



Motion Minima for Different Directions in Color Space

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We have used the minimum-motion stimulus of Cavanagh, MacLeod & Anstis [(1987) *Journal of the Optical Society of America A*, 4, 1428–1438] to examine how signals along different directions in color space interact in motion perception. Stimuli were pairs of counterphasing gratings combined 90 deg out of phase in both space and time and modulated along different color–luminance axes. The axis for one of the gratings was fixed, while the axis for the second was varied so as to null perceived motion in the stimulus. The motion nulls show that observers are sensitive to motion signals carried by each of the cardinal directions of color space [an achromatic axis and L–M and S–(L + M) chromatic axes], but that signals along different cardinal axes are not combined to yield a net direction of motion. Pairing an achromatic and chromatic grating resulted in a motion null regardless of the relative or overall contrast of the two gratings, while the null directions for intermediate axes shifted depending on contrast. This result points to the special status of the luminance and chromatic axes. However, our results do not reveal a special pair of axes within the equiluminant plane. When contrasts along the cardinal axes are scaled for equal multiples of their respective detection thresholds, the L–M and S chromatic contrasts contribute roughly equally to the perceived motion, but are many times weaker than luminance contrast. Moreover, sensitivity to luminance motion is little affected by the presence of chromatic contrast, whereas sensitivity to chromatic motion is strongly masked by either luminance or chromatic contrast. These asymmetric interactions suggest that the motion of the luminance and chromatic components is encoded in qualitatively different ways. © 1997 Elsevier Science Ltd.

Motion nulling Color Equiluminance Color–luminance interactions

INTRODUCTION

Motion perception is impaired when stimuli are defined only by chromatic contrast. Thus chromatic stimuli are poor at supporting apparent motion in random-dot kinematograms (Anstis, 1970; Ramachandran & Gregory, 1978), perceived velocity can be much slower for chromatic than for luminance gratings (Moreland, 1980; Cavanagh *et al.*, 1984; Teller & Lindsey, 1993), and drifting chromatic gratings may fail to give rise to smooth perceived motion (Mullen & Boulton, 1992). In stimuli with both luminance and chromatic contrast, perceived motion is strongly dominated by the luminance contrast (Carney *et al.*, 1987; Ramachandran, 1987; Kooi & De Valois, 1992). Such results are consistent with physiological evidence suggesting that motion and color are encoded by distinct, parallel subsystems, and that sensitivity to moving stimuli depends primarily on the magnocellular pathway, which exhibits only weak color

opponency (Zeki, 1978; Maunsell & Newsome, 1987; Livingstone & Hubel, 1988; Schiller *et al.*, 1990; Shapley, 1990; Merigan & Maunsell, 1993). Yet chromatic signals can clearly contribute to the perception of motion: motion aftereffects can be elicited by an equiluminant adapting stimulus (Wohlgemuth, 1911; Cavanagh & Favreau, 1985; Derrington & Badcock, 1985; Mullen & Baker, 1985), chromatic contrast can act as a strong linking cue for apparent motion (Gorea & Papathomas, 1989), and luminance motion can be nulled by chromatic motion in the opposite direction (Cavanagh & Anstis, 1991; Agonie & Gorea, 1993; Chichilnisky *et al.*, 1993).

In the present study we have examined the spectral sensitivities of motion mechanisms, by examining how signals along different directions in color space are integrated to yield a perceived direction of movement. We used a motion nulling task based on the minimum-motion stimulus that was developed by Anstis and Cavanagh (1983) and (in the form we used) by Cavanagh *et al.* (1987). Two counterphase gratings—neither of which has a net direction of motion on its own—can combine to form a drifting grating when they are added together 90 deg out of phase in both space and time (Stromeyer *et al.*, 1984). The minimum-motion paradigm

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allows one to examine the spectral sensitivities of the mechanisms underlying this integration, by examining the perceived direction of motion when the two counterphase gratings have different luminance and/or chromatic contrasts—or in other words, when they are defined by different directions in color–luminance space.

Anstis and Cavanagh (1983) and Cavanagh *et al.* (1987) originally devised the minimum-motion stimulus as a way of measuring the relative luminosities of two different colors. In their studies one of the counterphase gratings (the “pedestal”) varied only in luminance, while the second (the “test”) was heterochromatic (e.g. red–

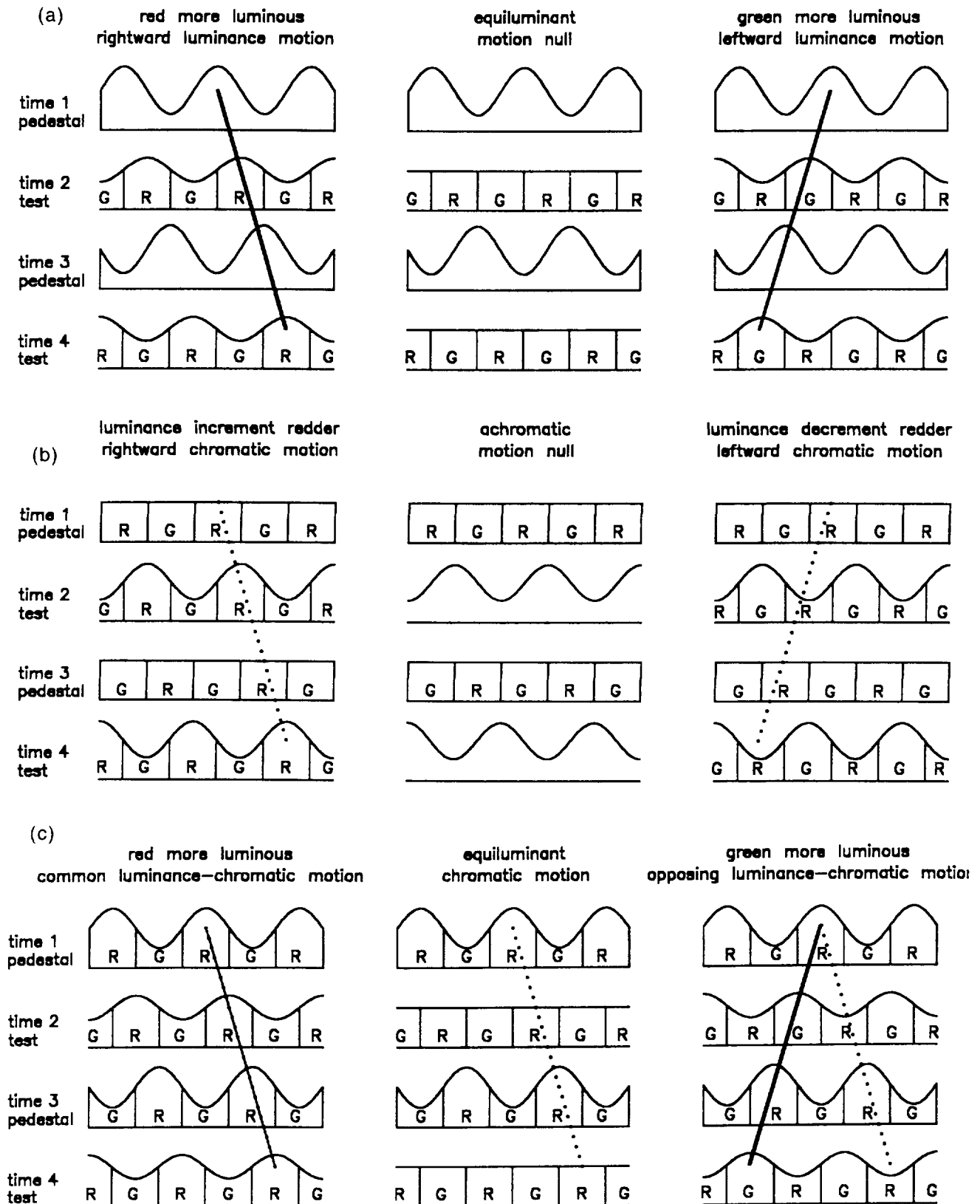


FIGURE 1. *Caption on facing page.*

green). If the two colors making up the test grating differed in luminance, then this luminance contrast would combine with the pedestal grating to generate a drifting luminance component [Fig. 1(a)]. The direction of motion would depend on which of the two colors had the higher luminance, and thus motion should be nulled when the two colors are equiluminant. An operational measure of equiluminance is thus the relative luminosities of the two colors at which motion is minimized in the stimulus (Anstis & Cavanagh, 1983; Cavanagh *et al.*, 1987).

Note that because the pedestal grating in their stimulus was always achromatic, only luminance contrast, and not chromatic contrast, could be common to the two gratings. Thus the stimulus conditions examined by Anstis and Cavanagh (1983) and Cavanagh *et al.* (1987) were designed to exclude chromatic motion. In the present study we generalized the minimum-motion technique by using a wide variety of pedestal gratings defined by different combinations of luminance and chromatic contrast, or different types of chromatic contrast. We then examined what combination of luminance and chromatic contrast in the test grating was required to null the motion. Stromeyer *et al.* (1990) and Webster and Mollon (1993) have shown previously that minimum-motion settings deviate from the equiluminant axis as chromatic contrast is added to the luminance pedestal grating. Here we systematically examine these deviations for different pedestal gratings. For example, Fig. 1(b) illustrates a case in which the luminance pedestal grating of Fig. 1(a) is replaced by a pure chromatic grating. In this case only chromatic contrast could be integrated across the two gratings to give rise to a net direction of motion, and the motion null should thus occur when the test grating has no chromatic contrast (i.e. when the test is a pure luminance grating). Observers can reliably set nulls for these pure chromatic pedestals, showing that chromatic contrast can alone support minimum-motion settings (Webster & Mollon, 1993; Stromeyer *et al.*, 1995).

Figure 1(c) illustrates a case in which the pedestal has both luminance and chromatic contrast. Consequently the stimulus could give rise to both luminance and chromatic motion. For certain combinations of pedestal and test

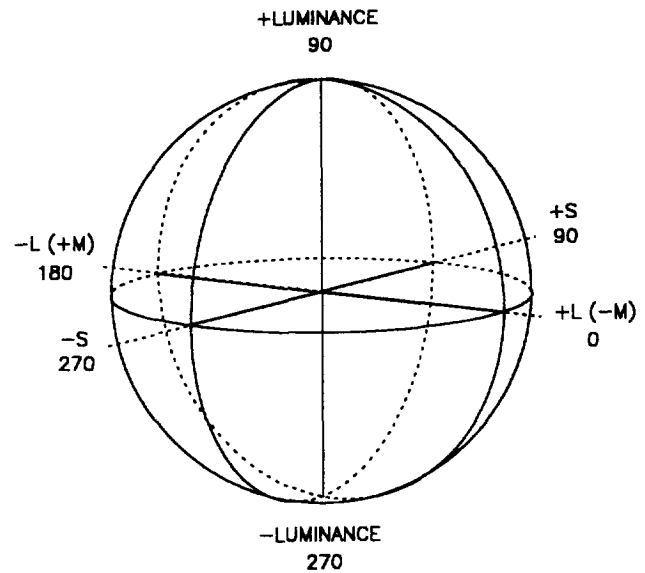


FIGURE 2. The luminance, L-M, and S color space used to specify the luminance-chromatic angles and contrasts of the stimuli [after MacLeod and Boynton (1979) and Derrington *et al.* (1984)].

contrasts, these luminance and chromatic components will drift in opposite directions. In Fig. 1(c) for example, if the pedestal is a bright-red/dark-green grating, while the test is a bright-green/dark-red grating, then chromatic (red-green) contrast will drift to the right while luminance (bright-dark) contrast will drift to the left. Opposing luminance and chromatic motion will occur whenever the correlations between luminance and chromaticity are of opposite sign in the test and pedestal gratings. Perceived motion due to luminance contrast can be nulled by chromatic contrast drifting in an opposite direction (Cavanagh & Anstis, 1991; Agonie & Gorea, 1993; Chichilnisky *et al.*, 1993), and thus in these cases the motion null should occur when the luminance and chromatic contrasts are equated such that their opposing motion signals are balanced.

The examples in Fig. 1 illustrate only a single plane within color-luminance space, but can be generalized to include any color-luminance direction by adding a second chromatic dimension, or alternatively, by directly

FIGURE 1. (a) An example of the minimum-motion stimulus of Cavanagh *et al.* (1987), shown at four successive time frames one quarter cycle apart. A counterphasing red-green test grating (with maximum contrast but opposite phase at times 2 and 4) is paired with a pure luminance pedestal grating that varies 90 deg out of phase with the test grating in both space and time (thus reaching maximum contrast but opposite phase at times 1 and 3). Luminance contrast in the test grating (shown by the sinusoidal envelope) can combine with the pedestal grating to generate a drifting luminance component, which moves to the right if the red component is more luminous but to the left if the green component is more luminous. Perceived motion is minimized when the red and green components are equiluminant. (Note that like the luminance contrast, the red-green spatial contrast in the test grating varies sinusoidally.) (b) Minimum-motion for a pure chromatic pedestal. In this example only chromatic contrast is common to the pedestal and test gratings. Motion based on chromatic contrast should be nulled when chromatic contrast is removed from the test grating (i.e. when the test is a pure luminance grating). (c) A pedestal with both luminance contrast and chromatic contrast could combine with a test grating to generate both luminance motion (solid line) and chromatic motion (dotted line). If luminance and chromatic contrast covary in the same way within the test and pedestal (e.g. both gratings are "bright-red" and "dark-green") then luminance and chromatic contrast will drift in the same direction (left column). If the test and pedestal instead combine luminance and chromatic contrast in opposite phases, then luminance and chromatic contrast will drift in opposite directions (right column). The motion null should therefore occur when the opposing luminance and chromatic motion signals are balanced.

representing the modulations within each of the three classes of cone. We defined our stimuli in terms of a three-dimensional color space whose principal axes corresponded to the achromatic axis (along which only luminance varies) and two equiluminant chromatic axes defined by: (a) signals in the long-wavelength cones opposed by signals in the medium-wavelength cones (L–M); or (b) signals in the short-wavelength cones opposed by a combination of signals in the long- and medium-wavelength cones [S–(L + M), which we abbreviate as S] (Fig. 2). Many properties of post-receptoral color vision appear to be organized in terms of these three “cardinal directions” (Le Grand, 1949; Krauskopf *et al.*, 1982; Derrington *et al.*, 1984; Mollon, 1989; Webster, 1996), and Krauskopf *et al.* (1996) have suggested that these dimensions might be central to the color organization underlying judgments of coherent motion in plaid stimuli. In the present experiments we sampled the motion nulls within each of the three planes defined by different pairs of cardinal axes. Specifically how the nulls vary as a function of the pedestal direction should in theory depend on such factors as the contrast sensitivity, spectral sensitivity, and number of mechanisms encoding the motion. We have therefore used these measurements in order to examine how the cone signals are organized within the pathways mediating minimum-motion judgments. A preliminary account of this work was given in Webster and Mollon (1992).

METHODS

Stimuli were displayed on a Sony monitor controlled by a Cambridge Research Systems graphics board (which allowed radiances on the monitor to be specified to an accuracy of 14 bits/gun). Luminances of the three guns were calibrated with a Minolta Chromameter, and linearized through look-up tables. Chromaticities (CIE, 1931) of the three guns were estimated with the Chromameter to be ($x = 0.616$, $y = 0.350$) for the red gun, ($x = 0.295$, $y = 0.588$) for the green gun, and ($x = 0.144$, $y = 0.056$) for the blue gun. Subjects (author MW and three trained observers) viewed the display monocularly with natural pupils from a distance of 1.5 m. Subjects had normal color vision and normal or corrected (observer SM) visual acuity.

Stimuli were presented in a 2-deg square field with a central fixation cross. Narrow black borders delimited the field from a surround (4.8-deg vertical \times 9.6-deg horizontal) of the same average luminance and chromaticity. The stimuli were horizontally oriented sinewaves with a spatial frequency of 1.5 c/deg, and were sinusoidally counterphased at 1 Hz. The pedestal grating had a fixed contrast and was presented in cosine phase with the fixation cross and the beginning of the trial. The test grating had a variable contrast and was modulated 90 deg out of phase with the pedestal in both space and time. On each trial the sign of the test contrast was randomly selected to be positive or negative, so that the perceived direction of motion would be uncorrelated with the color-luminance angle defining the test grating.

TABLE 1. Equations for converting times-threshold contrasts to MacLeod and Boynton (1979) r, b coordinates and Michelson luminance contrast

Observer MW	$r_{mb} = 0.000518(L-M)_{th} - 0.0000482S_{th} + 0.6568$ $b_{mb} = -0.0000090(L-M)_{th} + 0.000356S_{th} + 0.01825$ $LUM_m = 0.0065LUM_{th}$
Observer SM	$r_{mb} = 0.000855(L-M)_{th} - 0.0000733S_{th} + 0.6568$ $b_{mb} = -0.0000149(L-M)_{th} + 0.000542S_{th} + 0.01825$ $LUM_m = 0.0090LUM_{th}$

The two sets of equations are for the two principal observers. Angles for the L–M and S axes were defined empirically for one observer (MW) and differed slightly from the nominal r, b directions in the MacLeod–Boynton diagram (–1 vs 0 deg and 98 vs 90 deg).

During a trial the gratings were presented for 1 sec, with the parameters for the displayed composite grating recalculated on each frame (60 Hz).

All stimuli had the same average luminance (27.5 cd/m²) and chromaticity (equivalent to Illuminant C), but varied along different axes through this neutral point within the luminance, L–M, and S space of Fig. 2. The equiluminant plane was determined by the minimum-motion settings for an achromatic pedestal and test gratings with either L–M or S chromatic contrast. Initial estimates of these settings were used to calculate and correct for the relative luminosities of the three guns for each subject. Stimulus variations in our display that isolated variations along the S axis or along the L–M axis were empirically defined for one observer (MW), following the procedures described in Webster *et al.* (1990) and Webster and Mollon (1994). To equate contrast sensitivity along the three cardinal axes, for each observer the contrast thresholds were measured for detecting a single counterphasing grating lying along the luminance, L–M, or S axis. Contrasts along each axis were then scaled as multiples of the respective detection threshold. Table 1 gives equations for converting the two subjects' times-threshold L–M and S contrasts to the r, b coordinates of the MacLeod and Boynton (1979) chromaticity diagram and for converting times-threshold luminance contrast to Michelson luminance contrast.

Motion nulls were measured for a range of different pedestal directions within the three planes that isolated pairs of cardinal axes (i.e. the luminance vs L–M, the luminance vs S, and the L–M vs S planes). On a single run, the angle defining the pedestal grating remained fixed, while the angle defining the test grating was initially selected at random and then varied in four randomly interleaved staircases (10–12 reversals each), with the observer required to respond after each trial whether the direction of motion was up or down. Step size in the staircases was initially 16 deg and was then reduced to 2 or 8 deg (for pedestals on or near the equiluminant axis). These step sizes were based on pilot measurements of the psychometric functions for the motion nulls for different pedestal directions, though very similar results were obtained in additional runs using a constant step size. The angle at which minimum-motion

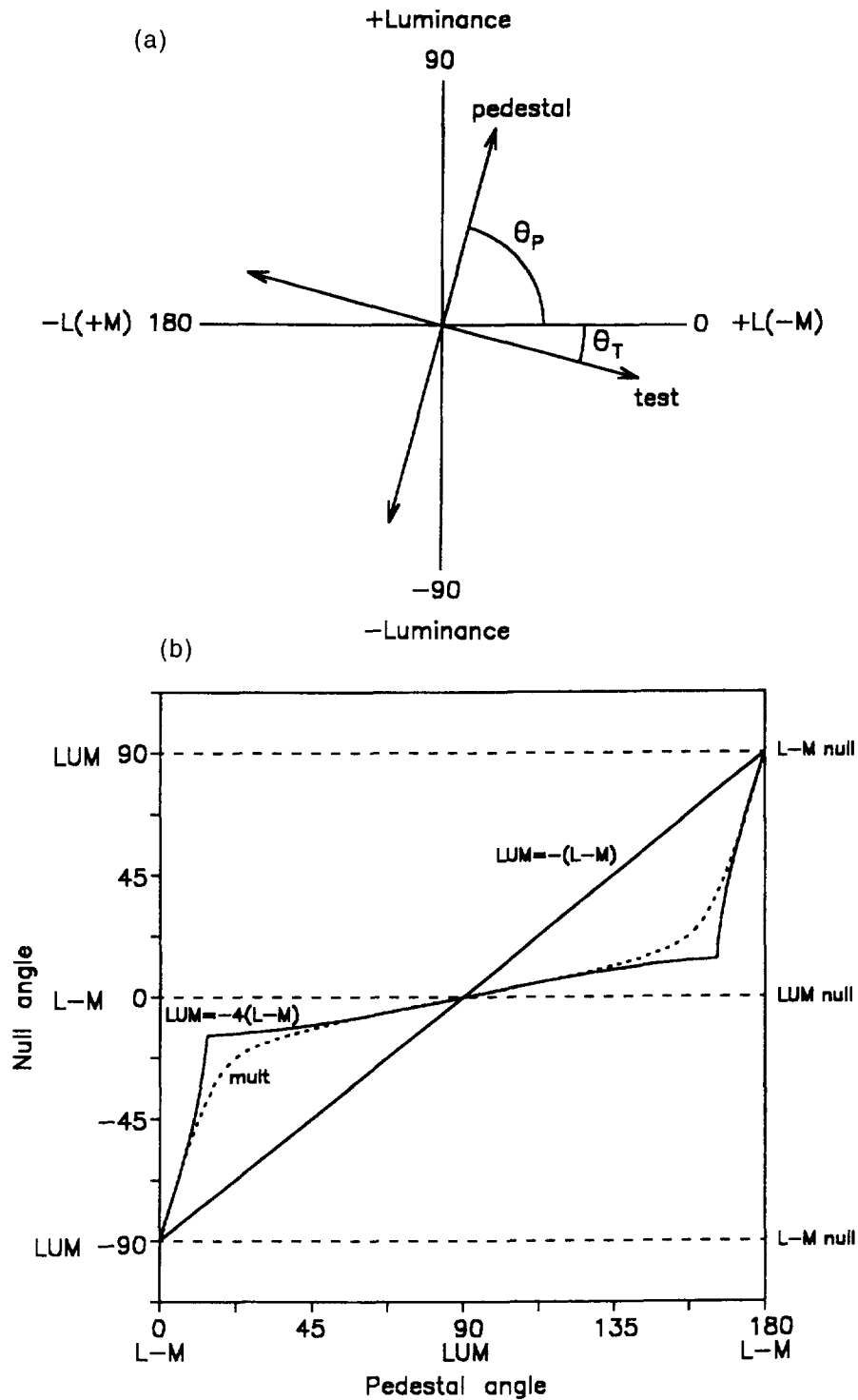


FIGURE 3. Motion nulls predicted for different pedestal and test directions within the luminance vs L-M plane. (a) Shows an example of pedestal and test gratings that vary along axes at angles θ_P and θ_T , respectively. (b) Plots, as a function of pedestal angle, the angle of the test grating at which motion reverses for one or two mechanisms or for a continuum of mechanisms. Dashed lines are predicted nulls for a single mechanism sensitive only to luminance contrast (null angle = 0) or L-M contrast (null angle = ± 90). Solid diagonal line represents the nulls based on luminance and L-M mechanisms with equal sensitivity. In this case the nulls always occurs when θ_P and θ_T are 90 deg apart. Reducing sensitivity of the L-M mechanism biases the nulls toward the L-M axis (as shown by the solid line for the case in which luminance contrast is four times stronger than L-M contrast). Dotted line shows predictions for a continuum of mechanisms whose sensitivity envelope forms an ellipse within the plane. With equal luminance and L-M sensitivities the predicted nulls again fall along the diagonal.

occurred was estimated both from the average of the last eight to ten reversals in the staircases, and from probit fits (Finney, 1971) to the accumulated responses at the different levels visited by the staircases. The two

alternative estimates were very similar, and only the latter are reported. Between two and four runs were made for each pedestal angle, with the order of the angles roughly counterbalanced across sessions.

In a second set of experiments we examined how sensitivity to motion in stimuli defined by the three cardinal axes was affected by the counterphase flickering components that are present in the minimum-motion stimulus (Stromeyer *et al.*, 1984; Cavanagh *et al.*, 1987). A luminance pedestal was combined with a test grating of fixed chromatic contrast, and luminance contrast was then varied in the test grating to estimate the motion null, again by four randomly interleaved staircases. The resulting psychometric functions were used to compare how the precision of luminance minimum-motion nulls depended on the magnitude of the chromatic contrast in the test grating. In the converse case, minimum-motion settings for chromatic pedestals were measured for test gratings that had different magnitudes of counterphasing luminance contrast. We then measured contrast thresholds for discriminating the direction of motion of a drifting luminance or chromatic grating in the presence of a luminance or chromatic counterphasing grating. The drifting test grating was randomly presented in phase with either the upward or downward component of a fixed contrast, counterphase pedestal, and test contrast was varied to estimate the discrimination threshold using a QUEST routine (Watson & Pelli, 1983). For these measurements the gratings were ramped on and off with 200 msec cosine ramps and 1 sec plateau, and feedback was given for incorrect responses.

RESULTS AND DISCUSSION

Our experiments are designed to examine three general questions about the influence of color on minimum-motion judgments. First, we explore the color organization underlying the motion nulls by measuring the nulling directions for a wide range of pedestal directions within the three planes defined by different pairs of cardinal axes. The resulting nulls strongly constrain the color organization, but as we show, do not define a unique organization or privileged set of axes. Second, we test whether some color–luminance directions do have a special status by examining how the motion nulls depend on the relative contrasts of the test and pedestal gratings. The results suggest that only the nulls for the achromatic and equiluminant axes remain unaffected by the contrast

changes, implying that these directions are important in the color organization. In the third set of experiments, we ask whether observers can detect the motion signals carried by luminance and chromatic contrasts independently, or whether these stimuli—which we show are not combined to yield a perceived direction of motion—interact to influence sensitivity. Our results reveal strong and asymmetric interactions which suggest that the processes underlying detection of luminance and chromatic motion are qualitatively different.

Motion-minima for Different Color–Luminance Directions

Predicted nulls

As a benchmark for interpreting the observed motion nulls, we compare them to the nulls that would be predicted by a linear combination of the motion signals carried by one or more motion-sensitive mechanisms that have different spectral sensitivities. This analysis is not intended as a formal model of minimum-motion judgments, and we show several ways in which our data depart from its predictions. However, the model provides a useful tool for assessing how the pattern of motion nulls could be affected by different organizations of the cone signals, and is a simple generalization of the single luminance-sensitive mechanism (that is typically assumed to underlie conventional minimum-motion settings) to the case of one or more mechanisms with arbitrary spectral sensitivities. For this analysis we assume that each mechanism draws on a linear combination of the cone signals, and we do not distinguish between separate mechanisms versus separate inputs to a single mechanism.

Figure 3 illustrates the pattern of nulls predicted for pedestal and test gratings defined by different angles within the luminance and L–M plane. The angle of the test grating (θ_T) at which the direction of motion reverses is plotted as a function of the angle of the pedestal grating (θ_P). The luminance and chromatic motion inherent in the minimum-motion stimulus can be seen by rearranging the terms for luminance and chromatic contrast in the counterphasing test and pedestal as follows (Cavanagh *et al.*, 1987):

$$\begin{aligned}
 & m_{P_l} \cos(2\pi f_x x) \cos(2\pi f_t t) + m_{T_l} \sin(2\pi f_x x) \sin(2\pi f_t t) + \\
 & \quad \text{pedestal luminance counterphase} + \text{test luminance counterphase} \\
 & m_{P_c} \cos(2\pi f_x x) \cos(2\pi f_t t) + m_{T_c} \sin(2\pi f_x x) \sin(2\pi f_t t) \\
 & \quad \text{pedestal chromatic counterphase} + \text{test chromatic counterphase} \\
 & = \\
 & [(m_{P_l} - m_{T_l})/2] \cos[2\pi(f_x x + f_t t)] + [(m_{P_l} + m_{T_l})/2] \cos[2\pi(f_x x - f_t t)] + \\
 & \quad \text{leftward luminance motion} \quad \text{rightward luminance motion} \\
 & [(m_{P_c} - m_{T_c})/2] \cos[2\pi(f_x x + f_t t)] + [(m_{P_c} + m_{T_c})/2] \cos[2\pi(f_x x - f_t t)]. \\
 & \quad \text{leftward chromatic motion} \quad \text{rightward chromatic motion}
 \end{aligned} \tag{1}$$

where f_x and f_t are the spatial and temporal frequencies of the gratings, and the m s are the contrasts of the luminance or chromatic components of each counterphase grating (expressed relative to the mean luminance and chromaticity of the stimulus). As this expression shows, the counterphasing luminance pedestal in Fig. 1(a) is equivalent to two identical luminance gratings drifting in opposite directions. Luminance contrast in the test grating adds to one of these directional components and subtracts from the other, inducing a net bias to the right or left depending on the sign of the contrast. The net luminance motion has a contrast equal to the counterphase grating with the lower luminance contrast, while excess luminance contrast in the second counterphase grating remains as residual flicker (Stromeyer *et al.*, 1984). A similar equivalence applies to chromatic motion in the stimulus (or to the signals along any arbitrary direction within color–luminance space).

Single mechanism. Suppose that the motion nulls depended on only a single mechanism that detected the net direction of the luminance contrast. This luminance-sensitive mechanism would signal net motion whenever both the test and the pedestal contained luminance contrast, but would be nulled whenever the test grating or pedestal grating was equiluminant. Thus for all pedestal angles the nulls in Fig. 3(b) should fall along the 0-deg (equiluminant) axis, and a unique null would not exist if the pedestal were itself equiluminant. Similarly, a mechanism that detected motion only of the L–M chromatic contrast would be nulled only when either or both gratings were achromatic, so that in Fig. 3(b) the nulls would always fall along the 90-deg axis. More generally, for any single mechanism that linearly combines the cone signals, sensitivity will vary as the cosine of its preferred direction (θ_{pref}) within the plane of Fig. 3(a); and there will be a single axis orthogonal to θ_{pref} to which the mechanism is insensitive and along which the test or pedestal grating would have to vary to null its net motion signal (unless the spectral sensitivity is such that the channel does not respond to any direction within the plane) (Derrington *et al.*, 1984). Thus we assume that the net motion response of any single mechanism is given by:

$$r_i = f[(m_{\text{Pi}} + m_{\text{Ti}}) - (m_{\text{Pi}} - m_{\text{Ti}})]/2.$$

where

$$m_{\text{Pi}} = \alpha_i c_{\text{P}} \cos(\theta_{\text{P}} - \theta_{\text{pref}})$$

and

$$m_{\text{Ti}} = \alpha_i c_{\text{T}} \cos(\theta_{\text{T}} - \theta_{\text{pref}}).$$

The term α_i represents the contrast sensitivity of the mechanism, while c_{P} and c_{T} are the times-threshold contrasts of the pedestal and test gratings, respectively. $f\{\}$ represents a monotonically increasing function of net motion contrast.

Note that a luminance-sensitive mechanism is the only single such mechanism that is consistent with the minimum-motion measurements of Cavanagh *et al.* (1987). That is, it is the only linear cone combination

that would predict motion nulls at equiluminance for their achromatic pedestal. However, Stromeyer *et al.* (1990), but vary depending on the luminance and chromatic contrast in the pedestal. Their results suggest that observers are sensitive to the motion of both the luminance and chromatic components of the stimulus. Moreover, as we noted in the Introduction, it is well established that chromatic contrast can support motion. Together these facts rule out the possibility that motion is carried by only a single spectrally selective mechanism, as verified empirically by Chichilnisky *et al.* (1993).

Two mechanisms. The solid diagonal line in Fig. 3(b) illustrates the settings that would be predicted if the nulls depended on the net response in two mechanisms with equal sensitivity, one signalling luminance motion (r_l) and the second signalling chromatic motion (r_c). Since we assume for this illustration that the responses of the two mechanisms simply add to determine the perceived direction of motion, for each pedestal angle θ_{P} , the null occurs for the test angle θ_{T} at which $r_l = -r_c$. Note that in this case a motion null could arise in one of two ways. If the pedestal is achromatic and the test is equiluminant (or vice versa) the nulls occur because each mechanism detects only one of the gratings, and thus there is no net motion *within* either mechanism. However, for all other pedestal-test combinations the nulls occur because the two gratings give rise to equal but opposite motion signals, so that there is no net motion *across* the two mechanisms.

The specific null angles predicted for two mechanisms could depend on a number of factors, such as the relative sensitivities of the mechanisms. For example, the “bent” line in Fig. 3(b) shows the nulls predicted if the response in the luminance mechanism is four times stronger than the response in the chromatic mechanism. This would have the effect of biasing toward the axis of lower sensitivity all null angles that reflect opposing motion, but would not affect the nulls at 0 or 90 deg, which instead reflect an absence of motion within either mechanism. The predictions are independent of the specific form of the contrast response function $[f\{\}]$ as long as it is the same within a scale factor for different mechanisms. However, the predicted pattern of nulls could change if, for example, the contrast response functions do differ for the different mechanisms or if there are interactions between the mechanisms. We show that the observed results are in fact inconsistent with linear summation in independent mechanisms that we assume for illustration here, and argue from our results that responses to luminance and chromatic motion are qualitatively different. However, we do not attempt to model this feature of our results, which could arise from a large number of factors.

A set of nulls defined by the diagonal line of Fig. 3(b) would strongly constrain the possible spectral sensitivities of the mechanisms encoding the motion. The only sets of mechanisms consistent with these nulls are those that preserve the orthogonality of the axes. As a counterexample, suppose the preferred directions of the

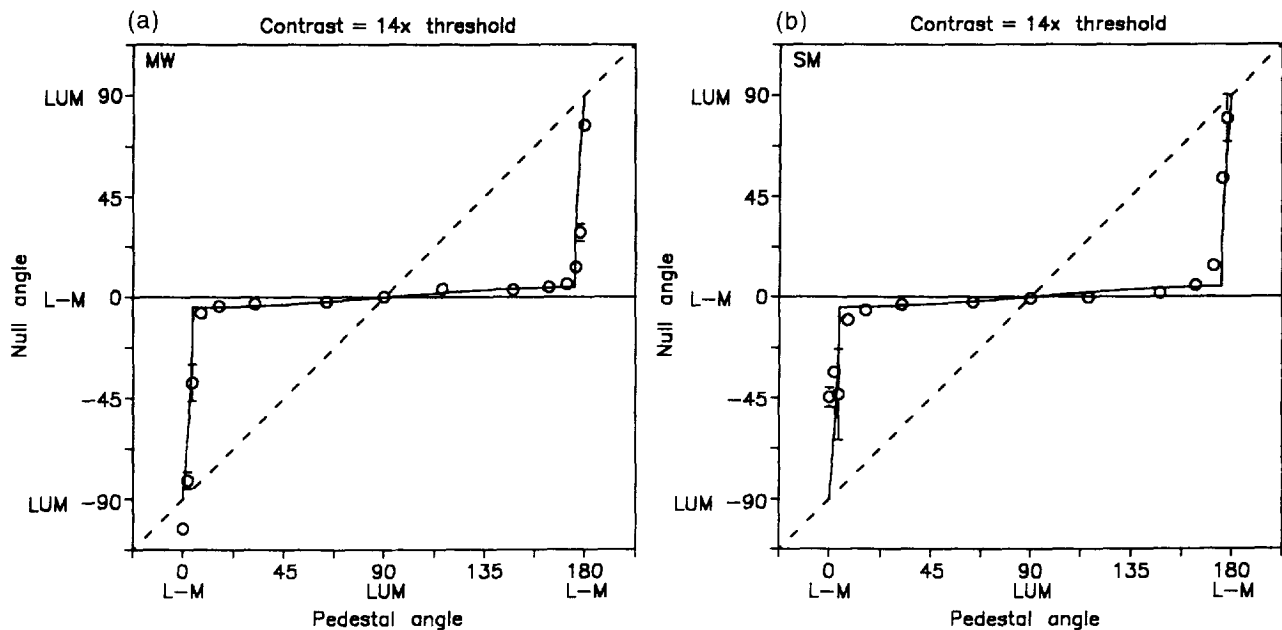


FIGURE 4. Motion nulls for 14 \times -threshold pedestal and test gratings within the luminance and L-M chromatic plane. Symbols plot the angle of the test grating (± 1 SEM) at which the perceived direction of motion reverses for different pedestal angles. The two figures show the motion nulls for two observers (MW and SM). Solid line shows the nulls predicted by the sum of independent responses in mechanisms sensitive to luminance and L-M contrast. The best fits were obtained when the response to luminance contrast was 12.8 (MW) to 14.1 (SM) times stronger than L-M contrast.

two mechanisms were at 90 and 135 deg within the plane of Fig. 3(a). The set of nulls would have to pass through the pair of directions that isolate each mechanism (0 and 45 deg) and thus would not fall along the diagonal. We show below that this provides a test for discriminating between alternative models of the chromatic channels.

While the nulls constrain the set of possible mechanisms, they do not define a unique set of mechanisms. For example, the nulls defined by the diagonal line in Fig. 3(b) are consistent with any pair of mechanisms that have equal sensitivity and whose preferred directions differ by 90 deg. Thus the null directions measured for a fixed stimulus contrast do not distinguish between many alternative spectral sensitivities, because they do not distinguish between motion minima based on nulls within either mechanism (which are tied to the mechanisms' tuning functions) vs nulls from opposing responses across the two mechanisms. However, in the second set of experiments we show that these two alternative bases for the nulls may be affected in different ways by changing stimulus contrasts, and we can thus test for preferred stimulus directions by examining the nulls for a wide range of test and pedestal contrasts.

Three or more mechanisms. Finally, motion within the luminance and L-M plane of Fig. 3(a) might plausibly be encoded by more than two mechanisms that are tuned to different combinations of luminance and chromatic contrast, or to different chromatic axes. The predicted nulls for multiple mechanisms can be calculated by generalizing the case for two mechanisms above to include additional mechanisms with arbitrary θ_{pref} , with the direction of motion again given by the sum of responses across mechanisms. As an extreme example,

the dotted curve in Fig. 3(b) illustrates the nulls that would be predicted by a uniform distribution of spectral mechanisms, each tuned to a different direction in the luminance and L-M plane (but with a bias in sensitivity along the luminance axis). The addition of many mechanisms has only a subtle effect on these predictions, by smoothing out the discontinuities in the nulls that arise from assuming only two discrete mechanisms with different sensitivities. And if the mechanisms all have equal sensitivity, then the nulls again fall along the diagonal, and thus are indistinguishable from the predictions for only two mechanisms. Thus the nulls at a fixed contrast do not uniquely define the number of mechanisms or their spectral sensitivities, though they again strongly constrain the set of possible color organizations [for example, for the nulls of Fig. 3(b), to those that again are consistent with the orthogonality of the axes]. However, if the two stimulus dimensions (luminance and L-M) are encoded by more than two mechanisms, then there will always be some mechanisms that detect both gratings and thus signal motion. The nulls for any plane encoded by more than two mechanisms must therefore always reflect the balanced motion signals across mechanisms, and never a null within all mechanisms. If in the extreme the plane is represented by a uniform distribution of mechanisms, then there are no preferred directions within the plane, and we show in the second set of experiments that this predicts a pattern of nulls which differs from the nulls predicted by two discrete mechanisms.

Observed nulls

Figure 4 shows actual measurements of the color-

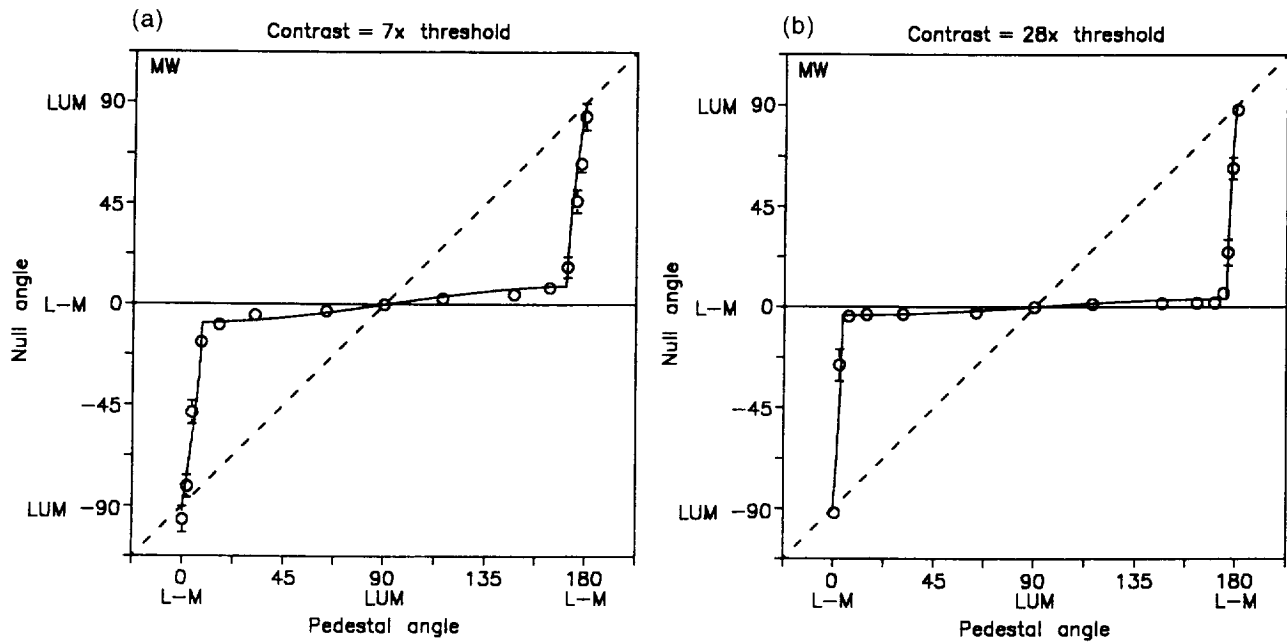


FIGURE 5. Motion nulls for gratings within the luminance and L-M plane that had contrasts of $7\times$ threshold (a) or $28\times$ threshold (b). Circles plot the observed null angles (± 1 SEM). Solid lines plot the predicted nulls based on independent luminance and chromatic mechanisms. Luminance contrast was estimated to be 8.4 times stronger than L-M contrast at $7\times$ threshold (a) while 15.9 times stronger at $28\times$ threshold (b).

luminance angles at which motion is nulled for pairs of gratings within the luminance and L-M plane. In these measurements the test and pedestal gratings had a fixed contrast of $14\times$ threshold. The two panels plot the results for two different observers. Very similar results were obtained for a third observer in each of the three planes examined.

Within the luminance and L-M plane the test angle required to minimize perceived motion varies system-

atically with the pedestal angle, suggesting that both the luminance contrast and the chromatic contrast in the gratings contribute to the perceived motion (Stromeyer *et al.*, 1990, 1995; Webster & Mollon, 1993). When the pedestal grating contained both luminance and chromatic contrast, the motion null occurred when the test grating also included both luminance and chromatic contrast but combined in opposite phase, consistent with a null that reflects balanced opposing responses to the luminance

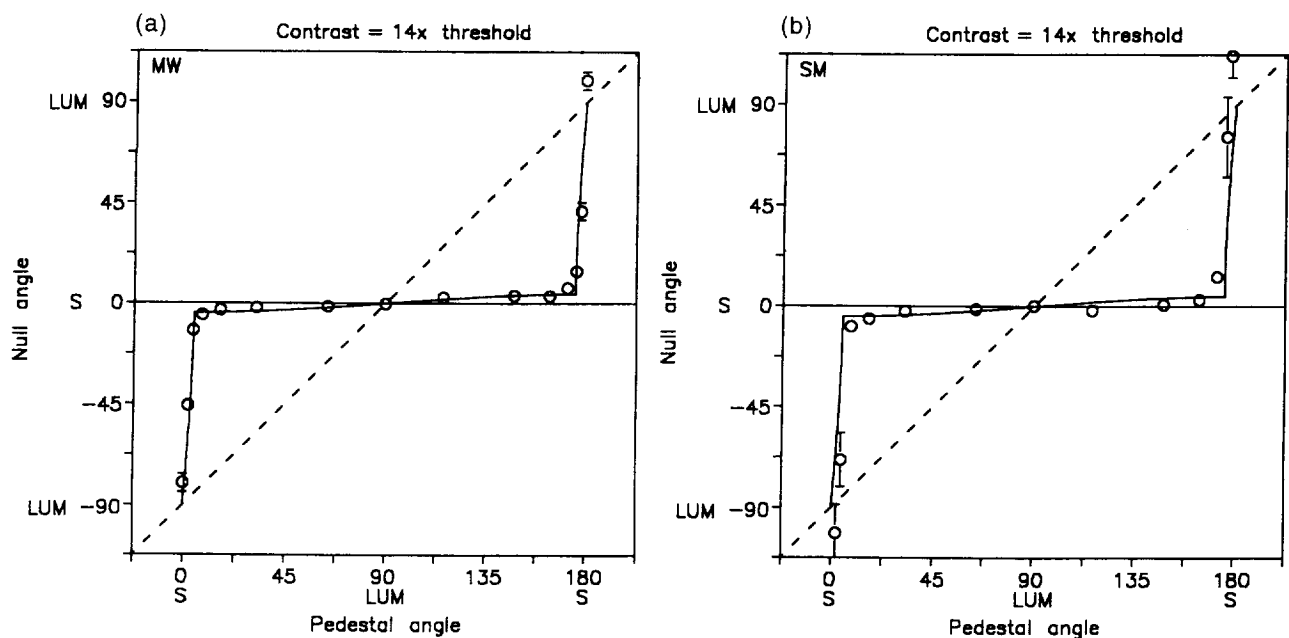


FIGURE 6. Motion nulls for gratings of $14\times$ threshold within the luminance and S chromatic plane, shown for two observers. Circles plot the observed nulls (± 1 SEM) based on the threshold scaling of luminance and S chromatic contrast. Solid lines plot the model fit, as in Fig. 4, but for two mechanisms encoding the luminance or S contrasts. Luminance contrast was estimated to be 15.0 (MW) to 11.9 (SM) times stronger than S contrast.

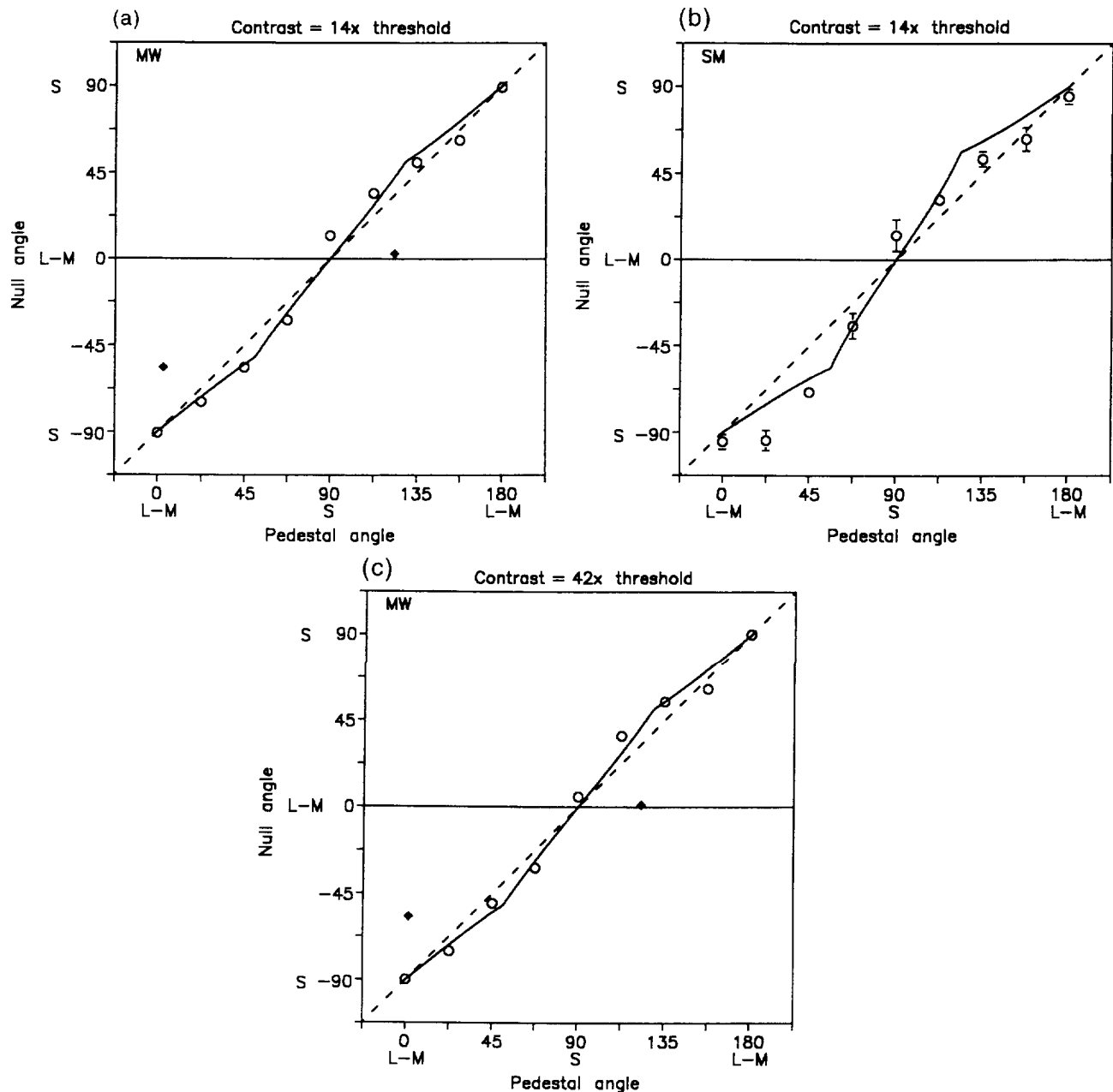


FIGURE 7. Motion nulls for gratings within the equiluminant L-M and S plane, for two observers. Circles plot the observed nulls (± 1 SEM) based on the threshold scaling of L-M and S chromatic contrast. Solid lines plot the model fit, as in Fig. 4, but for two mechanisms encoding the L-M or S contrasts. L-M contrast was estimated to be 1.2 (MW) to 1.3 (SM) times stronger than S contrast at 14 \times threshold, and 1.2 (MW) times stronger at 42 \times threshold. Filled diamonds in (a) and (c) plot the pair of axes corresponding to unique blue-yellow (125 deg) or unique red-green variations (2 deg) in the perceived color of the stimuli.

and chromatic motion. However, the angles of the test gratings at the nulls are strongly biased toward the equiluminant axis, and this bias suggests that luminance contrast was much stronger than chromatic contrast in determining the perceived motion. For example, the solid line shows the nulls predicted by the model outlined above by assuming two mechanisms, one sensitive to luminance contrast and the second sensitive to the L-M chromatic contrast. The relative sensitivities of the two mechanisms were varied to find the least-squares fit of predicted to observed null angles, and this required the luminance contrast to be 13 times stronger than L-M

contrast. [This estimate is relative to the contrast detection thresholds for the counterphase patterns, and thus could vary widely if a different reference contrast were chosen. For example, detection thresholds are lower for drifting luminance gratings than for counterphase luminance gratings, though a similar advantage is not observed for chromatic patterns (e.g. Lee & Stromeyer, 1989). This difference is illustrated in Fig. 13. Had we instead used these alternative thresholds to scale contrasts then the luminance/L-M ratio would be substantially lower.]

As we noted, the motion nulls illustrated in Fig. 4 were

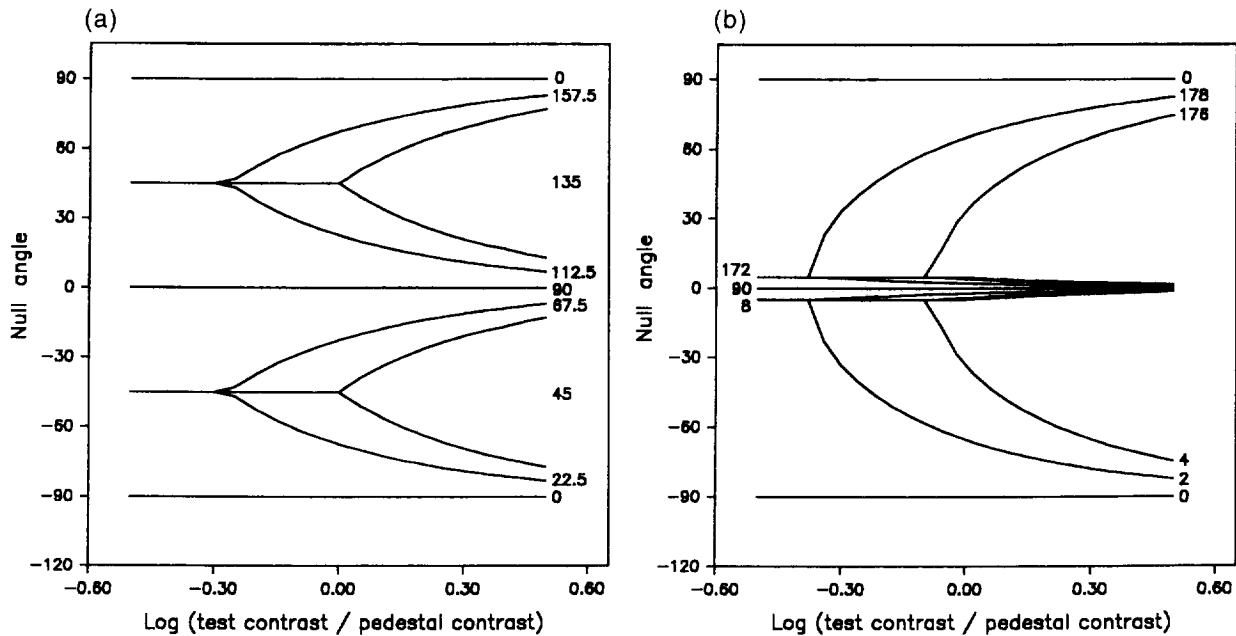


FIGURE 8. Motion nulls for test and pedestal gratings with different contrasts predicted by two mechanisms tuned to the luminance and L-M axes. (a) Illustrates the nulls predicted if the two mechanisms have equal sensitivity. Each line plots the nulls for a single pedestal angle as a function of relative contrast. Pedestal angles are labeled in the figure. For pedestals of 45 or 135 deg, a unique null exists for low test contrasts while an increasing range of nulling angles are predicted as the test contrast exceeds the pedestal contrast. (b) Illustrates similar predictions for the case in which luminance sensitivity is 12 times greater than L-M sensitivity.

for test and pedestal gratings that had a fixed contrast of $14\times$ threshold. To examine whether the null angles depended on overall contrast, MW made additional settings for gratings that instead had contrasts of $7\times$ or $28\times$ threshold. The resultant null angles are plotted in Fig. 5. For the three different contrast levels the pattern of the motion nulls is qualitatively similar, but the contributions of the luminance and chromatic components appear to differ. For example, the best-fitting sensitivity ratio for the $7\times$ threshold gratings required luminance contrast to be eight times stronger than L-M contrast, while at $28\times$ threshold luminance contrast was estimated to be 16 times stronger. Thus as the contrast in the patterns increased the motion nulls became increasingly dominated by the luminance components in the stimulus, and consequently there is no single scaling factor that can equate luminance and chromatic signals in this task. The change in relative sensitivity is inconsistent with the model we outlined above, but could arise if, for example, the response functions for luminance and chromatic contrast were qualitatively different, and/or if there were interactions between luminance and chromatic contrast that affected sensitivity to the motion. We consider evidence consistent with the latter possibility in the final set of experiments.

Figure 6 plots motion nulls for gratings defined by different directions within the luminance and S chromatic plane. As in Fig. 4 the gratings had a contrast of $14\times$ threshold. Again systematic variations are evident in the null angles, showing that the motion nulls were influenced by the S chromatic contrast in the gratings. The strength of the luminance signals was estimated as

before to be 12–15 times higher than the S chromatic signals. This value is similar to the value estimated for the $14\times$ -threshold luminance and L-M gratings, and suggests indirectly that the contributions of the S and L-M contrasts to the motion judgments are roughly equal once their contrast thresholds are equated.

Figure 7 plots the motion nulls for pairs of gratings that varied within the equiluminant S and L-M plane. In Fig. 7(a,b) the gratings again had contrasts of the $14\times$ threshold, while Fig. 7(c) shows the settings for a higher contrast of $42\times$ threshold. If the motion inputs from signals along the S and L-M chromatic axes were orthogonal, then pairs of gratings that varied along these separate axes should fail to generate motion, and Fig. 7 shows that this is close to the result observed (i.e. motion nulls for L-M pedestals occurred for test gratings near the S axis and vice versa). Moreover, throughout the equiluminant plane the motion null remained roughly 90 deg from the pedestal axis, so that the scaling of the L-M and S contrasts (estimated by fitting the nulls predicted by two mechanisms tuned to these axes) differed only slightly (1.2–1.3 times) from the original threshold scaling. This suggests that the opposing S and L-M motion signals that arise from these grating pairs are of roughly equal strength once their contrasts are equated for detectability. A similar pattern of results for equiluminant gratings has been obtained independently in an unpublished study by E. Switkes and M. Crognale (personal communication).

The independence of the S and L-M axes in the motion nulls can be contrasted to the nulls predicted by alternative models of chromatic mechanisms. For

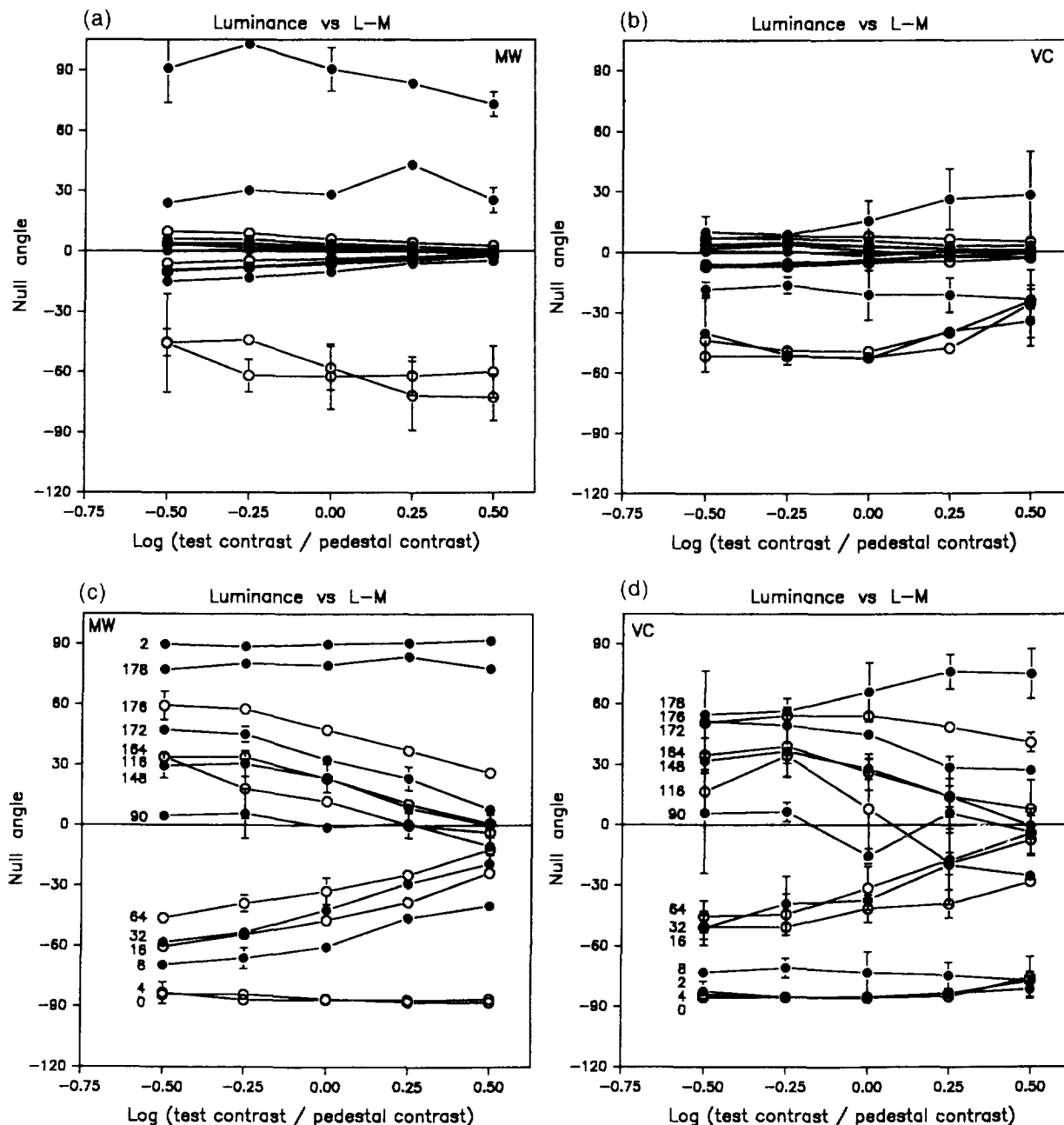


FIGURE 9. Observed motion nulls within the luminance vs L-M plane for test and pedestal gratings with different contrasts. (a) and (b) show for two observers the nulls (± 1 SEM) measured for 14 different pedestal angles. Each pedestal had a fixed contrast of $14\times$ threshold, while the contrast of the test grating was varied over a range from 4.43 to $44.3\times$ threshold. (c) and (d) replot the nulls after stretching the luminance axis by a factor of 10 (see text).

example, the diamonds in Fig. 7(a,c) plot the angles of counterphase gratings that appeared to vary along a pure blue-yellow or pure red-green axis. (Note each diamond plots the red-green angle along the pedestal axis and the blue-yellow angle along the null axis or vice versa.) These had angles of roughly 2 deg (red-green) and 125 deg (blue-yellow), as estimated by varying the angle in four randomly interleaved staircases while the observer judged on each trial the color deviation from the unique hues (see Webster & Mollon, 1994). The estimated angles were very similar for the two component colors in the gratings (i.e. both red and green or both blue and yellow) and at the two contrasts examined

($14\times$ and $42\times$ threshold). If the chromatic motion were encoded in only two mechanisms isolated by the two perceptual axes, then the nulls for the red-green pedestal should have occurred when the test was blue-yellow, or vice versa. Yet the nulls are predicted more closely by the orthogonal S and L-M axes.

While orthogonal S and L-M signals provide a good approximation to the observed nulls, there are nevertheless small but significant deviations. These deviations could reflect the actual spectral sensitivities of the chromatic channels, but they could also arise from a number of additional factors, including small residual luminance contrast in the gratings or a contribution of

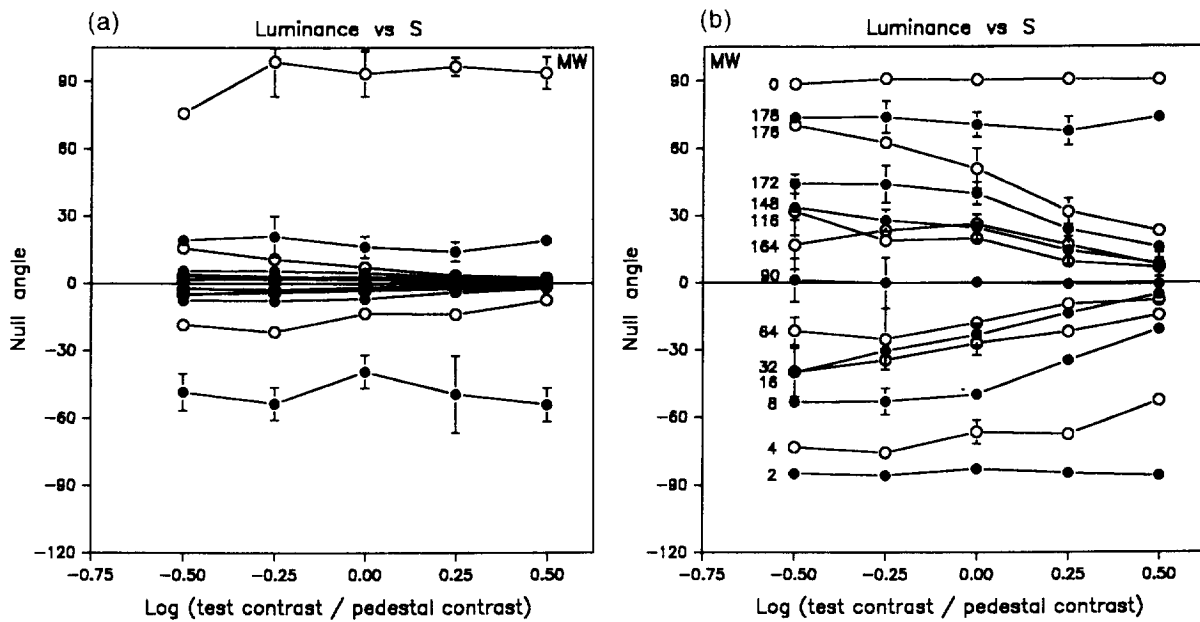


FIGURE 10. Observed motion nulls within the luminance vs S plane for test and pedestal gratings with different contrasts. (a) Shows the measured nulls (± 1 SEM) for one observer. (b) shows the nulls after stretching the luminance axis by a factor of 10 (see text).

rods to the motion nulls. Because of the very low sensitivity to the chromatic motion, our results do not readily discriminate between these factors. As an example, suppose that our equiluminance settings were in error, and as a result the nominal equiluminant plane was in reality tilted out of the true equiluminant plane along the 45-deg chromatic axis. In that case luminance contrast along different chromatic axes would vary as $\cos(\theta - 45)$. Now suppose that this error introduced a $1 \times$ -threshold luminance contrast (e.g. 0.0065 for MW) into the $14 \times$ -threshold L-M pedestal. If the nulls depended on the signals along the three cardinal axes, then luminance contrast in the pedestal would drive the null toward the 135-deg axis (the only equiluminant chromatic axis), while the null for the L-M chromatic contrast would be at 90 deg (the S-axis). Figure 4 suggests that the luminance signals are roughly 13 times stronger, and the resultant null should occur when the luminance and L-M signals cancel [$13(1/0.707)\cos(\theta - 45) + 14\cos(\theta) = 0$; $\theta \sim 116$ deg]. Thus even a threshold luminance contrast could in principle induce a large (e.g. 26 deg) deviation from the predicted null. The fact that the observed deviations are generally small therefore suggests that any residual luminance contrast in our chromatic gratings had little influence on these nulls.

Motion Minima for Pedestal and Test Gratings with Different contrasts

Predicted nulls

The preceding results suggest that within the mechanisms mediating minimum-motion judgments the responses to the luminance axis and L-M and S chromatic axes are orthogonal. This result limits the possible mechanisms underlying minimum-motion judg-

ments, but as we noted above, does not uniquely define the number of mechanisms or their spectral sensitivities. To try to test for preferred color-luminance directions in this task, we examined how the motion nulls varied as a function of the relative contrasts of the test and pedestal gratings. Thus the present conditions differed from the preceding conditions because we no longer constrained c_P and c_T to be equal.

Figure 8 illustrates the predicted effects of varying contrast, again for two mechanisms isolated by the luminance and L-M axes. In the example in Fig. 8(a) the two mechanisms had equal times-threshold contrast sensitivity, while Fig. 8(b) shows the predictions assuming the luminance mechanism was 12 times more sensitive than the chromatic mechanism. Each curve shows, for a single pedestal angle, the test angles at which motion is nulled as the ratio of c_T to c_P varies over a range of -0.5 to $+0.5$ log units. When the pedestal is achromatic and the test is equiluminant (or vice versa) changes in the relative contrast of the two gratings have no effect on the null angles, for as we noted previously, the null results because each mechanism detects only one of the two gratings and thus both mechanisms are silenced. However, for intermediate pedestal angles, varying the contrast ratio biases the test angle at which minimum motion occurs, and this arises because the nulls for these intermediate angles instead reflect the balance of opposing motion across the two mechanisms. In Fig. 8(a) for example, for a pedestal grating at 30 deg the sensitivity of the luminance mechanism is $\cos(30 - 90) = 0.5$, and the null should occur when the test grating is 90 deg away [so that the response in the L-M mechanism is -0.5 , or $\cos^{-1}(-0.5) - 0 = 120$ deg]. However, if the contrast of the test grating is doubled, then an L-M response of -0.5 instead occurs when the

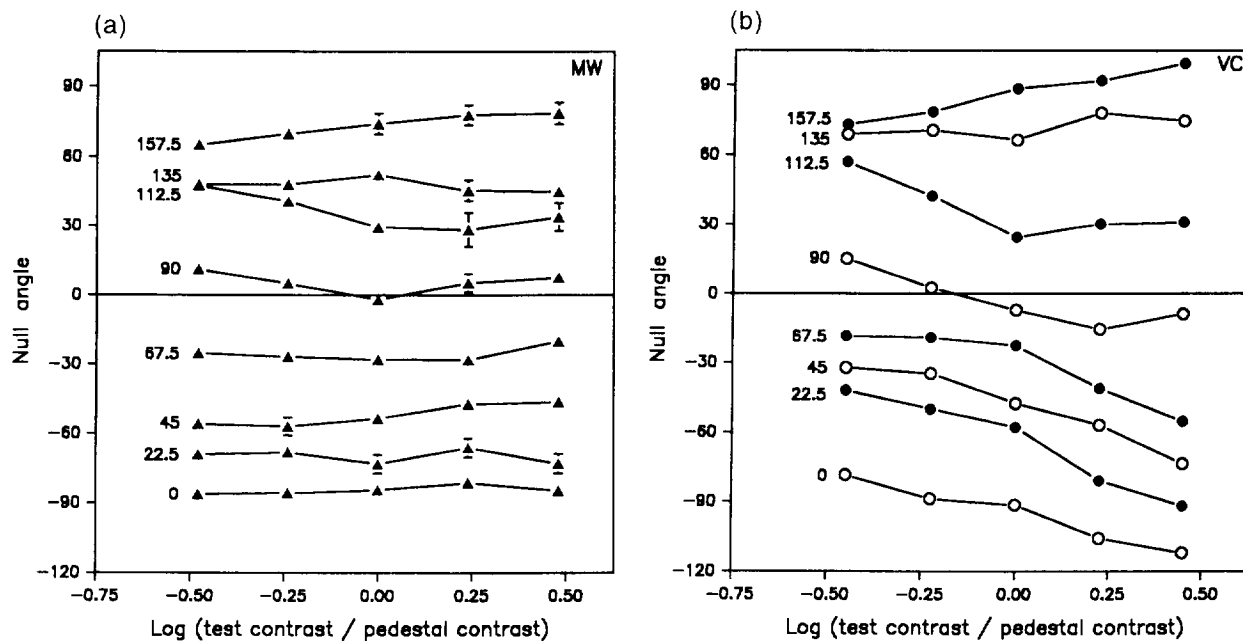


FIGURE 11. Observed motion nulls within the L-M vs S plane for two observers. In these settings it was necessary to vary both the test and pedestal contrasts to achieve a given ratio. Points plotted for each pedestal angle correspond to test/pedestal contrasts of 14/42, 24/42, 42/42, 42/24, and 42/14.

test is at an angle of 104.5 deg [i.e. $2 \cos(104.5) = -0.5$]. Thus as the ratio of c_T to c_P is varied, the angle of minimum-motion should remain constant only for the pedestal and test directions that isolate the two different mechanisms. Alternatively, if there is a uniform distribution of mechanisms tuned to different directions within the plane, then the nulls for all pedestal angles should remain constant. We therefore tested for invariant null angles in order to examine whether certain color-luminance axes had a special status in the minimum-motion settings. (The predictions in Fig. 8 are unlikely to be quantitatively correct, because the results of Fig. 5 suggest that the relative strength of luminance and chromatic signals varies as a function of contrast, which we do not attempt to model. Our motive in these experiments was not to test the specific changes that occur in axes whose nulls do vary with contrast, but rather to examine whether there were any stimulus axes whose nulling directions did not change.)

Observed nulls

Figures 9 and 10 show measurements of the actual minima within the two luminance and chromatic planes for test and pedestal gratings with different contrasts. The pedestal contrast was fixed at 14 \times threshold, while the contrast of the test grating was varied from 4.4 to 44 \times threshold. Figure 9 plots for two observers the null angles measured within the luminance and L-M plane, while Fig. 10 shows for one observer nulls within the luminance vs S plane. For both planes, as test contrast is increased there is a systematic bias in the nulls toward the equiluminant axis for most pedestal angles. Conversely, the null directions for the achromatic and equiluminant pedestals remain relatively constant. In the raw data these

trends are partly obscured by the unequal sensitivities to luminance and chromatic contrast, which strongly biases the nulls to lie near the equiluminant axis, and increases the variance in nulls near the achromatic axis. To see the structure more clearly, the nulls are also replotted in the figures after "stretching" the luminance axis by a factor of 10 so that all pedestal and test angles are redefined as:

$$\theta_{\text{new}} = \tan^{-1}[10 \tan(\theta_{\text{old}})]$$

(see Webster & Mollon, 1994). The invariance of the nulls for the luminance and chromatic axes compared to intermediate axes is now more evident and confirms their cardinal status in the minimum-motion settings. (Note this stretching is merely an alternative representation of the data that shows more clearly the variations in the nulls relative to the equiluminant axis. The transformation does not assume a model of the motion nulls, and in particular is not equivalent to equating luminance and chromatic contrast in the specific model outlined above, since the stretching takes no account of changes in the relative contrasts of the components on which predictions of the model depend. The predictions of Fig. 8 are qualitatively consistent with the observed results insofar as they correctly predict which color-luminance directions remain invariant. However, they do not correctly predict the magnitude of the shifts for axes whose nulls do vary. This discrepancy is similar to the results of Fig. 5, and could again reflect such factors as asymmetric interactions in the responses to luminance and color or qualitative differences in the response functions for different mechanisms.)

Figure 11 shows analogous measurements for stimuli within the L-M vs S plane. In this case we found that observers could not make reliable settings at low test

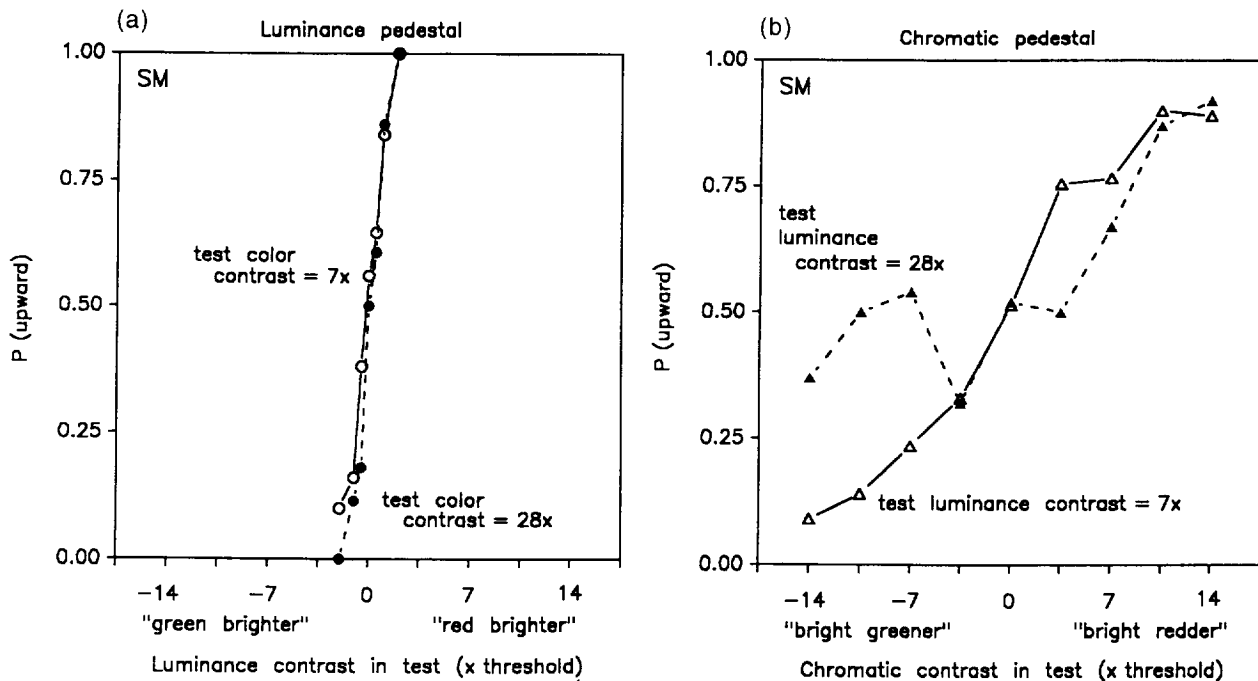


FIGURE 12. Psychometric functions for judging the perceived direction of motion in the minimum-motion stimulus when the pedestal grating was either a pure luminance grating (a) or a pure chromatic grating (b). For the luminance pedestal, motion nulls were estimated by varying luminance contrast in a test grating that had a fixed chromatic contrast of $7\times$ threshold (\circ) or $28\times$ threshold (\bullet). For the chromatic pedestal, chromatic contrast was varied in a test grating that had a fixed luminance contrast of $7\times$ threshold (\triangle) or $28\times$ threshold (\blacktriangle). The symbols plot the percentage of "upward" responses as a function of times-threshold luminance (a) or chromatic (b) contrast in the test grating.

contrasts, so to achieve a wide range of contrast ratios we instead varied both c_T and c_P . For observer MW, the resulting nulls remained relatively constant for all pedestal angles, so that there are no preferred directions within the plane. As noted above, this pattern of results would be predicted if the chromatic motion were encoded by an effectively uniform distribution of mechanisms rather than a single pair. However, the nulls for a second observer did vary systematically, with only the nulls for the 135-deg pedestal remaining constant. Because strong biases in the nulls could have arisen from very small luminance mismatches in our stimuli, we cannot rule out luminance artifacts as the basis for differences between the two observers. However, in neither case is there evidence that the S and L-M axes are special.

As an alternative test for preferred directions within the equiluminant plane, we also attempted to examine the chromatic mechanisms underlying the motion nulls by testing for motion aftereffects in our stimuli. Previous studies have shown strong transfer of motion aftereffects between luminance and chromatic gratings (Cavanagh & Favreau, 1985; Derrington & Badcock, 1985; Mullen & Baker, 1985), suggesting that the aftereffect might exhibit little color selectivity. However, tilt aftereffects have revealed selectivity for different color-luminance directions—in addition to a strong nonselective influence—when observers adapt to pairs of gratings with opposing orientations that are defined by different color directions (Flanagan *et al.*, 1990). We therefore examined whether opposite aftereffects might be induced in

gratings defined by different chromatic axes, after adapting to motion nulls in stimuli composed of opposite directions of motion within the cardinal axes (in test and pedestals defined by the $+45$ and -45 deg chromatic axes) or within intermediate axes (in test and pedestals defined by the S and L-M axes, respectively). However, adaptation to a motion null failed to produce motion aftereffects in any of our test stimuli, even though adaptation to the individual component motions induced pronounced aftereffects.

Interactions between Luminance and Chromatic Contrast in Minimum-motion Settings

In the preceding results we considered only the directions of the nulls for different pedestals in color-luminance space, yet the nulls for some pedestals can be set much more reliably than others. In the final set of experiments we examined sensitivity to the motion nulls along the different cardinal directions, both in order to test for interactions between the responses to signals along different cardinal axes and to test more directly whether luminance and chromatic signals are encoded in qualitatively different ways. As Cavanagh *et al.* (1987) noted, the net motion in the minimum-motion stimulus must in general be detected in the presence of both luminance and chromatic flicker. We examined how the presence of these flickering components along different color directions influenced the sensitivity to luminance or chromatic motion. Stromeyer *et al.* (1984) have previously examined the influence of luminance counter-

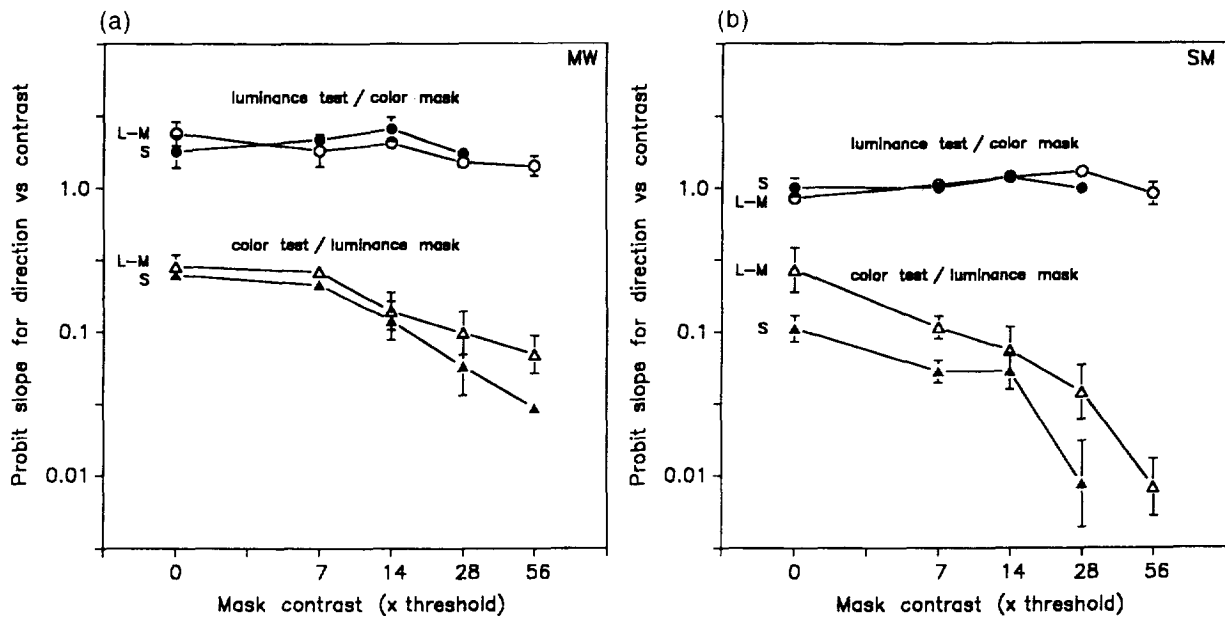


FIGURE 13. Slopes of probit functions fitted to the psychometric functions for judging perceived direction in the minimum-motion stimulus. Each point plots the mean of the slopes estimated from four runs (± 1 SEM). Circles plot the slopes for judging motion based on luminance contrast: subjects were presented with a pure luminance pedestal and varied the luminance contrast in a test grating that had a fixed chromatic contrast [as in (a)]. Slopes are plotted as a function of the contrast of the L-M (\circ) or S (\bullet) counterphasing component in the test. Triangles plot slopes for the converse case of judging either L-M (\triangle) or S (\blacktriangle) chromatic motion, by varying chromatic contrast in test gratings that had a fixed counterphasing luminance contrast [as in (b)].

phase flicker on luminance motion detection, and in the present study we extended their analysis to examine these interactions for both luminance and chromatic contrast.

Figure 12 shows examples of the psychometric functions for judging perceived direction in the minimum-motion stimulus based either on luminance contrast [Fig. 12(a)] or on chromatic contrast [Fig. 12(b)]. The two different curves for the luminance judgments show performance when a $14\times$ threshold luminance pedestal was combined with a test grating that had a fixed chromatic contrast of either $7\times$ threshold or $28\times$ threshold. Luminance contrast in the test grating was then varied to estimate the motion null [as in Fig. 1(a)]. Conversely, the two curves for the chromatic judgments show performance based on a $14\times$ threshold chromatic pedestal, combined with a test grating that had a fixed luminance contrast of $7\times$ or $28\times$ threshold. Thus in this case chromatic contrast in the test grating was varied to determine the point of minimum motion [as in Fig. 1(b)]. In the two figures luminance and chromatic contrasts along the x -axis have again been scaled to represent equal multiples of the detection thresholds for the luminance or chromatic counterphase gratings. When plotted in this way, two differences are evident between the luminance and chromatic settings. First, sensitivity to the chromatic motion is substantially lower than to the luminance motion, as indicated by the substantially shallower slopes for judging the direction of chromatic motion. Second, while the luminance motion judgments appeared to depend little on how much color contrast was present in the test grating, the sensitivity to chromatic motion appeared to decrease as more luminance contrast was

added to the test grating. Thus chromatic motion was judged less consistently when the test grating had a luminance contrast of $28\times$ threshold than when it had a luminance contrast of $7\times$ threshold. These results therefore suggest that the presence of counterphasing luminance contrast interfered with the ability to judge chromatic motion, while the presence of counterphasing chromatic contrast had little effect on the ability to judge luminance motion.

As an index of these interactions, the different psychometric functions were fitted by probit analysis, and the resulting probit slopes were then used as an estimate of sensitivity to motion under the different conditions. Figure 13 plots the probit slopes either for judging the direction of luminance motion in the presence of different amounts of counterphasing color contrast (circles), or for judging the direction of chromatic motion in the presence of different amounts of counterphasing luminance contrast (triangles). These slopes show that sensitivity to luminance motion depended little on the magnitude of the chromatic contrast in the test grating. This is an important property of the minimum-motion stimulus, because it suggests that the stimulus provides a sensitive measure of equiluminance over a wide range of chromatic contrasts. Conversely, sensitivity to chromatic motion was markedly lower than for luminance motion, and became progressively worse as the counterphasing luminance contrast in the test grating increased. Thus when the test grating had a high luminance contrast, subjects were largely unable to judge consistently the direction of motion on the basis of chromatic contrast.

To characterize these interactions more fully, we

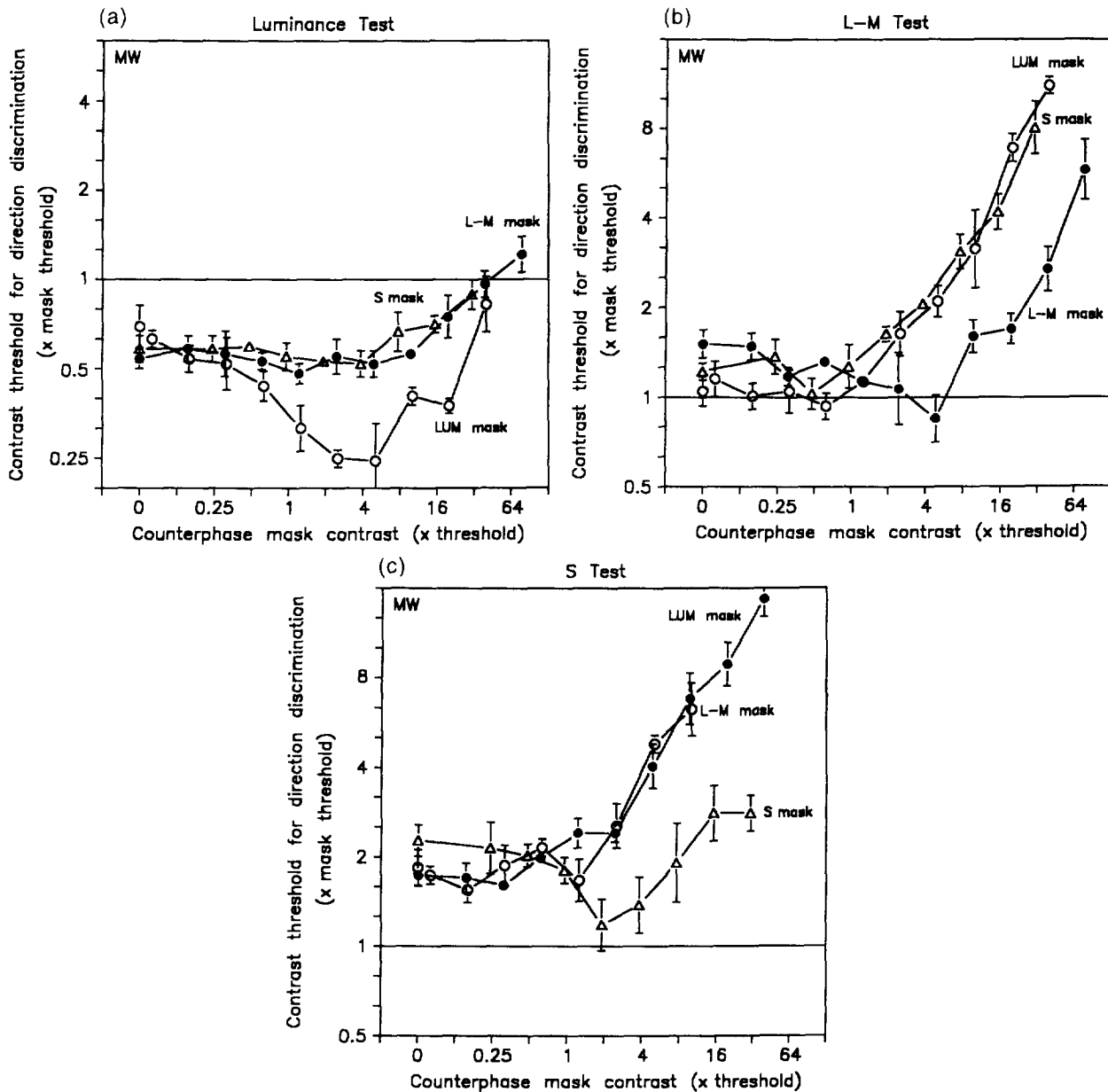


FIGURE 14. Contrast thresholds for discriminating the direction of motion of a drifting grating, as a function of the contrast of a superposed counterphasing mask. (a) Plots the direction discrimination thresholds (± 1 SEM) for a luminance test grating in the presence of a luminance (\circ), L-M (\bullet) or S (\triangle) mask. (b) Plots corresponding thresholds for a drifting L-M chromatic grating, while (c) shows thresholds for a drifting S chromatic grating.

presented a drifting luminance or chromatic test grating, and then measured the contrast threshold for identifying the direction of motion in the grating. The test gratings were superposed on a counterphasing luminance or chromatic pedestal grating of variable contrast. Figure 14(a) plots the direction discrimination thresholds for a drifting luminance grating as a function of the contrast of the counterphasing luminance, L-M, or S pedestal. Figure 14 (b,c) shows corresponding thresholds when the pedestal was either an L-M counterphasing grating or an S counterphasing grating. To maintain the same contrast metric as in the results above, the contrasts are again scaled as multiples of the detection thresholds for

the counterphase grating, which in this case is a mask stimulus. Note that this scaling does not equate the direction-discrimination thresholds for the drifting luminance and chromatic gratings. The relative differences between these thresholds for the luminance and chromatic gratings are consistent with differences between luminance and chromatic contrast in (a) contrast detection vs direction discrimination thresholds for drifting gratings (Lee & Stromeyer, 1989; Lindsey & Teller, 1990; Cavanagh & Anstis, 1991; Mullen & Boulton, 1992; Palmer *et al.*, 1993; Gegenfurtner & Hawken, 1995; Stromeyer *et al.*, 1995) and (b) contrast detection thresholds for drifting vs counterphase gratings (Lee &

Stromeyer, 1989), though we have not systematically examined the relationship between these three thresholds in the present study.

If luminance and chromatic contrast behaved similarly in this task, then all of the curves in Fig. 14 should have the same shape, but might be shifted in position depending on the relative sensitivity to the pedestal and test. Instead, the interactions are clearly asymmetric, suggesting that the processes encoding the luminance and chromatic motion are very different. Sensitivity to luminance motion improved substantially in the presence of the luminance pedestal (Stromeyer *et al.*, 1984) but was little affected by the chromatic pedestals (though weak masking is suggested for high contrast chromatic pedestals). Conversely, sensitivity to chromatic motion showed less facilitation. Instead, the chromatic motion was masked by both the luminance and chromatic pedestals, and the strongest masking occurred when the pedestal and the chromatic test fell along different cardinal axes. This pattern of interactions is very different from the interactions between luminance and color in contrast detection tasks (Switkes *et al.*, 1988). This suggests that the pedestal was not changing the motion thresholds simply by altering the detectability of the test grating, but rather was specifically altering the ability to see the motion in the test. The "inverse selectivity" of the masking for chromatic motion is the opposite of the thresholds predicted by independent signals within the cardinal axes, but is consistent with the relative losses in sensitivity to the chromatic signals in the minimum motion stimulus as the overall contrast in the stimulus is increased (e.g. Figs 5 and 9).

CONCLUSIONS

Color–luminance selectivity in minimum-motion

Our results suggest that in the minimum-motion paradigm observers are sensitive to stimulus variations along each of the three cardinal directions, but do not encode signals across different cardinal axes to perceive a net direction of motion (see Figs 4–7). This suggests that the motion nulls depend on mechanisms that are isolated by the cardinal axes, or that lead to balanced opposing responses along the cardinal axes. Conversely, the nulls are not readily accounted for by models of chromatic selectivity such as those based on perceptual red–green and blue–yellow color axes, since such models do not predict balanced responses to the S and L–M axes (Fig. 7).

The set of null directions we measured at a fixed test contrast do not uniquely define the number of mechanisms or their spectral sensitivities, for there are many different ways that the cone signals could be organized to preserve orthogonal responses to the cardinal axes. However, as contrast is varied, only the achromatic pedestal or equiluminant pedestals appear to retain a constant nulling direction (Figs 5 and 9–11). This invariance points to a special status for the luminance and chromatic axes in the motion nulls. Krauskopf *et al.*

(1996) similarly reported a special status for these axes in studies of coherent motion, yet unlike the results for plaid motion, our minimum-motion settings do not point to a special pair of axes within the equiluminant plane (Fig. 11). Moreover, even within the luminance–chromatic planes we tested, our results do not rule out the involvement of multiple mechanisms each tuned to a different direction. Multiple color–luminance channels have been suggested by a number of other psychophysical and physiological studies [reviewed in Webster (1996)], and have been implicated in previous studies of motion perception (Kooi *et al.*, 1992; Webster & Mollon, 1993; Krauskopf *et al.*, 1996). For example, Webster and Mollon (1993) showed that contrast adaptation to gratings with covarying luminance and chromatic contrast biases minimum-motion settings by tilting the equiluminant axis away from the axis of adaptation, and this tilt is inconsistent with sensitivity losses in independent luminance and chromatic mechanisms.

Luminance contrast vs chromatic contrast in minimum-motion settings

While luminance contrast and chromatic contrast both contributed to the motion nulls, their effects differed both quantitatively and qualitatively. Motion signals along the S and L–M axes were of roughly equal strength once their contrasts were equated for detectability (Fig. 7). However, these times-threshold chromatic contrasts were many times weaker than an equivalent times-threshold luminance contrast (Figs 4–6). These results are consistent with the many studies [e.g. of coherent motion (Kooi & De Valois, 1992); or comparing direction discrimination vs contrast detection (Lee & Stromeyer, 1989; Lindsey & Teller, 1990; Cavanagh & Anstis, 1991; Mullen & Boulton, 1992; Palmer *et al.*, 1993; Gegenfurtner & Hawken, 1995; Stromeyer *et al.*, 1995)] that suggest that, relative to their detection thresholds, chromatic contrasts are weaker than luminance contrasts in measures of motion perception. Qualitatively, the masking interactions we observed between luminance and chromatic contrast were highly asymmetric, and consequently, there is no contrast metric that could equate the properties of luminance and chromatic motion in our task (Figs 13 and 14). Several previous studies have demonstrated that the chromatic inputs to motion are not equivalent to a scaled version of luminance inputs (e.g. Cavanagh & Favreau, 1985; Kooi & De Valois, 1992; Agonie & Gorea, 1993; Gegenfurtner & Hawken, 1996). Such differences could reflect differences in the mechanisms sensitive to luminance and chromatic contrast and/or differential inputs of luminance and chromatic contrast to the various processes (e.g. Cavanagh, 1992; Lu & Sperling, 1995) and pathways (e.g. Merigan & Maunsell, 1993) thought to underlie motion perception.

Minimum-motion and equiluminance

The minimum-motion stimulus is used widely as a measure of the luminous efficiency of different colors.

While we have found that the motion nulls can be influenced by signals along any direction in color space, two aspects of our findings suggest that within this paradigm the nulls for the achromatic pedestal are particularly well defined. First, the achromatic and equiluminant pedestals are the only stimuli whose null directions appear independent of test contrast and are thus confined to a plane in color space (Figs 9 and 10). Thus in our measurements it is only these pedestal directions that come close to defining an additive sensitivity [though weak additivity failures in the conventional minimum-motion stimulus have been reported; Kaiser *et al.* (1989)]. Second, the counter-phasing components inherent in the minimum-motion stimulus serve to enhance sensitivity to luminance contrast while masking sensitivity to chromatic contrast, so that the achromatic pedestal appears uniquely well suited for facilitating the detection of stimulus motion (Fig. 14).

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