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Bipolar or rectified chromatic detection mechanisms?

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Abstract

It is widely accepted that human color vision is based on two types of cone-opponent mechanism, one differencing L and M cone types (loosely termed "red–green"), and the other differencing S with the L and M cones (loosely termed "blue–yellow"). The traditional view of the early processing of human color vision suggests that each of these cone-opponent mechanisms respond in a bipolar fashion to signal two opponent colors (red vs. green, blue vs. yellow). An alternative possibility is that each cone-opponent response, as well as the luminance response, is rectified, so producing separable signals for each pole (red, green, blue, yellow, light, and dark). In this study, we use psychophysical noise masking to determine whether the rectified model applies to detection by the postreceptoral mechanisms. We measured the contrast-detection thresholds of six test stimuli (red, green, blue, yellow, light, and dark), corresponding to the two poles of each of the three postreceptoral mechanisms. For each test, we determined whether noise presented to the cross pole had the same masking effect as noise presented to the same pole (e.g. comparing masking of luminance increments by luminance decrement noise (cross pole) and luminance increment noise (same pole)). To avoid stimulus cancellation, the test and mask were presented asynchronously in a "sandwich" arrangement (mask-test-mask). For the six test stimuli, we observed that noise masks presented to the cross pole did not raise the detection thresholds of the test, whereas noise presented to the same pole produced a substantial masking. This result suggests that each color signal (red, green, blue, and yellow) and luminance signal (light and dark) is subserved by a separable mechanism. We suggest that the cone-opponent and luminance mechanisms have similar physiological bases, since a functional separation of the processing of cone increments and cone decrements could underlie both the separation of the luminance system into ON and OFF pathways as well as the splitting of the cone-opponent mechanisms into separable color poles.

Keywords: Human color vision, Chromatic mechanisms, Contrast sensitivity

Introduction

Human daylight vision is subserved by three types of photoreceptor: the long (L), medium (M), and short (S) wavelength-sensitive cones. At a second, postreceptoral stage of processing, responses from the three cone types are combined to provide the basic mechanisms of color vision at the retinal, subcortical, and early cortical levels. It is widely accepted that three such postreceptoral mechanisms are manifest at the psychophysical level: a "*red–green*" mechanism that opposes L- and M-cone responses (L−M and M−L), a "*blue–yellow*" mechanism that opposes S-cone inputs with a combination of L- and M-cone responses (S–(L+M), (L+M)–S), and a "*luminance*" (achromatic) mechanism that sums L- and M-cone responses. These three psychophysical detection mechanisms have been extensively investigated using threshold summation and masking techniques, which show that they are based on the linear summation of cone inputs, followed by an independent, nonlinear combination to detection threshold (Kranda & King-Smith, 1979; Stromeyer et al., 1983; Noorlander et al., 1981; Cole et al., 1993; Sankeralli & Mullen, 1996; Giulianini & Eskew, 1998; Eskew et al., 1999 for a review).

In previous studies, each of the chromatic mechanisms is typically assumed to be bipolar. For example in Fig. 1, which shows the red–green cone-opponent and the luminance mechanism in a cone-contrast space, the red–green mechanism is represented as a vector passing through the origin of cone-contrast space, composed of both the +L−M (red) and +M−L (green) poles of the mechanism, and the same formulation applies to the blue–yellow mechanism. So far there has been little evidence to contradict this bipolar view of cone opponency. Differences in detection thresholds, or in cone weights supporting the "red" and "green" poles, could suggest the two poles of each cone-opponent process are separable or distinct. However, the foveal detection thresholds are identical in both the "red" and "green" directions, as are the "blue" and "yellow" thresholds, although there is some evidence to suggest that an asymmetry emerges in the red–green mechanism in the periphery (Stromeyer et al., 1992). Furthermore, the "red" and "green" threshold contours in cone-contrast space are parallel, indicating the same cone weights apply to each pole but with opposite sign (see references cited above). There is one psychophysical study, however, which suggests that chromatic adaptation is pole

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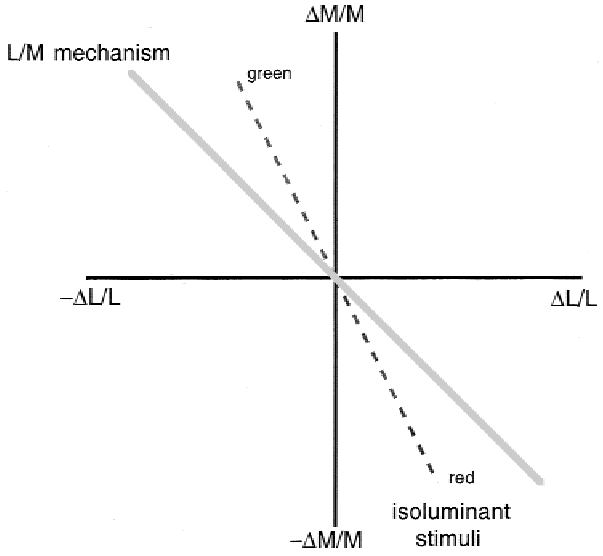

Fig. 1. The representation of the L/M cone-opponent mechanism (thick line) and the isoluminant chromatic stimuli (thin line) in the L,M plane of cone-contrast space. Note the L/M cone-opponent mechanism draws on L and M cones with equal weights but opposite sign. "Red" or "green" isoluminant Gaussian stimuli are used to isolate this mechanism, as sketched on the figure. The "green" cardinal stimulus increments M cones and decrements L cones of the opponent mechanism, whereas the "red" cardinal stimulus does the reverse. We test whether the "red" and "green" poles of this cone-opponent process can be considered as separable, or whether they are part of a single mechanism with a bipolar response to the "red" and "green" stimuli. We apply similar tests to the S cone-opponent and the luminance mechanisms.

specific; a red adaptive field raises thresholds for red tests, but not for green tests, supporting separability between cone-opponent poles (Krauskopf et al., 1982). Several earlier studies have also hinted at asymmetries of adaptation between the red and green poles (Walraven, 1977; Reeves, 1981, 1983).

There is much greater psychophysical evidence, however, to suggest that the luminance mechanism is represented as two separable poles, at least under some conditions. Several psychophysical studies using narrow-band masking or background adaptation techniques suggest that cone decrements and cone increments in the luminance system are encoded separately (DeValois, 1977; Krauskopf, 1980; Tyler et al., 1992; Bowen & Wilson, 1994; Chichilnisky & Wandell, 1996; Bowen, 1997; DeMarco et al., 2000). This psychophysical evidence is well supported by a large body of physiological data revealing anatomically distinct populations of neurons in mammalian vision responsive to luminance increments (ON cells) and decrements (OFF cells) (e.g. Kuffler, 1953; see Schiller et al., 1992, or Calkins, 1999 for reviews). A primate lesion study (Schiller, 1986) suggests that these pathways functionally separate the detection of light increments and decrements. It thus seems logical to extend this view of the luminance system to the cone-opponent systems, and to propose that cone increments and decrements within the cone-opponent mechanisms are also encoded separately. Psychophysically, this predicts that the two poles of each cone-opponent process are separable. For example, as Fig. 1 illustrates, changes in the "red" versus "green" cone-opponent directions are each coded by opposite pairs of cone increments and decrements.

The bipolar view of the chromatic mechanisms, however, remains part of the "textbook view" of color vision, which maintains that psychophysical postreceptoral mechanisms respond in a bipolar fashion to signal two opponent colors (e.g. Sekular & Blake, 1990; Kaiser & Boynton, 1996). Because these cone-opponent responses loosely resemble the perceptual phenomena collectively known as "color opponency" (e.g. Hurvich & Jameson, 1957), the textbook model directly links cone opponency to color opponency. It is assumed that color-opponent phenomena arise from the excitatory and inhibitory responses of chromatic neurons found early in the primate visual system (e.g. De Valois, 1960). At one time this was a reasonable suggestion, since many examples have been reported of spectrally opponent cells in the retina and lateral geniculate nucleus (LGN) that respond in a bipolar fashion, by excitation to one color and inhibition to another (De Valois et al., 1958, 1966; Wiesel & Hubel, 1966; Gouras, 1968; De Monasterio & Gouras, 1975; DeValois & DeValois, 1975). More recently, however, the bipolar model has been questioned for a number of reasons.

Firstly, color opponency (color appearance) cannot be predicted from the responses of the psychophysically isolated cone-opponent mechanisms. For instance, stimuli that isolate the L/M cone-opponent mechanism do not appear uniquely red or green, but pinkish and blue–green, and those that isolate the blue–yellow mechanism appear more purplish and lime-green than blue or yellow. Thus, the unique hues predicted by color opponency cannot directly arise from the responses of cone-opponent mechanisms, and these two should not be linked (see De Valois & De Valois 1993; De Valois et al., 1997; Eskew & Kortick, 1997). Secondly, our knowledge of the physiological chromatic mechanisms indicates that there are four different classes of red–green neuron at the subcortical stage, two responding to red (+L−M, −M+L) and two to green (+M−L, −L+M) (see references above, and Lennie & D'Zmura, 1988 for a review), thus potentially providing the building blocks for separable red and green mechanisms. Furthermore, given the loss in maintained neural discharge at the primate cortical level, it is thus neither practical nor necessary for the inhibitory response of any one neuron to signal a separate stimulus attribute. For these reasons, we consider a psychophysical model in which each postreceptoral mechanism consists of two separable pathways acting in a unipolar or rectified manner. In this "rectified" model, the response of each psychophysical cone-opponent mechanism signals only one color sensation, and the four different poles are each separable submechanisms. In this study, we test psychophysically for the "rectified" as opposed to the "bipolar" models of the cone-opponent mechanisms. We isolate each pole of each mechanism using cardinal stimuli, and use a noise-masking technique to test for their psychophysical separation. We use a standard signal-detection model of detection threshold (e.g. Barlow, 1956; Green & Swets, 1966; Burgess et al., 1981; Thomas, 1985; and Sankeralli & Mullen, 1997 as applied to cone-contrast space). The addition of noise raises the signal-to-noise ratio (threshold) of the neural pathways sensitive to the masking noise, reflected in a change in detection threshold for the test stimulus, providing these contribute to test detection. In our task, the detection threshold of a test stimulus that isolates one pole of a postreceptoral mechanism (e.g. red, +L −M) is measured in the presence of a noise mask isolating either the same pole (red, +L −M) or the opposite pole (green, +M −L) of the postreceptoral mechanism (see Fig. 1). If the two poles of a postreceptoral mechanism consist of separable pathways, stimulus noise of the opposite polarity as the test should have little masking effect on test detection. On the other hand, if the two poles are part of a common neural pathway, then noise of opposite polarity should have a masking effect comparable to noise of the same polarity as the test.

Methods

Stimuli and apparatus

Six test stimuli were used, corresponding to the four poles of the cone-opponent mechanisms (red, green, blue, and yellow) and the two poles of the luminance mechanism (light and dark). The test was presented at an optimal duration for detection: 17 ms for the luminance stimuli and 100 ms for the chromatic stimuli. To prevent the physical stimulus cancellation that occurs when a test and mask of opposite polarity are presented simultaneously, the mask in all conditions was displayed asynchronously with the test (Fig. 2). The mask was presented in 100-ms time intervals preceding and following the test stimulus, with blank interstimulus intervals of 50 ms inserted between the test and mask presentations. This "sandwich" arrangement was used to provide an effective masking of test stimulus by the noise mask without incurring physical cancellation of the test and mask stimuli. Because of the rapid sequence of the test and mask, the test appeared to the subject as being embedded within the noise mask.

The test stimulus was a horizontal bar 4-deg long and Gaussian enveloped vertically ($\sigma = 0.35$ deg). The noise mask consisted of one-dimensional (1D) (horizontally oriented) binary noise, generated by setting each screen raster line to a contrast relative to the background of zero or of some fixed value (termed the *peak mask contrast*). For chromatic masks, this binary noise was then spatially low-pass filtered (20-dB cutoff at 3 cycles/deg) to reduce artefacts arising from chromatic aberration (Flitcroft, 1989). Both the signal and the noise were confined by software windowing to a vertical 4-deg-wide strip along the central portion of the screen; the remainder of the screen was fixed at the background white (Fig. 2).

The stimulus was presented on a BARCO CCID 7651 RGB monitor (frame rate: 75 Hz, line rate: 60 kHz) driven by a Cambridge Research Systems VSG2/1 video controller interfaced with a Dell 333D computer. The VSG software permitted linearization of the video output to within a contrast error of 0.17 log units. The screen (11 deg $\times$ 11 deg) was fixed at a background luminance of 55 cd m^{-2} near equal energy white [CIE (0.28, 0.30)].

We use a color space (a cone-contrast space) that directly encodes the outputs of the three cone responses. This stimulus space, denoted by (L, M, and S), is defined as the incremental quantal catches of the three cone types to a given stimulus, normalized by the respective quantal catches to the fixed, white background. A stimulus in this space may also be represented in polar coordinates (R, θ, ϕ), where the distance R from the origin represents the stimulus contrast in cone-contrast units, and the two angular coordinates (θ, ϕ) represent the direction of a unit vector in the three-dimensional space. To define the chromaticity of our six test stimuli, we defined three fixed cardinal axes within this space (Derrington et al., 1984; Krauskopf et al., 1982). Each cardinal axis was chosen so as to isolate one of the postreceptoral mechanisms. From this determination, stimuli in the cardinal axes stimulated the (L, M, and S) cone responses in the ratios of 0:0:1 (blue/yellow), 1:1:1 (light/dark). For the red–green cardinal axis, an individual determination was obtained for each subject using a minimum motion paradigm (Mullen & Sankeralli, 1999). This was done in order to account for the intersubject variability in the L- and M-cone weights to the luminance mechanism (Stromeyer et al., 1997). This procedure yielded a red/green cardinal axis stimulating cone responses in ratios of (1:−2.78:−0.89) for subject MJS and DMD, and (1:−3.63:−1.32) for subject KTM. In a previous study, we showed that this selection indeed produces independent red–green, blue–yellow, and luminance cardinal stimuli that exhibit little mutual cross masking (Sankeralli & Mullen, 1997). Contrast is defined in cone-contrast units of the visual stimuli.

Procedure

In each trial, two stimulus trains were presented in random order; one containing the test, the other containing a blank interval in the place of the test. The subject was required to identify which presentation contained the test. To assist the subject, each train was preceded by a brief tone, and a small (2 minutes) fixation spot was continuously placed at the center of the screen. In addition, audio feedback was provided to inform the subject whether their response was correct or not. A staircase procedure was used, in which the test contrast was raised by 0.10 log units following an incorrect response, and lowered by 0.05 log units following two consecutive correct responses. The threshold value was evaluated as the mean of the last six reversals of the staircase. This value

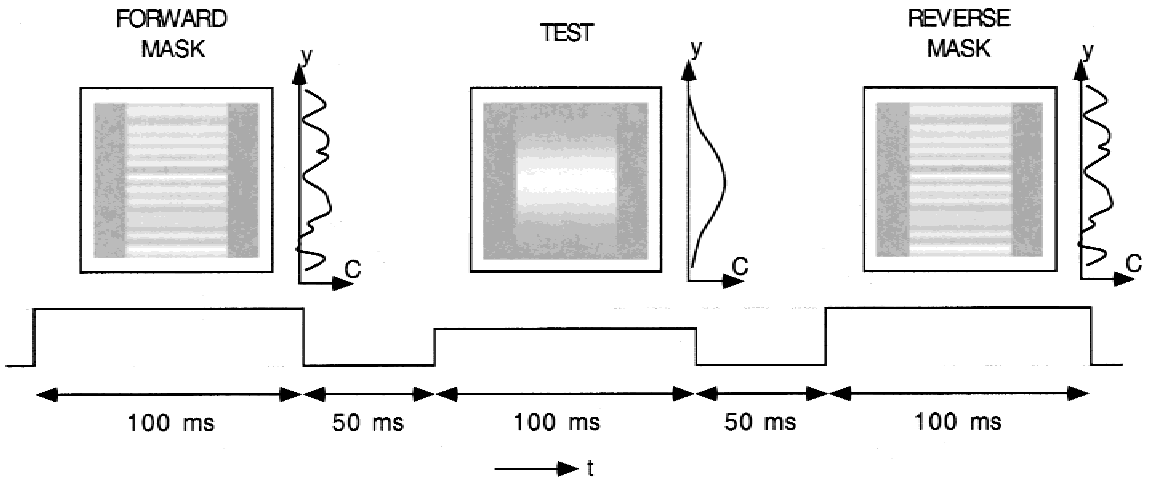

Fig. 2. Stimulus train for asynchronous noise masking. The duration of each noise mask was 100 ms and that of the test was 100 ms for red, green, blue, and yellow stimuli and 17 ms for light and dark stimuli. The intervals between the test interval and each noise mask were 50 ms.

estimated the 81.6% correct level for this task. Each threshold data point was obtained as the average of at least three such measurements. For each test stimulus, the test detection threshold was measured as a function of the contrast energy of the mask, for same-pole and cross-pole masks in turn. Three color-normal subjects (the two authors and one observer naive to the purpose of the experiment) performed the experiments.

Results

Masking functions

Fig. 3 shows the measured variation of test threshold with peak mask contrast for the six test stimuli. The axes are expressed in contrast-squared (*energy*) units. An energy representation is used as it predicts a linear variation of the measured function, given standard assumptions concerning detection mechanisms (Pelli, 1981). For convenience, positive mask energy is used to represent the same-pole mask condition (test and mask having the same polarity), and negative mask energy denotes cross-pole masking (test and mask having opposite polarities). The data for each masking condition for each subject were fitted by linear regression. The slope of this fit (shown on each panel) yields the masking effect of each type of mask. The ratio of these two slopes gives the relative magnitude of the masking effect in the same-pole condition to that in the cross-pole condition. A high ratio ($\gg 1$) indicates that the cross-pole masking effect is much lower than that for same-pole masking, in support of the rectified model of postreceptoral mechanisms. A low ratio (≈ 1) indicates that cross-pole masking has the same effect as same-pole masking, favoring the bipolar model. Our results yield a high masking-effect ratio for all six test conditions and for all three subjects (Table 1). We conclude that the two poles of each postreceptoral mechanism are each subserved by a distinct, rectified pathway.

We considered the possibility that our brief red, green, blue, and yellow flashes may contain sufficient artefacts to behave like luminance stimuli. For the red–green mechanism, it has been shown that temporal delays between the L- and M-cone projections to this mechanism may give rise to luminance artefacts (Stromeyer et al., 1997). To test for this, we measured the detection thresholds of the red, green, blue, and yellow tests in the presence of luminance noise of a contrast of up to twice that of the luminance noise mask used in the main experiment (i.e. up to 50% contrast). Such noise will have a strong masking effect on the luminance mechanism, and would therefore reduce the detectability of a nominally chromatic test stimulus if this stimulus were detected on the basis of luminance artefacts. Our results for both subjects tested (MJS and KTM) show that the introduction of luminance noise has no effect on detection of the red, green, blue, and yellow test stimuli, even for the highest noise-mask contrasts (Fig. 4). We therefore conclude that our chromatic stimuli are indeed being detected by the appropriate chromatic mechanism, and not on the basis of luminance artefacts.

Chromatic tuning functions

As a further demonstration of the asymmetric masking properties between the poles of each postreceptoral mechanism, we measured the chromatic masking function of each test stimulus. These functions act as signatures of the postreceptoral mechanisms, and reveal which postreceptoral mechanism is detecting a given stimulus (Gegenfurtner & Kiper, 1992; Sankeralli & Mullen, 1997). The tuning functions are obtained by measuring the detection threshold of the test as a function of the mask direction in color space (Fig. 5). If the test is being detected by a single postreceptoral mechanism, the tuning function takes the form of a pair of circular lobes, whose major axis points in the direction of the detecting mechanism in color space.

The tuning functions of the red and green test stimuli for subject MJS are shown in Fig. 5. These results are plotted in the cone-contrast plane containing the red/green and luminance axes (boxed letters). The arrow shows the test direction in cone-contrast space. The individual data points (diamonds) represent each threshold measurement of the test corresponding to each masking direction. The radial distance of the data point from the origin represents the test threshold in units of cone contrast, whereas the direction of the data point with respect to the origin represents the color-space direction of the mask. The orientation of the fitted masking function (dashed lines) yields the color-space direction corresponding to the postreceptoral mechanism detecting the test. For both stimuli, this axis is oriented along the L−M direction, which is the previously obtained direction corresponding to the red–green mechanism (Eskew et al., 1999). The separability of the red and green poles of this mechanism is observed in the asymmetry between the lobe sizes in each plot. For the red test stimulus, the lobe oriented in the L−M vector direction is larger, illustrating that noise stimulating the red pole of the red–green mechanism has a greater masking effect than noise affecting the green pole. The reverse is true for the green test stimulus. This result therefore demonstrates that, for the red and green tests, same-pole noise has a greater masking than cross-pole noise, indicating an inherent separability between the red and green poles. The result also confirms that the red and green tests are detected by an L−M red–green mechanism, and are not due to the presence of luminance artefacts.

Effect of interstimulus interval

Previous studies suggest that the small degree of cross-pole masking observed may arise as a result of the temporal response of individual detection mechanisms (Fiorentini et al., 1990). It is well known, for instance, that the OFF luminance mechanism responds to both the offset of a light stimulus and the onset of a dark

Table 1. *Same-/cross-pole masking ratios*[a]

	MJS	KTM	DMD
Red	20	35	14
Green	18	8.7	3
Blue	5.0	22	70
Yellow	11	5.7	4
Light	5.2	3.5	2.4
Dark	5.0	3.0	2.6
Average	**8.9**	**8.6**	**6.5**
Upper 69%	17	23	25
Lower 69%	4.7	3.2	1.7

[a]Results for the six test conditions and three subjects are shown. A ratio greater than one indicates that the cross-pole masking effect is smaller than the same-pole masking effect. The average (mean on a log scale) of the ratios is calculated for each subject, as is the 69% confidence interval (calculated from the standard deviations on a log scale). The results show that the same-/cross-pole masking ratios are significantly greater than one, in favour of a Rectified Model of postreceptoral mechanisms.

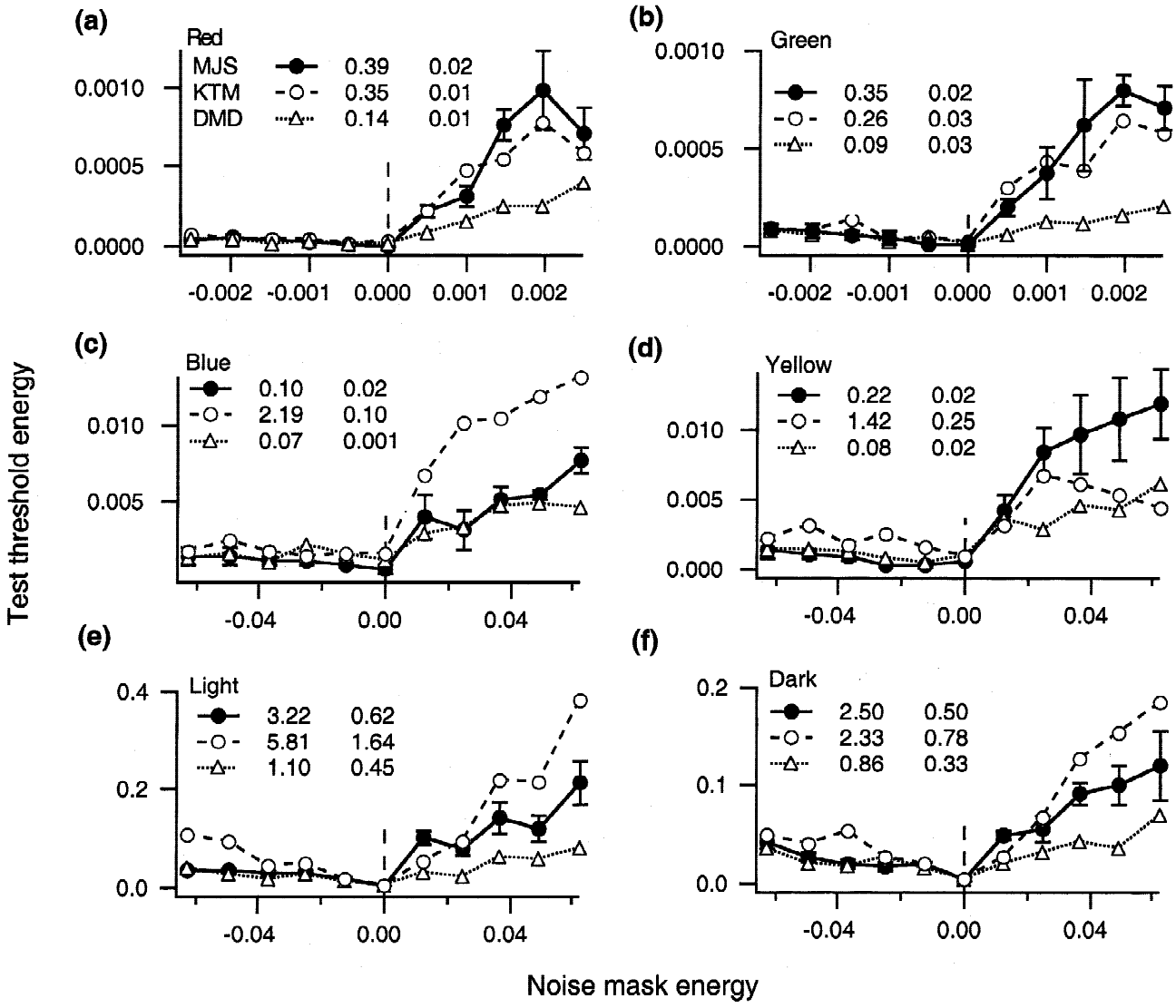

Fig. 3. Noise masking functions. Variations of signal threshold with peak noise mask contrast in energy (contrast squared) units are shown for the three subjects. Masking by noise of the same polarity as the same polarity is denoted by positive units, masking by the opposite polarity as negative units on the x-axis. The standard error for each data point is approximately 20% of the test threshold squared value, as shown for subject MJS. For the blue test for subject KTM, the signal threshold squared axis is scaled by a factor of 0.2. In each plot, the slope of the linear fit for noise masking by the same (left column) and opposite (right column) polarity as the test for each subject. These slopes show that same-pole masking is more effective than the corresponding opposite-pole masking, by a factor varying between 2.4 and 80 (see Table 1).

stimulus. Furthermore, at least for the luminance mechanism, there is a delayed, inverted neural response, such that the transient excitation to a bright flash in the ON pathway at flash onset is followed by a delayed secondary response in the OFF pathway even when the flash is sustained (Uchikawa & Yoshizawa, 1993; Bowen & Wilson, 1994; Metha & Mullen, 1996). For either of these reasons, a light test intended to stimulate only the light pole of the luminance mechanism may evoke a secondary response in the dark pole following a fixed delay. If this were the case, the same-/cross-masking ratios would depend critically on the time course of our test-mask presentations. To test for this, we measured same-/cross-pole masking ratio as a function of the duration of the blank period (the interstimulus interval, or ISI) before and after the test presentation. The results for both subjects and all six test stimuli are shown in Fig. 6. The horizontal axis represents the interstimulus interval between the test and each mask interval, whereas the vertical axis represents the ratio of the same- to cross-pole masking effect expressed in log units (zero therefore denotes that the same- and cross-pole masking effects are the same). The results show that, for the chromatic test stimuli, there is a gradual roll-off of the masking ratio, corresponding to a simultaneous reduction of same- and cross-pole masking as the test becomes increasingly distinguishable from the mask. Two features of the results are striking. Firstly, for the luminance tests, there is a distinct "dip" in the ratio, such that, at ISIs of approximately 100 ms, the effect of cross-pole masking may, in fact, be greater than that of same-pole masking. This finding is consistent with the measured impulse–response function of the luminance mechanism, which has a negative

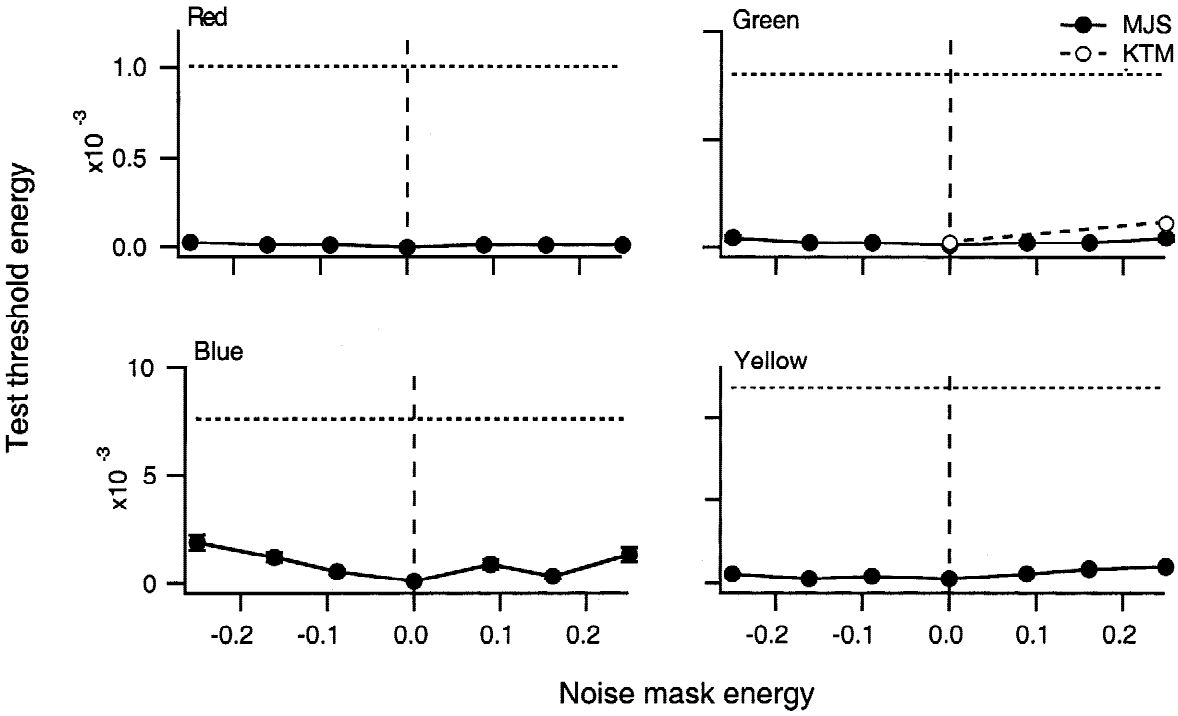

Fig. 4. Masking functions for red, green, blue, and yellow test stimuli in luminance noise. The horizontal axis represents the energy (peak contrast squared) of the luminance noise mask. Note that the maximum noise energy (0.25, corresponding to 50% peak luminance contrast) is five times higher than that used in the main experiment (Figs. 3e–3f). The vertical axis represents the test threshold energy (contrast squared), on the same scale as that in Figs. 3a–3d. The results show that even luminance noise masks of high energy do not produce the masking effects observed in Figs. 3a–3d. This demonstrates that the chromatic masking observed in Figs. 3a–3d was not the result of the presence of luminance artefacts in the chromatic noise masks.

lobe peaking between 80 and 100 ms following flash onset (Uchikawa & Yoshizawa, 1993). The second striking feature is of a definite decrease in the masking ratio for the chromatic stimuli at very short ISIs. This corresponds to a sharp rise in cross-polar masking, which may result from the linear addition of the test and mask stimuli in these mechanisms at brief ISIs.

Discussion

We demonstrate, using a cone selective cross-pole masking technique, that each pole of the two cone-opponent and one luminance postreceptoral mechanism is subserved by a separable submechanism, so yielding six separable psychophysical detection mechanisms (red, green, blue, yellow, light, and dark) rather than the three presently proposed in the literature. Our results have a number of implications, both for early processing in terms of ON and OFF pathways, and for the higher visual stage of color opponency.

Firstly, our results, showing a lack of masking between achromatic cone incremental (+L, +M, +S, and "light") and cone decremental (−L, −M, −S, and "dark") stimuli, provide further behavioral evidence for the separability of the ON and OFF processes in the luminance pathways, observed first from single-cell recordings (Hartline, 1938; Kuffler, 1953; Schiller, 1992; Calkins, 1999 for reviews). The range of psychophysical evidence supporting the separable processing of light increments and decrements is not yet comprehensive, but includes measurements of differential cone weights and adaptation effects for the detection of increments versus decrements (Chichilnisky & Wandell, 1996), and asymmetric masking or adaptation of achromatic increments and decrements (De Valois, 1977; Krauskopf, 1980; Bowen & Wilson, 1994; Bowen, 1997). Coupled with observed difference in spatial characteristics of increment and decrement processing (Whittle, 1986; Tyler et al., 1992), we conclude that luminance ON and OFF pathways are functionally segregated in human vision, at least under some conditions.

Secondly, our results suggest that a similar segregation exists between ON and OFF processes within the cone-opponent neurons of the chromatic pathways, functionally separating each pole of the cone-opponent process. We find that a +L −M ("red") mask fails to elevate threshold detection of a −L+M ("green") test stimulus (or *vice versa*), and that an +S–(L+M) ("blue") mask fails to elevate threshold detection of a −S+(L+M) ("yellow") test stimulus (or *vice versa*). This lack of cross-pole interaction suggests that the separation between the processing of cone incremental and decremental stimuli is also found in cone-opponent pathways, with masking only occurring when both cone type and sign are the same in both test and masking stimuli. Our results thus suggest that at some point in the visual system rectified L-cone center ON or M-cone center OFF neurons can potentially signal "red", with the reverse arrangement (rectified M-cone ON or L-cone center OFF neurons) signalling "green". They also point to the existence of similar rectified units processing increments and decrements within the S-cone opponent system. Separable processing of S-cone increments and decrements has also been reported using adaptation methods (McLellan & Eskew, 2000). It is not clear at what stage the two cone-opponent processes become functionally or behav-

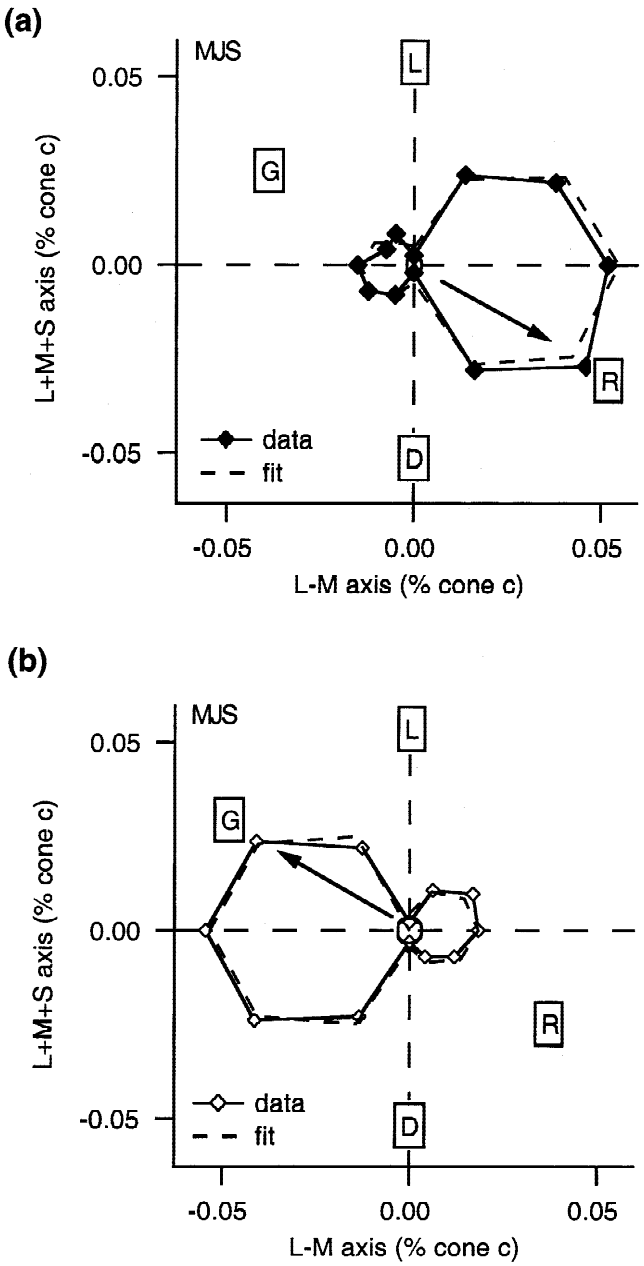

Fig. 5. Chromatic tuning functions for the red and green test stimuli. In the plane of cone-contrast space shown, the axes are defined by the L−M (horizontal axis) and L+M+S (vertical axis) directions. This plane isolates the red–green and luminance mechanisms: the blue–yellow mechanism direction lies perpendicular to the plane. The red [R], green [G], light [L], and dark [D] test stimulus directions are shown in the figure. Diamond symbols represent the test thresholds (distance from origin) as a function of the direction in color space of the noise mask (peak contrast = 0.1). The dotted circular lobes represent the fits of a Cosine Model: the lobe size shows the masking effect, the lobe direction reveals the direction in color space of the detecting mechanism. The figure shows that, for the red test (a), the detecting mechanism is in the L−M direction (major axis of larger lobe), corresponding to the L−M (red) pole of a red–green mechanism. For the green test (b), the detecting mechanism is in the M−L direction (green pole of a red–green mechanism). The smaller lobes reflect a limited degree of cross-pole masking. The figure confirms that both the red and green test stimuli are detected by red–green chromatic mechanisms, and not on the basis of luminance artefacts.

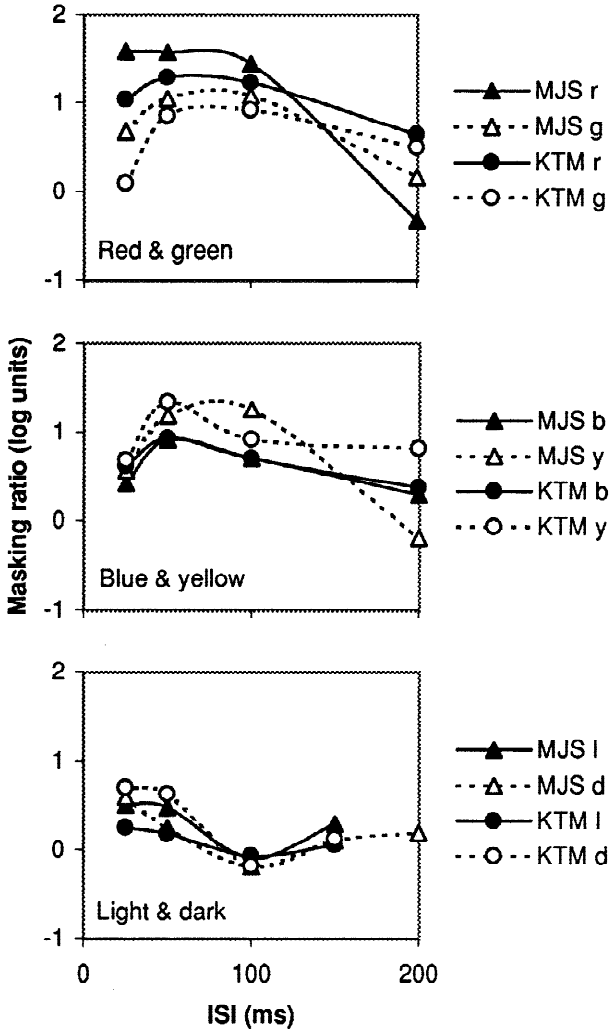

Fig. 6. Variation of same-/cross-pole noise masking ratio with ISI. The horizontal axis (ISI) represents the blank interval before and after each test presentation. The test and mask durations were the same as those in the main experiment, and the peak noise mask contrast was fixed at the maximum values used in the main experiment (5% red–green, 25% blue–yellow, and luminance). The vertical axis (expressed in log units) represents the ratio of the test threshold energy (contrast squared) in the same-pole condition to that in the cross-pole condition. A ratio of 0 log units indicates that the same- and cross-pole masking effects were equal. The figure shows that the noise-masking ratio depends on the ISI, with a relative maximum of cross-pole masking at 25 ms (red, green, blue, and yellow tests) and 100 ms (light and dark tests). This result suggests that the cross-pole masking observed in our experiments may arise from the temporal responses within each rectified subpathway.

iorally rectified. A retinal stage of rectification is possible since the presence of cone-selective ON and OFF neurons have been reported in both the red–green and the blue–yellow systems (Mariani, 1984; Schiller, 1992; Dacey & Lee, 1994; Calkins, 1999), but a cortical process could equally well be considered. A similar rectification process is proposed in the "multistage model" of color vision proposed by De Valois and De Valois (1993) and is placed at the complex cell level.

We find that the two opposing submechanisms of the red–green cone-opponent mechanism have close mirror symmetry between

the cone inputs. This is revealed by our measurements of the chromatic tuning functions in Fig. 5, which yield directly the cone weights to an isolated detecting mechanism. The measurements revealed that the red subpathway uses balanced inputs between L- (excitatory) and M- (inhibitory) cones, whereas the green pathway has balanced M- (excitatory) and L- (inhibitory) cones. This observed symmetry in cone weights between the poles demonstrates that, for much psychophysical work, it is practical to consider the red–green mechanism as a single unit with a bipolar response. This is assumed, for instance, in psychophysical tests using spatial or temporal sinewave-modulated stimuli. A further feature of the close association between opponent poles is the small measure of cross-pole masking observed both in our threshold-versus-contrast masking functions and in our chromatic tuning functions. Previous studies (e.g. Uchikawa & Yoshizawa, 1993) suggest that this may be the result of negative lobes (due perhaps to a neural undershoot) of the temporal responses of these subpathways. In this light, our observation of the dependence of the relative degree of cross-polar masking with temporal parameters is particularly revealing.

In our masking experiment, the temporal parameters of the mask presentation were chosen so as to preferentially and temporarily desensitize the mechanism detecting the test (Foley & Boynton, 1993), but not to cause long-term chromatic habituation, which has a much longer time course (e.g. Krauskopf et al., 1982). It is worth considering, however, whether the asymmetry observed between same- and cross-pole masking could be accounted for by some effect of the stimulus presentation. We consider two possibilities: temporal summation between test and mask components, and adaptation to the mask. In the case of temporal summation, the temporally asynchronous test and mask displays will reduce the task to one of test detection in the presence of a fixed pedestal: an incremental test in the case of same-pole masking (because the test is increased in the same direction as the mask) and a decremental test in the case of cross-pole masking (because the test is decreased in the opposite direction to the mask). Under such pedestal conditions (with a mask contrast up to between five and ten times that of the test), we would expect Weber's Law to prevail, and we would not expect to find, for any given background, the large asymmetry that we observed between detection of test stimulus increments (same-pole condition) and decrements (cross-pole condition). In the case of effective adaptation to the mask, the task can again be considered as a pedestal paradigm with sensitivity to the test stimulus reduced by the adapting background, but there is no *a priori* reason to suppose that the adaptation to a fixed background will differentially affect sensitivity to test stimulus increments (same-pole condition) and decrements (cross-pole condition). Thus, simple adaptation of a common mechanism could not account for the large observed asymmetry between the same- and cross-pole masking conditions. We therefore argue that the lack of masking in the cross-pole condition compared to the same-pole condition indicates the presence of separable mechanisms mediating detection of each pole.*

The notion of separability between the poles of the cone-opponent mechanisms (red–green and blue–yellow) significantly augments the prevailing understanding of the involvement of these mechanisms in the perceptual phenomena of color opponency. We emphasize, however, that the existence of separate submechanisms at the level of cone opponency does not conflict with perceptual color opponency. As mentioned in the Introduction, recent research supports the idea that the cone-opponent mechanisms mediating stimulus detection are not directly responsible for the phenomena of color opponency. Our results further strengthen this idea by showing that the poles of the cone-opponent processes are separable mechanisms, whereas the phenomena of color opponency represent perceptual interactions presumably arising from a higher order stage of perceptual opponency between individual cells or cell populations (De Valois & De Valois, 1993; De Valois et al., 1997). There is also evidence that our perception of opponent colors is not static, but may be supported by a dynamic opposition between separate "red" and "green" cell pools, exhibiting some form of hysteresis (Billock et al., 1997). Thus, our observation of psychophysically separable red and green, blue and yellow cone-opponent processes provides a useful step in the understanding of how perceptual color opponency is ultimately achieved.

*Our referees also suggested that under the bipolar model adaptation between mask and test stimulus there might be expected to produce an enhancement of test threshold (facilitation) in the cross-pole condition. However, our results show no evidence of any such facilitation, but rather a slight elevation of threshold.

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