



Absence of Linear Subthreshold Summation between Red–Green and Luminance Mechanisms over a Wide Range of Spatio-temporal Conditions

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We have tested the independence of red–green chromatic and luminance mechanisms at detection threshold using a method of subthreshold summation. Stimuli were isoluminant red–green gratings and yellow–black luminance gratings that uniquely activate the red–green color and luminance mechanisms, respectively. Stimuli were Gaussian enveloped 0.25, 1 or 4 cpd sinewave gratings, counter-phase flickered at 0, 5 or 9 Hz. The threshold detection of red–green color contrast was measured in the presence of a subthreshold amount of luminance contrast, and vice versa. The results allow a model of linear summation between the color and luminance mechanisms to be rejected, but are well fitted by a model, assuming that these mechanisms are independent but combine to determine detection by probability summation, with a high summation index (median value = 4). We conclude that there are independent red–green chromatic mechanism and luminance detection mechanisms over this range of spatio-temporal conditions. © 1997 Elsevier Science Ltd. All rights reserved.

Color vision Isoluminance Red–green mechanism Subthreshold summation

INTRODUCTION

A substantial body of evidence suggests that the outputs of primate cones are linearly combined into at least two chromatic (opponent) and one luminance (additive) post-receptoral detection mechanism (Sperling & Harwerth, 1971; Kranda & King-Smith, 1979; Thornton & Pugh, 1983; King-Smith & Carden, 1976; Krauskopf *et al.*, 1982; Mullen & Kulikowski, 1990; Cole *et al.*, 1993; Metha *et al.*, 1994). Furthermore, measurements of detection thresholds expressed as contours in a cone contrast space have indicated that one of the chromatic mechanisms is a red–green mechanism which linearly combines L and M cone outputs in balanced opposition (Noorlander *et al.*, 1981; Stromeyer *et al.*, 1983, 1985; Cole *et al.*, 1993; Sankeralli & Mullen, 1996). This mechanism is the most sensitive when thresholds are expressed in terms of L and M cone contrasts (Chaparro *et al.*, 1993). It determines detection thresholds over a

wide range of L and M cone combinations and maintains remarkably stable cone weights for a wide range of spatio-temporal conditions (Chaparro *et al.*, 1994; Metha *et al.*, 1994). By contrast, the luminance mechanism combines cones additively, but with cone weights that appear to be considerably variable between both spatio-temporal conditions and subjects (Cole *et al.*, 1993; Metha *et al.*, 1994; Stromeyer *et al.*, 1995; Sankeralli & Mullen, 1996).

It is frequently assumed that these detection mechanisms are independent and undergo some form of nonlinear combination to determine threshold. This assumption provides a plausible account of the shape of detection threshold contours in a color space. It also potentially provides a theoretical basis for the interpretation of threshold contours as revealing one mechanism as distinct from another, so allowing a single mechanism's cone weights to be assessed (Noorlander *et al.*, 1981; Stromeyer *et al.*, 1983, 1985). In many cases, ellipsoidal fits to the detection contours have been preferred: this fit corresponds to probability summation between mechanisms with an exponent of 2 (quadratic combination), and it has been argued that this fit is always adequate (Poirson *et al.*, 1990; Knoblauch & Maloney, 1995). However, in the case of an ellipsoidal fit, it is controversial whether a threshold contour alone can provide sufficient evidence for the specification of the underlying post-receptoral mechanisms. It is argued

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(Poirson *et al.*, 1990; Knoblauch & Maloney, 1995) that an ellipsoidal fit fails to allow the specification of the detection mechanisms since, once linearly transformed into a circle, an infinite number of different sets of mechanisms could theoretically account for the data. Furthermore, interpretations involving multiple detection mechanisms cannot be excluded. In other cases, however, it has been argued that models assuming at least three independent detection mechanisms, combined by probability summation with an exponent greater than two (providing a parallelogram-like fit to the data) best describe detection threshold contours (Cole *et al.*, 1993; Metha *et al.*, 1994; Sankeralli & Mullen, 1996). These fits are related to a unique set of visual mechanisms which can then be successfully derived from the data (Poirson *et al.*, 1990).

An established approach to the determination of the independence of underlying detection mechanisms is the measurement of subthreshold summation (Graham, 1989, Part III). Of course, a nonlinear combination of independent detection mechanisms is implicit in the fitting of the threshold contours described above, and independence is assumed in many post-receptoral models of color vision (e.g., Guth & Lodge, 1973) as well as in the interpretation of post-receptoral spectral sensitivity functions (e.g., King-Smith & Carden, 1976). Other approaches have measured directly the subthreshold summation between two stimuli (Boynton *et al.*, 1964; Kranda & King-Smith, 1979; Gur and Akri, 1992). Boynton *et al.* (1964) found evidence for independent mechanisms combined by probability summation, although the specific type of post-receptoral mechanisms determining detection is unclear. Kranda & King-Smith (1979, 1984) found evidence that red-green opponent mechanisms and luminance mechanisms were independent and combined by probability summation, although their stimuli were not specifically chosen to isolate one or other type of post-receptoral mechanism. There is also further limited psychophysical evidence to support the existence of independent red-green and luminance mechanisms at detection threshold: measurements of masking functions (detection threshold vs mask contrast) suggest little or no subthreshold summation between isoluminant red-green and achromatic stimuli, since interactions only occur once one of the stimuli is at suprathreshold contrasts (Switkes *et al.*, 1988; Cole *et al.*, 1990; Mullen & Losada, 1994; Chaparro *et al.*, 1994). However, in the studies just mentioned there are only a small number of data points in the relevant subthreshold regions of the functions. On the other hand, in an extensive study, evidence for linear subthreshold summation between red-green and achromatic stimuli was found, contradicting the existence of independent red-green and luminance detection mechanisms (Gur & Akri, 1992). Thus, there is some disagreement over the issue of subthreshold interaction between red-green and luminance mechanisms.

In this study, we aim to test directly for the independence of red-green chromatic and luminance

mechanisms at detection threshold, using a method of subthreshold summation. Our first aim is to examine the matter of subthreshold summation of color and luminance contrast once again, in an attempt to clarify the apparent contradictions in the literature. Our second aim is to test whether the independence of color and luminance detection depends upon the spatial and temporal conditions used. This is a relevant question because the spatio-temporal conditions of the stimulus are likely to determine the type of subcortical pathways that subserve color and luminance contrast detection. Primate lesions of the LGN suggest that for low spatial frequencies at mid to high temporal frequencies, luminance detection is mediated by the M cell pathway and color contrast detection by the P cell pathway, whereas under other conditions the P cell pathway is a common substrate for both luminance and color contrast detection (Merigan, 1991). This is broadly consistent with the physiology of magnocellular and parvocellular neurones of the macaque LGN (Derrington *et al.*, 1984). Thus, the medium to high spatial frequency and low temporal frequency range could be considered to provide conditions favorable for dependencies between color and luminance contrast.

We measure the amount of subthreshold summation between cardinal chromatic and luminance stimuli over a wide range of spatial and temporal conditions (0.25–4 cpd, 0–9 Hz), using a method similar to that of Graham *et al.* (1978) (see also Graham, 1989). We test whether our results are best fitted by a detection mechanism which linearly sums color and luminance contrast or by independent mechanisms which determine threshold by probability summation. Our results support the independence of the red-green and luminance mechanisms over this spatio-temporal range.

This paper confines itself to the controversial question of the independence of the post-receptoral mechanisms at their detection thresholds. A separate question arising is whether these detection mechanisms remain independent at suprathreshold contrasts (when one or both stimuli are visible), or in the execution of higher order tasks such as motion, form or stereo perception. In general, there is ample evidence that color-luminance interactions occur for suprathreshold conditions, revealing both masking and facilitation, providing one of the stimuli is suprathreshold ((Switkes *et al.*, 1988; Cole *et al.*, 1990; Mullen & Losada, 1994; Hilz *et al.*, 1974) and demonstrating a range of interactions between color and luminance contrast for higher order tasks such as velocity perception (Cavanagh *et al.*, 1984; Cavanagh & Anstis, 1991; Mullen & Boulton, 1992), contour localization (Rivest & Cavanagh, 1996; Greene & Brown, 1995), contour integration (McIlhagga & Mullen, 1996), and in the spatial interactions responsible for the perception of Mach bands (Gur & Syrkin, 1993). Since it is known that different tasks are mediated within different levels and areas in the visual system, it is not surprising that independent chromatic and luminance mechanisms may occur at one level to subserve detection (for example at

an early cortical stage), but may occur in combination at another (for example, to mediate the execution of the more complex tasks above). This issue is explored in more detail in the Discussion.

METHODS

Stimuli

Stimuli were horizontal, isoluminant, red–green chromatic sinewave gratings or yellow, isochromatic, luminance gratings. Stimuli were Gaussian enveloped along the axis of modulation with a half-width at 1/e height of 1.5 cycles of the stimulus to render them spatially narrow band, providing a Fourier bandwidth at 1/e height of 0.3 octaves. They were sharply truncated on the horizontal axis at a bar length of 4 cycles of the stimulus. These are standard Gabor stimuli (Graham, 1989). The stimuli were also restricted in time by a Gaussian temporal envelope with a half-width of 1/e of 125 msec, corresponding to a Fourier bandwidth of 2.5 Hz. Stimuli within the envelope were either stationary (0 Hz) or counterphase flickered by a cosinusoidal function of time at 5 or 9 Hz. Spatially and temporally bandpass stimuli were used for two reasons: (i) bandpass stimuli are required in order to separate effectively the different test temporal and spatial frequencies used; and (ii) spatial bandpass filtering of the chromatic stimuli reduces the effects of chromatic aberrations.

The luminance profile across space of the combined red (r) and green (g) component gratings is given by:

$$L = Mr + Mg + Mr(C + \Delta C)\sin\omega x \pm Mg(C - \Delta C)\sin\omega x \quad (1)$$

where Mr and Mg are their respective mean luminances, C is their contrast, ΔC is an added contrast increment or decrement to the component gratings, and ω is the spatial frequency. Red and green component gratings are added to produce a luminance grating and subtracted for a chromatic grating. To obtain an isoluminant chromatic grating or a homochromatic luminance grating $\Delta C = 0$, and the component gratings have equal contrasts (C). The contrasts of both the isoluminant chromatic grating and the homochromatic luminance grating are defined as the contrast of the component gratings (C). To produce gratings with combined color and luminance contrast, the contrast of one component grating is incremented and the other decremented by a fixed amount (ΔC). Thus, if C is the contrast of the original isoluminant stimulus, ΔC is the contrast of the added luminance stimulus, and vice versa. The phase relationship between the chromatic and luminance contrast was fixed at 0 deg (red chromatic peaks added to luminance peaks) unless given otherwise. The overall phase of the stimulus (within the envelope) was randomly varied between each presentation. The mean luminance and chromaticity are not affected by presentation of the stimuli.

Isoluminance of the two colors was measured using a method of adjustment to determine the point at which the perceived drift rate reached a minimum. Subjects viewed

a continuously drifting grating (in the same Gaussian window) of the same temporal rate and spatial frequency to be used in the experiment. When isoluminance was required for a static grating, minimum motion was determined using a low temporal drift rate (4 Hz). The ratio of the red to green mean luminances in the stimulus was varied while their contrasts are held constant. Thus, at isoluminance, the two component gratings have equal "sensation luminance" and only the color of the combined stimulus is modulated (Kaiser, 1988). An average of at least 10 measures was obtained.

We have chosen chromatic (red–green) and luminance stimuli that uniquely activate their respective color and luminance mechanisms. A plot of the two stimuli in an L, M cone contrast space can be seen elsewhere (Mullen & Losada, 1994, Fig. 2). We assume that red–green chromatic mechanism is cone opponent with equal L and M cone weights (a vector at 135 deg in a plot of M cone contrast as a function of L cone contrast). The cone weights to this mechanism are found to be remarkably stable between subjects and spatial conditions (Stromeyer *et al.*, 1985; Cole *et al.*, 1993; Chaparro *et al.*, 1994). The luminance stimulus is represented in the same space by a vector lying at 45 deg. This stimulus is orthogonal to the chromatic mechanism, and is, therefore, a cardinal luminance stimulus. The direction of the vectors representing the isoluminant (cardinal) chromatic stimuli depend on the individual subject, but fall below 135 deg, reflecting the dominance of the luminance mechanism by the L cones.

Apparatus and calibration

Two luminance modulated gratings were displayed on separate Joyce (DM2) display screens with white P4 phosphors, and were viewed through narrow band interference filters (Melles Griot, center wavelengths of 525 and 605 nm and full bandwidths at a half-height of 21–22 nm). These two monochromatic gratings were optically combined 180 deg out of phase by a beam splitter to produce a chromatic grating, or in phase to produce a luminance grating of the same mean luminance and chromaticity. Longitudinal and transverse chromatic aberrations were corrected (Mullen, 1985), and a bite bar was used to align the subject's head. Viewing was monocular and with a natural pupil. Stimuli were centrally fixated using a small fixation spot, and had a mean luminance of 22 cd m⁻². Linearizing calibrations of the phosphor nonlinearities of the display monitors were made using a UDT optometer (model S370) fitted with a photometric head (No. 265). The goodness of the fits of the linearizing look-up tables to the light output of the monitors produced a contrast error for the displayed stimuli of within 0.017 log units. Calibrations of the absolute luminance values of the component colors were carried out using a Universal spot photometer, and were checked regularly. All stimuli were generated using a VSG2/1 waveform generator (Cambridge Research Systems) with 14 bit DACs.

Paradigm

Detection thresholds were measured using a two-alternative forced-choice staircase procedure, in which the test stimulus appeared in one of two time intervals and the other interval was blank. The subject indicated by pressing a button in which interval the test stimulus appeared, and feedback was given after each trial. The staircase procedure was terminated after eight reversals in the contrast presented, and the threshold was determined as the mean of the contrasts of the last five reversals. Each plotted threshold represents the mean of at least three measured thresholds. Results were obtained on two or three subjects (KTM, SJC, MAL) with normal color vision measured on the standard tests (Farnsworth Munsell 100 Hue Test and The City University Colour Vision Test).

In all the experiments, an isoluminant chromatic detection threshold and a luminance detection threshold were determined first. Detection threshold was then measured for a range of subthreshold combinations of color and luminance contrast. For half of the threshold measurements of each experiment, the luminance contrast was the independent variable: a stimulus with a fixed subthreshold luminance contrast was presented in the test interval and the amount of color contrast required to raise the stimulus to detection threshold was determined. For the remaining data points, the color contrast was the independent variable and luminance contrast was varied to determine detection threshold. Some results were repeated using a modification of this paradigm, in which the stimulus with the fixed subthreshold contrast was presented in both intervals and the test stimulus with the variable contrast in one interval, and no change was found in the results.

Model predictions

The results were assessed in the light of two possible models. The first is linear physiological summation between the color and luminance detection mechanisms, occurring at a stage in the visual system preceding that at which the threshold criterion operates. This model holds that at detection threshold of the combined stimulus, the subthreshold values of color and luminance contrast, expressed as proportions of their respective detection thresholds, sum to unity. This model predicts that the data lie on a line joining the color and luminance thresholds, and is given on the figures by a dashed line.

The second model considered is one of probability summation of independent color and luminance mechanisms. This model assumes that the detection mechanisms are independent. However, the likelihood of detection is greater when independent mechanisms are stimulated together, than when any single mechanism is stimulated alone. The psychophysical effect of probability summation has been described thoroughly elsewhere (Boynton *et al.*, 1964; Sachs *et al.*, 1971; Quick, 1974; Graham, 1989). As a test of this model, we have fitted all our results with the vector-magnitude model described by Quick (1974), which provides a very close approximation

to the effects of probability summation and is more convenient mathematically. The fitted equation has the form:

$$S^K = (1/L)^K + (1/C)^K \quad (2)$$

S represents the overall contrast sensitivity to the combined color and luminance stimulus. K represents the power of the combination of the mechanisms, and also corresponds to the slope of their psychometric functions. L represents the luminance contrast detection threshold in the absence of color contrast, and C represents the color contrast detection threshold in the absence of luminance contrast.

This equation was fitted to the data using a method of least χ^2 . Because both axes can be independent variables, standard deviations were measured in either the horizontal or the vertical direction. For the purposes of determining the fit, these values were assumed to be applicable to the vector joining the origin of the figure and the data point. Standard deviations were converted from logarithmic to linear units, and for the fit the averaged color and averaged luminance standard deviation was calculated for each condition, and are given on each figure. The goodness of fit is given by the χ^2 value, and the degrees of freedom, both shown on each figure in parentheses. In the fitting procedure the value of K was constrained to be less than or equal to 8. In two of the fits the constrained K value of 8 was reached, and in these two cases there were insufficient data in the "corners" of the function to determine whether K was significantly greater than 8.

The best fit of the model is given by the solid line, and the fitted value of K in equation (2) is given on each figure. The fit is elliptical (circular) for a K value of 2, and a "squared-off" fit occurs for K values greater than 2. This model assumes that the slopes of the psychometric functions for color and luminance detection are the same. It is presently controversial whether there is any difference in the slopes of the psychometric functions for color and luminance detection (Maloney, 1990; Cole *et al.*, 1993; Knoblauch & Maloney, 1995; Eskew *et al.*, 1994).

RESULTS

Figures 1 and 2 show the results for the summation to threshold for a combination of luminance and color contrast for three temporal conditions (0, 5 and 9 Hz) at one spatial frequency (1 cpd). Results for two subjects are shown. The fitted K values for the three temporal conditions are: 3.7, 5.4, and 4.2, respectively for KTM; and 6.4, 3.2, and 8, respectively for SJC.

In Fig. 3, results are shown for two relative phases of the combination of color and luminance contrast at one condition (1 cpd, 0 Hz): red chromatic bars added to yellow luminance bars (a relative phase of 0), and green chromatic bars added to luminance bars (a relative phase of 180 deg). The fitted K values for these two conditions are 8 and 5.1. The results show no dependence of the data

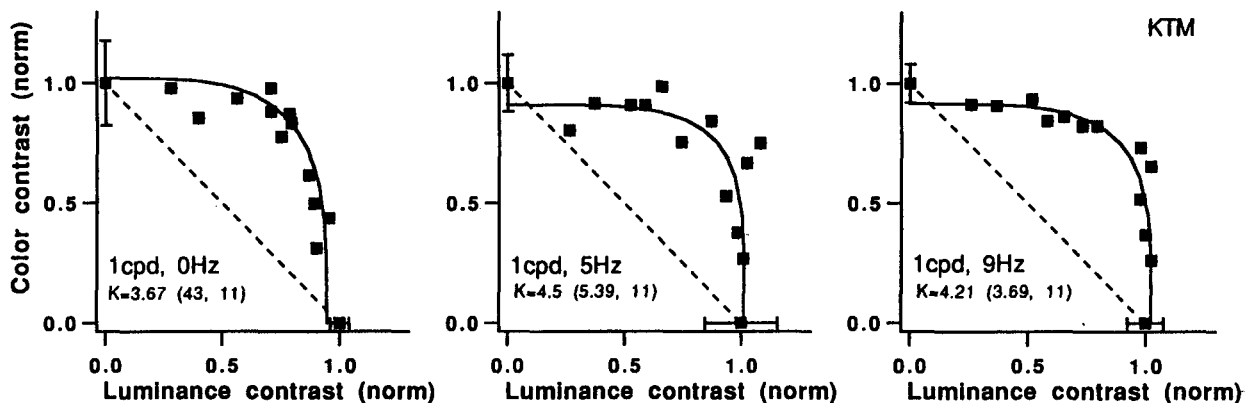


FIGURE 1. Detection thresholds for the combination of color and luminance contrast. x and y axes have been normalized to the detection threshold for the cardinal red-green and luminance stimuli, respectively. Stimuli are 1 cpd gratings of different temporal frequencies from 0 to 9 Hz as marked. From left to right panels, measured chromatic contrast thresholds are: 0.01, 0.027 and 0.061. Measured luminance contrast thresholds are: 0.012, 0.009 and 0.009. The solid line indicates the fit of the probability summation model, with the power of K given on each figure. Figures in parentheses give the χ^2 value and degrees of freedom for the fit. The dashed line is the prediction of a linear summation model. Error bars give ± 1 SD. Subject: KTM.

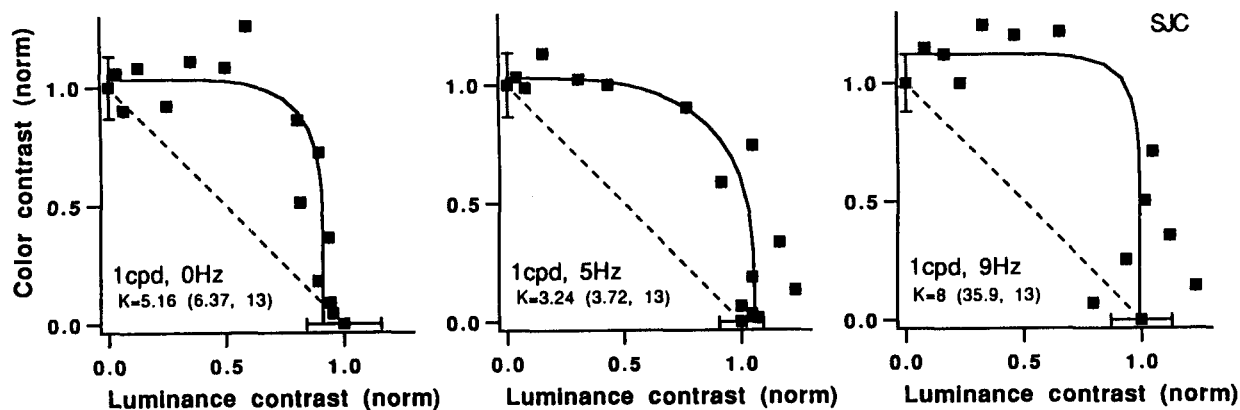


FIGURE 2. Legend as for Fig. 1. From left to right panels, measured chromatic contrast thresholds are: 0.011, 0.03 and 0.056. Measured luminance contrast thresholds are: 0.016, 0.013 and 0.012. Subject: SJC.

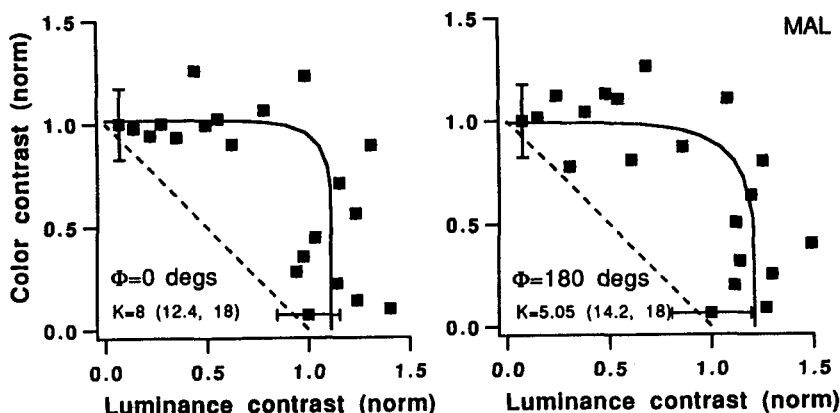


FIGURE 3. Legend as for Fig. 1, but both panels are for a stimulus of 1 cpd, 0 Hz. The relative phase of the color-luminance contrast combination is 0 deg in the left panel (red peak adding to yellow peak) and 180 deg in the right panel (green peak adding to yellow peak). From left to right panels, measured chromatic contrast thresholds are: 0.007 and 0.008. Measured luminance contrast thresholds are: 0.007 and 0.007. Subject: MAL.

on the relative phase of the color and luminance combination.

Figures 4 and 5 show the results for summation to threshold for two further spatio-temporal conditions on two subjects: a low spatial frequency presented at a high

temporal frequency (0.25 cpd, 9 Hz), and a high spatial frequency (relative to the color contrast sensitivity function; Mullen, 1985) presented at a low temporal rate (4 cpd, 0 Hz). The fitted K values are: 2.4 and 3.7, respectively for KTM; and 3.1 for both data sets of SJC.

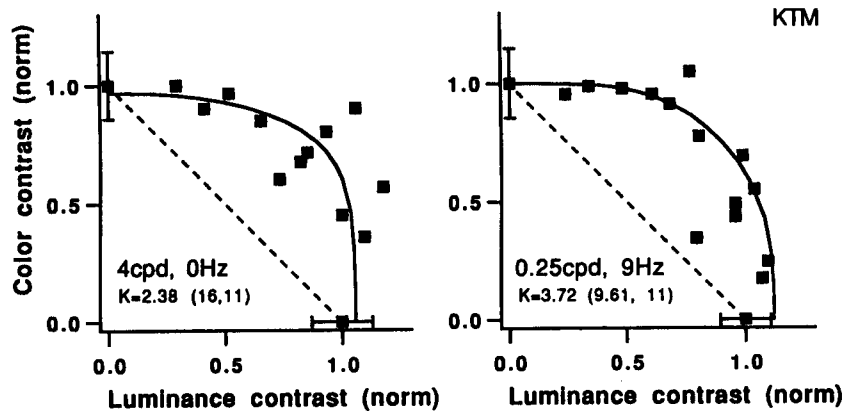


FIGURE 4. Left panel: the stimulus is 4 cpd, 0 Hz. Right panel: the stimulus is 0.25 cpd, 9 Hz. For other details see Fig. 1 legend. From left to right panels, measured chromatic contrast thresholds are: 0.062 and 0.051. Measured luminance contrast thresholds are: 0.023 and 0.007. Subject: KTM.

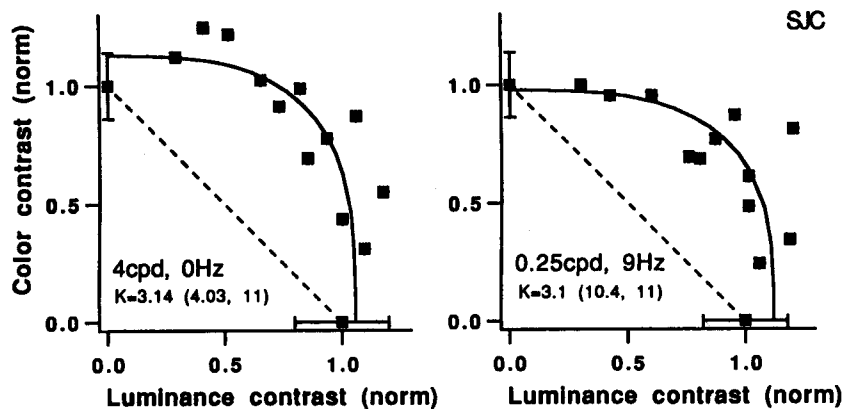


FIGURE 5. Legend as for Fig. 4. From left to right panels, measured chromatic contrast thresholds are: 0.041 and 0.052. Measured luminance contrast thresholds are: 0.017 and 0.011. Subject: SJC.

Values of K significantly greater than 1 indicate that the linear model should be rejected. As explained in the Methods, for two data sets the constrained K value of 8 was reached and we therefore cannot determine whether the best fitting K value is 8 or higher. The averaged K value for all the fits is 4.7 ± 2 , and the mean excluding the two constrained K values is 4 ± 1.2 . Since the two highest values, and hence the overall mean, cannot be accurately determined, we have also calculated the median value which is 4. These results show that the best fitting average K value is significantly greater than 1, allowing the model of linear summation to be rejected at the 95% confidence level.

DISCUSSION

Under all the spatio-temporal conditions tested, the results we obtained are not compatible with the model of linear summation ($K = 1$) between color and luminance mechanisms. Instead they are best fit by a vector magnitude model, which is the equivalent in its predictions to a probability summation model (Quick, 1974). Thus, the results suggest that the color and luminance detection mechanisms are independent of each other, but combine by probability summation to deter-

mine detection. The lack of phase dependence of the color and luminance contrast combination is compatible with previous results demonstrating a lack of phase dependence of the threshold vs masking functions obtained between color and luminance contrast (Switkes *et al.*, 1988; Mullen & Losada, 1994).

Knoblauch & Maloney (1995) and Poirson *et al.* (1990) have reported conditions in which threshold contours are best fitted by an ellipsoid. If the best fit to our data had been circular ($K = 2$), the threshold contours would be rendered ellipsoidal in another linearly transformed color space. For our results, however, all the fits have a K value greater than 2 (median = 4), which is reflected in the relatively square shape of the detection contours. These squared-off contours support the existence of independent detection mechanisms in the direction of the axes of the space [as opposed to an elliptical or circular fit, which, it is argued, remains ambiguous as to the direction of the underlying mechanisms (Poirson *et al.*, 1990)]. Thus, this result aids in the interpretation of detection threshold contours in a cone contrast space since it supports the assumption that the elongated contours in an L, M cone contrast space reflect the existence of at least two independent mechanisms (red-green and luminance) determining

detection threshold. They are, thus, compatible with the model of Cole *et al.* (1993), Metha *et al.* (1994), and Sankeralli & Mullen (1996), who have modeled detection thresholds by the probabilistic combination of independent mechanisms; these and other studies report best fitting K values for detection thresholds averaged across subjects and conditions of 4 (Metha *et al.*, 1994; Kranda & King-Smith, 1979), 4.2 (Cole *et al.*, 1993) and 3.2 (Sankeralli & Mullen, 1996), which are very similar to our values reported here. Our results suggest that these two isolated mechanisms are independent for grating detection over a wide spatio-temporal range, and this indicates that changes in the shape of the detection threshold contours with the spatio-temporal conditions reflect the independent translation of the contours of these mechanisms as their relative sensitivities change. Furthermore, a recent study of the slopes of the psychometric functions for cardinal red-green, luminance, and combined color-luminance stimuli, which uses a definition of color contrast which is a linear transform of our own, finds evidence for independent red-green and luminance detection mechanisms (Metha, 1994).

For our high spatial and low temporal frequency condition (4 cpd, 0 Hz), primate lesion studies suggest that the P cell pathway mediates the detection of both the color and luminance stimuli (Merigan, 1991). Our results demonstrate the existence of independent color and luminance detection mechanisms, even under these spatio-temporal conditions. Thus, we suggest that the color and luminance signals of the P cell pathway are subsequently separated (demultiplexed) into independent psychophysical detection mechanisms at a cortical level. Possible models for this separation are reviewed by Kingdom & Mullen (1995). It should be noted, however, that the present experiments do not provide a basis for excluding the possible existence of additional independent mechanisms which combine luminance and color contrast. The possible intrusion of a relatively insensitive "intercardinal" mechanism represented by a vector, for example, around 45 deg in the plots, cannot be excluded by our data, and might be acting to round the corners of the plotted functions and lower their K value.

Our results contrast with those of Gur & Akri (1992), who found complete linear summation over a wide spatial frequency range (0.3–20 cpd). It is not clear why this conflicting result has been obtained. We consider two possibilities. Granger & Heurtley (1973) first reported that nominally isoluminant red-green stimuli presented on a RGB monitor above about 3 cpd are achromatic in appearance at threshold. It is also known that for stimuli displayed on an RGB monitor with no correction for chromatic aberrations, detectable luminance artifacts arising from chromatic aberrations are likely to occur in chromatic stimuli above about 5 cpd, most likely accounting for Granger & Heurtley's observation (Bradley *et al.*, 1992). Thus, the higher spatial frequency stimuli used by Gur & Akri (1992) (9–20 cpd) are likely to contain significant luminance artifacts which may

combine linearly with the achromatic contrast of the luminance stimuli. Nonetheless, this explanation is unlikely to provide an account of their finding of linear summation at the lower spatial frequencies (0.3 and 0.9 cpd). A second possibility that we have considered arises from the different measures of color contrast used by the two studies. Gur & Akri (1992) use a measure of color contrast which is not independent from luminance contrast. The color profile of the stimulus was considered in terms of a modulation in chromaticity, and the color contrast was defined as the difference in the chromaticities at the peak and trough of the grating: i.e., $r/(r+g)_{\max} - r/(r+g)_{\min}$, where r and g are the phosphor luminances at the peak and trough of the grating. This definition of color contrast is not independent from the Michelson luminance contrast of the stimulus, as the color profile will no longer vary sinusoidally when sinusoidal luminance modulations are added to it and nonlinear distortions will result (Mullen *et al.*, 1992). We have re-calculated the thresholds for our data using the color contrast definition of Gur & Akri (1992). The results show that this produces small but insignificant changes in our data plots. Thus, the use of two different definitions of color contrast fail to account for the differences between the two studies. Although our results combine with a body of data compatible with the existence of independent contributions of color and luminance mechanisms to detection threshold (Cole *et al.*, 1993; Metha *et al.*, 1994; Sankeralli & Mullen, 1996; Kranda & King-Smith, 1979; Palmer *et al.*, 1993) we can provide no specific explanation for why our results differ from those of Gur & Akri (1992), who used broadly similar methods to our own.

As raised in the Introduction, further questions which arise are whether the luminance and color mechanisms remain independent at suprathreshold levels of contrast, or when higher order tasks are performed. Sinewave masking studies demonstrate that the luminance and chromatic mechanisms display masking interactions at high suprathreshold levels of contrast (approximately over 20 times detection threshold) (Switkes *et al.*, 1988; Cole *et al.*, 1990; Mullen & Losada, 1994). With noise masking these high contrast interactions are less evident, probably due to the broader spatio-temporal distribution of the energy of the masking stimulus (Gegenfurtner & Kiper, 1992; Losada & Mullen, 1995). At lower suprathreshold contrasts (approximately 2–20 times threshold), facilitatory interactions occur which are highly dependent on the stimulus arrangement and the manner of its presentation (Switkes *et al.*, 1988; Cole *et al.*, 1990; Mullen & Losada, 1994). Evidence suggests, however, that these facilitatory interactions are compatible with independent transduction by distinct color and luminance mechanisms (see models of Switkes *et al.*, 1988 and Mullen & Losada, 1994), and probably reflect some form of higher order interaction (Eskew *et al.*, 1991).

In the performance of higher order tasks, there is evidence for a range of different types of interactions

between color and luminance mechanisms, both linear and nonlinear. The literature suggests that the type of combination obtained depends on the particular task. There is some evidence that color and luminance contrast combine (possibly linearly) in their contribution to velocity perception (Cavanagh *et al.*, 1984; Cavanagh & Anstis, 1991; Mullen & Boulton, 1992), whereas for direction discrimination the evidence is inconclusive but indicates a nonlinear combination of color and luminance mechanisms (Palmer *et al.*, 1993; Gegenfurtner & Hawkin, 1995). For suprathreshold spatial tasks, a variety of interactions between color and luminance contrast have been reported affecting, for example, border localization (Greene & Brown, 1995; Rivest & Cavanagh, 1996), contour integration (McIlhagga & Mullen, 1996), and the perception of Mach bands (Gur & Syrkin, 1993). For stereo vision it is clear that color vision can support some form of stereopsis (Stuart *et al.*, 1992; Jordan *et al.*, 1990), however, there is evidence from summation square experiments that the color and luminance mechanisms remain independent and combine by probability summation (Simmons & Kingdom, 1997). Thus, the present paper indicates the existence of independent red-green and luminance mechanisms for the determination of detection thresholds, and this implies that a successful demultiplexing of the chromatic and luminance signals occurs to mediate detection thresholds, probably at an early cortical level (Kingdom & Mullen, 1995 for models). At the higher visual stages which are presumed to mediate more complex tasks discussed above, either these mechanisms may be recombined, or these tasks are based on the outputs of cortical neurons which have not undergone demultiplexing and so retain univariant color-luminance responses.

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