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On the Independence of Chromatic and Achromatic Stereopsis Mechanisms

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The extent to which the processing of stereoscopic depth information can take place separately in colour-contrast-sensitive and luminance-contrast-sensitive mechanisms has been investigated. Contrast thresholds for stereoscopic depth identification (front/back) were measured using 0.5 c/deg Gabor patches. The stimuli possessed different amounts of colour and luminance contrast ranging from isoluminance (red/green) to isochrominance (yellow/black) through intermediate values. Two models for combining chromatic and achromatic stereopsis information were tested. The first (*single-pathway*) model assumed colour and luminance contrast summation within a single luminance-contrast-sensitive mechanism before stereoscopic judgement. The second (*dual-pathway*) model assumed probability summation between independent chromatic and achromatic stereopsis mechanisms. The latter model provided the better fit to the data. In providing evidence in favour of an independent chromatic stereopsis mechanism, it was shown that luminance artifacts were unlikely to be the cause of maintained stereopsis at isoluminance. The possible neural substrates of chromatic stereopsis are discussed. © 1997 Elsevier Science Ltd. All rights reserved.

Colour Stereopsis Contrast sensitivity Isoluminance Binocular vision

INTRODUCTION

To what extent do chromatic mechanisms independently contribute to performance in spatial tasks such as stereoscopic depth perception? This problem has traditionally been addressed by measuring stereoscopic performance at *isoluminance*, when the contribution of luminance mechanisms is theoretically zero (Lu & Fender, 1972; Comerford, 1974; Gregory, 1977; de Weert, 1979; de Weert & Sadza, 1983; Osuobeni & O'Leary, 1986; Livingstone & Hubel, 1987; Tyler & Cavanagh, 1991; Osuobeni, 1991; Scharff & Geisler, 1992; Simmons & Kingdom, 1994, 1995; Kingdom & Simmons, 1996). A brief review of these studies is given in Howard and Rogers (1995).

Perhaps the most extreme views on what happens to stereopsis at isoluminance are represented by the studies of Livingstone and Hubel (1987) and Scharff and Geisler (1992). Livingstone and Hubel (1987) suggested that one can always find a ratio of red to green luminances at which stereoscopic depth perception is impossible, whatever the nature of the stimulus (specifically random-dot stereograms and short vertical bars) so long as one is careful enough to eliminate any potential luminance artifacts. Scharff and Geisler (1992), on the other hand, suggested that the reduction in performance at isoluminance was entirely due to the reduced effective contrast of isoluminant stimuli. Using an 'equivalent-contrast' metric derived from an ideal observer model, they showed that stereoscopic performance for some of their subjects was as good with red–green isoluminant patterns as with isochromatic patterns. These results and conclusions were, broadly speaking, consistent with those of Grinberg and Williams (1985) who used blue–yellow stimuli.

In a series of studies, Simmons and Kingdom (1994, 1995) and Kingdom and Simmons (1996) put forward a middle view. They used multiples of stimulus detection threshold as their contrast metric and found that stereoscopic depth perception using vertically oriented isoluminant Gabor stimuli was impaired but not eliminated. Thus, although they found that stereoscopic performance was worse at isoluminance, their results clearly showed that there was a chromatic input to stereopsis under some conditions.

It does not follow from these results, however, or any others demonstrating maintained stereoscopic performance at isoluminance, that there is a dedicated chromatic stereopsis mechanism that is distinct from the luminance stereopsis mechanism. The reasons for this are as follows. First there are the technical difficulties involved in creating a stimulus totally free of luminance artifacts. Livingstone and Hubel (1987) listed a number of these difficulties, the main one being variations in the

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isoluminant point with eccentricity. They suggested that unless the stimulus was very small (i.e. confined to the central 1 deg of the visual field) one could never be certain that the entire stimulus was at isoluminance and thus totally free from luminance contrast. Second there is the nature of isoluminance itself. Given a luminance-contrast-sensitive *neuron* it should always be possible to manufacture an isoluminant heterochromatic stimulus to which the cell does not respond. However, not all of these neurons will necessarily share the same isoluminant point and thus it may be impossible to silence the whole population with one such stimulus (Logothetis *et al*., 1990; Dobkins & Albright, 1993, 1995).

A third problem with interpreting the maintenance of stereoscopic performance at isoluminance concerns the potential contributions of luminance-contrast-sensitive mechanisms that have a residual chromatic sensitivity. This problem differs from the previous one in that the neurons in question would not necessarily possess an isoluminant point at all because they demonstrate a significant response to isoluminant stimuli, although this response may be qualitatively different from that to luminance-defined stimuli. Indeed, psychophysical evidence from the motion domain raises just such a possibility for stereopsis. Dobkins and Albright (1993) have provided evidence for a motion mechanism that is sensitive to the presence but not the sign of isoluminant chromatic borders. This mechanism is thought to have a neural substrate in the human visual area V5/MT, and could be relayed via the so-called "frequency-doubled" response of magnocellular LGN neurons to isoluminant stimuli (Schiller & Colby, 1983; Dobkins & Albright, 1994). The same signal could carry information useful for stereopsis to V1 and beyond, and thus stereoscopic performance at isoluminance could therefore be subserved solely by activity in the Magno processing stream, consistent with the scheme of Livingstone and Hubel (1987).

These three challenges to the notion of the involvement of a colour-opponent mechanism in stereopsis have already been partially answered by previous studies. Experimental evidence for significant variation in the isoluminant point with eccentricity is scarce (see Dobkins & Albright, 1993). Indeed, in the study of Mullen (1991) there appeared to be little variation up to eccentricities of 5 deg. Furthermore, the isoluminant stereoscopic stimuli used by Tyler amd Cavanagh (1991) and Simmons and Kingdom (1994) were relatively small. Thus, at least in these two studies, it would appear that the stimuli were free of luminance *artifacts*. Two lines of evidence argue against an "unsigned", Magno-based, colour-contrast-sensitive mechanism (Dobkins & Albright, 1993) being the substrate of stereoscopic performance at isoluminance. First, Simmons and Kingdom (1995) found that when the disparity of vertically oriented Gabor stimuli was varied through a wide range of phase disparities (from zero up to 1.3 cycles), colour contrast thresholds for stereoscopic depth identification showed a cyclic dependence on disparity. This result showed that the sign of the colour contrast was important at isoluminance (i.e. that red bars were matching red bars and green were matching green). Second, the study of Stuart *et al*. (1992) demonstrated that a purely chromatic signal could support stereopsis in the presence of uncorrelated luminance noise, and also that this percept was adversely affected by the contrast of the noise. They suggested from these results that they had observed stereoscopic processing within a "double-duty" visual pathway which was multiplexing chromatic and achromatic signals [for a review see Kingdom & Mullen (1995)] and that this was consistent with the stereoscopic signals being carried by the Parvo processing stream.*

Nevertheless, the second objection to the maintenance of stereopsis at isoluminance, that it may be impossible to reach isoluminance for all luminance-contrast-sensitive stereoscopic mechanisms simultaneously, still remains a possibility, and evidence for a truly independent† low-level colour-opponent input to stereopsis mechanisms has yet to be provided. In this study, therefore, an explicit test of independence of the chromatic and achromatic contributions to stereoscopic depth perception is presented. The method used is similar to that first employed by Graham *et al*. (1978) for estimating the independence of spatial mechanisms, and is fully described in Graham (1989). Stereoscopic stimuli (0.5 c/deg, vertically oriented Gabor patterns) were generated which possessed different amounts of colour and luminance contrast. Contrast thresholds for depth identification were measured for a range of disparities. The range was designed to be optimal for chromatic stereopsis mechanisms in that it was set close to the disparities which provided best performance in a previous study (Simmons & Kingdom, 1994). The contrast thresholds obtained were then predicted from two hypotheses: first, that a single luminance-contrast-sensitive mechanism was responsible for stereoscopic performance at all levels of nominally luminance contrast (including zero) and second, that performance was subserved by two "independent" stereopsis mechanisms, one being sensitive to luminance contrast and the other sensitive to chromatic contrast. The results favoured the second hypothesis. The approach is similar to that taken by others to study motion perception (e.g. Palmer *et al*., 1993).

METHODS

The methods used in this study were similar to those presented in previous publications (Simmons & Kingdom, 1994, 1995), so only a brief summary will be provided here, except where the methods deviate substantially from those employed previously.

Stimuli

The stimuli used were "Gabor" patches, consisting of a sinusoidal variation in luminance and/or colour (the

*This argument is presented in more detail in the Discussion section.
†The nature of the definition of 'independence' in this context is considered in the Discussion section.

"carrier") modulated by a Gaussian (the "envelope"). The spatial frequency of the carrier was 0.5 c/deg and the standard deviation of the envelope was 1 deg, resulting in a spatial bandwidth of approx. 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 always vertically 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. A pair of high-contrast vertical nonius lines, each 36 min arc long and 1.8 min arc (1 pixel) wide, was present both before, between, and immediately after stimulus presentation. These nonius lines served as an additional disparity reference, and ensured that subjects' eyes were correctly positioned. The ensemble of fixation stimuli was designed to provide a strong depth reference at zero disparity [see Fig. 1 of Simmons & 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 approx. 10 cd/m^2.

Stereo display method

Stimulus 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 "crosstalk" 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 crosstalk was undetectable. Further control experiments indicated that the crosstalk contrast was approx. 20 dB (a factor of 10) lower than that of the actual stimulus, which suggests that it may

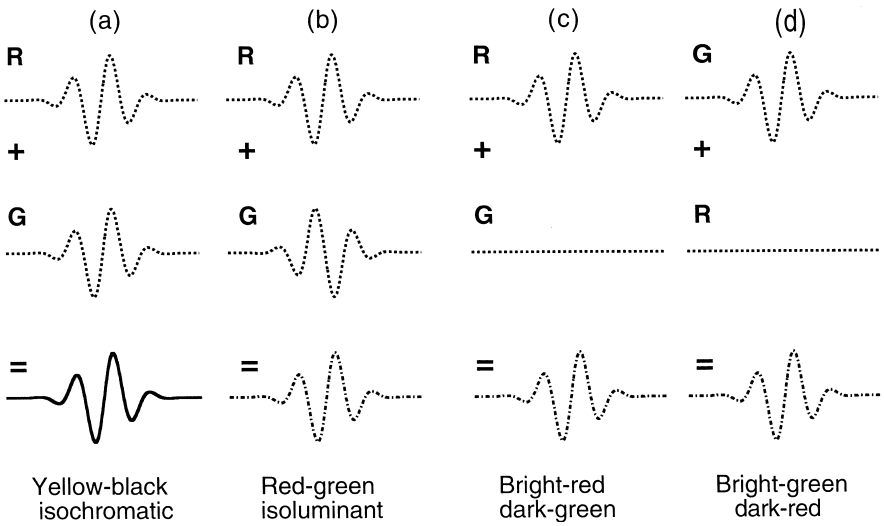

FIGURE 1. Schematic diagram to illustrate the construction of colour/luminance compound stimuli. Columns (a) and (b) show how the in-phase and anti-phase modulations of the red (R) and green (G) monitor guns produced the nominally isochromatic (bright and dark yellow bars) and isoluminant (red and green 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.

have been above detection threshold for some of the very highest stimulus contrasts used (e.g. those used for estimating stereoscopic performance with zero luminance contrast). However, given the evidence that low-contrast stereoscopic signals have little effect on perceived depth of higher contrast signals (Boothroyd & Blake, 1984) and also evidence for a contrast similarity constraint on stereo matching (Smallman & McKee, 1995), it was assumed that the crosstalk did not significantly affect stereoscopic performance in this study.

Subjects

Subjects were the two authors. Both are colour normal. One (FK) is emmetropic and the other (DS) wore his prescribed optical correction. Both subjects were highly experienced in stereoscopic depth discriminations.

Procedure—depth identification

In the main series of experiments, stimuli were constructed with six disparities, three crossed and three uncrossed (± 10, ± 30 and ± 50 min arc). The range of disparities was chosen to optimally stimulate chromatic stereopsis mechanisms (Simmons & Kingdom, 1994). 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. Irrespective of the interval in which the stimulus was presented, the subject was asked to judge whether the stimulus appeared to be in front of or behind the disparity reference. The nonius lines were always present except during stimulus presentation. In the course of a single experimental run, stimuli were presented at a range of contrasts. The range was selected to bracket the required contrast threshold. A given experimental run consisted of six presentations at each of the six disparities and five contrasts together with 36 zero-contrast "catch" trials to probe for subject biases.* There were thus 216 trials in each experimental run. The duration of a run was approx. 10 min. The CLC ratio was never changed during the course of a run, but runs at different ratios were interleaved in a random order.

Data from a number of runs at each CLC ratio were collated to construct psychometric functions relating the proportion of "front" responses to the stimulus contrast.

Procedure—contrast detection

In the detection experiments there were also two presentation intervals, in one of which the stimulus was presented. The subject was now 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 (216) was exactly the same as in the depth-identification experiments. Experiments were performed at an eccentricity of 15 min arc, thus corresponding to the monocular half-image location of a stimulus with 30 min arc of disparity.

Procedure—isoluminance setting

The isoluminant point was determined using the method of worst performance [see e.g. Kingdom & Simmons (1996)]. Pilot experiments indicated the range of R/(R + G) ratios at which depth-identification contrast thresholds were highest. A series of more detailed measurements was then performed at a series of R/(R + G) ratios close to this point. The step size in R/(R + G) ratio was 2%. The procedure for these depth-identification experiments was similar to that described above except that only two disparity values were employed (± 30 min arc), and the number of presentations at each disparity and contrast was ten in each experimental run. Consequently the run was shorter, at 120 trials (including 20 "catch" trials).

The R/(R + G) values obtained using this method were 0.51 and 0.52 for subjects FK and DS, respectively. Errors in this determination were likely to be no greater than ± 2% given the resolution of sampling and the size of the error bars. It was found, however, that there was quite a broad range of R/(R + G) values at which stereopsis was impaired by almost the same amount [see Fig. 4 of Simmons & Kingdom (1994) for a similar measurement] and thus that small errors in the location of the isoluminant point would have made little difference to performance measures. Interestingly, the values are close to those determined in a separate study where worst stereoacuity was the performance measure (Kingdom & Simmons, 1996), although they are slightly different from those found using the minimum-motion technique (Simmons & Kingdom, 1994, 1995).

Data analysis

A maximum-likelihood procedure, similar to that employed by Watson (1979), was used to fit the depth-identification and simple-detection psychometric functions with Weibull–Quick functions. A "bootstrap" procedure (Maloney, 1990; Foster & Bischof, 1991) was used to determine 95% confidence limits on the estimates of the threshold (α) and slope (β) parameters of the fitted functions. These confidence limits are the error bars plotted on the figures (i.e., the error bars are *not* standard errors).

MODEL PREDICTIONS

The main goal of this study was to compare the predictions made under two hypotheses, namely that stereoscopic 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-sensitive and luminance-contrast-sensitive pathways. These predictions were made in the following way.

*The catch trials and the use of two temporal intervals were included to allow valid comparison with the detection experiments [see Simmons & Kingdom (1994)].

†Binocular detection thresholds were measured concurrently because a simultaneous study of binocular summation was being performed.

Single-pathway hypothesis

If a single luminance-contrast-sensitive pathway were responsible for stereoscopic performance 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 assuming that depth-identification performance with the nominally isoluminant stimulus was entirely due to activation by some form of luminance input. Thus, if the psychometric function for the nominally isoluminant stimulus was:

$$P_D(c_{col}) = 1 - 0.5\exp[-(c_{col}/\alpha_{col})^{\beta_{col}}], \quad (1)$$

where P_D is the probability of correctly identifying the stereoscopic depth of the stimulus, c_{col} is chromatic contrast, and α_{col} and β_{col} are the psychometric function parameters, and, furthermore, if the psychometric function for the isochromatic stimulus was:

$$P_D(c_{lum}) = 1 - 0.5\exp[-(c_{lum}/\alpha_{lum})^{\beta_{lum}}], \quad (2)$$

with c_{lum} being luminance contrast, and α_{lum} and β_{lum} the psychometric function parameters, then c_{col} was taken to have an equivalent luminance contrast c_{eq}, which corresponded to the luminance contrast required to obtain the same level of performance (P_D). In mathematical terms c_{eq} could be calculated by equating the right-hand sides of Eq. (1) and (2) giving the expression:

$$c_{eq} = \alpha_{col}(c_{lum}/\alpha_{lum})^{\beta_{lum}/\beta_{col}}. \quad (3)$$

Psychometric functions could then be calculated for stimuli at different CLC ratios by substituting the calculated modified luminance contrast c_{mod}, given by:

$$c_{mod} = c_{lum} + c_{eq}, \quad (4)$$

into the expression for the isochromatic psychometric function, thus:

$$P_D(c_{mod}) = 1 - 0.5\exp[-(c_{mod}/\alpha_{lum})^{\beta_{lum}}]. \quad (5)$$

From these psychometric functions, predicted thresholds for different compound stimuli could be determined and plotted in terms of c_{col} and c_{lum}.

These predictions are shown in Fig. 3 as dot-dashed and dotted lines. These lines correspond to a "red-bright" or "green-bright" luminance input, meaning that the phase of the effective luminance input was such that either the redder parts of the isoluminant stimulus were brighter than the green or the green brighter than the red, respectively.

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 depth identification 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 conventional 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 share the same or similar slope parameters [i.e. the same β values—see Eq. (3)], as in Fig. 3(a). Second, the predictions exhibit a "null" region where the luminance contrast provided by the chromatic component of the compound stimuli destructively interferes with the luminance component. Notice that, in Fig. 3, the null regions cover almost the entire opposite quadrant for a given polarity of effective luminance contrast. For example, the lower quadrants of the panels of Fig. 3 correspond to the range of CLC ratios over which the effective luminance contrast coming from the chromatic stimulus component is in opposite phase to that of the luminance stimulus component itself, if it is assumed that redward-going chromaticity changes correspond to increases in luminance.

Dual-pathway hypothesis

An alternative to the single-pathway hypothesis was that stereoscopic depth identification was taking place "independently" in separate chromatic and luminance stereopsis mechanisms. Such a hypothesis suggested that stereoscopic performance at different CLC ratios could be predicted via probability summation (Graham, 1989) between the two mechanisms. Predictions were thus made in the following way.

If the probability of correctly identifying the depth of a luminance-defined stimulus was given by Eq. (2), and that for correctly identifying the depth of a chromatic stimulus was given by Eq. (1), then the probability of correctly identifying the depth of a compound stimulus possessing both luminance and colour contrast was thus:

$$P_D(c_{lum}, c_{col}) = 1 - 0.5\left\{\exp[-(c_{lum}/\alpha_{lum})^{\beta_{lum}}]\right\} \cdot \left\{\exp[-(c_{col}/\alpha_{col})^{\beta col}]\right\}. \quad (6)$$

Again, contrast thresholds for all CLC ratios could be predicted from these psychometric functions and are shown as the solid lines in Fig. 3.

Goodness-of-fit assessment

The goodness-of-fit of the models described above was assessed by calculating χ^2 statistics for each data set (Press *et al*., 1988). These statistics were calculated in two ways, one based on the threshold data at each CLC ratio, and the other based on the raw proportion-correct data at each CLC ratio. The latter calculation was performed because it entailed making fewer assumptions about the data, such as that the Weibull–Quick function was a good description of the psychometric function.

In the first calculation, that based on the threshold data, the following calculation was performed:

$$\chi^2 = \sum(O_i - E_i)^2/\sigma_i^2, \quad (7)$$

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

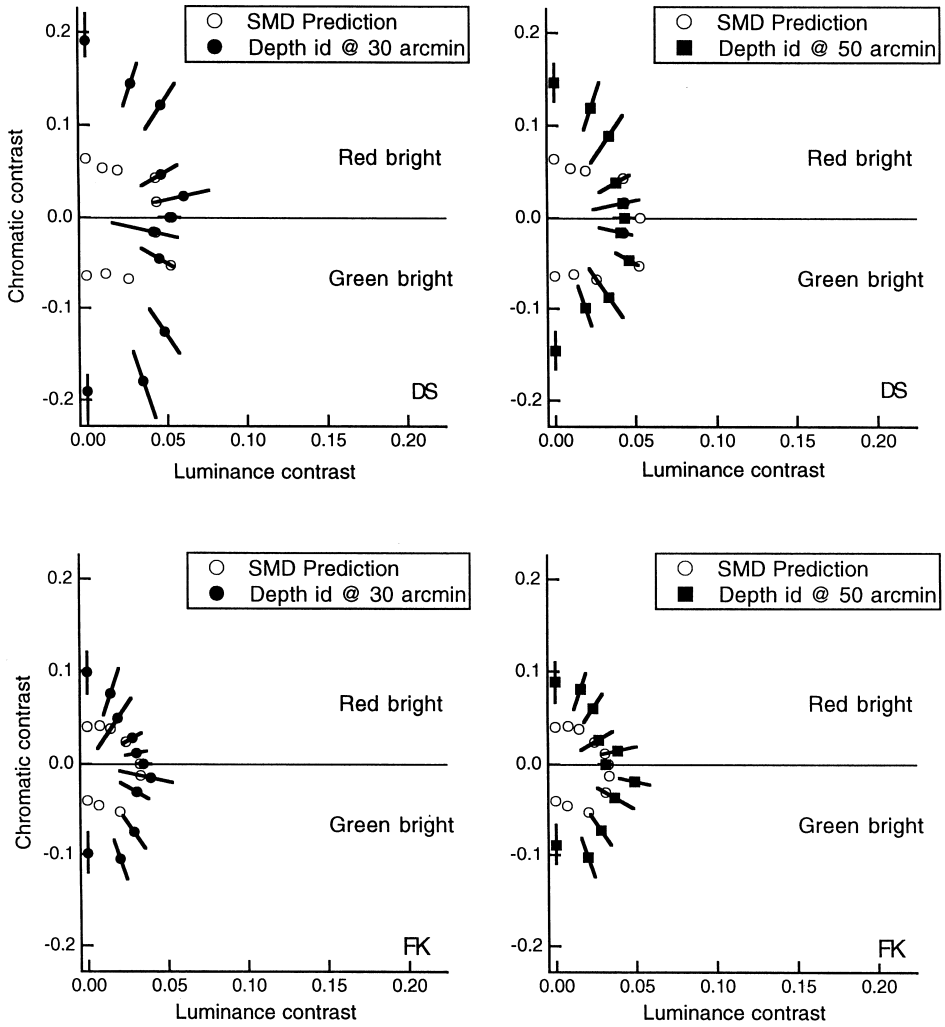

FIGURE 2. Contrast thresholds for depth identification at two disparities [$\pm$30 min arc (●) and $\pm$50 min arc (■)] at a range of different CLC ratios for two subjects. Data are plotted with chromatic contrast as ordinate and luminance contrast as abscissa. The sign of the chromatic contrast corresponds 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. The open circles are the contrast thresholds for simultaneous monocular detection (see text).

threshold, estimated from the inter-quartile range of the 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.

In the second calculation, that based on the raw proportion-correct data, Eq. (7) was used again, except with O_i being the proportion correct at a given contrast, E_i being the expected proportion correct from each of the model predictions, and σ_i being calculated by assuming that the data followed a binomial distribution.* This calculation is essentially the same as assessing the goodness-of-fit of each model to the psychometric function. Again the number of degrees of freedom corresponded to the number of data points in the psychometric function (usually 5). These could then be collated for each data set to give an overall χ^2 statistic.

Relationship to predictions in Simmons and Kingdom (1994)

The data were also analysed to confirm previous findings concerning the relative contrast requirements of isochromatic compared to isoluminant stimuli for depth identification. Simmons and Kingdom (1994) showed that, for isochromatic stimuli, depth identification at an appropriate disparity was possible once the stimuli were simultaneously detectable in both eyes. For isoluminant stimuli, however, more contrast than that required for simultaneous monocular detection was necessary for depth identification. A full discussion of the significance

*i.e. $\sigma = \sqrt{(Pq/n)}$ where P is probability correct at a given contrast, q is probability incorrect at this contrast, and n is the number of trials.

of this contrast threshold gap is given in Simmons and Kingdom (1994).

RESULTS

The data are first presented in their raw form, prior to presenting them in the manner most suitable for testing the main hypothesis of this study. In Fig. 2, contrast thresholds for depth identification are plotted with chromatic contrast as the ordinate vs luminance contrast as abscissa. Data are shown for two different subjects at two disparity conditions (± 30 and ± 50 min arc). The data for the ± 10 min arc disparity condition are not shown because it was not possible to obtain thresholds at all CLC ratios at this small disparity, probably because of relatively poor stereoacuity at isoluminance (Kingdom & Simmons, 1996). Each graph is divided into two "quadrants" which correspond to different phase relationships between the luminance and chromatic stimulus components. The upper quadrant, marked "red bright" corresponds to positive luminance excursions being in phase with the redward chromatic excursions. This condition is taken to be "positive" chromatic contrast. The lower quadrant, marked "green bright", corresponds to positive luminance excursions being in phase with greenward chromatic excursions and is taken to be "negative" chromatic contrast. Depth-identification data are shown as solid circles or squares with associated 95% confidence limits as error bars. The hollow circles show the amount of contrast required for simultaneous monocular detection, calculated separately for each CLC ratio from monocular detection data (Simmons & Kingdom, 1994).

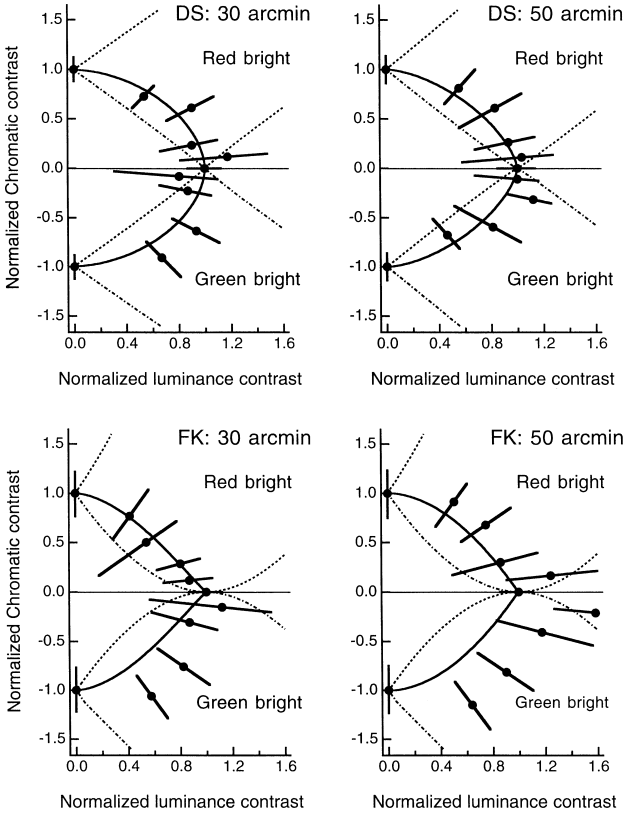

FIGURE 3. Depth-identification data from Fig. 2 replotted in terms of normalized chromatic and luminance contrast, where thresholds were normalized by the thresholds for the nominally isoluminant and isochromatic stimuli. The sign conventions and symbol allegiances are as in Fig. 2. Three predictions are shown on each graph. The dot-dashed and dotted curves are the single-pathway 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.

Threshold contrast values on the luminance axis are much lower than those on the chromatic axis. This observation in itself has no particular significance, because the contrast metrics for luminance and colour were not equivalent. However, the predictions of the simultaneous monocular detection model do provide a basis for comparison across different CLC ratios. It is clear from Fig. 2 that, whereas thresholds closer to the luminance axis overlap with the prediction, those closer to the chromatic axis do not. The size of the "contrast gap" for the isoluminant stimulus varies between different conditions, ranging from a factor of 2.2 to a factor of 3.1. The existence of this contrast gap has been reported previously (Simmons & Kingdom, 1994), and was taken to be evidence for a different type of processing underlying chromatic stereopsis as opposed to luminance stereopsis. The gap normally begins to appear when the contrasts of the chromatic and luminance stimulus components are equal (i.e. a CLC ratio of 1.0) and increases as the contrast of the chromatic stimulus component increases, although, again, there are variations between subjects and conditions.

The depth-identification data from Fig. 2 are replotted in Fig. 3 with axes normalized to the depth-identification contrast thresholds for the isoluminant and isochromatic stimuli, respectively. Hence thresholds are 1.0 on each axis, but vary at different CLC ratios. The depth-identification symbols and error bars have the same allegiances as in Fig. 2. Also shown on the graphs are the predictions from the two different models which directly address the issue of the independence of chromatic and luminance stereopsis mechanisms, namely the single- and dual-pathway models. The dot-dashed curves are the predictions of a single-pathway model with the sign of redward-going chromaticity being equivalent to positive-going luminance. The dotted curves are similar predictions except that greenward-going chromaticity is now equivalent to positive-going luminance. The solid curves are the predictions of the dual-pathway (probability summation) model. Details of how these predictions were made are given in the Model Predictions section.

The question addressed by Fig. 3 is the extent to which the data are well described by any of the proposed models. A cursory inspection of Fig. 3 shows that, across all conditions, the dual-pathway model appears to fit the data better. This conclusion is backed up by goodness-of-fit calculations. In Table 1 two sets of χ^2 statistics are presented. In the first set, the statistics are based on the

TABLE 1. Summary of χ^2 statistics for different data sets, calculated by comparing thresholds (left-hand columns) and psychometric functions (right-hand columns)

	χ^2-statistic			
	By threshold		By Ψ function	
Condition	Best single-pathway	Dual-pathway	Best single-pathway	Dual-pathway
FK 30 min arc	105.5	19.2	138.3	44.9
FK 50 min arc	186.3	71.8	196.2	98.0
DS 30 min arc	69.7	12.0	80.9	46.0
DS 50 min arc	46.1	7.0	73.5	68.7

The number of degrees of freedom for each of these comparisons was 8 and 40, respectively. Each individual column corresponds to the χ^2 statistic based on the best-fitting single-pathway prediction or the dual-pathway prediction.

threshold data alone, and in the second they are based on the raw proportion-correct data (for further details again see the Model Predictions section). In both cases the dual-pathway model gave a better fit to the data than the better of the single-pathway predictions.*

Another area in which the single-pathway model fails is in the location of a "null" point. Any model that proposes that chromatic contrast provides an input to a linear luminance mechanism that is solely interpreted as luminance contrast also requires that the chromatic input should have a "sign" such that redward-going chromaticity is equivalent to either positive-going luminance or negative-going luminance and vice versa for greenward-going chromaticity. If this is true then there must be some CLC ratio at which the equivalent luminance contrast of the chromatic stimulus component cancels out or nulls the luminance contrast component. At this CLC ratio it should be impossible to find a threshold, as is indicated by both single-pathway predictions in Fig. 3. Indeed, the predictions are "off the scale" of the graph for intermediate CLC ratios when the polarity of the proposed equivalent luminance contrast for the chromatic stimulus component is opposite to the luminance contrast of the luminance stimulus component. The data do not exhibit this behaviour.

DISCUSSION

Stereopsis at isoluminance and luminance artifacts

Although there have been a number of demonstrations of maintained stereoscopic performance at isoluminance under some conditions (Comerford, 1974; Gregory, 1977; de Weert & Sadza, 1983; Grinberg & Williams, 1985; Osuobeni & O'Leary, 1986; Tyler & Cavanagh, 1991; Osuobeni, 1991; Scharff & Geisler, 1992; Simmons & Kingdom, 1994, 1995; Kingdom & Simmons, 1996), luminance artifacts have been invoked to explain these results (Livingstone & Hubel, 1987). In this study, the effects of potential luminance artifacts were modelled by assuming that, if stereoscopic performance at nominal isoluminance was entirely due to luminance artifacts, then there would be consequences for stereoscopic performance at other CLC ratios. These consequences would be that contrast thresholds for depth identification at different CLC ratios would follow one of the single-pathway predictions illustrated in Fig. 3. The data did not follow either of these predictions and thus it can be concluded that the stereoscopic performance at nominal isoluminance demonstrated in this study was not due to artifactual stimulation of a luminance-contrast-sensitive mechanism. The potential artifacts that are inconsistent with the data include those due to inhomogeneities in the isoluminant point across the retina (Livingstone & Hubel, 1987), rod-mediated responses (Dobkins & Albright, 1993), and temporal phase lags between L- and M-cone signals (Stromeyer *et al*., 1994). All of these potential artifacts would have resulted in a "signed" luminance artifact at the same spatial frequency as the luminance component of the compound stimuli. The more complex effects of longitudinal and transverse chromatic aberrations may not have been accounted for by this analysis, but the stimuli were designed to minimize the effects of chromatic aberration artifacts, having a narrow spatial bandwidth centred about 0.5 c/deg. In any case, even when present, chromatic aberration artifacts do not seem to affect stereoscopic performance greatly (Scharff & Geisler, 1992).

Evidence for independence of chromatic and achromatic stereopsis mechanisms?

Exactly how do chromatic mechanisms influence stereoscopic judgements? In Fig. 4 four possibilities are illustrated in schematic form. The first, that the influence of colour contrast is artifactual [Fig. 4(a)], has already been dismissed. The second possibility is that chromatic- and luminance-contrast-sensitive mechanisms summate linearly before stereoscopic judgements are made [Fig. 4(b)]. The third is that chromatic and luminance mechanisms summate nonlinearly before stereoscopic judgements are made [Fig. 4(c)]. The fourth and final possibility is that there are separate mechanisms for chromatic and luminance stereopsis that influence each other only by virtue of probability summation [Fig. 4(d)].

The predictions of the second of these models, namely a conventional linear-summation model, would appear on Fig. 3 as a straight line joining the nominally isoluminant and isochromatic contrast thresholds in each quadrant. This conventional model, however, relies on the assumptions that: (a) the psychometric functions for both classes of stimuli have the same slopes; and (b) that the chro-

*A better fit is demonstrated by a lower χ^2 statistic. For both subjects the single-pathway model could be rejected at the 5% level. Note also that if only one of the single-pathway models had been used for comparison, rather than the better of the two, the fit would have been even worse. The dual-pathway model cannot be rejected at the 5% level for subject DS, but does not provide an acceptable fit for FK. However, the direction of the difference is towards greater rather than less independence. It is also important to bear in mind that there were no free parameters incorporated into the model predictions.

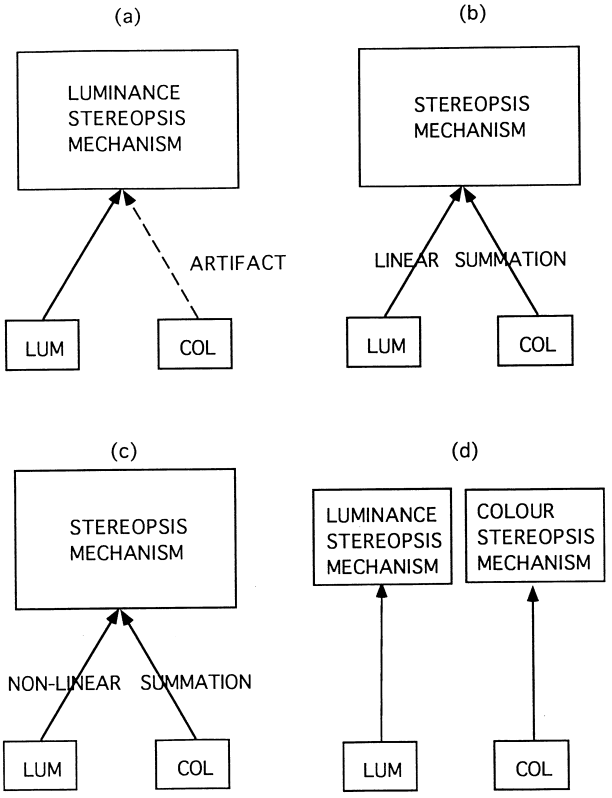

FIGURE 4. Schematic diagram of possible mechanisms underlying performance in the stereoscopic depth-identification task at different CLC ratios.

matic signal is somehow rectified before linear summation with the luminance signal, such that the sign of the colour contrast does not matter. Our single-pathway model does not rely on these assumptions. For one subject (DS), the slopes of the psychometric functions had similar slopes*, and this is reflected in Fig. 3 by straight lines in the prediction. For subject FK the slopes were significantly different†, consequently the prediction is more curved. Finding different slopes for isoluminant and isochromatic psychometric functions itself argues against linear summation. Our single-pathway model allows for a limited amount of non-linear transformation of the chromatic input before addition to the luminance contrast. Even with this modification the fit to the data is relatively poor. It seems that the linear summation of chromatic and luminance contrast before stereoscopic judgements are made is not a viable possibility, and thus the model illustrated in Fig. 4(b) can be rejected.

The non-linear summation of chromatic and luminance contrasts into a common stereoscopic pathway does remain a possibility. This non-linear summation could be as simple as a threshold on the chromatic input to the combined mechanism, such that only very high chromatic contrasts influence performance. Even if this suprathreshold summation were perfectly linear the prediction would be hard to distinguish from the probability-summation prediction, so long as the threshold was high enough (judging from the data in Fig. 3, the threshold would have to be at least 0.75 of the contrast required to reach threshold with the isoluminant stimulus). Presumably, if stereoscopic performance at isoluminance were subserved by the "unsigned" chromatic mechanism described by Dobkins and Albright (1993) then the summation of chromatic and luminance contrast would also be non-linear, but there are other arguments against this mechanism being the substrate for performance in the experiments described here (see below). Therefore the model presented in Fig. 4(c) cannot be rejected, but the evidence in favour of it is weak.

The relatively good fit of the probability-summation (dual-pathway) model at a range of CLC ratios suggests, however, that an explanation of stereoscopic performance at isoluminance that is both consistent with the data and parsimonious is that there are both luminance-contrast-sensitive and colour-contrast-sensitive stereopsis mechanisms [Fig. 4(d)]. These mechanisms appear to be independent in the sense that if a determination of the "sign" of a stereoscopic depth is required (i.e. a front/back judgement) then suprathreshold activity in either or both mechanisms may allow the subject to respond correctly. Notice, however, that this independence may not be maintained at high levels of suprathreshold contrast in each mechanism. Presumably full independence of chromatic and achromatic stereopsis mechanisms would admit the possibility of two potentially different depth signals for a surface defined by both luminance and colour contrast. In that situation, in order to assign an unambiguous depth percept to the surface, the visual system may have to combine the chromatic and achromatic stereo information in some way. The form of "independence" described here for threshold levels of stereoscopic performance does not rule out that possibility.

Neural mechanisms of chromatic stereopsis

The most obvious neural substrate for the chromatic stereopsis mechanism would be a colour-opponent signal carried at least as far as V1 by the parvocellular pathway. It is well known that neurons in this pathway have a strong response to isoluminant heterochromatic stimuli (Derrington *et al*., 1984) and that there is at least some binocular sensitivity that remains even when Magnocellular neurons are ablated (Schiller *et al*., 1990).

Could performance at isoluminance in this study have been mediated by a "frequency doubled" response from the Magnocellular pathway? The cyclic dependence of contrast thresholds for depth identification on phase disparity (Simmons & Kingdom, 1995) suggests that stereopsis at isoluminance is dependent on a mechanism that cares about the polarity of colour contrast [i.e. a "signed" mechanism, according to the terminology of

*β values for DS were 1.7 and 1.8 for isochromatic and isoluminant stimuli, respectively, at 30 min arc disparities and 1.6 and 1.5 at 50 min arc disparities.

†β values for FK were 1.7 and 0.9 for isochromatic and isoluminant stimuli, respectively, at 30 min arc disparity and 1.9 and 1.0 at 50 min arc. Both of these differences are significant at the 5% level based on a simple *z*-score analysis of the bootstrap histograms.

Dobkins & Albright (1993)]. Indeed, the fact that stereoscopic depth perception is possible at the 30 min arc disparity suggests that the "unsigned" mechanism of Dobkins and Albright (1993) is not mediating performance because this disparity corresponds to an interocular phase displacement of 90 deg and should thus provide an ambiguous depth percept. Furthermore, the temporal properties of the nominally isoluminant stimuli used in this study, with most of the stimulus energy confined to low temporal frequencies, would certainly not be ideal to evoke the sort of response in area MT/V5 that is thought to underlie the "unsigned" motion mechanism (Gegenfurtner *et al*., 1994; Dobkins & Albright, 1994, 1995). Hence, it seems likely that the stereoscopic performance at isoluminance reported here is not subserved by frequency-doubled responses in the Magnocellular pathway.

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