# Role of chromatic and luminance contrast in inferring structure from motion

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We measured the ability to infer structure from motion (SFM) in several directions in three-dimensional color space. Only motion cues are useful to subjects in performing this three-dimensional shape-identification task. We report the following results: (1) SFM performance is at chance for equiluminant stimuli that isolate short-wavelength-sensitive cones. Hence the short-wavelength-sensitive-cone input to SFM is negligible. (2) SFM performance increases with the  $|\Delta L - \Delta M|$  signal when  $\Delta L + \Delta M = 0$  (i.e., only chromatic and no luminance contrast is available). We reject the hypothesis that SFM obtains input from a single chromatic mechanism combining the long- and medium-wavelength-sensitive cones linearly. Our data are compatible with SFM that uses the output of two mechanisms, one taking the difference between the long- and medium-wavelength-sensitive-cone signals and the other taking the respective sum. We reject the particular hypothesis that SFM utilizes only the magnitude and not the sign of the long- and medium-wavelength-sensitive-cone signal. (3) We compare SFM performance with threshold performance for velocity and motion discrimination. Stimuli with luminance contrast yield SFM performance that is superior to stimuli without luminance contrast when they are expressed as multiples of velocity discrimination threshold. This superiority is even greater when SFM performance is compared with motion-direction discrimination thresholds.

#### INTRODUCTION

Some researchers have suggested that the motion system is restricted to an analysis of the luminance component of the retinal image. Equiluminant chromatic gratings appear to move more slowly than luminance gratings,1 apparent motion is reduced at equiluminance,2 and motion of an equiluminant pattern is easily captured by motion as a result of luminance.3 However, chromatic information can disambiguate apparent motion,4 equiluminant chromatic gratings appear to move in depth,5 chromatic information can be used in motion segregation and motion-integration tasks,6 motion aftereffects occur for equiluminant stimuli,7 and results on the perception of coherent motion suggest that motion is analyzed in chromatic channels.8 In general, models assuming that only luminance<sup>9</sup> is computed in the motion task have been rejected. However, whereas L- and M-cone signals of opposite sign (equiluminant red and green lights) can be utilized for various motion tasks, S cones contribute little to the motion system.10

In the present study we investigate the chromatic mechanisms that are utilized to infer structure from motion (SFM). First, we ask whether a single chromatic mechanism suffices to explain SFM performance or whether we must postulate that SFM performance depends on the output of more than one chromatic mechanism. By "(chromatic) mechanism" we mean a linear combination of the L-, M-, and S-cone signals followed by a rectifying nonlinearity. We call an SFM model that assumes exactly one chromatic mechanism a single-mechanism model. For example, a model that states that SFM performance is a function of the luminance contrast of the stimulus is a specific single-mechanism model. We refer to a model that states that two chromatic mechanisms are required to account for SFM performance as a two-mechanism model,

for example, a model that assumes that SFM performance is a function of the combined output of a luminance mechanism (adding L- and M-cone signals) and an opponent mechanism (subtracting L- and M-cone signals). To test these hypotheses we measure SFM performance in the following directions<sup>11</sup> in three-dimensional color space: in an S-cone-isolating direction, in a direction such that only the difference between the L- and M-cone signals varies, in a direction such that the intensity is increased, and in several intermediate directions.

Second, if more than one chromatic mechanism must be postulated to account for the SFM performance, we ask whether identical chromatic mechanisms are utilized in tasks that conceptually precede the SFM computation. In other words, we ask whether the cone signals are combined in an identical fashion for different tasks. If the performance in the SFM task is the same when stimuli are equal multiples of their relevant threshold (e.g., motion or velocity discrimination threshold), then we may retain the hypothesis of identical mechanisms for different tasks.

#### **METHODS**

# Description of the Stimuli in Color Space

We express our stimuli in cone-excitation space as increments in the L-, M-, and S-cone coordinates  $(\Delta L, \Delta M, \Delta S)$  with respect to the gray background. The S-cone excitation is scaled arbitrarily such that  $[S(\lambda)]/[L(\lambda)+M(\lambda)]=1.0$  at  $\lambda=400$  nm. The L- and M-cone fundamentals of Smith and Pokorny (based on the original Judd-modified CIE 1931 x,y,z standard functions) are scaled such that their integral (over wavelength) equals the  $V(\lambda)$  function; that is, we assume that only L and M cones contribute to luminance. Equiluminant red or green stimuli are lights with  $\Delta L=-\Delta M$  and  $\Delta S=0$ ,

achromatic stimuli are lights that are simply increments and decrements of the background intensity b, nominally equiluminant yellowish-greenish or violet stimuli are lights with  $\Delta L = \Delta M = 0$  and  $|\Delta S| > 0$ . The background is metameric to an equal-energy white light with cone excitations  $L_b = 0.67$ ,  $M_b = 0.33$ , and  $S_b = 0.016$ .

We employed stimuli at different chromatic contrasts. The low, medium, and high cone contrasts  $[(\Delta L/L_b), (\Delta M/M_b)]$  for the equiluminant red lights were (0.0456, -0.0907), (0.0639, -0.127), and (0.0821, -0.1633). The cone contrasts for the equiluminant green lights were of the same magnitude but of reversed sign. The S-cone contrast was zero for red and green lights. The low and high S-cone contrasts of the yellowish lights were -0.56 and -0.75, respectively. Violet lights had contrasts of the same magnitude but of reversed sign. The L- and M-cone contrast was zero for the yellowish and violet lights.

A problem in evaluating performance for equiluminant stimuli is the luminance artifact resulting from chromatic aberration. To reduce these effects, we blur the stimuli with a Gaussian mask such that the relative amplitude is 0.5 at a spatial frequency of 2 cycles per degree (c/deg) (and lower at all higher frequencies). For sine-wave gratings of spatial frequencies lower than 3 c/deg there is a negligible effect of the luminance contrast introduced by chromatic aberration on the perceived velocity.1 Furthermore, assuming an optimal focus<sup>14</sup> (i.e., a focal state that maximizes the retinal contrast for the luminance mechanism  $V_{\lambda}$ ), we predict that the luminance artifact resulting from chromatic aberration is largest for the violet (S-cone-isolating) lights, intermediate for the red and green lights, and smallest for the yellowish lights. assumption of an optimal focal state is plausible since the observer is adapted to a white background and the stimuli are presented only briefly. Hence we will be able to evaluate the magnitude of the luminance artifact resulting from chromatic aberration by comparing the performance for the (nominally equiluminant) red, green, violet, and yellowish lights. Since performance for equiluminant violet and yellowish lights is comparable, we conclude that chromatic aberration does not produce a significant luminance contrast with our stimulus conditions.

#### SFM: Stimuli and Task

Sperling et al. 15 introduced the shape-identification task that was used in this research. The shapes consist of bumps and concavities on a flat ground. Each stimulus is based on one of two triangular layouts (denoted u and d), as shown in Fig. 1(a). At each of these three points the stimulus can be perceived as closer to the observer than the ground (+), in the ground (0), or behind the ground (-). The depths of all locations outside the circle surrounding these points are set to be in the ground. The depth is interpolated between and around these points by use of a smooth spline, resulting in shapes consisting of a small number of bumps or concavities varying in shape and location of each bump. Observers were required to identify the shape, which includes the specification of the triangular layout (u or d) and the depth sign at each corner of the triangle (+, 0, or -). Figure 1(b) shows four of the 53 possible shapes. Observers also indicated which of two rotation paths (l or r) were used, as indicated in Fig. 1(c).

Stimuli were generated by randomly scattering points

on the chosen surface, rotating that surface back and forth about a vertical axis, and projecting the resulting points to the image plane by using parallel projection. In addition, the points scintillated slightly (points were deleted and new points added) to remove any density cues to the task (see Ref. 15 for further details). As with any SFM stimuli, the interpretation is ambiguous, and the depth values and direction of motion may perceptually reverse. Instead of perceiving a bump moving to the left, one may perceive a concavity moving to the right. Either of these responses is scored as correct. After each trial the observer received as feedback the set of possible correct responses.

Three practiced observers participated in the experiment. One was an author, and the others were naïve to the purpose of the experiment. The subjects were instructed to fixate a cross located at the lower edge of the stimulus pattern. The SFM stimulus subtended a visual angle 6.6 deg wide and 6.0 deg high. Trials were run at two different mean luminance levels (15 and 60 cd/m²). Since we did not find any significant differences between the low and high mean luminance conditions, we report data only for the high mean luminance condition.

Stimuli were displayed on a Conrac 7211 RGB color monitor operating at a refresh rate of 60 Hz. The stimuli were stored on a Vax 11/750 computer and downloaded to an Adage RDS-3000 frame buffer. In each trial a new movie consisting of 30 frames was presented. Each stimulus frame was presented for four successive video frames at 60 Hz, resulting in a display rate of 15 new frames/s and a stimulus duration of 2 s. The convolution with the Gaussian mask was computed on line.

The velocities ranged between 0.6 and 4 deg/s, where the peak velocity was achieved in only one or two frames. The average velocity in the vicinity of a peak or a valley was  $\sim$ 1.6 deg/s. The ground dots at the edges of the display moved at a velocity of  $\sim$ 0.6 deg/s.

## **Threshold Measurements**

We will compare SFM performance for chromatic and achromatic stimuli with the psychophysical performance in simpler tasks. This enables us to decide whether these chromatic mechanisms are identical for different tasks or whether the cone signals are weighted differently.

The choice of the threshold that is used to normalize SFM performance is determined by the model that we assume for the SFM computation. Clearly, several stages are prerequisites to SFM: the moving stimulus must be visible, and the direction of motion must be identified. Detection of motion by itself is not sufficient to yield a correct answer in our SFM task. The task may be solved if the local motions are identified and classified accurately as leftward, static, or rightward. However, there is strong evidence that local velocity measurements are used to infer three-dimensional shape given this kind of stimulus. For example, subjects discriminate quite well between different bump heights, which requires the discrimination of velocities in addition to correct identification of direction of motion. 16

We measured thresholds for visibility of either a steady or a moving Gaussian blob, for identification of direction of motion, and for velocity discrimination. For the chromatic stimuli, detection and discrimination thresholds

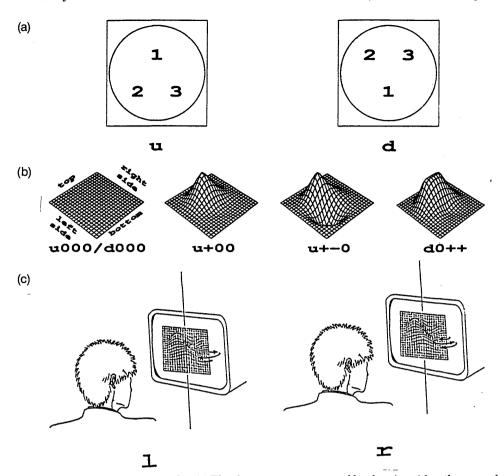


Fig. 1. Stimulus shapes and shape-identification task. (a) The shapes were constructed by choosing either the upward- or the downward-pointing triangular layout (u or d). Each of the three designated locations within the triangle was associated with either a positive depth (peak), zero depth (flat), or a negative depth (valley), denoted by +, 0, and -, respectively. Depth outside the circle was fixed at zero, and depths at all other locations were interpolated by use of a spline. (b) Four representative shapes given by this construction. (c) The shapes rotated either first left, then right, then left or in the opposite series, as indicated. The task of the observer was to determine which triangular layout (upward or downward pointing) was used, to identify the depth at each of the three locations, and to indicate the rotation direction (l or r).

will be compared with SFM performance for the chromatic conditions that yield the minimum performance. As such, the chromatic stimuli will be chosen based on the results of the SFM data so that they are commensurate. This ensures that the normalization by threshold data will be sensitive to changes in the chromatic direction, free of any assumption regarding the definition of equiluminance for the SFM task. Hence, for the contrast thresholds, contrast was varied along the line connecting the background color and the SFM minimum.

The stimuli were generated by using the HIPS software<sup>17</sup> by convolving a dot with a Gaussian mask such that the relative amplitude was 0.5 for a spatial frequency of 2 c/deg and smaller than 0.5 for all higher frequencies, identical to the blurred dots of the SFM stimuli. To the extent possible we chose all other stimulus parameters similar to the SFM stimulus. For visibility and discrimination of motion-direction threshold the duration of the stimulus was 500 ms. The stimulus moved at a velocity of 1.7 deg/s, which is representative of the velocities present in the SFM stimuli. The subject either had to judge in which of the two intervals (two-interval forced choice) the stimulus occurred (visibility threshold) or had to identify the direction of motion as right or left (two-alternative forced choice). To obtain thresholds for velocity discrimi-

nation as a function of contrast, two rather different velocities (0.9 and 1.7 deg/s) were used, and the subject was asked whether the slower stimulus appeared in the first or the second interval (two-interval forced choice). Since either stimulus duration or traversed distance is sufficient for a decision as to which of the two stimuli moves faster, the traversed distance (and hence the duration) was randomized for both stimuli.

Employing an adaptive procedure with three interleaved staircases, we assessed the contrast at which 81% correct responses were given. The chance performance was 50% for the two-interval forced-choice task (visibility) as well as for the two-alternative forced-choice tasks (direction of motion and velocity discrimination). For each condition the final threshold is the average of at least six midrun estimates. Within one session the direction in color space and the task were kept constant. For example, velocity discrimination thresholds in the red direction were measured in one block of trials.

# Hypotheses

Our first goal is to test various hypotheses on the combination of the cone signals for the SFM task. That is, we seek to assess the weight of each cone class for the SFM task and test whether the cone signals are recombined in

one or more than one mechanism. We now describe four models and their predicted outcomes.

Figure 2 depicts four hypothetical outcomes for stimuli in the L-M direction (equiluminant red and green lights), the intensity direction (achromatic lights), and several intermediate directions (red and green lights of a luminance slightly above or below the background luminance). Model (a)'s hypothesis is the most specific one, model (d)'s the most general. In the predictions, we make the strong and unacceptable assumption that the percent of correct responses is proportional to the output of the mechanism. However, below we use only qualitative aspects of these predictions, which are preserved by any monotonic transformation of these predictions. In each figure, the predicted percent correct is plotted as a function of luminance increment  $(\Delta L + \Delta M)$ . The nominal value of  $\Delta L$  +  $\Delta M = 0.1$  refers to a luminance contrast of 10%. Outcomes (a) and (b) correspond to single-mechanism models

for SFM, whereas (c) and (d) are predictions of two-mechanism models.

The simplest model that we consider is one in which SFM performance is a function of luminance only. Model (a) predicts that performance will drop to chance at the point  $\Delta L + \Delta M = 0$  for all the equiluminant stimuli.

Model (b) is slightly more general. Here we allow the L and M cones to receive different weights. In other words, performance is a function of  $|w_L \Delta L + w_M \Delta M|$ . This model predicts that minimum SFM performance will vary for the red and green lights as a function of the weights  $w_L$  and  $w_M$ . The predicted performance will drop to chance only if the weights of the L and M cones are such that  $w_L \Delta L + w_M \Delta M = 0$ . The example illustrated in model (b) assumes that  $w_L = 2$  and  $w_M = 1$ . If the weighted sum  $2\Delta L + \Delta M$  equals zero, then  $\Delta L = -(\Delta M/2)$ , and the sum  $\Delta L + \Delta M$  equals  $\Delta M/2$ , which is smaller than zero for reddish lights and larger than zero

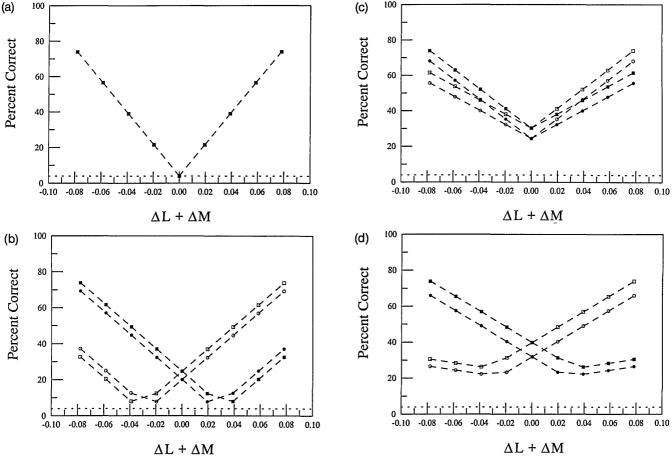


Fig. 2. Hypothetical outcomes of an SFM experiment under the assumption that performance in the SFM task is proportional to the output of the following mechanisms. Percent correct in the SFM task for lights of different chromatic contrasts is plotted as a function of the luminance increment ( $\Delta L + \Delta M$ ). SFM performance is measured for various luminance levels around the point of zero luminance contrast. Hypothesis (a) is the most specific one, hypothesis (d) the most general. (a) Under the hypothesis that only luminance ( $\Delta L + \Delta M$ ) is utilized for the SFM task, we expect to see the same SFM performance for lights of different chromatic contrasts and of the same luminance contrast. (b) We allow for different weights of the L- and M-cone signals. That is, SFM performance is proportional to  $|w_L \Delta L + w_M \Delta M|$ , where  $w_L, w_M > 0$ . We illustrate the case  $w_L = 2$  and  $w_M = 1$ . In this case the minimum SFM performance for red lights (open symbols) will be shifted toward a negative luminance contrast ( $\Delta L + \Delta M < 0$ ), and SFM performance for green lights (filled symbols) will reach the minimum at a positive luminance contrast. Squares denote lights of high chromatic contrast, and circles denote lights of low chromatic contrast. (c) Here we assume that a luminance mechanism ( $w_{\text{lum}}|\Delta L + \Delta M|$ ) and a chromatic mechanism ( $w_{\text{ch}}|\Delta L - \Delta M|$ ) feed into the SFM system with different weights. Under this hypothesis we expect the minimum SFM performance to occur always at the point of nominal equiluminance ( $\Delta L + \Delta M = 0$ ). However, the minimum SFM performance will not drop to chance for any  $w_{\text{ch}} > 0$ . (d) In the most general case two mechanisms are used, one close to a pure luminance mechanism ( $|w_L \Delta L - w_M \Delta M|$ , where  $w_L, w_M > 0$ ) and the other close to a pure chromatic mechanism ( $|w_L \Delta L - w_M \Delta M|$ , where  $w_L, w_M > 0$ ). The two mechanisms may be weighted unequally (i.e.,  $w_{\text{lum}} \neq w_{\text{ch}}$ ).

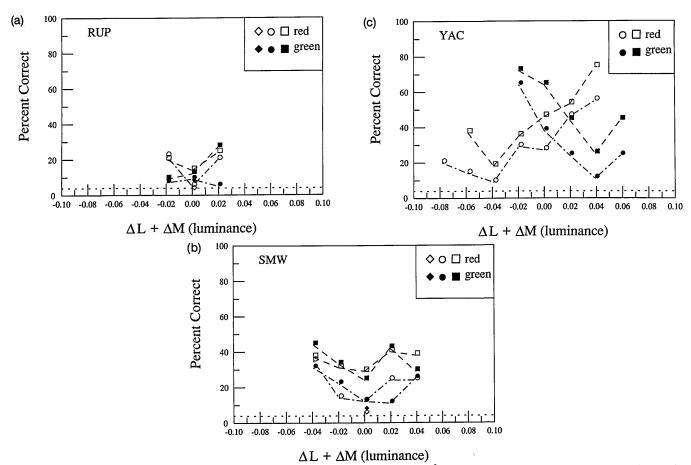


Fig. 3. Results of the shape-identification task for the high luminance level (60 cd/m²). Percent correct in the SFM task for chromatic lights with added luminance increments or decrements is plotted as a function of the sum of the L- and M-cone signals ( $\Delta L + \Delta M$ ). Error bars are identical to those in Fig. 4. That is, the same percent correct in both figures results in the same confidence intervals. Filled symbols denote greenish lights, and open symbols denote reddish lights; diamonds, circles, and squares symbolize lights of increasing chromatic contrast. For example, filled squares illustrate SFM performance for green lights of the highest chromatic contrast as a function of an added luminance increment or decrement. The minimum SFM performance for one subject is clearly different from the nominal equiluminance point (c): minimum SFM for the green lights is shifted toward a positive luminance increment; minimum SFM for the reddish lights is located at a negative luminance increment. In other words, for this subject the plane of minimum SFM performance. However, SFM performance plane such that reddish lights require a negative luminance to yield minimum SFM performance. However, SFM performance increases with increasing chromatic contrast (squares compared with circles). These data are consistent with a two-mechanism model that allows for different weights of the L and M cones within each mechanism [Fig. 2(d)]. For the other two subjects the minimum SFM coincides with the nominal equiluminance point [(a) and (b)]. Again, performance in the SFM task improves with increasing chromatic contrast (squares are above circles, which are above diamonds). This is best seen for the equiluminant chromatic lights (i.e., at the point  $\Delta L + \Delta M = 0$ ). Comparing the data with the hypothetical outcome in Fig. 2(c) reveals that the data for subject SMW and RUP are compatible with a two-mechanism model and equal weights for L and M cones.

for greenish lights. In other words, minimum performance will be reached at a  $\Delta L + \Delta M$  value that is smaller than zero if  $\Delta M < 0$  and greater than zero if  $\Delta M > 0$ . In general, the larger the relative weight of the L cones, the farther leftward the minimum SFM performance shifts from the nominal equiluminance point for the red lights. The location of the minimum also depends on the chromatic contrast, where chromatic contrast is expressed as the absolute values of  $\Delta L$  and  $\Delta M$ . This singlemechanism hypothesis predicts that chance performance will result from any chromatic contrast as long as the appropriate luminance increment is found such that  $w_L \Delta L + w_M \Delta M = 0$ . The important feature of hypothesis (b) is that the SFM performance for lights of high chromatic contrast (squares) is not uniformly higher than for the low chromatic contrast stimuli (circles).

Model (c) assumes that both chromatic and luminance information are utilized by the SFM system and that the

L and M cones are weighted equally. Thus performance will be monotonically increasing in  $w_{\rm lum}|\Delta L + \Delta M| + w_{\rm ch}|\Delta L - \Delta M|$ . In this model, for red and green lights the minimum performance will occur at  $\Delta L + \Delta M = 0$ . In the example shown in model (c),  $w_{\rm lum} = 2$  and  $w_{\rm ch}$  is set to 1. A slightly asymmetric SFM performance for luminance increments and decrements is predicted. The extent of the asymmetry depends on the relative weighting of the luminance and chromatic omponents. When L and M cones are weighted equally in the chromatic and luminance components, the predicted performance for the red and green lights of high chromatic contrast (squares) is never below performance for the low-chromatic-contrast lights (circles).

Model (d) states that SFM performance increases with  $w_{\text{lum}}|w_L\Delta L + w_M\Delta M| + w_{\text{ch}}|w_L\Delta L - w_M\Delta M|$ . When L and M cones are weighted unequally, the minima for red and green lights will be shifted depending on their respec-

tive weights as outlined for outcome (b). In model (d) the L cones are weighted twice as much as the M cones for both mechanisms and the luminance and chromatic mechanisms are weighted equally.

#### **RESULTS**

#### L- and M-Cone Input to SFM

Figure 3 depicts the SFM performance for red and green lights for increasing chromatic contrasts as a function of the luminance component of the stimulus.  $\Delta L + \Delta M =$ 0 denotes the nominal equiluminance point. SFM performance improves with increasing chromatic contrast: percent correct in the SFM task is higher for colored lights of high chromatic contrast (squares) compared with lights of medium chromatic contrast (circles) and low chromatic contrast (diamonds). For all observers, the minimum SFM performance is above chance (dashed lines at 4% correct). Since we sampled the luminance contrast in steps of 2% of contrast, there could be an intermediate luminance contrast at which performance drops to zero. However, especially for subject SMW, percent correct as a function of luminance contrast varies rather smoothly. Hence we do not expect an abrupt drop to chance performance at an intermediate contrast level. In addition to the above-chance performance, the location of the minimum SFM point varies between observers: for subject YAC the minimum SFM performance occurs at a luminance decrement ( $\Delta L + \Delta M < 0$ ) for the reddish lights and at a luminance increment for the greenish lights<sup>18</sup>; for the other two subjects the minimum SFM occurs at zero luminance contrast ( $\Delta L + \Delta M = 0$ ).

Figure 4 compares SFM performance for chromatic (red and green) and achromatic stimuli (dark gray and light gray) as a function of the sum of the magnitudes of L- and M-cone signals  $(|\Delta L| + |\Delta M|)$ . Filled symbols denote chromatic stimuli, and open symbols denote achromatic stimuli with a positive (upward-pointing triangles) or a negative (downward-pointing triangles) luminance contrast. The error bars denote 95% confidence intervals. For the chromatic direction we plotted the stimuli that produced minimum SFM performance (from Fig. 3).19 Figure 4 shows that L- and M-cone signals of the same sign (achromatic stimuli) are more effective for SFM than are L- and M-cone signals of opposite sign (chromatic stimuli).20 Furthermore, for subjects RUP and SMW the achromatic and equiluminant chromatic stimuli that are plotted in Fig. 4 were chosen to be of the form  $-\Delta L$ ,  $+\Delta M$ or  $+\Delta L$ ,  $-\Delta M$  (equiluminant chromatic lights) and  $+\Delta L$ ,  $+0.5\Delta M$  or  $-\Delta L$ ,  $-0.5\Delta M$  (achromatic stimuli). Hence we can compare performance for lights of the same L-cone signal when an M-cone signal of the same or opposite sign is added. If only the sum of the magnitudes of the L- and M-cone signals is utilized in the SFM task, then a light of the form  $+\Delta L$ ,  $-\Delta M$  (chromatic) is predicted to yield a performance superior to a light of the form  $+\Delta L$ ,  $+0.5\Delta M$ (achromatic). However, comparison of the chromatic (filled symbols) and achromatic lights (open symbols) in Fig. 4 demonstrates that the sign of the M-cone signal is crucial: for a given L-cone signal, adding on M-cone signal of the same sign and small magnitude yields a higher SFM performance than does adding an M-cone signal of opposite sign but larger magnitude.

#### S-Cone Input to SFM

Figure 5 shows the SFM performance for achromatic and equiluminant S-cone-isolating stimuli plotted as a func-

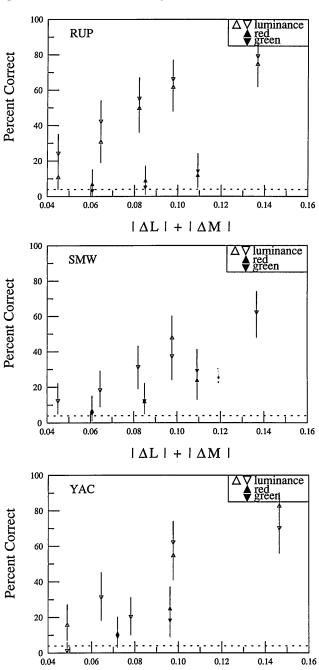
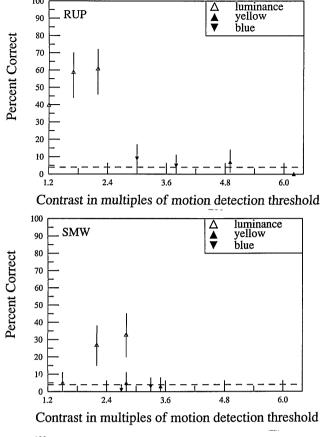
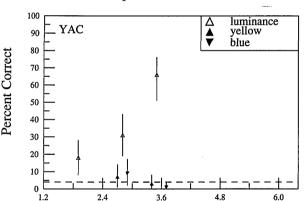


Fig. 4. Results of the shape-identification task for chromatic and achromatic stimuli. Percent correct in the SFM task is plotted as a function of the sum of the magnitudes of the incremental Land M-cone signals. SFM performance for chromatic lights yielding a minimum SFM performance (from Fig. 3) as well as for achromatic lights is plotted. Open symbols represent the performance for achromatic stimuli, either below (downward-pointing triangles) or above (upward-pointing triangles) the mean luminance. Closed symbols denote chromatic stimuli, either red (upward-pointing triangles) or green (downward-pointing tri-The dashed lines indicate chance performance (4%). angles). Vertical bars denote 95% confidence intervals. For all subjects and both mean luminance levels we find a consistent superiority of the achromatic-defined stimuli over the stimuli defined primarily by chromatic contrast.

 $|\Delta L| + |\Delta M|$ 

100





Contrast in multiples of motion detection threshold

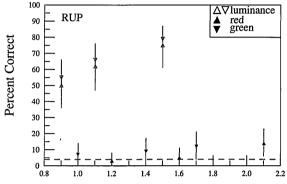
Fig. 5. Normalized SFM: results of the shape-identification task for achromatic stimuli and for the S-cone-isolating (yellowish-greenish and violet) lights. Percent correct is plotted as a function of multiples of threshold for detection of motion. For all subjects SFM performance for S-cone-isolating lights is at chance.

tion of detection threshold of a moving Gaussian target. For all subjects performance drops to chance (dashed lines at 4% correct) for yellow and blue lights.

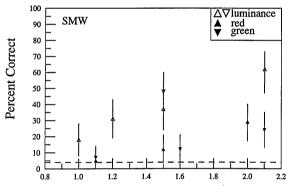
We attempted to measure velocity discrimination threshold as a function of the contrast in the S-cone-isolating direction as well. However, we were not able to produce a contrast high enough that we could obtain reliable estimates of the thresholds. The thresholds were close to or beyond the contrast range that we could produce with our monitor. However, since SFM performance for S-cone-isolating stimuli is at chance, equating with threshold is not crucial.

# SFM Performance Compared with Velocity Discrimination Thresholds

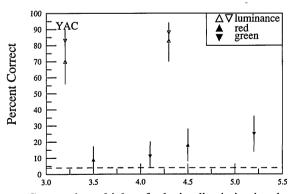
In this section we evaluate the input of chromatic and achromatic contrast to SFM by comparing SFM performance with performance at tasks prerequisite to performing the SFM task. We compare performance for two directions in color space: a red–green direction and an achromatic direction. As is pointed out above, performance of the SFM task requires, at a minimum, accurate classification of motion at several spatial locations. If the SFM performance is comparable between chromatic and achromatic stimuli when contrast is expressed in units of contrast



Contrast in multiples of velocity discrimination threshold



Contrast in multiples of velocity discrimination threshold



Contrast in multiples of velocity discrimination threshold

Fig. 6. Normalized SFM: results of the shape-identification task for red, green, and achromatic stimuli. Percent correct is plotted as a function of multiples of contrast threshold for velocity discrimination. The velocity discrimination threshold is measured as a function of contrast. The direction in color space along which contrast is varied is defined by the minimum SFM performance as illustrated in Fig. 3. For all subjects SFM performance for achromatic stimuli is superior to SFM performance for chromatic lights when both kinds of stimulus are expressed as multiples of their respective velocity discrimination thresholds.

thresholds for motion detection, direction discrimination, or velocity discrimination, then no additional deficit in the SFM mechanism need be postulated for chromatic stimuli compared with achromatic stimuli.

Hence we determined the thresholds for various relevant psychophysical tasks for both achromatic and chromatic stimuli and scaled the SFM performance with these thresholds. In Fig. 6 we plot SFM performance when the chromatic and achromatic stimuli are expressed as multiples of their contrast thresholds for velocity discrimination. Each threshold is the average of at least six midrun estimates. The chromatic stimuli (filled symbols) are the stimuli yielding minimum SFM performance (from Fig. 3) and are not necessarily identical with the stimuli of zero luminance contrast. The various thresholds were measured along the line in color space defined by the coordinates of the background and the coordinates of the minimum SFM stimulus. We did this so that the interpretation of our results is not affected by a potential shift of the point of the observed minimum SFM performance away from the point of zero luminance contrast.

When scaled by the threshold for velocity discrimination, achromatic stimuli remain more effective for SFM than do chromatic stimuli (Fig. 6). In addition, velocity discrimination shows a larger deficit for chromatic stimuli than does motion-direction discrimination or detection. In other words, the ratio between thresholds for chromatic and achromatic stimuli for visibility and direction of motion is smaller than or equal to the ratio for velocity discrimination (for all subjects). Hence, the SFM performance for achromatic and chromatic stimuli will not be superimposed when normalized by these thresholds either.

#### Note on Stimulus Appearance

Our result that SFM performance for chromatic and achromatic stimuli is not comparable when equated with various thresholds reflects the actual appearance of the stimuli rather truthfully. Chromatic and achromatic contrast, which give rise to identical SFM performance (same percent correct), do not appear to be equally visible. Barely visible achromatic stimuli are perceived as moving quite fast, and structure can be inferred from a barely visible stimulus. For chromatic stimuli, although the pattern is clearly visible, the subject reports a perceptual slowing down of the motion and is not able to infer structure from this slow motion.

#### DISCUSSION

## Role of the S Cones in SFM

We define a chromatic mechanism as a linear combination of the L-, M-, and S-cone signals followed by a function f that increases monotonically with the magnitude of the linearly combined cone signals, that is,  $f(w_L \Delta L + w_M \Delta M + w_S \Delta S)$ . Under the conditions of our experiment, we could not produce an S-cone-isolating stimulus yielding SFM performance above chance (Fig. 5). Consequently the weight  $w_S$  is zero, and it suffices to consider only mechanisms that take as input the L- and M-cone signals. This finding is consistent with data collected in a motion-cancellation task, suggesting that S cones contribute little to the motion system. 10

#### Rejection of a Single Chromatic Mechanism

Comparison of Figs. 2 and 3 reveals the basic properties for the combination of the L- and M-cone signals. For subjects RUP and SMW [Figs. 3(a) and (b)] the minimum SFM occurs at the nominal equiluminance point ( $\Delta L$  +  $\Delta M = 0$ ), yet at the minimum SFM point that SFM performance is higher for the high chromatic contrast (squares) than for the low chromatic contrast (diamonds). This is incompatible with a single chromatic mechanism [Fig. 2, models (a) and (b)], which predicts chance performance (dashed line at 4%) at the minimum SFM point regardless of the chromatic contrast. For subject YAC [Fig. 3(c)] the minimum SFM occurs at a luminance contrast that is different from zero, yet the performance for the high chromatic contrast (squares) is always above the performance for lights of lower chromatic contrast (circles). These data are incompatible with hypotheses (a) and (b).

To summarize, the data are not compatible with a single-mechanism model stating that SFM performance is proportional to (or monotonically increasing with)  $|w_L \Delta L| + w_M \Delta M|$ . No linear combination of the L- and M-cone signals predicts SFM performance for chromatic and achromatic stimuli. In particular, this excludes SFM models that assume that only luminance is used to infer SFM.

#### **Evidence for at Least Two Chromatic Mechanisms**

The data of subjects SMW and RUP [Figs. 3(a) and (b)] are compatible with a two-mechanism model, as illustrated in Fig. 2(c). The minimum SFM performance coincides with the nominal equiluminance point but never drops to chance. In fact, it increases with increasing chromatic contrast (squares above circles). In the framework of the general two-mechanism model, this feature is predicted only if the weights of the L and M ones are approximately the same for the luminance mechanism. This result seems to contradict the common belief that the L-cone weight is twice as large as the M-cone weight in the luminance mechanism. However, we defined the L- and Mcone excitation as incremental cone excitation with respect to the background as opposed to cone contrast, that is, the ratio between the incremental cone excitation and the cone excitation of the background. Since the gray background's L-cone excitation is approximately twice as large as its M-cone excitation, the L-cone contrast of a chromatic stimulus presented on this background is approximately half of the M-cone contrast. Hence, if we had defined our stimuli in terms of their cone contrasts rather than of their incremental cone excitations, we would have concluded that the L-cone weight has to be twice as large as the M-cone weight to predict our data. To our knowledge there is no general agreement on whether the cones encode contrast or incremental cone excitation. The fact that the minimum SFM point occurs at  $\Delta L + \Delta M = 0$  as opposed to  $(\Delta L/L_b) + (\Delta M/M_b) = 0$  supports our assumption that cones do not encode contrast.

The data of subject YAC are in qualitative agreement with a two-mechanism model weighting the L and M cones differently [Fig. 3(c)]. For prediction of YAC's data the weight for the L cones must be approximately twice as large as the weight of the M cones.

The last model we consider is a specific two-mechanism model stating that SFM is proportional to (or monotonically increasing with)  $w_L|\Delta L| + w_M|\Delta M|$ . That is, we hy-

pothesize that only the magnitude, and not the sign, of the L- and M-cone signal is used to infer SFM. This model proved successful to predict vernier acuity data for stimuli with and without luminance contrast. Thresholds for vernier acuity for chromatic and achromatic stimuli are equated when the stimuli are expressed as the sum of the absolute L- and M-cone contrasts. The data in Fig. 5 are at variance with a model stating that the magnitudes of the L- and M-cone signals are combined linearly  $(w_L|\Delta L| + w_M|\Delta M|)$ . Given a positive L-cone signal, a higher SFM performance is achieved when a positive M-cone signal is added (resulting in a luminance signal) than when that same M-cone signal is subtracted (resulting in a chromatic signal).

To summarize, our data are compatible with the hypothesis that the SFM system obtains input from two mechanisms: one mechanism that computes  $|w_L \Delta L + w_M \Delta M|$ , and hence responds optimally to lights with L-and M-cone signals of the same sign, and a second mechanism that computes  $|w_L \Delta L - w_M \Delta M|$  and hence responds optimally to stimuli with the L- and M-cone signals of opposite sign. We reject the particular model that only the magnitudes, and not the signs, of the L- and M-cone signal are used in the SFM task.

#### **Normalized SFM Performance**

When we normalize SFM performance for achromatic and red-green chromatic stimuli with respect to their contrast thresholds for velocity discrimination (or direction discrimination), we find that achromatic stimuli yield superior SFM performance (Fig. 6). In other words, this suggests that there is an additional deficit in the SFM task for chromatic compared with achromatic input that is not accounted for by the velocity discrimination performance. A potential explanation is the different nature of the stimuli we used for the threshold measurements and the SFM task: whereas the spatial-frequency content and the velocities were comparable, the SFM stimuli consisted of a large number of Gaussian blobs as opposed to a single Gaussian blob employed for the threshold measurements.

Yet another possible cause for the different performance for normalized chromatic and achromatic lights is the fact that the SFM stimulus was not foveal but extended over several degrees of visual angle, whereas the stimulus that was used for threshold measurements was a small Gaussian blob. If the relative weight of the L- and M-cone signal varies as a function of eccentricity, then we would expect the minimum performance for SFM (measured with a large stimulus) to occur at a different L:M cone ratio than the minimum performance for motion detection or discrimination (measured with a small target). To explore this possibility we measured the thresholds for red-green and achromatic lights under different spatial conditions: the Gaussian target was presented foveally, peripherally, or at a spatial location chosen randomly at each trial. These pilot data did not demonstrate any systematic change in the relative performance of chromatic and achromatic lights.

We believe that comparing the performance for chromatic and achromatic lights for different tasks is interesting because it demonstrates that the effectiveness of the chromatic contrast decreases with the complexity of the

task. The ratio between the threshold for detecting a moving achromatic target and the threshold for detecting a moving chromatic target is larger than the comparable threshold ratio for velocity discrimination. Lindsey and Teller<sup>22</sup> measured thresholds for motion detection, motion discrimination, and form detection. They found that thresholds for discrimination were always larger than for motion detection (3:1) for equiluminant lights. Cavanagh and Anstis<sup>23</sup> reported ratios of 2:1 for equiluminant lights, whereas Watson et al.<sup>24</sup> found ratios of 1:1 for achromatic lights. These results are consistent with our threshold measurements: we find discrimination/detection ratios between 1:1 and 3:2 for equiluminant lights. Velocity discrimination/detection ratios are between 3:2 and 2:1.

To summarize, normalizing the chromatic and achromatic stimuli with respect to their velocity discrimination threshold (or motion discrimination or detection thresholds) does not equate them in structure-from-motion performance. The superiority of stimuli with luminance contrast increases with the complexity of the task.

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- 18. Subject YAC was also more red sensitive in the heterochromatic flicker task than was the average observer. YAC required a smaller L:M cone ratio than was predicted by the

- cone fundamentals of the average observer. Hence the L cones must have a larger weight than the M cones for this observer in the SFM and heterochromatic flicker tasks.
- 19. Instead of plotting the SFM performance for all stimuli (i.e., achromatic, chromatic, and those of combined contrast), we compare the achromatic stimuli only with those stimuli that produced the minimum SFM. This comparison suffices, since the performance of all other stimuli is intermediate.
- 20. The superiority of the achromatic signals would be even greater if we expressed the stimuli in terms of the absolute cone contrasts. Our experiment does not permit us to discriminate between these two possible inputs, since we kept the adaptation level constant throughout all experiments. For our conditions, the use of cone contrast (cone excitation of the test increment divided by the cone excitation of the background light) instead of the incremental cone excitation is equivalent to weighting the M cones twice as much as the L cones.
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