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The Spatial Tuning of Chromatic Mechanisms Identified by Simultaneous Masking

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We have investigated the spatial transfer characteristics of the mechanisms sensitive to color in the human visual system using a method of simultaneous spatial masking with isoluminant chromatic stimuli. The test stimuli were Gaussian enveloped red–green gratings of three spatial frequencies in the lowpass region of the color domain (0.25, 0.5 and 1 c/deg). The masking stimuli were red–green gratings at the orientation and phase of the test, presented at the same spatial frequency, and at ±1, and ±2 octaves from its spatial frequency. We obtained test contrast threshold as a function of mask contrast for a wide range of mask contrasts (TvC functions). Tuning functions were derived from linear fits of the masking data, by taking the mask contrast that doubled the minimum test threshold at each spatial frequency. Chromatic tuning functions show bandpass characteristics for all test spatial frequencies examined with an average full bandwidth at half-height of 2.6 octaves, which is similar to the luminance bandwidths obtained under comparable conditions. Thus, our results suggest that the color contrast sensitivity function is the upper envelope of a range of bandpass mechanisms whose peaks extend to very low spatial frequencies.

Color vision Isoluminance Spatial masking Chromatic spatial tuning Chromatic mechanisms

INTRODUCTION

The performance of the human visual system in the detection of spatial distributions of color is characterized psychophysically by the color contrast sensitivity function (CSF) (Schade, 1958; Van der Horst & Bouman, 1969; Granger & Heurtley, 1973; Kelly, 1983; Mullen, 1985). These studies reveal that the color CSF has lowpass characteristics, distinct from the bandpass characteristics of the luminance CSF. The mechanisms that underlie the luminance CSF are spatially tuned filters whose bandpass characteristics have been estimated by a number of different psychophysical techniques, including suprathreshold masking (Stromeyer & Julesz, 1972), spatial adaptation (Blakemore & Campbell, 1969), and subthreshold summation (Sachs, Nachmias & Robson, 1971). Although the overall shape of the color contrast sensitivity function has lowpass characteristics, this does not imply that the psychophysical mechanisms determining threshold are also lowpass. A lowpass color CSF may represent the upper envelope of numerous bandpass mechanisms whose peaks extend to low spatial frequencies. In this case, a decline in color contrast sensitivity at low spatial frequencies may only be revealed by extending contrast sensitivity measurements to lower spatial frequencies than have previously been reported (below 0.1 c/deg). Alternatively, the peaks of bandpass mechanisms may extend to such low frequencies that the size of the human visual field ultimately limits the measurement of any low spatial frequency decline in contrast sensitivity.

Relatively few psychophysical studies have examined the spatial tuning of the chromatic detection mechanisms. Masking techniques have been used to obtain the spatial frequency selectivity of chromatic detection mechanisms (De Valois & Switkes, 1983; Switkes, Bradley & De Valois, 1988). Their results suggest that the spatial filters underlying the detection of chromatic stimuli are bandpass in shape, and are similar to the filters underlying luminance contrast detection. These functions, however, were obtained for gratings centered on a spatial frequency of 2 c/deg, and little is known about the spatial selectivity of masking at lower frequencies to which chromatic sensitivity is the greatest.

The spatial tuning of the chromatic detection mechanisms has also been investigated using adaptation techniques (Bradley, Switkes & De Valois, 1988). Adaptation to red–green chromatic gratings temporarily elevates chromatic contrast thresholds with a time–course similar to the elevation found for luminance contrast. The spread of the adaptation effect across spatial frequency for the chromatic gratings shows bandpass characteristics, with some asymmetry also characteristic of luminance adaptation (Blakemore & Campbell, 1969), and overall the selectivity of chromatic adaptation was found to be slightly broader than for the luminance domain. This study, however, was also confined to chromatic spatial frequencies at the upper end of the color CSF (0.5 c/deg, and above). Moreover, the spatial tuning of

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chromatic mechanisms cannot presently be inferred from primate cortical neurophysiology which is ambiguous in revealing both bandpass and lowpass neurones sensitive to color (Thorell, De Valois & Albrecht, 1984; Livingstone & Hubel, 1984; Lennie, Krauskopf & Sclar, 1990; Bertulis & Glezer, 1984; Michael, 1978; Gouras, 1974).

In this work, we have addressed the question of the tuning characteristics of the chromatic mechanisms using a simultaneous masking technique in the low spatial frequency region of the color domain. We measured the effect of masking stimuli on test detectability for spatial frequencies of 0.25, 0.5, and 1 c/deg. Test and mask were presented at the same orientation and relative phase. For each test frequency, five masking stimuli were used whose spatial frequencies were the same as the test, ± 1, and ± 2 octaves from the test. We obtained complete masking functions covering the whole contrast range from subthreshold to high suprathreshold levels for each combination of test and masking frequency (TvC functions). The TvC functions show the standard "dipper" shape, with subthreshold facilitation and subsequent masking. Tuning functions were calculated from linear fits of the rising segments of these TvC functions by taking the contrast of the mask that produced a two-fold elevation in the minimum test threshold at each spatial frequency. The chromatic tuning functions derived show bandpass characteristics with an average full bandwidth at half height of 2.6 octaves, similar to the luminance bandwidth under comparable conditions.

METHODS

The stimulus generation and apparatus have been described elsewhere and are given only briefly here (Mullen, 1985; Mullen & Boulton, 1992). Test and masking stimuli were both isoluminant chromatic gratings, or were both isochromatic luminance gratings. Chromatic stimuli were horizontal red–green gratings produced by displaying two luminance modulated gratings, each on a Joyce (DM2) display screen with white P4 phosphors. These were viewed through narrow band interference filters (Melles Griot) with center wavelengths of 527 and 606 nm, respectively, and full bandwidths at half height of 21–22 nm. The two monochromatic component gratings were combined by a beam splitter 180 deg out of phase to produce a chromatic grating, or in phase to obtain a luminance grating of the same mean luminance and chromaticity. Longitudinal and transverse chromatic aberrations were corrected (Mullen, 1985). 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}.

Test and mask stimuli were sinewaves of the same orientation and combined in phase. Both were Gaussian enveloped along the axis of modulation with a half-bandwidth at 1/e height of 1.5 cycles of the test stimulus, and were sharply truncated on the horizontal axis at a bar length of 6 cycles of the test stimulus. Thus, the spatial extent of the stimuli was determined by the spatial frequency of the test grating, and the number of cycles in the masking stimulus varied inversely to the spatial frequency of the test. For test spatial frequencies of 0.25 c/deg, a Zeiss ($\times 3$) telescope was used to magnify the display.

Contrast of the two luminance component gratings was defined by the usual formula:

$$C = \frac{I_{max} - I_{min}}{I_{max} + I_{min}}$$

where I_{max} and I_{min} are the peak and trough luminance values of the monochromatic grating respectively. Although their respective mean luminances may differ, the contrasts of these two component gratings were always equal, and the contrast of the chromatic stimulus was defined by their contrast. All stimuli were generated using a VSG2/1 waveform generator (Cambridge Research Systems) with 14-bit analog output DACs.

Isoluminance of the two colors was measured using a minimum motion method. Subjects found the point at which the perceived drift rate reached a minimum by varying the ratio of the red to green mean luminance in the stimulus with a method of adjustment. This was repeated at least 10 times and an average obtained. This is a convenient method of obtaining the isoluminant point as there is a sharply defined minimum in perceived drift rate at isoluminance for these stimuli (Moreland, 1982; Cavanagh, 1987; Mullen & Boulton, 1992).

In the masking experiments, thresholds were measured using a standard two-alternative forced-choice staircase procedure. A masking stimulus appeared in each of two time intervals, and was accompanied by the test stimulus in one of the intervals. The contrast of the stimulus was ramped on and off with a temporal Gaussian envelope with a spread of 125 msec. The stimulus was stationary, and the phase of its presentation within the envelope was randomly varied between each interval. The subject indicated by pressing a button in which interval the test stimulus had appeared, and feedback was given after each trial. The staircase procedure was terminated after 12 reversals in the contrast presented, and the threshold was determined as the mean of the contrasts of the last seven reversals. Each plotted threshold represents the mean of at least three measured thresholds. Results were obtained from three subjects (KTM, MAL, MJS) with normal color vision measured on the standard tests (Farnsworth–Munsell 100 hue test; The City University colour vision test).

RESULTS

Threshold vs contrast functions for color

The contrast threshold of the test in the presence of the masking stimuli was measured for test spatial frequencies of 0.25, 0.5 and 1 c/deg. The spatial frequencies of the masking stimuli were the same spatial frequency as the test, and ± 1 and ± 2 octaves from it. We

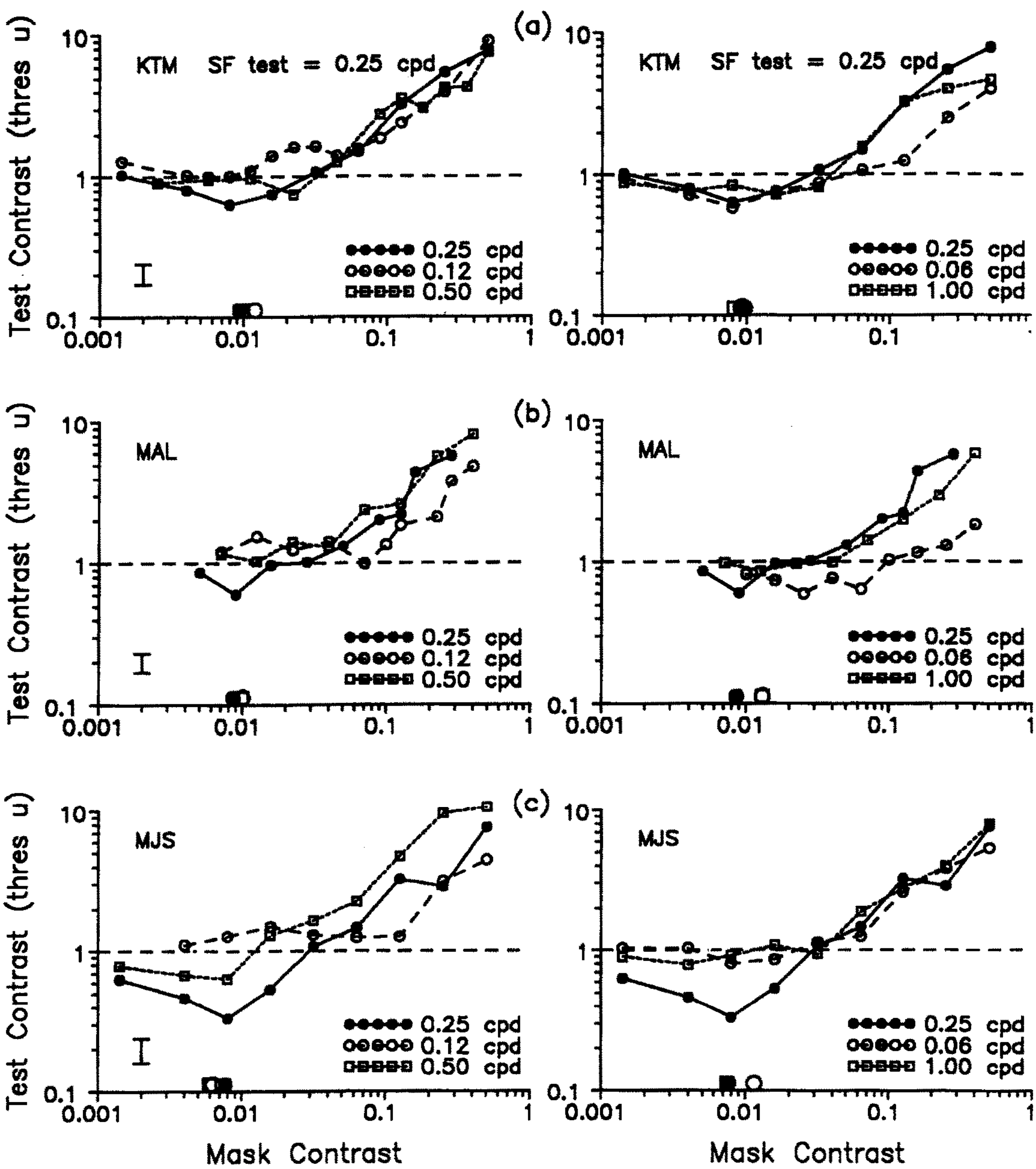

FIGURE 1. TvC functions for test stimulus of 0.25 c/deg. In the left panels, the TvC functions for masking stimuli of spatial frequencies of ± 1 octave (0.125 and 0.5 c/deg) are plotted, and in the right panels functions for ± 2 octaves (0.0625 and 1 c/deg) are shown. In all the TvC plots open squares indicate a mask frequency above that of the test, and open circles indicate a mask frequency below the test. The TvC function for the masking stimulus at the spatial frequency of the test (0.25 c/deg) is shown in both graphs with the solid symbols. On the ordinate, test contrast threshold is given in multiples of the unmasked test threshold. The abscissa shows the contrast of the mask. The horizontal dotted line indicates the unmasked test threshold. The thresholds of the masking stimuli are represented on the abscissa by the symbol corresponding to the relevant TvC function. The error bars represent twice the average standard deviation (2 SD) for each subject and condition. Sections (a)–(c) show data for subjects KTM, MAL, MJS, respectively.

measured the test contrast threshold for contrasts of the masking stimuli that varied from low subthreshold contrasts (0.3–1.6%) to high suprathreshold contrasts (25–50%). Figures 1–3 give the TvC functions for test stimuli of 0.25, 0.5 and 1 c/deg, respectively. Sections (a)–(c) show the data for three subjects (KTM, MAL, and MJS, respectively). The left panels of each figure show the TvC functions for spatial frequencies of the mask ± 1 octave from the test spatial frequency, and the right panels show the TvC functions for masking stimuli ± 2 octaves from the test frequency. In these figures open squares are used to indicate a mask frequency above that of the test, and open circles indicate a mask frequency below the test. The TvC function for test and masking stimuli of the same spatial frequency is shown in both graphs with the solid symbols. The test contrast thresholds are given as multiples of the unmasked test threshold, which is given by horizontal dotted lines. The absolute contrast of the masking stimuli are given on the abscissa, with the thresholds of the masking stimuli represented on the abscissa by the symbol for the corresponding TvC function. Error bars represent twice the average standard deviations (2SD) for each subject and test spatial frequency.

When the test and mask have the same spatial frequency, the TvC functions for all subjects show the characteristic dipper shape. At subthreshold contrasts of the masking stimuli, the test thresholds show facilitation which is maximal at or near the threshold of the masking stimulus, and at higher contrasts the test thresholds increase. For mask contrasts above 5 or 6 times threshold, the test thresholds rise above the unmasked threshold. Facilitation diminishes sharply or disappears when the spatial frequency of the masking stimuli differs from the test spatial frequency, in keeping with previous results for chromatic (Switkes *et al.*, 1988) and luminance stimuli (Legge & Foley, 1980; Speed & Ross, 1992). For all the conditions, facilitation shows a strong inter-subject variability. Facilitation may be explained by a positively accelerating non-linearity in the detection function. Non-linear transducer models (Stromeyer & Klein, 1974; Nachmias & Sansbury, 1974; Legge & Foley, 1980; Foley & Legge, 1981) and uncertainty models (Pelli, 1985) are consistent with such an accelerating detection function. Models of masking typically suppose a compressive non-linearity in the transducer function which reduces the incremental sensitivity of the detecting mechanism (Legge & Foley, 1980; Wilson, McFarlane & Phillips, 1983). Based on the differences in the properties of masking and facilitation, it has been suggested that

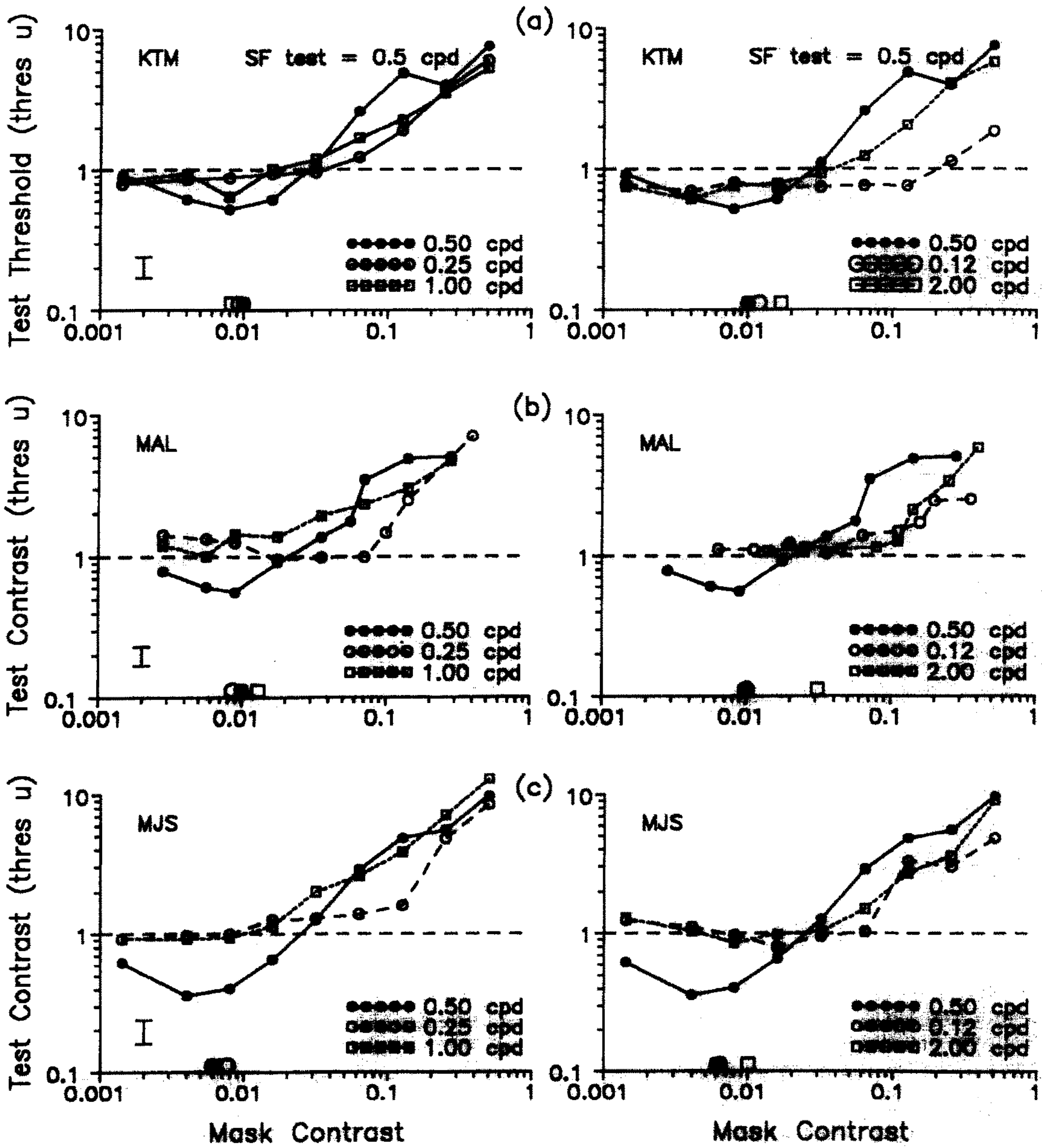

FIGURE 2. TvC functions for test stimulus of 0.5 c/deg. In the left panels, the TvC functions for masking stimuli of 0.25 and 1 c/deg are plotted and, in the right panels, for masking stimuli of 0.125 and 2 c/deg. The TvC function for masking stimuli of 0.5 c/deg is shown in both graphs for reference. The axis and threshold values are represented as in Fig. 1. Sections (a)–(c) show the data for KTM, MAL, and MJS as before.

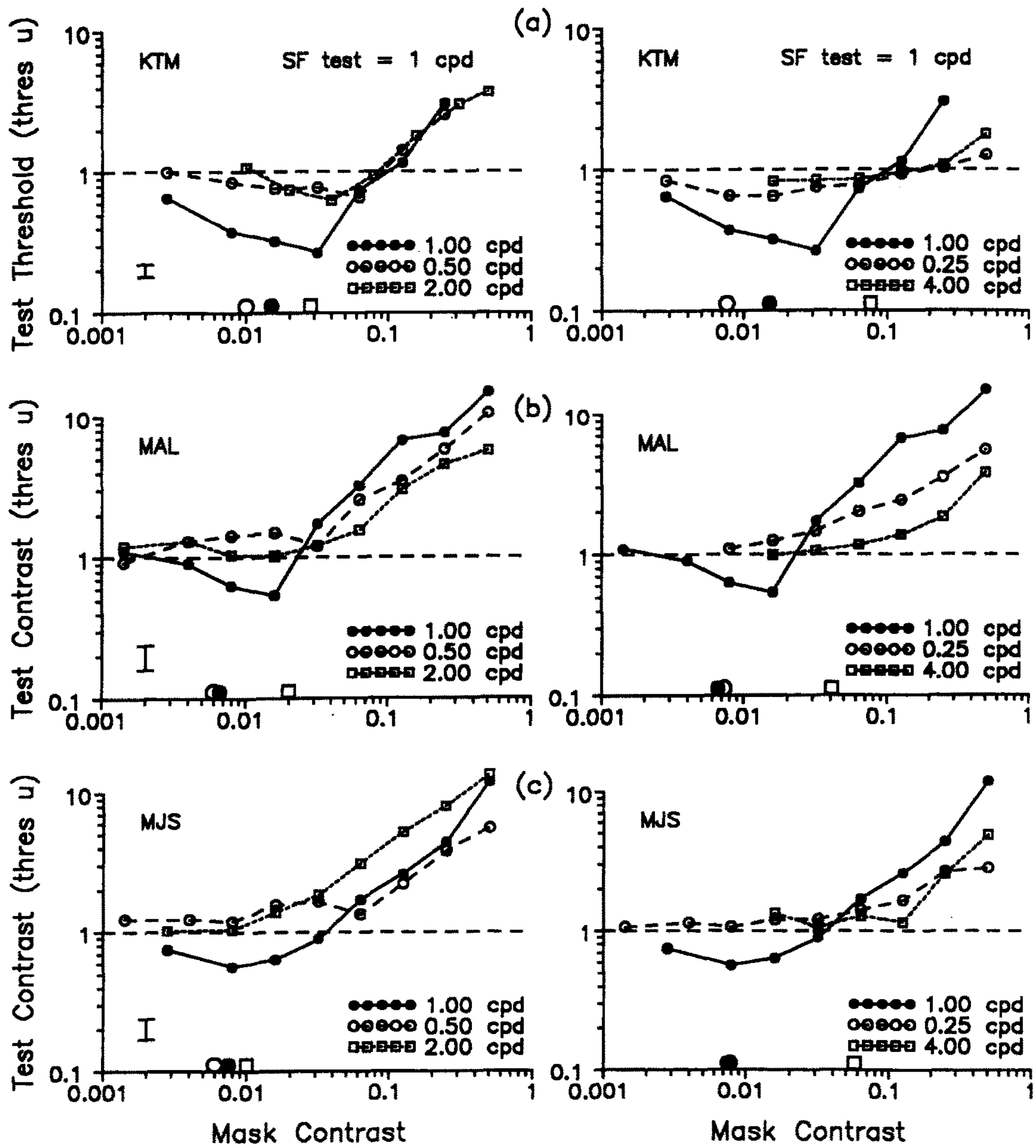

FIGURE 3. TvC functions for test stimulus of 1 c/deg. In the left panels, the TvC functions for masking stimuli of 0.5 and 2 c/deg are plotted and, in the right panels, for masking stimuli of 0.25 and 4 c/deg. The TvC function for masking stimuli of 1 c/deg is shown in both graphs for reference. The axis and threshold values are represented as in Fig. 1. Sections (a)–(c) show the data for KTM, MAL, and MJS as before.

these may reflect separate underlying mechanisms (Legge & Foley, 1980; Ross & Speed, 1991). A conventional criterion for masking is threshold elevation above the unmasked threshold. Alternatively, masking may be defined as any rise in the test threshold, and hence would begin from the upturn in the TvC function indicating entry into the compressive phase of the non-linear transducer function. In this study we use this latter definition for masking.

We noticed that the threshold elevations for mask spatial frequencies above and below the test frequency are often similar to those obtained at the test frequency. Occasionally, the greatest threshold elevations occur at a mask spatial frequency different from the test spatial frequency, specifically this tends to occur for masks 1 octave above the test frequency for subject MJS. We return subsequently to the influence of this effect on the tuning function we derive.

Threshold vs contrast functions for luminance

In order to compare the tuning characteristics of the luminance and color mechanisms, we obtained TvC functions for luminance (isochromatic) test and masking stimuli for one subject (MAL) at the same three test spatial frequencies (0.25, 0.5 and 1 c/deg), and for all three subjects at one test frequency (0.5 c/deg). The luminance TvC functions for MAL are presented in Fig. 4(a, b, c) for test stimuli of 0.25, 0.5 and 1 c/deg,

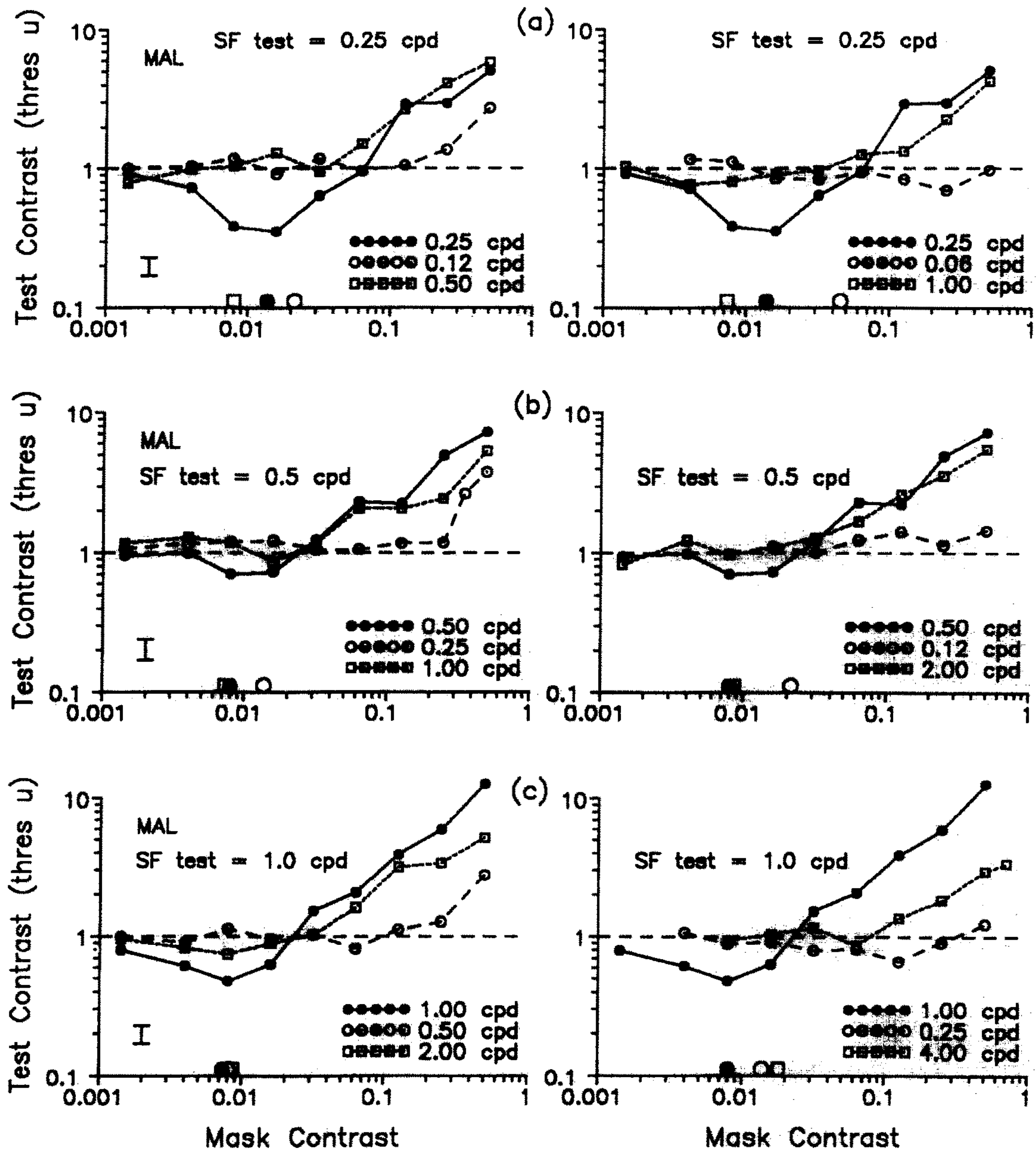

FIGURE 4. Luminance TvC functions. In the left panels, the TvC functions for masking stimuli of ±1 octave from the test are plotted. In the right panels, the TvC functions for masking stimuli of 2 octaves above and below the test are plotted. The TvC function for masking stimuli of the test spatial frequency is shown in both graphs for reference. The axis and threshold values are represented as in Fig. 1. Sections (a)–(c) show the data obtained with test stimuli of 0.25, 0.5 and 1 c/deg, respectively. Subject MAL.

respectively, using the same format. Data for the other two subjects at 0.5 c/deg are not shown, but are used in the subsequent calculations. The overall characteristics of all these luminance TvC functions are similar to those previously reported (Legge, 1979; Legge & Foley, 1980). In agreement with Switkes *et al.* (1988), we find that luminance and color TvC functions are very similar within the range of the variability of the data, and we find this at all test spatial frequencies.

One can see that the luminance masking stimuli with lowest frequency do not produce any effect on the detectability of the test whereas some masking still occurs for chromatic stimuli, suggesting that low spatial frequency masks are less effective in the luminance domain.

Calculation of the tuning functions

To obtain a smoothed version of the rising segments of the TvC functions, we fitted each rising segment with a linear regression. If facilitation is present, the fit includes all data points at and after maximum facilitation. Facilitation is defined as a test threshold reduction >2 SDs from the unmasked threshold. If the facilitation is absent, all data points 2 SDs above the unmasked threshold, and the last data point at unmasked threshold, are included in the fit. These fits

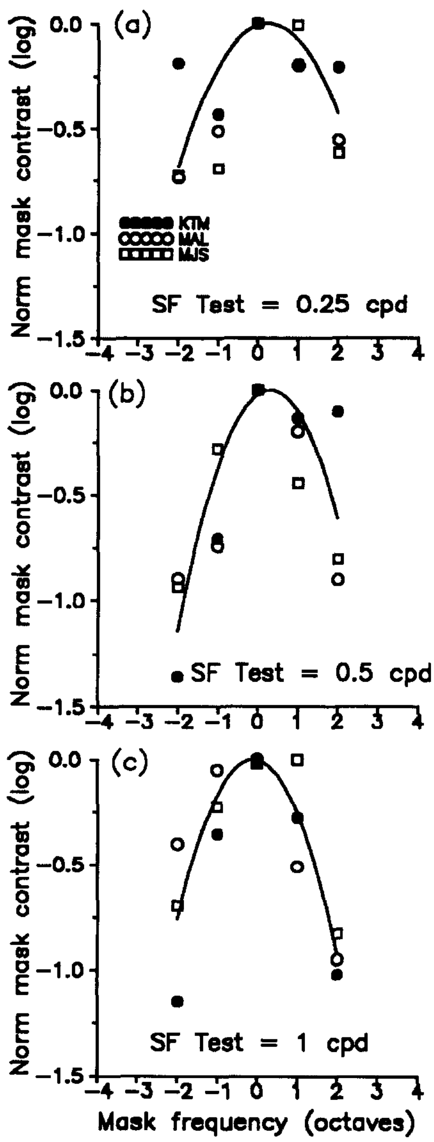

FIGURE 5. Chromatic tuning functions obtained using the two-fold elevation criterion. Tuning functions obtained for test centered at 0.25, 0.5 and 1 c/deg are shown in (a), (b) and (c) respectively. The spatial frequency of the masking stimulus is represented in octaves. On the ordinate, the logarithm of the normalized masking contrast is shown. The data points are the normalized values for each subject and the solid line represents the Gaussian fit to the normalized average over subjects.

allow us to obtain the value of the masking contrast for a given test threshold. We took as our measure of the magnitude of masking, the mask contrast required to produce a two-fold elevation from the minimum test threshold. This provides individual tuning functions.

The chromatic tuning functions are shown in Fig. 5 for test spatial frequencies of 0.25, 0.5 and 1 c/deg in (a), (b), and (c) respectively. The contrast of the masking stimulus with the maximum normalized to unity is represented in log units on the ordinate, and the different symbols represent the results for each of our three subjects. The abscissa shows the spatial frequency in octaves relative to the test frequency. A Gaussian was fitted to the average across subjects (solid line), and is given by:

$$y = \exp\{-(2.77(f-f_0)^2/\sigma^2)\}$$

where y is mask contrast; f is the spatial frequency in octaves of the test frequency; f_0 is the spatial frequency corresponding to the peak of the Gaussian, and σ is the full bandwidth at half height.

All the tuning functions show bandpass characteristics, including the lowest spatial frequency of 0.25 c/deg. The data points show no marked asymmetry. In keeping with Stromeyer *et al.* (1982), we find that the maximum masking usually occurs at the test spatial frequency, with no evidence for displaced peaks in the tuning functions at the low spatial frequencies as has sometimes previously been reported (Legge, 1978, 1979).

As we already pointed out for the TvC functions of Figs 1–4, threshold elevations by a mask at the test frequency may be similar to, or less than, elevations by a mask ± 1 octaves away from the test. A good example of these effects can be observed in the data of MJS at 1 c/deg [Fig. 1(c)]. Thus if the criterion for the effectiveness of the mask was based simply on test threshold elevation at a particular mask contrast, the tuning function would be rather flat, with peaks that tend to skew away from the test frequency. Our criterion, however, takes into account the initial lowering of test threshold by facilitation and measures the effectiveness of the mask at elevating the test threshold from the *minimum* threshold. Clearly when facilitation occurs, greater elevation (masking) is required to reach a given test threshold than with no facilitation. Since facilitation is maximum when the masking and test stimuli have the same spatial frequency, adopting this criterion reveals a greater mask effectiveness at frequencies at and close to the test. Furthermore, with this criterion the peaks of the tuning functions lie closer to the test spatial frequency, any apparent shift in the peaks of the tuning functions is reduced, and the tuning functions become more peaked.

The bandwidths (σ) and peak frequencies (f_0) of the tuning functions were obtained from the Gaussian fits and are shown in Tables 1 and 2, respectively. In Table 1, the values of the bandwidths (σ) for all subjects and test frequencies are given as well as the average across subjects. The values of the bandwidths show no significant trend for an increase with spatial frequency, using an F-test on the data with a 95% confidence limit. Averaging across spatial frequencies, we found a full bandwidth at half height of 2.6 octaves. In Table 2, the

TABLE 1. Bandwidths (σ) for the color and luminance mechanisms

	0.25 c/deg		0.5 c/deg		1 c/deg	
SF	Color	Luminance	Color	Luminance	Color	Luminance
KTM	4.3		2.8	1.8	2.1	
MAL	2.6	1.7	2.2	2.9	2.7	1.6
MJS	2.6		2.3	1.8	2.5	
AVE	3.0		2.4	2.0	2.4	

The full bandwidths at half-height for the mechanisms centered at 0.25, 0.5 and 1 c/deg are shown for color and luminance Gaussian fits for three subjects. The bandwidth for the combined data across subjects is shown at the bottom.

TABLE 2. Peak frequencies (f_0) for the color and luminance mechanisms

	0.25 c/deg		0.5 c/deg		1 c/deg	
SF	Color	Luminance	Color	Luminance	Color	Luminance
KTM	0.2		1.0	0.4	0.1	
MAL	0.2	0.6	0.1	1.1	−0.5	0.6
MJS	0.3		0.0	0.2	0.0	
AVE	0.2		0.3	0.4	−0.1	

The peak frequencies expressed as octave deviation from the test frequency for test spatial frequencies of 0.25, 0.5 and 1 c/deg are shown for color and luminance Gaussian fits for three subjects. The peak frequency for the combined data across subjects is shown at the bottom.

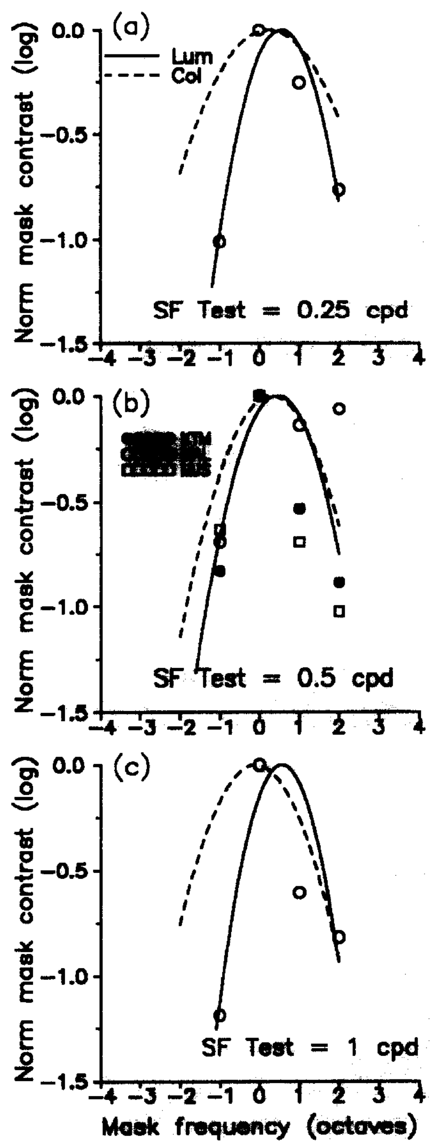

FIGURE 6. Luminance tuning functions. The luminance tuning functions obtained by using the two-fold elevation criterion are given with the solid lines and data points. The middle panel shows the luminance tuning function for a test spatial frequency of 0.5 c/deg for three subjects (KTM, MAL, MJS). (a, b) Functions for 0.25 and 1 c/deg, respectively, for MAL only. The average color tuning functions from Fig. 5 have also been plotted for reference (dashed line).

values of the peak frequency (f_0) in octaves of the test spatial frequency are given. The peaks of the Gaussian tuning functions show a small and insignificant degree of skewing to other frequencies.

Comparison with luminance tuning functions

In order to compare the tuning characteristics of the psychophysical mechanisms that process luminance and color under the same conditions, we have obtained the tuning functions from the luminance TvC functions. We used the same criterion and bandwidths calculations. In Fig. 6(b), the luminance tuning functions for three subjects at 0.5 c/deg are shown with a fit based on the combined data (solid line, symbols according to subject), (a) and (c) show tuning functions for one subject (MAL) for 0.25 and 1 c/deg, respectively (solid line with open circles). The Gaussian fit to the average color tuning function is also represented at each spatial frequency for comparison (dashed line, no data points shown). The data for the luminance stimuli for all test spatial frequencies show a low frequency decline which is greater than for the higher spatial frequencies, resembling the asymmetrical effects found previously for luminance masking (Stromeyer, Klein, Dawson & Spillmann, 1982; Henning, Hertz & Hinton, 1981; Legge & Foley, 1980), luminance adaptation (Blakemore & Campbell, 1969), and color adaptation (Bradley *et al.*, 1988).

The values of σ and f_0 are given on the bottom lines of Tables 1 and 2, respectively. The values of σ obtained with luminance masking are typically smaller than the ones obtained with color at all spatial frequencies. However, an F-test shows that this is not significant at the 95% confidence level. Comparing color and luminance at the same spatial frequency for the same three subjects gives bandwidths of 2.4 and 2.0 octaves, respectively. Results for further subjects are needed to assess whether this difference is significant.

DISCUSSION

It has sometimes been assumed in previous studies that the rising parts of the TvC functions are unitary and the detection of the test is mediated by only one mechanism (Legge & Foley, 1980). Following this model, masking stimuli desensitize the detection mechanism to produce a threshold elevation of the test in a multiplicative manner, depending on the gain of the mechanism to the mask spatial frequency. Thus, the test threshold elevation is expected to vary linearly on log–log coordinates, and the rising segments of the TvC functions should be unitary and all of the same slope. There are similarities with this model in our approach to the treatment of the TvC functions, although we recognize that our masking functions may not be unitary but subserved by multiple mechanisms. We have fitted the TvC functions with a linear fit which is appropriate if the masking function is unitary. If, however, multiple mechanisms underlie the masking function, our fit represents an averaging across these mechanisms. Unlike Legge and Foley (1980), we have allowed the slope to vary when fitting the rising segments of TvC function for different spatial frequencies of the mask, and thus we are not restricting the fit by the assumption of unitary detection mechanisms.

It has also been suggested that particularly in the presence of a high contrast masking stimulus, the detection of the test may be subserved by mechanisms centered not at the test frequency, but at a frequency shifted away from the test which optimizes the detection threshold. This effect was first found in auditory masking and termed off-frequency listening (Patterson & Nimmo-Smith, 1980). It has been suggested that a similar effect, termed off-frequency looking (Pelli, 1980), occurs in vision for temporal masking (Hess & Snowden, 1991) and spatial masking (Wilson *et al.*, 1983; Perkins & Landy, 1991; Foley & Yang, 1991). For a multiple mechanism model with strong probability summation between channels the rising segments of the TvC curves for different mask frequencies show different slopes, becoming shallower when mask spatial frequency differs from the test. Therefore, the accuracy of the derived tuning functions as a representation of the underlying mechanism depends on the particular range of mask contrasts used. The estimates will appear a little broader than the underlying channel for very low mask contrasts (when the mask begins to be effective) but become narrower as mask contrast increases. If there is weak probability summation, the rising segments are not unitary, but show inflections at high mask contrasts as other mechanisms with different peak spatial frequency sensitivities are recruited. In this case, the tuning functions derived from data at low mask contrasts, before the intrusion of any other mechanism, are good estimates of the underlying mechanism tuning functions but become too narrow as mask contrast increases. It is worth mentioning that with a multiple mechanisms model a set of lowpass mechanisms, which could be expected to underlie color processing given the shape of the color CSF, will *always* produce lowpass masking effects even when the test is detected by off-frequency looking. Thus, although the assessment of the bandwidth of the mechanisms may be influenced by the adoption of single vs multiple mechanism models for detection, the assessment of the nature of the mechanisms, whether lowpass or bandpass is not.

In our data there are some features which suggest a possible intrusion of multiple mechanisms at high contrasts. Firstly, as we mentioned before, we fitted the rising segments with lines of different slopes, which vary over a wide range between conditions, from 0.18 to 1.6, although with an average value of 0.67 (± 0.25) similar to that (0.62) found by Legge and Foley (1980). Secondly, it has been reported that, in general, the luminance tuning functions obtained by taking the threshold elevation produced by masks of fixed contrast become narrower as contrast increases (Foley & Yang, 1991). We have looked for this effect in our data for chromatic masking and results are shown in Fig. 7 where the raw data of Figs 1(a) and 3(c) have been replotted as an example. Test thresholds in log units for fixed mask contrast ranging from low contrasts (6%) to high (50%) are shown as a function of mask frequency in octaves. Data for all mask contrasts are plotted on the same graph and the threshold elevation values have not been normalized. Solid lines represent Gaussian fits to the data. The full bandwidths at mask contrasts of 6% are 5.3 and 3.5 (two subjects), and at 50% are 3.5 and 2.9 (same two subjects). The data show some narrowing at the higher mask contrast, which may suggest the intrusion of multiple detection mechanisms. We also observed that in some of the TvC functions the rising segments of the TvC functions in some conditions (test and mask stimuli of the lowest spatial frequencies) appear to show inflections. It is difficult, however, to establish whether these effects in our data are genuine, or due to the variability in the data. We have been unsuccessful in replicating specific inflections in the TvC functions.

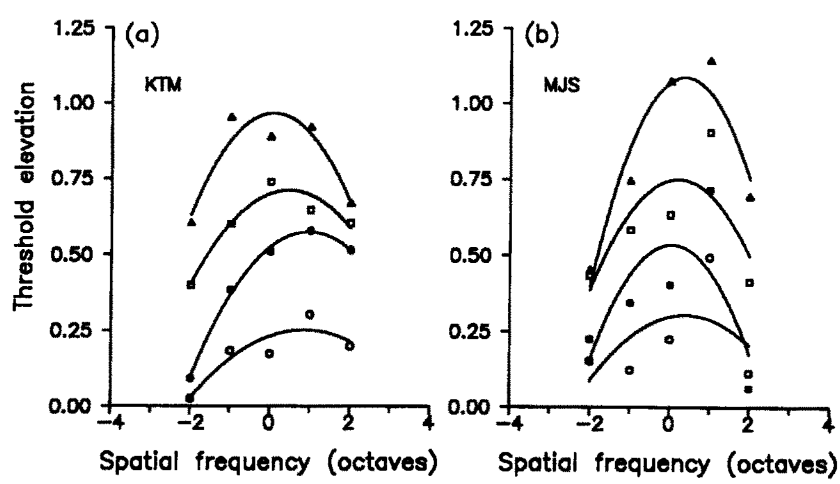

FIGURE 7. Chromatic tuning functions obtained for a fixed mask contrast. Test threshold elevation in log units from Figs 1(a) (KTM, sf = 0.25 c/deg) and 3(c) (MJS, sf = 1 c/deg) have been plotted for fixed mask contrasts as follows: 6, 13, 25 and 50%. On the abscissa, the mask frequency is shown in octaves relative to the test spatial frequency. The threshold elevation values have not been normalized. The solid lines represent the Gaussian fits to the data. The values of σ increased from 5.3 (at 6%) to 3.5 (at 50%) for KTM, and from 3.5 (at 6%) to 2.9 (at 50%) for MJS.

In order to reduce the effects of off-frequency looking Hess and Snowden (1991) used only low contrast masks. The contrast of the test stimulus was fixed at a value just above its unmasked threshold, and the contrast of the masking stimulus needed to bring the test back to detection threshold was obtained. Our criterion measure of masking (the mask contrast producing a two-fold increase in threshold) resembles this. It is worth pointing out, however, that as we fitted the data over the complete range of mask contrast and not just over the near-threshold contrast range, the derived tuning functions represent an average over the possible effects of multiple mechanisms intruding at high contrasts, and thus our bandwidth estimates will only be slightly narrower than those we would have obtained by using only low mask contrasts. Furthermore, the use of methods based only on low contrast masks are restricted in this study for two reasons. Firstly, we found methods which vary mask contrast to obtain a criterion test contrast threshold (Patterson & Moore, 1986; Hess & Snowden, 1991; Foley & Boynton, 1992) to be highly variable in this task since our TvC functions are often very shallow around unmasked threshold. Secondly, alternative methods which determine tuning relative to mask contrasts at the point of maximum facilitation are restricted since facilitation is often shallow and the maximum difficult to determine (Speed & Ross, 1992).

On the other hand, there are alternative models available which may explain a non-unitary TvC function and the presence of inflections. These models are based on the detection of the envelope modulation (beats) which appears when two gratings of different spatial frequencies and similar contrast are added. This stimulus has a periodicity at which there is no Fourier energy. There is some evidence that subjects are able to detect the envelope in a complex grating stimulus, possibly reflecting a non-linearity prior to spatial filtering (Henning, Hertz & Broadbent, 1975). Under some combinations of test and mask, this effect may underlie stimulus detection. Nachmias (1993) provided further evidence that the observer uses changes in local features (phenomenal appearance of the test-plus-masker waveforms as opposed to the masker alone) to decide whether a test stimulus has been added to the masker.

Our data in Figs 5 and 6 suggest that tuning functions for luminance are narrower than for color. Part of this narrowing is caused by the steeper decline at low frequencies of the luminance tuning functions, which may be explained by the different sensitivities to color and luminance contrast at lower and higher spatial frequencies in the context of a multiple channel model. The fact that contrast sensitivity for luminance is higher than for color at high spatial frequencies implies that luminance mechanisms have higher gains than color mechanisms in this range. When masking with low spatial frequencies in luminance, the use of high frequency luminance channels in the detection of the test causes an absence of masking. For color, however, the use of high frequency mechanisms does not improve the detection of the test as they have low gains.

Previous masking studies on the spatial tuning of luminance mechanisms give bandwidth estimates similar to ours. Legge and Foley (1980) obtained tuning functions for luminance gratings of 2 c/deg with field sizes of 6 deg (12 test cycles presented) and 0.75 deg (1.5 test cycles). They obtained full bandwidths at half height of 1.75 octaves for the wide field and of 3 octaves for the narrow field. Our estimates obtained presenting three test cycles lie between both of these results. Wilson *et al.* (1983) found bandwidths that ranged from 1.25 octaves at high frequencies (2.8–16 c/deg) to 2.5 octaves at low frequencies (0.75–1.5).

In a previous study, Switkes *et al.* (1988) obtained the TvC functions for three subjects with a test spatial frequency of 2 c/deg. They obtained color tuning characteristics similar to ours when they plotted the threshold elevation for a mask contrast of 32% vs the spatial frequency of the masking stimuli. The full bandwidth at half height for the chromatic mechanism centered at 2 c/deg was 3 octaves. This is close to our 2.6 octaves in spite of the fact that they used a different criterion to obtain the masking functions. Preliminary reports from an on-going study also indicate the existence of bandpass chromatic mechanisms (Pandey & Vimal, 1993). Bradley *et al.* (1988) obtained color and luminance tuning functions using a method of adaptation. They found color mechanisms, whose full bandwidths are of 3.8 octaves, broader than the equivalent luminance mechanisms (2 octaves full bandwidth). Humanski and Wilson (1992) have reported the tuning characteristics of the mechanisms subserved by S-cones and found two bandpass mechanisms (with peak frequencies of 0.7 and 1.4 c/deg). Webster, De Valois and Switkes (1990) report that spatial frequency discrimination is slightly poorer for chromatic than luminance gratings. Overall, these results suggest similar underlying mechanisms for color and luminance contrast detection.

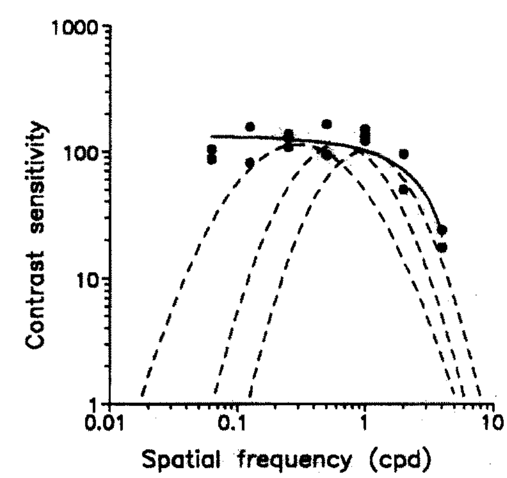

FIGURE 8. Chromatic mechanisms underlying the chromatic CSF. The figure shows the contrast sensitivity data obtained for the three subjects and the Gaussian fits to the averaged tuning functions obtained with the two-fold elevation criteria for test frequencies centered at 0.25, 0.5 and 1 c/deg. The gain of the mechanisms have been adjusted to fit the shape of the CSF.

In summary, Fig. 8 shows how the average color mechanisms we have obtained underlie the color CSF. Our results suggest that color vision, like luminance vision, encodes the scene into a range of spatial scales by bandpass filtering.

REFERENCES

Bertulis, A. & Glezer, V. (1984). Color-spatial vision. *International Journal of Psychophysiology, 2,* 147–165.

Blakemore, C. & Campbell, F. W. (1969). On the existence of neurons in the human visual system selectively sensitive to the orientation and size of retinal images. *Journal of Physiology, 203,* 237–260.

Bradley, A., Switkes, E. & De Valois, K. K. (1988). Orientation and spatial frequency selectivity of adaptation to color and luminance gratings. *Vision Research, 28,* 841–856.

Cavanagh, P. (1987). Reconstructing the third dimension: Interactions between color, texture, motion, binocular disparity and shape. *Computer Vision, Graphics and Image Processing, 37,* 171–195.

De Valois, K. K. & Switkes, E. (1983). Simultaneous masking interactions between chromatic and luminace gratings. *Journal of the Optical Society of America, 73,* 11–18.

Foley, J. M. & Boynton, G. M. (1992). Simultaneous pattern masking: Mechanisms are revealed by threshold versus masker contrast functions and the direct measurement of masking sensitivity. *Investigative Ophthalmology and Visual Science (Suppl.), 33,* 1256.

Foley, J. M. & Legge, G. E. (1981). Contrast detection and near-threshold discrimination in human vision. *Vision Research, 21,* 1041–1053.

Foley, J. M. & Yang, Y. (1991). Forward pattern masking: Effects of spatial frequency and contrast. *Journal of the Optical Society of America A, 8,* 2026–2037.

Gouras, P. (1974). Opponent color cells in different layers of foveal striate cortex. *Journal of Physiology, 238,* 583–607.

Granger, E. M. & Heurtley, J. C. (1973). Visual chromaticity-modulation transfer function. *Journal of the Optical Society of America, 63,* 1173–1174.

Henning, G. B., Hertz, B. G. & Broadbent, D. E. (1975). Some experiments bearing on the hypothesis that the visual system analyses spatial patterns in independent bands of spatial frequency. *Vision Research, 15,* 887–897.

Henning, G. B., Hertz, B. G. & Hinton, J. L. (1981). Effects of different hypothetical detection mechanisms on the shape of spatial frequency filters inferred from masking experiments—I. Noise masks. *Journal of the Optical Society of America, 71,* 574–581.

Hess, R. F. & Snowden, R. J. (1991). Temporal properties of human visual filters: Numbers, shapes and spatial covariation. *Vision Research, 32,* 47–59.

Humanski, R. A. & Wilson, H. R. (1992). Spatial frequency mechanisms with short-wavelength-sensitive cone inputs. *Vision Research, 32,* 549–560.

Kelly, D. H. (1983). Spatiotemporal variation of chromatic and achromatic contrast thresholds. *Journal of the Optical Society of America, 73,* 742–750.

Legge, G. E. (1978). Sustained and transient mechanisms in human vision: Temporal and spatial properties. *Vision Research, 18,* 69–81.

Legge, G. E. (1979). Spatial frequency masking in human vision: Binocular interactions. *Journal of the Optical Society of America, 69,* 838–847.

Legge, G. E. & Foley, J. M. (1980). Contrast masking in human vision. *Journal of the Optical Society of America, 70,* 1458–1471.

Lennie, P., Krauskopf, J. & Sclar, G. (1990). Chromatic mechanisms in striate cortex of Macaque. *Journal of Neuroscience, 10,* 649–669.

Livingstone, M. S. & Hubel, D. H. (1984). Anatomy and physiology of a color system in the primate visual cortex. *Journal of Neuroscience, 4,* 309–356.

Michael, C. R. (1978). Color vision mechanisms in monkey striate cortex: Dual-opponent cells with concentric receptive fields. *Journal of Neurophysiology, 41,* 572–588.

Moreland, J. D. (1982). Spectral sensitivity measured by motion photometry. *Documenta Ophthalmologica Proceedings Series, 33,* 61–66.

Mullen, K. T. (1985). The contrast sensitivity of human color vision to red–green and blue–yellow chromatic gratings. *Journal of Physiology, 359,* 381–409.

Mullen, K. T. & Boulton, J. C. (1992). Absence of smooth motion perception in color vision. *Vision Research, 32,* 483–488.

Nachmias, J. (1993). Masked detection of gratings: The standard model revisted. *Vision Research, 33,* 1359–1365.

Nachmias, J. & Sansbury, R. V. (1974). Grating contrast: Discrimination may be better than detection. *Vision Research, 14,* 1039–1042.

Pandey, R. & Vimal, R. L. P. (1993). Threshold elevation curves for the red–green channel estimated by oblique masking. *Investigative Ophthalmology and Visual Science (Suppl.), 34,* 751.

Patterson, R. D. & Moore, B. C. J. (1986). Auditory filters and excitation patterns as representations of frequency resolution. In Moore, B. C. J. (Ed.), *Frequency selectivity in hearing* (pp. 123–177). London: Academic Press.

Patterson, R. D. & Nimmo-Smith, I. (1980). Off-frequency listening and the auditory filter asymmetry. *Journal of the Acoustic Society of America, 67,* 229–241.

Pelli, D. G. (1980). Channel properties revealed by noise masking. *Investigative Ophthalmology and Visual Science (Suppl.), 19,* 44A.

Pelli, D. G. (1985). Uncertainty explains many aspects of visual contrast detection and discrimination. *Journal of the Optical Society of America A, 2,* 1508–1531.

Perkins, M. E. & Landy, M. S. (1991). Nonadditivity of masking by narrow-band noises. *Vision Research, 31,* 1053–1065.

Ross, J. & Speed, H. D. (1991). Contrast adaptation and contrast masking in human vision. *Proceedings of the Royal Society of London, 246,* 61–69.

Sachs, M. B., Nachmias, J. & Robson, J. C. (1971). Spatial frequency channels in human vision. *Journal of the Optical Society of America, 61,* 1176–1186.

Schade, O. H. (1958). On the quality of color-television images and the perception of color detail. *Journal of the Society of Motion Picture Television Engineers, 67,* 801–819.

Speed, H. D. & Ross, J. (1992). Spatial frequency tuning of facilitation by masks. *Vision Research, 32,* 1143–1148.

Stromeyer, C. F. & Julesz, B. (1972). Spatial frequency masking in vision: Critical bands and spread of masking. *Journal of the Optical Society of America, 62,* 1221–1232.

Stromeyer, C. F. & Klein, S. (1974). Spatial frequency channels in human vision as asymmetric (edge) mechanisms. *Vision Research, 14,* 1409–1420.

Stromeyer, C. F., Klein, S., Dawson, B. M. & Spillman, L. (1982). Low spatial-frequency channels in human vision: Adaptation and masking. *Vision Research, 22,* 225–233.

Switkes, E., Bradley, A. & De Valois, K. K. (1988). Contrast dependence and mechanisms of masking interactions among chromatic and luminance gratings. *Journal of the Optical Society of America A, 5,* 1149–1162.

Thorell, L. G., De Valois, R. L. & Albrecht, D. G. (1984). Spatial mapping of monkey V1 cells with pure color and luminance stimuli. *Vision Research, 24,* 751–769.

Van der Horst, G. J. C. & Bouman, M. A. (1969). Spatiotemporal chromaticity discrimination. *Journal of the Optical Society of America, 59,* 1482–1488.

Webster, M. A., De Valois, K. K. & Switkes, E. (1990). Orientation and spatial frequency discrimination for luminance and chromatic gratings. *Journal of the Optical Society of America A, 7,* 1034–1049.

Wilson, H. R., McFarlane, D. K. & Phillips, G. C. (1983). Spatial frequency tuning of orientation selective units estimated by oblique masking. *Vision Research, 23,* 873–882.

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