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The perceived speed of drifting chromatic gratings is mechanism-dependent

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Abstract

The perceived speed of chromatic motion was investigated for gratings that stimulate each chromatic mechanism [$L-M$ and $S-(L+M)$] in isolation and for gratings that stimulate both chromatic systems. The observers' task consisted of adjusting the speed of a drifting achromatic grating to match the perceived speed of an isoluminant chromatic grating, drifting at 8 deg/s (temporal frequency of 4 Hz). Every observer reported a substantial decrease in perceived speed for chromatic gratings modulated along the $S-(L+M)$ (blue–yellow) cardinal axis compared to other directions in color space. One observer even reported motion standstill for gratings modulated along this axis. Further testing demonstrates that the perceived speed of an isoluminant chromatic grating depends solely on the extent to which it stimulates the $L-M$ (red–green) mechanism. Thus, under the conditions that were tested, the $S-(L+M)$ postreceptoral mechanism does not appear to contribute significantly to determining the perceived speed of chromatic motion.

Keywords: Motion; Chromatic; Speed; Equiluminance

1. Introduction

It has been proposed that color and motion are processed independently of each other in the visual cortex (Livingstone & Hubel, 1987; Ramachandran & Gregory, 1978; Zeki, 1978). It has further been suggested that the system that processes motion is only sensitive to luminance information (Ramachandran & Gregory, 1978). These suggestions have generated an interest in investigating the visual system's capability to process chromatic motion. Several studies have demonstrated that chromatic motion is perceived (e.g., Bilodeau & Faubert, 1997; Bilodeau & Faubert, 1999; Cavanagh & Favreau, 1985; Cavanagh, Tyler, & Favreau, 1984; Cropper & Derrington, 1996; Faubert, Bilodeau, & Simonet, 2000; Gorea & Papathomas, 1989; Moreland, 1982; Mullen & Baker, 1985). However, the perceived motion of isoluminant chromatic gratings has consistently been reported as slower and less smooth than that of achromatic gratings (e.g., Cavanagh & Anstis, 1991; Cavanagh & Favreau, 1985; Cavanagh et al., 1984; Derrington & Badcock, 1985; Kooi & De Valois, 1992; Mullen & Boulton, 1992; Troscianko & Fahle, 1988).

Different mechanisms have been proposed to underlie chromatic motion processing. It has been suggested that low-level systems, such as motion energy analyzers (Zaidi & DeBonet, 2000) or color-opponent mechanisms (Cavanagh & Anstis, 1991; Derrington & Badcock, 1985), process chromatic motion. A competing hypothesis is that a higher order mechanism, such as a third order motion mechanism (Lu, Lesmes, & Sperling, 1999a,b) or a position tracking system (Seiffert & Cavanagh, 1999) underlies chromatic motion processing. Finally, it has been suggested that two distinct mechanisms process chromatic motion (Gegenfurtner & Hawken, 1996; Seiffert & Cavanagh, 1999). These two mechanisms are thought to detect chromatic motion at different speeds and contrasts.

Psychophysical research has compared the contribution of the $L-M$ (red–green) and of the $S-(L+M)$ (blue–yellow) mechanisms to motion. Motion nulling experiments suggest that the $S-(L+M)$ mechanism

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contributes weakly, if at all, to chromatic motion processing (Cavanagh & Anstis, 1991; Cavanagh, MacLeod, & Anstis, 1987). This proposed weak contribution of the $S-(L+M)$ system to chromatic motion processing relatively to the $L-M$ system has not been found to affect perceived speed (Cavanagh et al., 1984). However, the blue–yellow and red–green gratings used in these experiments did not isolate the two postreceptoral chromatic mechanisms, which does not allow for a direct comparison between these systems.

2. Experiment 1

The purpose of Experiment 1 was to compare the efficiency with which information from the $L-M$ and $S-(L+M)$ systems is used in order to process chromatic motion. To assess this, the perceived speed of drifting chromatic gratings modulated along the cardinal axes of these two mechanisms was investigated. If a chromatic system is used more efficiently than the other to process motion, perceived speed should be diminished for gratings modulated along the cardinal axis of the mechanism that contributes the least to motion processing. However, if the inputs from both postreceptoral chromatic mechanisms are used equally well to process motion, perceived speed should be equal for the $L-M$ and the $S-(L+M)$ cardinal axes. In order to assess if inputs from these two systems interact to determine perceived speed, perceived speed was also assessed for axes along which both mechanisms are stimulated.

2.1. Methods

2.1.1. Observers

Three experienced psychophysical observers were tested for the purpose of this experiment (JF, CH and MS). All observers had normal or corrected to normal visual acuity as well as normal color vision, as assessed by H-R-R pseudoisochromatic plates and a Nagel anomaloscope. Observer JF is one of the authors of this paper. Observers MS and CH were naive to the objectives and hypotheses of the experiment.

2.1.2. Apparatus and stimuli

Observers were tested using a Power Macintosh G3 computer equipped with an 8-bit per gun video card and an Apple Multiscan CRT monitor. The CIE (x, y) coordinates of the monitor were $(0.60, 0.36)$ for the red phosphor, $(0.28, 0.59)$ for the green phosphor and $(0.14, 0.06)$ for the blue phosphor. Stimuli were generated and the data were collected using MATLAB and the extensions provided in the Psychophysics Toolbox (Brainard, 1997) and low-level Videotoolbox (Pelli, 1997). Lookup tables were used to ensure that phosphor irradiance was linear.

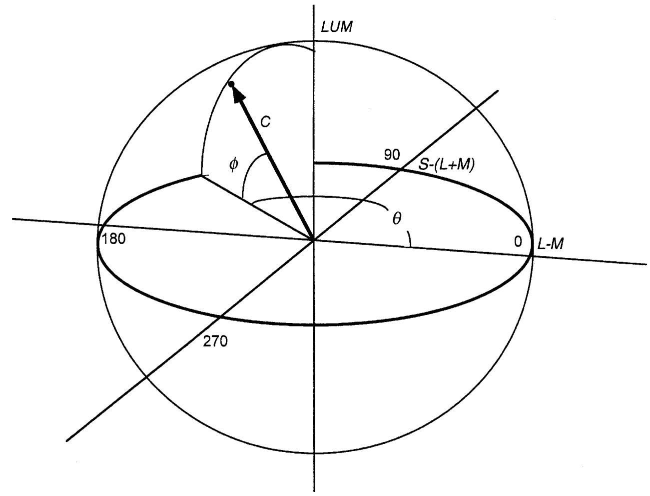

Fig. 1. Three-dimensional cardinal color space used in the experiment. The origin is at a white point. The vertical axis represents the luminance variation. The $L-M$ and $S-(L+M)$ axes represent the coordinates within the isoluminant plane. Three stimulus quantities were defined: contrast (C), azimuth (θ) and elevation (ϕ). The azimuth (θ) represents the angular deviation from the $L-M$ axis and the elevation (ϕ) represents the deviation of the stimulus from isoluminance. The vector length (C) represents the amplitude of modulation.

As in the experiments by Sankeralli and Mullen (1997, 1999), the $L-M$ cardinal axis corresponds to the axis orthogonal to the $S-(L+M)$ and luminance axes in a cone contrast space. The cardinal axes found in this space are similar to those used by Derrington, Krauskopf, and Lennie (1984). A representation of the color space used in this experiment is shown in Fig. 1.

A spherical system that defined three stimulus quantities (contrast C, azimuth θ, and elevation ϕ) was used. The three axes were scaled according to a cone contrast space. A near equal energy white adapting field [CIE (x, y, Y) coordinates: $(0.29, 0.30, 33)$] was presented. All gratings had an amplitude of modulation (m) of 15% in a cone contrast space (Cole & Hine, 1992; Sankeralli & Mullen, 1999). This value was determined by

$$m = \sqrt{(L_{\mathrm{MAX}} - L_{\mathrm{MIN}})^2 + (M_{\mathrm{MAX}} - M_{\mathrm{MIN}})^2 + (S_{\mathrm{MAX}} - S_{\mathrm{MIN}})^2},$$

in which L, M and S represent the grating's L, M and S maximum and minimum cone contrast values.

A black fixation point was present at the center of the monitor at all times during testing. Stimuli consisted of sinusoidal gratings modulated through the origin in color space. On each trial, observers were shown an achromatic grating and an isoluminant chromatic grating. Gratings were presented through square apertures, 4° in width, centered at eccentricities of 2.5° above and below fixation. To minimize potential luminance artifacts from transverse chromatic aberration, most evident at higher spatial frequencies in chromatic gratings (Faubert et al., 2000), gratings had a spatial frequency of 0.5 cpd.

Chromatic gratings drifted at a speed of 8 deg/s (temporal frequency of 4 Hz). Observers were tested with isoluminant chromatic gratings modulated along 12 different azimuths, ranging from the 0–180° ($L-M$) axis to the 165–345° axis in color space. The azimuth of the chromatic grating in color space was changed for each condition. To prevent observers from matching the spatial location of the achromatic and chromatic gratings, the gratings drifted in opposite directions.

2.1.3. Procedure

The display was viewed monocularly through natural pupils at a distance of 57 cm. A chin rest and forehead bar were used in order to maintain a constant viewing distance and head position. Isoluminance had been determined prior to testing for each observer at each azimuth in color space and for each testing position with a minimum motion technique using gratings with a spatial frequency of 0.5 cpd and a temporal frequency of 4 Hz.

Observers were instructed to maintain their gaze on the fixation point at all times during testing. In order to assess the perceived speed of chromatic motion, observers adjusted the speed of a drifting achromatic grating to match the perceived speed of the chromatic grating with the mouse. When the perceived speed of the two gratings appeared equal, observers indicated a response by pressing the mouse button.

The relative speed of the achromatic grating (speed of the achromatic grating, which matched the perceived speed of the chromatic grating, divided by the speed of the chromatic grating) was recorded on each trial. The direction of drift (left or right) and the position of the chromatic gratings (top or bottom) were block randomized across trials.

2.2. Results

The relative speed results are shown as a function of the chromatic grating's azimuth of modulation in color space in Fig. 2. The data were analyzed using a single factor within subjects ANOVA. The chromatic grating's azimuth was found to have a highly significant effect on results ($F(11,22) = 6.493$, $p < 0.0001$). A significant decrease in the perceived speed of chromatic motion occurred at azimuths near the $S-(L+M)$ cardinal axis (90–270° axis). For every observer, the largest reduction in perceived speed was reported for chromatic gratings modulated along the $S-(L+M)$ cardinal axis. Observer JF even reported motion standstill at this azimuth, but not at other azimuths in color space.

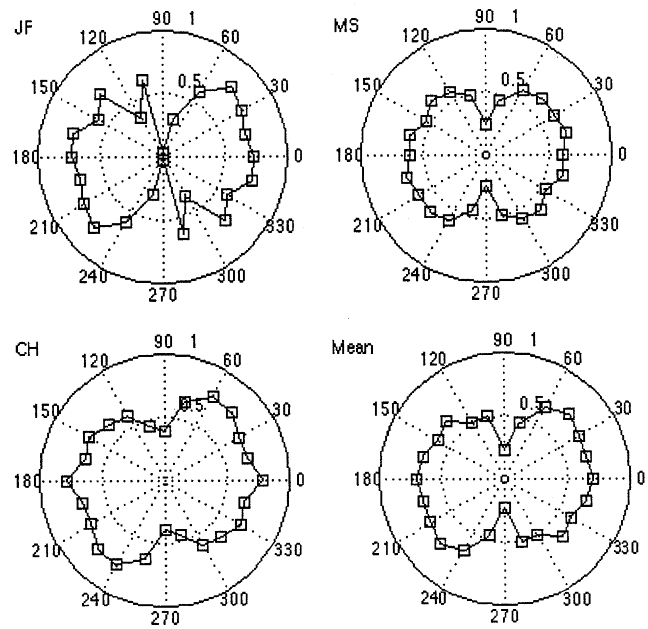

Fig. 2. Relative speed of an achromatic grating and a chromatic grating of the same perceived speeds (speed of the achromatic grating divided by the speed of the chromatic grating) as a function of azimuth in color space for observers JF, MS and CH. The bottom right graph is the mean results for all three subjects. Distance from origin represents the relative speed of the achromatic grating and angle represents the azimuth of modulation of the grating in cardinal color space. The $L-M$ cardinal direction is on the 0–180° axis and the $S-(L+M)$ cardinal direction is on the 90–270° axis.

2.3. Discussion

The results of Experiment 1 indicate that the perceived speed of a drifting chromatic grating depends on which of the two postreceptoral chromatic systems it stimulates. This mechanism dependence of the perceived speed of chromatic motion constitutes a novel finding. This finding is inconsistent with earlier reports of equal perceived speeds for isoluminant blue–yellow and red–green chromatics gratings (Cavanagh et al., 1984). It is likely that this is due to the blue–yellow gratings of earlier experiments not stimulating the $S-(L+M)$ mechanism in isolation. The mechanism dependence of perceived speed suggests that the $L-M$ and $S-(L+M)$ mechanisms do not contribute equally to motion perception. This conclusion is in agreement with earlier suggestions that the contribution of the $S-(L+M)$ mechanism to chromatic motion processing is weaker than that of the $L-M$ mechanism (Cavanagh & Anstis, 1991; Cavanagh et al., 1987; Gegenfurtner & Hawken, 1995).

2.3.1. Interactions between the two postreceptoral chromatic systems

A butterfly shaped pattern can be observed for the results presented in Fig. 1. This is due to a sharp decrease in perceived speed for chromatic gratings modulated along the $S-(L+M)$ cardinal axis and to a lesser decrease for gratings modulated along nearby azimuths in color space. Here, we propose two models that can potentially account for these results.

The first model presupposes that, when a drifting chromatic grating stimulates both chromatic mechanisms, the visual system receives two conflicting speed inputs. One speed input is derived using information from the $L-M$ system and the other, from the $S-(L+M)$ system. In these conditions, the amount of stimulation of $S-(L+M)$ and $L-M$ units is compared to determine perceived speed. According to this model, the perceived speed of chromatic motion is a weighted sum of the two chromatic mechanisms' speed inputs. This model proposes that the weights are proportional to the activity of the two mechanisms relative to each other. This model will be referred to as the weighted sum model.

The perceived speed of an isoluminant chromatic grating as a function of azimuth predicted by the weighted sum model could be described by the following function:

$$V_P(\theta) = \mathrm{abs}[V_{L-M}\cos(\theta)] + \mathrm{abs}[V_{S-(L+M)}\sin(\theta)].$$

In which V_P is the perceived speed of a chromatic grating, V_{L-M} is the perceived speed of a grating modulated along the $L-M$ cardinal axis and $V_{S-(L+M)}$, the perceived speed of a chromatic grating modulated along the $S-(L+M)$ cardinal axis.

A second possibility is that the perceived speed of chromatic motion is determined using a single chromatic mechanism. In this model, when a grating stimulates both chromatic mechanisms, the $S-(L+M)$ mechanism does not contribute significantly to motion perception. It is also possible that the $S-(L+M)$ mechanism does not contribute to chromatic motion processing at all. Any perceived motion in the $S-(L+M)$ cardinal direction could thus be the result of residual responses from other postreceptoral mechanisms or demands of the task. This model predicts a sharp decrease in perceived speed for gratings modulated along the $S-(L+M)$ cardinal axis because it is at this direction in color space that the $L-M$ mechanism is the least responsive. The perceived speed of a chromatic grating stimulating both mechanisms would thus be solely dependent on the $L-M$ input. We will refer to it as the residual model.

If the amplitude of modulation remains constant, the perceived speed of an isoluminant chromatic grating as a function of azimuth predicted by such a model can be described by

$$V_P(\theta) = \mathrm{abs}[(V_{L-M} - V_{S-(L+M)})\sin(\theta)] + V_{S-(L+M)}.$$

The predictions of these two models for Experiment 1 are shown against the averaged results for the three observers in Fig. 3.

Both models show a good fit with the results of Experiment 1. In Experiment 1, the amount of stimulation of the $S-(L+M)$ and $L-M$ systems covaried with azimuth. Because of this, it is currently impossible to determine which of the two proposed models best explains the results.

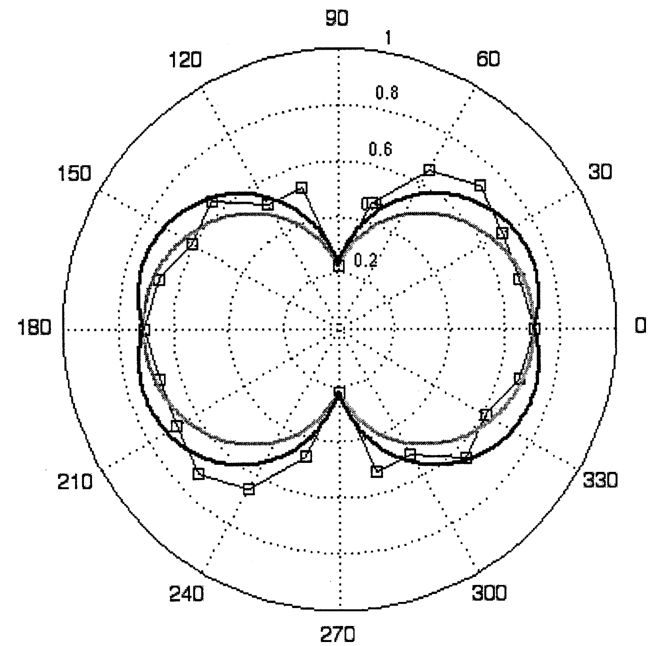

Fig. 3. Predicted relative speed results of a weight and a residual model as a function of azimuth in color space. The bold black line indicates the predicted relative speed of the weighted sum model. The bold gray line represents the predicted relative speed results of the residual model. The mean results from the three subjects of Experiment 1 are shown with the full black line with open squares.

3. Experiment 2

The purpose of Experiment 2 was to assess which of the two proposed models best accounts for the results of Experiment 1. Experiment 2 also aimed to assess if the $S-(L+M)$ system contributes significantly to determining perceived speed. In Experiment 2, the amplitude of modulation along the cardinal axis of one chromatic mechanism remained constant, while the amplitude of modulation along the other chromatic mechanism's cardinal direction was varied. This allows an assessment of whether perceived speed is determined using both mechanisms or a single mechanism. The two models differ in the predicted speed of a chromatic grating when the amplitude of modulation along the $L-M$ cardinal axis remains constant and the amplitude of modulation along the $S-(L+M)$ cardinal axis is increased. In such conditions, the residual model predicts that the perceived speed of a grating will remain constant. In contrast, the weighted sum model predicts that an increase in perceived speed should occur with increasing levels of $S-(L+M)$ stimulation.

3.1. Methods

3.1.1. Observers

Two of the observers from Experiment 1 were tested (MS and CH).

3.1.2. Stimuli and apparatus

The same apparatus as in Experiment 1 was used. The gratings had the same spatial and temporal parameters as those used in Experiment 1. In the constant $L-M$ condition, the amplitude of modulation along the $L-M$ cardinal direction remained constant at 15% in cone contrast space and the amplitude of modulation along the $S-(L+M)$ cardinal axis was varied. In the constant $S-(L+M)$ condition, the amplitude of modulation in the $S-(L+M)$ cardinal axis remained constant at 15% in cone contrast space and the amplitude of modulation in the $L-M$ cardinal direction was varied. The modulation along the $L-M$ and $S-(L+M)$ cardinal axes was always in phase (i.e., the maximum and minimum modulations along these two axes always corresponded).

3.1.3. Procedure

The same procedure as in Experiment 1 was used in order to assess the perceived speed of drifting chromatic gratings.

3.2. Results

The relative speed results of each observer for Experiment 2 are shown in Fig. 4. For both observers, in the constant $S-(L+M)$ condition, the perceived speed of chromatic motion increased with the amplitude of modulation in the $L-M$ mechanism cardinal direction.

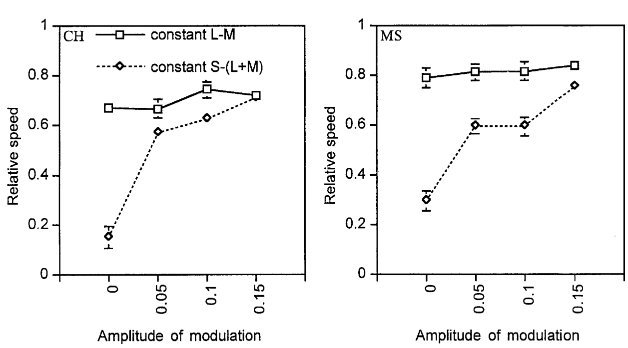

Fig. 4. Relative speed of an achromatic grating which matched the perceived speed of a chromatic grating as a function of amplitude of modulation. The solid line with squares represents the perceived speed results when the $L-M$ modulation was maintained constant and the amplitude of modulation in the $S-(L+M)$ was varied. The dashed line with diamonds represents the perceived speed results when the amplitude of modulation in the $S-(L+M)$ cardinal direction was held constant and the amplitude of modulation in the $L-M$ cardinal direction was varied. Error bars represent SEM.

In the constant $L-M$ condition, the amplitude of modulation along the $S-(L+M)$ cardinal axis did not affect the perceived speed of the grating. Thus, in the conditions that were tested, the level of $L-M$ stimulation alone determined the perceived speed of chromatic motion.

3.3. Discussion

Spatial variations in macular pigment would have increased the likelihood of a luminance artifact for the $S-(L+M)$ cardinal direction, so the present results cannot be attributed to this factor. The results of Experiment 2 indicate that, when a drifting isoluminant chromatic grating stimulates both postreceptoral chromatic mechanisms, only the $L-M$ input is used to determine perceived speed. This conclusion is consistent with earlier suggestions that the $S-(L+M)$ mechanism contributes weakly, if at all, to chromatic motion processing (Cavanagh & Anstis, 1991; Cavanagh et al., 1987; Gegenfurtner & Hawken, 1995). However, the conclusion of the current experiments is not consistent with that of Cropper, Mullen, and Badcock (1996), who suggest that the two chromatic systems interact to determine perceived direction in plaid patterns consisting of two chromatic gratings modulated along the two chromatic cardinal axes.

4. General discussion

Consistent with earlier experiments, which found that observers can detect chromatic motion (e.g., Bilodeau & Faubert, 1997; Bilodeau & Faubert, 1999; Cavanagh & Favreau, 1985; Cavanagh et al., 1984; Faubert et al., 2000; Gorea & Papathomas, 1989; Moreland, 1982; Mullen & Baker, 1985), motion standstill was not reported in this experiment, except by one observer along the $S-(L+M)$ cardinal direction. Thus, it appears that there is a contribution of color to motion perception. The results also call into question the contribution of the $S-(L+M)$ system to the perception of chromatic motion.

Other experiments have found evidence for an S-cone contribution to motion perception (Dougherty, Press, & Wandell, 1999; Wandell et al., 1999) in humans. However, these experiments used higher contrasts than those reported here. At the cone contrasts used in Experiments 1 and 2, the S-cone contribution to motion perception appears to be very weak compared to the $L-M$ contribution and perceived speed was solely determined by the level of $L-M$ excitation when both mechanisms were active.

It could be argued that, in Experiment 1, the decrease in perceived speed for gratings modulated along the $S-(L+M)$ cardinal axis may be caused by a difference in the contrast sensitivity of the two chromatic systems. However, at the temporal frequencies used in Experiment 1, it has been found that the perceived speed of a red–green chromatic grating does not increase with chromatic contrast (Gegenfurtner & Hawken, 1996). Because of this, it is unlikely that the decrease in perceived speed observed for chromatic gratings modulated along the $S-(L+M)$ cardinal axis is caused by a lower perceived contrast per se.

Our findings are inconsistent with those of research on sensitivity to chromatic motion for gratings modulated along different azimuths in a cardinal color space. Lindsey and Teller (1990) do not report a large decrease in sensitivity to motion for chromatic gratings modulated along the $S-(L+M)$ cardinal axis in a motion discrimination task. Additionally, Lindsey and Teller (1990) found that the highest and lowest sensitivity to chromatic motion occurred at azimuths of 40–60° and 140° respectively, whereas no differences in perceived speed were found between these azimuths in our results. It should be noted that there are several methodological differences between the two studies. The main difference is that Lindsey and Teller (1990) measured relative thresholds rather than relative speeds, as in our study.

It has been proposed that a position tracking mechanism underlies chromatic motion perception (Seiffert & Cavanagh, 1999). This system is thought to underlie the perception of chromatic motion primarily at temporal frequencies of 2 Hz and below (Seiffert & Cavanagh, 1999). Hence, it seems unlikely that the decrease in perceived speed for gratings modulated along the $S-(L+M)$ cardinal axis in Experiment 1 is due to a differential in the contribution of the two chromatic mechanisms to a position-tracking system. At the temporal frequency used in the present experiment, it has been suggested that chromatic motion is detected primarily by low-level motion mechanisms such as motion-energy analyzers (Gegenfurtner & Hawken, 1996; Seiffert & Cavanagh, 1999). If this is the case, our results suggest that the $S-(L+M)$ system does not make a significant contribution to these low-level motion mechanisms.

It has been argued that chromatic motion is perceived exclusively by a third order motion system (Lu et al., 1999a,b). Thus, it could be suggested that our results are due to the gratings modulated along the $S-(L+M)$ cardinal axis being closer to isosalience than gratings modulated along other azimuths in color space. However, there is no a priori reason to suppose that equisalience differs for stimuli modulated along the $S-(L+M)$ and $L-M$ cardinal axes. Lu et al. (1999b) report large individual differences in isosalience. In contrast, the minimal perceived speed occurred for gratings modulated along the $S-(L+M)$ cardinal axis for all our observers. Another possibility is that chromatic gratings modulated along the $S-(L+M)$ cardinal direction cannot be used as efficiently by the third order motion system as chromatic gratings modulated along the $L-M$ cardinal axis.

In conclusion, it appears that information coming from the two postreceptoral chromatic mechanisms cannot be used with equal efficiency in the processing of chromatic motion. The results of Experiments 1 and 2 suggest that the $S-(L+M)$ mechanism does not contribute to the processing of chromatic motion under the conditions tested in these experiments.

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