where c_{col} is the chromatic contrast of the chromatic stimulus component.

Goodness-of-fit assessment

The goodness of fit of the models described above was assessed by calculating Chi-squared statistics for each data set (Press, Flannery, Teukolsky & Vetterling, 1988). The following calculation was performed:

$$\chi^2 = \sum (O_i - E_i)^2 / \sigma_i^2, \qquad (4)$$

where O_i was the observed value of the ith threshold, E_i was the expected value of that threshold under a given model, and σ_i was the standard error associated with that threshold, estimated from the inter-quartile range of the

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*i.e. that the phase of the equivalent luminance contrast of the nominally isoluminant stimulus is such that the red parts of the stimulus are brighter than the green ("red bright") or the green parts brighter than the red ("green bright").
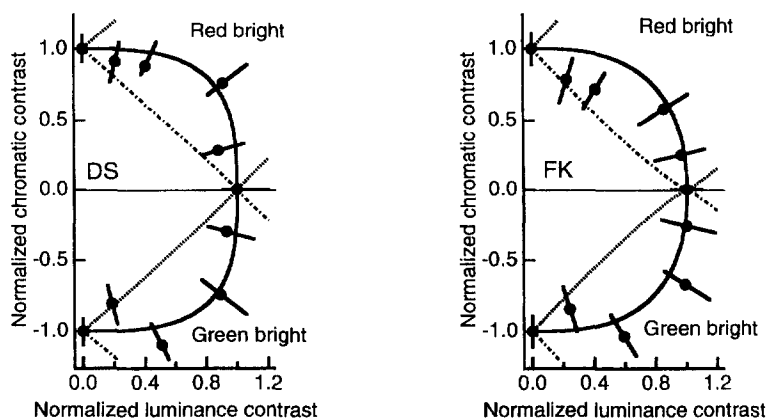
FIGURE 2. Normalized contrast thresholds for binocular detection at a range of different colour/luminance contrast (CLC) ratios for two subjects. Thresholds were normalized by the appropriate isoluminant or isochromatic threshold. Data are plotted with normalized chromatic contrast as ordinate and normalized luminance contrast as abscissa. The sign of the chromatic contrast corresponds to the relative phases of the chromatic and achromatic modulation. In the upper "quadrant" (marked "red bright") the red phases of chromatic modulation coincide with the bright phases of luminance modulation. In the lower "quadrant" (marked "green bright") the green and bright phases coincide. The error bars on the data are 95% confidence limits determined by bootstrap analysis. Three predictions are shown on each graph. The dot-dashed and dotted curves are the single-pathway model predictions with the sign of the equivalent luminance contrast of the chromatic content being such that red is bright and green is bright respectively. The solid curve gives the prediction of the dual-pathway (probability-summation) model, where probability summation is between independent luminance- contrast- and chromatic-contrast-sensitive mechanisms rather than between the left and right eyes (as later).

bootstrap threshold histogram (Maloney, 1990). The χ^2 values were collated separately for each data set and the number of degrees of freedom was equal to the total number of threshold values included in the analysis, given that there were no free parameters in the model predictions.

RESULTS

In Fig. 2, contrast thresholds for binocular detection are plotted with normalized chromatic contrast as the ordinate vs normalized luminance contrast as abscissa. The normalization factors for each axis were the contrast thresholds for the isoluminant and isochromatic stimuli. Hence thresholds are 1.0 on each axis, but vary at different CLC ratios.

A cursory inspection of Fig. 2 shows that, across all conditions, the dual-pathway model appears to fit the data better. This observation is backed up by goodness-of-fit calculations. For both DS and FK, the dual-pathway model provided a lower χ^2 statistic than the best single-pathway model (DS: best single-pathway 144.6, dual-pathway 16.4; FK: best single-pathway 171.9, dual-pathway 22.7). It was therefore concluded that these compound stimuli were not being detected by a single pathway and assumed that independent colour- and luminance-contrast-sensitive mechanisms were fulfilling this role.

BINOCULAR SUMMATION OF CHROMATIC AND ACHROMATIC CONTRAST

Having established that independent luminance-contrast- and chromatic-contrast-sensitive mechanisms were

probably involved in detecting these compound stimuli, the next step was to establish to what extent binocular summation (that is, summation between the eyes) was affected by the relative amounts of colour and luminance contrast in the stimulus.

Figure 3(a) shows a plot of the magnitude of binocular summation at a range of CLC ratios. The binocular summation data (filled circles) are weighted geometric means* (Topping, 1957) of binocular summation data obtained from the two subjects and the error bars are the associated standard errors. Also shown on the graph are two semicircles. The inner semicircle (dotted line) has a radius of 1.2 and thus represents the amount of binocular summation expected from *binocular* probability summation† alone. The outer semicircle (dashed line) has a radius of $\sqrt{2}$ and represents the amount of binocular summation usually obtained with luminance stimuli and conventionally termed neural summation (Campbell & Green, 1965; Legge, 1984a; Rose et al., 1988; Anderson & Movshon, 1989).

The main point to note from Fig. 3(a) is that the binocular summation level was above that predicted by probability summation at all CLC ratios. Indeed, there was no consistent variation of the binocular summation

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*For each individual data point, a standard error was estimated from the inter-quartile range of the bootstrap histogram. This standard error was then used to inversely weight the binocular summation ratios when they were combined and also to calculate the overall standard error.

†Note again that binocular probability summation refers to probability summation between the left and right eyes, not between the mechanisms of chromatic contrast and luminance contrast processing, as described in the analysis of the data presented in Fig. 2.
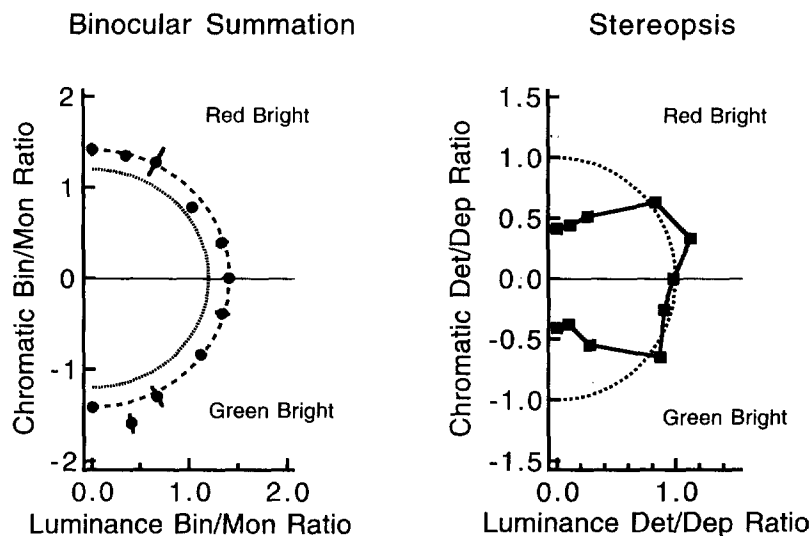
FIGURE 3. (a) Amount of binocular summation, expressed as the ratio of binocular to mean monocular contrast sensitivities, at a range of CLC ratios. The data are presented using the same polar format as Fig. 2, in that the angle between the vector to the data point and the chromatic (vertical) axis represents the relative amount of luminance contrast in the stimulus. Thus, data along the vertical axis were obtained with isoluminant (i.e., chromatic) stimuli, and data perpendicular to this axis were obtained with isochromatic (i.e., luminance) stimuli. The magnitude of the data vector represents the amount of binocular summation. The data points are weighted means of ratios obtained from two subjects and the error bars are the associated standard errors. The dotted semicircle shows the level of binocular summation expected from probability summation between the left and right eyes (1.2). The dashed semicircle represents the usual level of binocular summation obtained empirically with luminance stimuli ($\sqrt{2}$). (b) Stereoscopic data plotted in a similar way to that in (a). The length of the stimulus vector now represents the ratio of contrast sensitivities for simultaneous monocular detection to those for stereoscopic depth identification of the stimulus. These data are weighted means of those presented in Fig. 2 of Simmons and Kingdom (1997), 30 arcmin condition. The dashed semicircle represents a ratio of 1, which is the ratio expected if stereoscopic depth identification is possible at the contrast threshold for simultaneous monocular detection.

level with the amount of luminance contrast in the stimulus. This result provided evidence for neural summation within the mechanisms most sensitive to chromatic contrast.

The meaning of this result is put into perspective when compared with the data in Fig. 3(b), which shows the ratio of contrast sensitivities for simultaneous monocular detection to those for stereoscopic depth identification*. Where this ratio is equal to 1 (the locus indicated by the dotted semicircle) depth identification is possible at simultaneous monocular detection threshold†. Where this ratio is less than 1, more contrast is required for depth identification than for detection. Figure 3(b) shows that this ratio drops well below 1 when the CLC ratio is greater than 1, which is when the compound stimulus is dominated by the chromatic component. Hence, when

detection of the stimulus is primarily determined by the chromatic-contrast detection mechanism, stereoscopic depth identification is not possible at this detection threshold. It has been argued previously that the existence of such a "contrast gap" indicates that those mechanisms which detect the stimulus are separate from those which underlie stereoscopic depth processing (Simmons & Kingdom, 1994).

By comparing the two panels of Fig. 3 it can be seen that binocular neural summation is taking place at CLC ratios which do not support stereoscopic depth identification at detection threshold, suggesting that binocular neural summation is taking place in mechanisms that are not sensitive to stereoscopic depth.

This result encouraged a re-examination of previous binocular summation data that had been collected in the course of previous studies (i.e., Simmons & Kingdom, 1994, 1995, 1997; Kingdom & Simmons, 1996). Figure 4 shows a summary of these data.

The conditions were luminance vertical (LV), luminance horizontal (LH), chromatic vertical (CV), and chromatic horizontal (CH). Note that the horizontal and vertical orientations in this case were those of the Gabor carrier grating. The differently shaded bars of the histogram represent binocular summation data collected at the different eccentricities 0, 20, and 80 arcmin, corresponding to disparities of 0, 40 and 160 arcmin‡. The data are geometric means of data collected from both

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*These data are again weighted means of data from two subjects. These data were plotted in their raw form in Fig. 1 of Simmons and Kingdom (1997). The reader is referred to this study for a more detailed description of how the stereopsis data were obtained. The stimulus disparity for the depth identification experiments was 30 arcmin and the stimuli were identical to those used in the detection experiments.

†It has been argued previously that this calculated detection threshold is the most appropriate for comparison with stereoscopic data (Simmons, 1992; Simmons & Kingdom, 1994).

‡Different eccentricities were always obtained by equal and opposite shifts of the monocular half-images, hence the one-to-one relationship between eccentricity and disparity.

subjects and the error bars are standard errors on these data.

For all four conditions there is a significant decrease in binocular summation with increasing eccentricity. In all four conditions, significant neural summation was found at zero eccentricity. For both luminance conditions, binocular summation levels dropped to approximately those levels expected from probability summation at eccentricities of 80 arcmin. For both chromatic conditions, there were still significant levels of neural summation at this largest eccentricity. Only for the LV condition was stereoscopic depth identification possible at detection threshold (Simmons & Kingdom, 1994, 1995, 1997). For all other conditions (i.e. LH, CV, CH) there is no evidence that those mechanisms that are detecting the binocular stimuli are the same as those which process its stereoscopic depth (see Simmons & Kingdom, 1994).

Indeed, the ordering of the binocular summation data, with summation ratios being lowest for the luminance vertical condition and highest for the chromatic horizontal condition, is the reverse of what would be expected from stereopsis data. The worst stimulus as far as stereopsis is concerned is the chromatic horizontal. Subjects found it almost impossible to obtain depth perception with this stimulus, even at the highest contrasts obtainable on the equipment (Simmons & Kingdom, 1995; Kingdom & Simmons, 1996), yet the binocular summation ratios are actually very high and close to a factor of 2. They are higher than those obtained with the vertical luminance stimulus, which is a much better stimulus for stereopsis.

DISCUSSION

Binocular detection in mechanisms sensitive to chromatic contrast

One aim of this study was shared with that of a related study (Simmons & Kingdom, 1997), which was to ascertain whether a binocular function, in this case binocular detection rather than stereopsis, was possible in the mechanisms sensitive to chromatic contrast. The better fit of the model based on probability summation between independent luminance-contrast- and colour-contrast-sensitive mechanisms that is illustrated in Fig. 2 and backed up by the goodness-of-fit statistics reported above, suggests that binocular detection of stimuli which possess both chromatic and luminance contrast is obtained via independent detection processes in separate colour- and luminance-contrast-sensitive mechanisms. This finding is confirmed in a recent study by Mullen, Cropper and Losada (1997), although the presentation in that case was monocular. A better fit to the data may have been obtained by postulating more than two mechanisms sensitive to combinations of colour and luminance contrast, but such an analysis was beyond the scope of this study and would also have involved introducing free parameters.
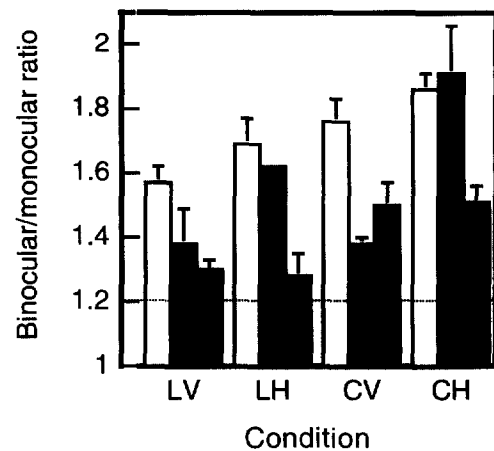

FIGURE 4. Histogram showing the binocular summation levels obtained in four different conditions (LV = Luminance Vertical, LH = Luminance Horizontal, CV = Chromatic Vertical, CH = Chromatic Horizontal). The different shaded bars represent data collected at 0 (open bars), 20 (shaded bars) and 80 (solid bars) arcmin of eccentricity. The error bars are standard errors based on the geometric means of the binocular summation ratios (no error bars are shown in one of the LH conditions because it is based on only one threshold measurement). Again, data were averaged across subjects and the dotted horizontal line represents the level predicted from interocular probability summation.

Evidence for binocular neural summation in chromatic detection mechanisms

The data presented in Figs 3 and 4 clearly show that significant amounts of binocular neural summation are obtained under conditions in which binocular detection is mediated by mechanisms that are primarily sensitive to chromatic contrast. Hence, whatever the utility of chromatic mechanisms for stereoscopic depth perception (Simmons & Kingdom, 1994, 1995, 1997; Kingdom & Simmons, 1996), they clearly have a high degree of binocularity.

Implications for the link between binocular neural summation and stereopsis

It has been suggested that binocular neural summation is linked to the mechanisms of stereopsis (Rose et al., 1988).

Figure 5 plots binocular summation data from Fig. 5 of Rose et al. (1988), which were obtained with 0.75 cpd D3 luminance stimuli, the most comparable stimulus to the vertically oriented luminance Gabor stimuli used in this study (thin solid line). Superimposed on Rose et al.'s data are data taken from Fig. 4 of this study. Only shown are data for the luminance vertical (LV; open circles) and chromatic horizontal (CH; filled squares) conditions. Note that in the current study, data obtained with crossed and uncrossed disparities were pooled so, for comparison purposes, the data have been reflected in the zero disparity axis.

The vertical luminance data are consistent with the study of Rose et al. (1988) in that binocular summation is maximal at zero eccentricity (1.57) and falls gradually
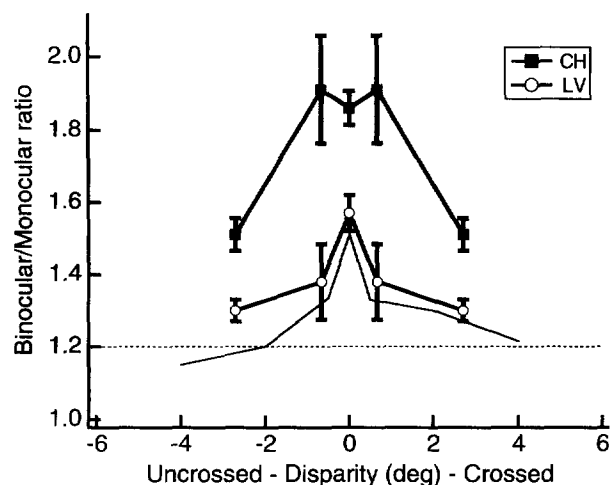
FIGURE 5. Binocular summation ratios plotted against disparity in degrees. The thin solid line joins data obtained from Fig. 5 of Rose *et al.* (1988) and was collected using a 0.75 cpd D3 stimulus that was vertically oriented. The open circles show data collected in this study using luminance contrast with a vertically oriented Gabor carrier (Luminance Vertical, LV); the filled squares represent data collected using chromatic contrast with a horizontally oriented carrier (Chromatic Horizontal, CH). The error bars in this case are standard errors based on the average (geometric mean) of the binocular summation ratios. Note that the summation ratios were averaged across subjects, as well as across separate threshold determinations. The data from this study have been pooled across equally sized crossed and uncrossed disparities. Again the horizontal dotted line represents the level of binocular summation expected from probability summation.

with increasing eccentricity. At the largest eccentricity tested, 80 arcmin (which corresponds to a disparity of 160 arcmin) the binocular summation level had dropped to 1.30. However, the horizontal chromatic data are strikingly different. First, the overall level of binocular summation is much higher (1.86 at zero eccentricity, dropping to 1.51 at 80 arcmin). Second, the levels are such that something close to full summation (a factor of 2) is being obtained for central viewing of the horizontally oriented chromatic stimulus, and even at the relatively large eccentricity of 80 arcmin, the levels obtained were appreciably above those expected from probability summation. This result is all the more surprising given the difficulty in obtaining any sort of stereoscopic depth percept with these stimuli (see Simmons & Kingdom, 1995; Kingdom & Simmons, 1996).

It is thus clear from these data that stimulus conditions under which stereoscopic depth discrimination is very difficult, and certainly not possible at detection threshold, give rise to levels of binocular summation that suggest that binocular neural summation is occurring. Whilst Rose *et al.* (1988) did not suggest that binocular neural summation *only* takes place in stereopsis mechanisms, the link between the two phenomena is weakened by the evidence presented in this study.

One explanation of the results presented here that is in keeping with the conclusions of Rose *et al.* (1988) is that binocular summation in the LH, CV, and CH conditions is taking place in binocular *fusion* mechanisms. The diplopia threshold was not examined with these stimuli, although subjects often reported diplopia at the largest eccentricity tested (80 arcmin), so binocular fusion mechanisms remain a possible substrate for the binocular

neural summation found here. However, it is relevant that for both luminance-contrast conditions, binocular summation levels had dropped very close to probability summation at the 80 arcmin eccentricity, but the same was not true for the chromatic conditions (see Figs 4 and 5).

Another interesting point is the high level of binocular summation found with the chromatic stimuli. In particular, for the CH condition, levels were close to *full* neural summation (i.e., apparently adding the contrasts from the two eyes) at zero eccentricity. This result would appear to indicate an even greater degree of binocularity in the chromatic mechanisms than the luminance mechanisms, despite the poor stereopsis obtained at low chromatic contrasts.

Perhaps there is, however, an explanation for this higher level of binocular summation with chromatic stimuli. Perhaps stereopsis in fact requires *inhibitory* interocular interactions in order to enable accurate cross-correlation of left- and right-eye inputs (Freeman & Ohzawa, 1990; Simmons, 1992; Simmons & Hawken, 1993; Kontsevich & Tyler, 1994; Smallman & McKee, 1995; Anzai *et al.*, 1995). These interactions may take the form of some sort of interocular contrast gain mechanism. Hence the high levels of binocular summation found with chromatic stimuli could reflect the lack of such a mechanism (or, at least, such a mechanism capable of operating at low input contrasts) and the presence of this mechanism could be crucial to operational stereopsis.

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