Perceived Speed of Colored Stimuli

Robert F. Dougherty,* William A. Press,
and Brian A. Wandell
Department of Psychology
Stanford University
Stanford, California 94305

Summary

The influence of contrast and color on perceived motion was measured using a speed-matching task. Observers adjusted the speed of an L cone contrast pattern to match that of a variety of colored test patterns. The dependence of speed on test contrast was the same for all test colors measured, differing only by a sensitivity factor. This result suggests that the reduced apparent speed of low contrast targets and certain colored targets is caused by a common cortical mechanism. The cone contrast levels that equate perceived speed differ substantially from those that equate visibility. This result suggests that the neural mechanisms governing speed perception and visibility differ. Perceived speed differences caused by variations in color can be explained by color responses that are characteristic of motion-selective cortex.

Introduction

In an ideal visual system, perceived speed does not depend on contrast or color. A stimulus moving at 5°/s should appear to move at the same speed whether it has high or low contrast, or whether it appears red or blue. The visual pathways do not achieve this goal. Low contrast achromatic luminance stimuli appear to move more slowly than otherwise matched high contrast stimuli (Stone and Thompson, 1992). Certain colored stimuli appear to move more rapidly than others (Cavanagh et al., 1984).

One explanation of this observation was the hypothesis that color and motion information are represented in independent processing streams (Livingstone and Hubel, 1988; Zeki, 1993). Colored stimuli with low luminance contrast targets were perceived to have low velocity, it was argued, because extrastriate motion areas receive luminance but not chromatic signals. Stimuli with zero luminance contrast, however, do appear to move and do evoke responses in extrastriate visual areas involved in motion perception (Cavanagh and Anstis, 1986, 1991; Saito et al., 1989; Chichilnisky et al., 1992; Gegenfurtner et al., 1994; Cropper and Derrington, 1996; McKeefry and Zeki, 1997; Thiele et al., 1999). Even so, it has been argued that there remains a quantitative discrepancy between the behavioral and neural measurements in motion-selective cortex (Hawken et al., 1994; Gegenfurtner and Hawken, 1996a). This discrepancy is explained by a new hypothesis that

*To whom correspondence should be addressed (e-mail: bobd@stanford.edu).

there are two cortical processing streams which process color information differently (Gegenfurtner and Hawken, 1996b).

In this and two companion papers we examine the cortical basis for the relationship between perceived speed, color, and contrast. Here, behavioral experiments designed to measure how perceived speed depends on color and contrast are described. The second paper reports functional magnetic resonance imaging (fMRI) measurements of color responsivity in a motion-selective portion of the human brain, region MT+ (Wandell et al., 1999 [this issue of *Neuron*]). The third paper describes measurements of neural activity in area MT of the awake monkey brain (Seidemann et al., 1999 [this issue of *Neuron*]). For the stimuli used in these studies, we find no significant discrepancy between the behavioral and neural measurements. Hence, the color information within the conventional motion pathway may be sufficient to explain behavioral judgments of relative speed.

Results

Each panel in Figure 1a shows how perceived speed increases with stimulus contrast, and different panels describe measurements for different observers. The curves within each panel show the relationship between contrast and speed for the three types of cone-isolating stimuli. In the experiment, subjects adjusted the physical velocity of a standard stimulus, an L cone–isolating stimulus at 2.5% contrast, to match the perceived speed of a colored test that always moved at 8.2°/s. Consider the curve measuring matches between an L cone test and the L cone standard. At 2.5% test contrast, the test and standard matched at the physical speed (8.2°/s), as expected. As test contrast increases, the L cone standard velocity increases as well. The smooth curve summarizes the covariation of speed and contrast. The function defining the curve is described in the Experimental Procedures.

For all three cone types, the curves relating test contrast to matching speed are the same. The curves differ only with respect to a horizontal shift along the log contrast axis. The size of the relative displacements measures the relative color sensitivity for the speed judgment task. For all three observers, the displacements show that L cone sensitivity is twice the M cone sensitivity and more than ten times the S cone sensitivity.

Figure 1b shows measurements of perceived speed using test colors formed by adding and subtracting M cone signals to the L cone test. Adding M cone contrast shifts the curve to the left, increasing the perceived speed. Subtracting M cone contrast shifts the curve to the right, decreasing the perceived speed.

The data in Figure 1 are plotted with respect to physical contrast of the test stimuli. Can the differences in perceived speed be explained in terms of the relative visual sensitivity to the contrast patterns? To answer this question, we replot the speed-matching data in Figure
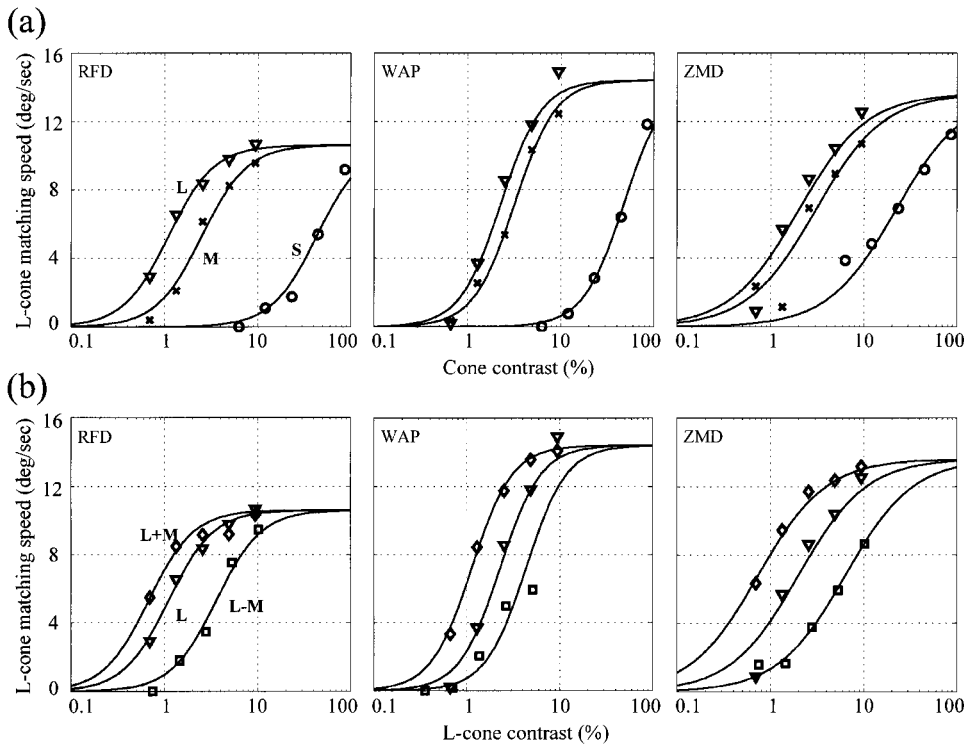
(a)

(b)

Figure 1. Speed Matches Between an L Cone Standard and Various Colored Tests

([a], Top Row) Matches to L, M, and S cone–isolating test stimuli are shown. The curves for the different cone types are labeled in the first panel. The contrast of the test, moving at a velocity of 8.2°/s (0.5 cycles/°), is shown on the horizontal axis. The speed of the 2.5% L cone standard is shown on the vertical axis.

([b], Bottom Row) Speed matches between an L cone standard and mixtures of L and M signals are shown. In each panel, the middle curve represents the same data as the L cone–isolating match in the upper panel. The other two curves show matches for colored targets in which an M cone signal was added or subtracted from the L cone test. The horizontal axis measures the cone contrast of the L cone component of the test mixture. In both (a) and (b), data for three observers are shown. Error bars indicating ±1 SEM were on the order of the symbol size and were omitted for clarity. Function-fit parameters: R. F. D.: for all conditions, $p = 1.8$, $m = 5.3$; $\sigma = 0.0111$ for L cone, $\sigma = 0.0251$ for M cone, $\sigma = 0.4307$ for S cone, $\sigma = 0.0068$ for L + M, and $\sigma = 0.0508$ for L − M; W. A. P.: for all conditions, $p = 2.0$, $m = 7.2$; $\sigma = 0.0228$ for L cone, $\sigma = 0.0320$ for M cone, $\sigma = 0.4773$ for S cone, $\sigma = 0.0159$ for L + M, and $\sigma = 0.0612$ for L − M; Z. M. D.: for all conditions, $p = 1.2$, $m = 6.8$; $\sigma = 0.0200$ for L cone, $\sigma = 0.0303$ for M cone, $\sigma = 0.2203$ for S cone, $\sigma = 0.0104$ for L + M, and $\sigma = 0.0898$ for L − M.

2 using a horizontal axis that measures cone contrast relative to threshold. This adjustment does not bring the curves together; the differences in the perceived speed of the colored targets are not explained by differences in color sensitivity. Observers detect the (L−M) and S cone patterns at very low contrast levels; nonetheless, these patterns appear to move quite slowly.

The data in the first two figures are all based on matches with respect to an L cone standard. Do the relative sensitivity judgments depend on the color of this standard? To answer this question, we carried out a control condition in which judgments were made using an S cone standard. The curves in Figure 3 show that the horizontal displacement along the log contrast axis was unchanged when measurements were made using a different standard.

Even at relatively high contrast, the S cone test appears to move very slowly (Cavanagh et al., 1984). Is it possible that S cone signals do not reach the motion pathways and that all of the perceived S cone motion is due only to small calibration errors in the S cone stimulus, resulting in unwanted L and M cone signals? To test this hypothesis, we superimposed an intense

yellow light on the display. The background light reduces the L and M cone contrast but spares the S cone contrast. Were the nominal S cone matches due to inadvertent L and M cone signals caused by the stimulus, the yellow background light should influence the S cone matches in the same way that it influences the L and M cone matches.

Figure 4 shows that the yellow background light influences the L and M cone stimuli differently from the S cone stimuli. A match between an L cone test and an L cone standard made upon a neutral background remains a match when the yellow light is added. The yellow background reduces the contrast of both L cone stimuli so that both appear to move more slowly. But, the match is preserved. A match between an L cone standard and an S cone test made on a neutral background is disturbed by adding the yellow background light. The yellow light slows the L cone standard but not the S cone test. In the presence of the yellow background, the S cone test appears to move more quickly than the L cone stimulus; hence, the speed of the L cone standard must be increased to achieve a speed match. Similarly, a match between a pair of M cone stimuli is preserved
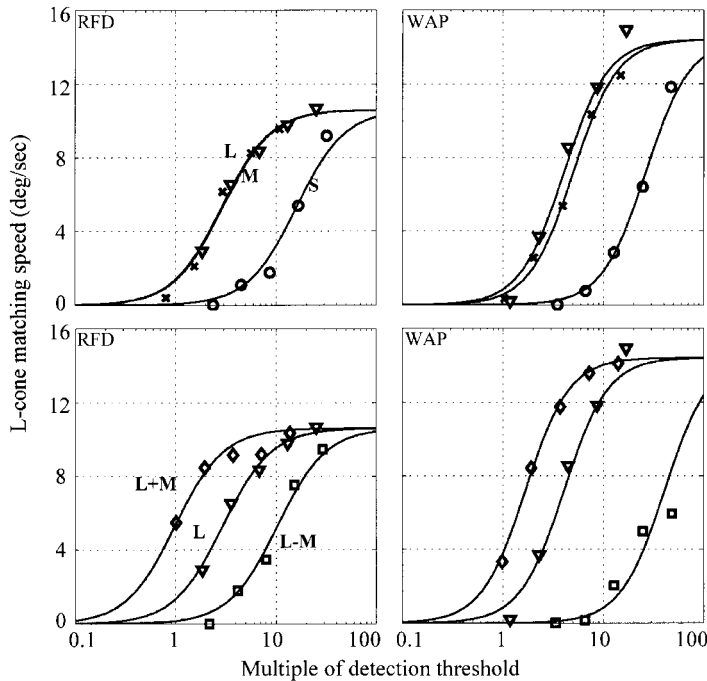
Figure 2. Speed Matches Plotted Relative to Threshold Contrast

Other details as Figure 1.

when the yellow background is added. But, the yellow background disturbs the match between an M cone stimulus and an S cone stimulus. We conclude that the S cone speed judgments are carried by S cone signals, not by unwanted signals in the L and M cones.

Discussion

The relative sensitivities of color and luminance as revealed by detection thresholds differ from the relative sensitivities revealed by speed judgments. This result suggests that the neural mechanisms that limit the visibility of these targets differ from those that compute speed. This supports the hypothesis that color information is distributed to various perceptual processes, including those involved in motion perception (Cavanagh and Anstis, 1991; Chichilnisky et al., 1993; Cavanagh et al., 1998; Dobkins and Albright, 1998). The 1.0–1.3 log unit difference in the S cone and luminance contributions to perceived speed measured behaviorally here
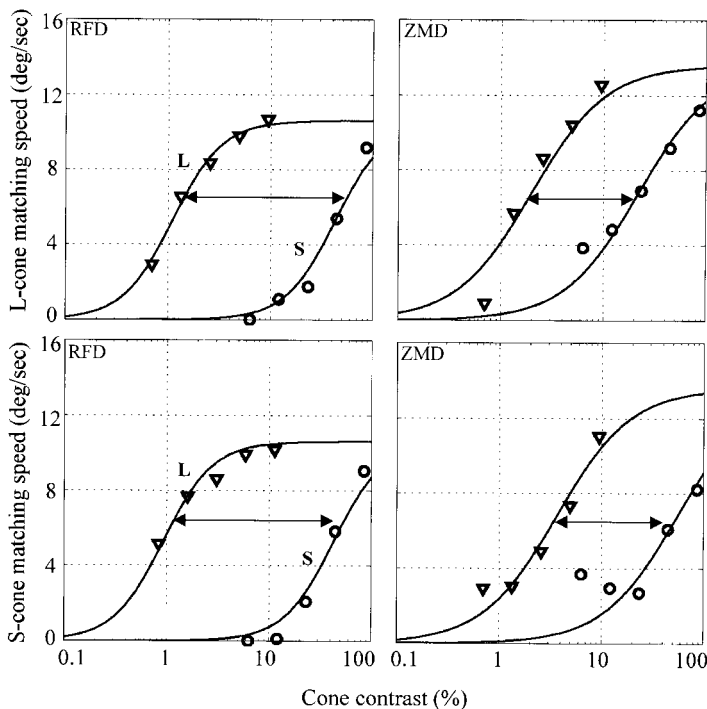

Figure 3. Transitivity Experiment

In the top row, the L cone and S cone data from Figure 1 are plotted. In the bottom row, measurements using an S cone standard rather than an L cone standard are shown. (Cone contrast of the S cone standard was 75% for R. F. D. and 86% for Z. M. D.) Other details as in Figure 1.
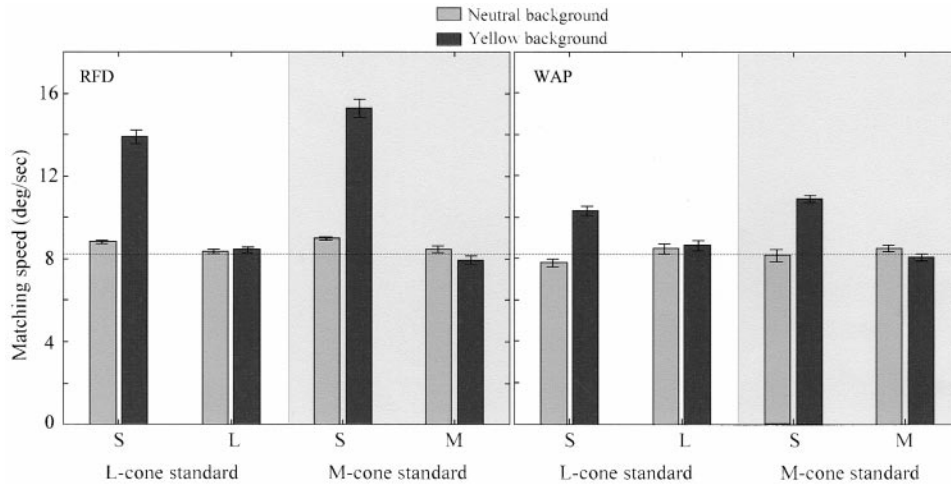
Figure 4. S Cone Isolation Control Experiments

The matching speed of various tests (8.2°/s) on a neutral (shaded bars) or yellow (closed bars) background was measured. The speed of an L cone standard (2.5% nominal contrast) was adjusted to match each test. The S and M cone contrasts were chosen to match the perceived speed of an L cone standard at 8.2°/s (horizontal dotted line) on a gray background. The L and M cone matches are not disturbed by the background change, while the S cone matches are. See text for further explanation. Error bars indicate ±1 SEM.

corresponds well with human MT+ signals measured using fMRI (Wandell et al., 1999) and macaque unit recordings in area MT (Seidemann et al., 1999). Hence, we suggest that the apparent speed of different colored targets is a consequence of the signals in human region MT+. Other perceptual quantities, such as visibility, are a consequence of signals at other cortical sites.

Related Literature
Hawken and colleagues (Hawken et al., 1994; see also Figure 5 in Burr et al., 1998) argue that the perceived motion of color and luminance signals is carried by different motion pathways. Their argument is based on a difference in the slope relating perceived speed to contrast in luminance and isoluminant targets. Yet, fitting the complete data set reported here while allowing

the slope to be a free parameter, we find no consistent difference between luminance and isoluminant stimuli.

Figure 5 shows that in the range of overlap, the measurements in these studies agree. The difference arises because these investigators made measurements over a smaller range of contrast levels than were used here. For example, Hawken et al. (1994) made perceived speed measurements at contrast levels exceeding five to eight times the detection threshold for both luminance and isoluminant stimuli. The data reported here show that the apparent speed of isoluminant targets rises sharply only at contrast levels significantly above threshold, while the apparent speed of luminance targets rises near threshold levels and is nearly saturated at higher contrasts. Figure 5b shows that when the data are restricted to this range, we too see a difference in
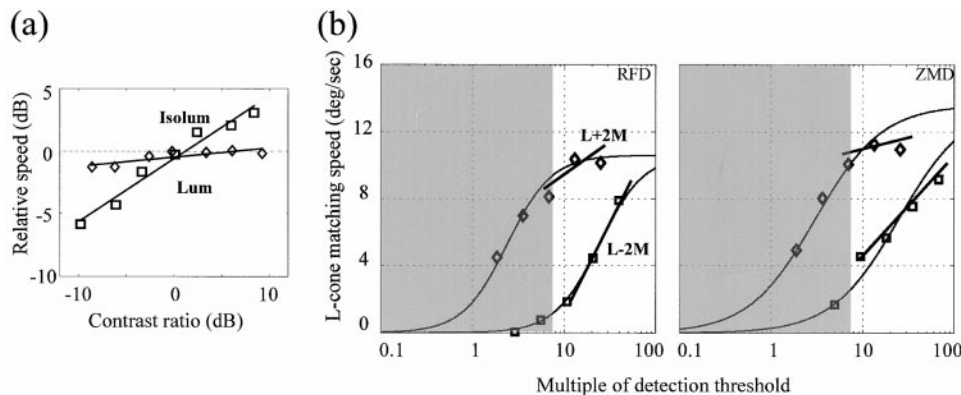

Figure 5. Speed-Matching Ratios for Luminance and Isoluminance Targets

(a) The ratio of target contrasts is measured on the horizontal axis, and the relative velocity is measured on the vertical axis. The slopes of the luminance and isoluminance measurements differ when test contrasts are measured relative to detection threshold. Data from Hawken et al. (1994).
(b) Comparisons of speed matches using a luminance (L + 2M) and isoluminance (L − 2M) target are shown for two observers. The shaded region marks contrasts at or below five times threshold. When restricting comparisons to contrasts above this range, the slopes differ. See text for details.
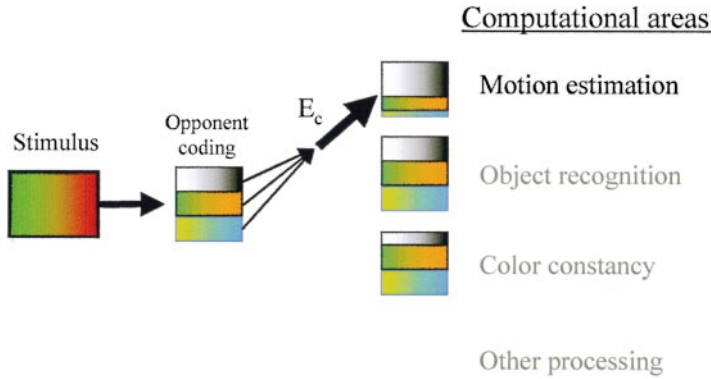
Figure 6. An Emerging View of the Distribution of Color Information in Cortex

See text for details.

slope. By including the larger contrast range, we find that all stimuli show the same dependence of perceived speed on contrast.

Stone and Thompson (1992) report that perceived speed of luminance stimuli does not saturate at high contrasts. For most of their measurements, the standard had higher contrasts (10%–70%) than the one used here (2.5%). With high contrast standards, the effects of contrast on perceived speed are modest. For example, Stone and Thompson point out that "at 2.5% test contrast, for all three subjects, the speed errors appear larger at a given contrast ratio than those [at higher contrasts]" (p. 1539). They go on to say that the failure to find saturation only applies to speed matches made using standards above 10% contrast. Gegenfurtner and Hawken (1996a) used lower contrast standards for their speed matches and found that "at contrast levels greater than the standard there tends to be some saturation" (p. 1285). Thus, it seems that with lower contrast standards, the effects are larger and saturation is evident.

Our results agree with those of Lee and Stromeyer (1989) and Cropper and Derrington (1996) who, through a variety of psychophysical experiments, provide evidence for color-specific computations in motion pathways. Lee and Stromeyer specifically demonstrate S

cone inputs to motion detection mechanisms. They also report that S cone stimuli can influence the motion of luminance stimuli. Like these authors, we find that S cones do contribute to motion perception. The interaction between isoluminance and luminance stimuli reported by Lee and Stromeyer and others (Cavanagh and Anstis, 1991; Chichilnisky et al., 1993) suggests that the S cones and the L and M cones contribute to the same motion mechanisms.

Expanding upon the measurements by Cavanagh and Anstis (1991), Chichilnisky et al. (1993) measured how effectively isoluminant stimuli cancel the motion of luminance stimuli. They concluded that motion responses from a variety of colored stimuli are represented by a common motion mechanism and that this mechanism is not monochromatic. Summarizing all of the measurements, we suggest that the motion mechanism color responses be described by an equation that combines the luminance, red–green, and blue–yellow opponent mechanisms, such as $E_c = \lambda(L + M)^2 + \rho(L - M)^2 + \beta(S - [L + M])^2$. In this equation, E_c represents a color energy signal that is communicated to motion-selective cortex. The signal is formed from the weighted sum of squared signals from the luminance and two opponent-color mechanisms. The luminance weight, λ, is the
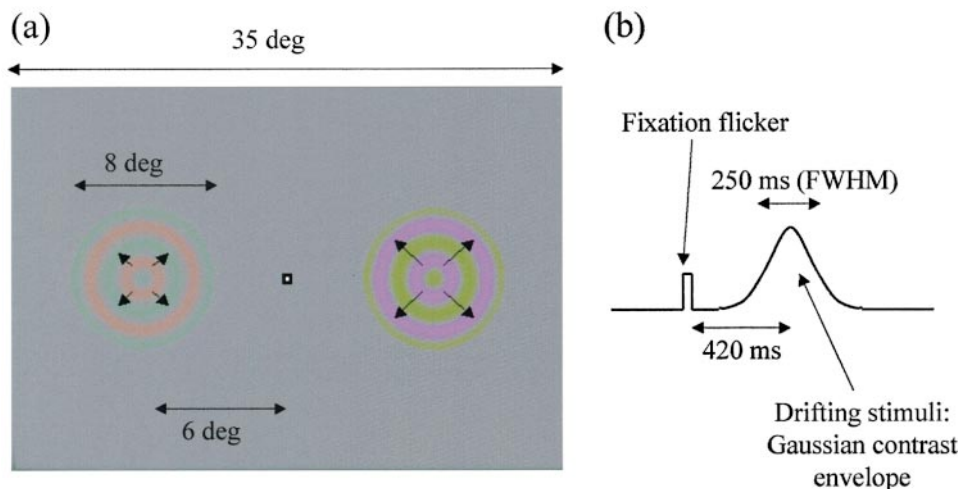

Figure 7. Stimulus Schematic

Spatial (a) and temporal (b) properties. See text for details.

largest, followed by the red–green weight, ρ, and a small blue–yellow weight, β. The color energy is analogous to the motion energy, which is used in standard models of motion perception to combine responses in the spatial and temporal frequency domains (Adelson and Bergen, 1985; van Santen and Sperling, 1985; Watson and Ahumada, 1985).

Cropper and Derrington's experiments (1996) illustrate how psychophysical results may be used to analyze where the putative color energy computation takes place. Their experiments show that direction discrimination of a chromatic grating is little affected by a static luminance grating mask, although this same mask disrupts the direction discrimination of a luminance test. These results suggest that the static luminance mask acts prior to the combination of luminance and chromatic signals into the putative color energy model.

Conclusions

The measurements described here and in the accompanying papers support an emerging view of the relationship between color and other visual computations (Dobkins and Albright, 1998). Figure 6 illustrates this view: color signals are distributed throughout cortex, including to pathways specialized for motion. In this view of cortical organization, information about stimulus color is widely distributed in cortex in a variety of forms. One mechanism for modulating the different amounts of color information is to alter the relative signal weights of a color energy signal. A second mechanism is to control whether the entire population of neurons in a pathway represents the same color energy signal or whether individual neurons within a pathway represent different color signals. Presumably, the color signals distributed to each pathway take a form that is suitable for the pathway's specific computational objective.

Experimental Procedures

Observers
Two of the authors (R. F. D. and W. A. P., males aged 30 years) and a naïve observer (Z. M. D., a male aged 18 years) served as subjects. All had normal or corrected-to-normal acuity and no measurable color deficits.

Apparatus
Stimuli were presented on a cathode ray tube display (Sony Multiscan 200sf, 17 inch, Trinitron) controlled by a graphics card with 10 bit intensity resolution for each color channel (Radius Thunderpower 30-1920). The stimuli were calibrated for intensity and wavelength using a Photo Research SpectraScan PR650 spectral photometer. The calibration procedures included (1) tests of the additivity of the red, green, and blue display channels, (2) measurements of the spectral power distribution of each display channel, and (3) characterization of the (nonlinear) relationship between the digital frame buffer values and each color channel's output intensity. These calibration measurements provide sufficient information to create cone-isolating stimuli (Brainard, 1989; Wandell, 1995). Cone absorptions were estimated using the Stockman fundamentals (Stockman et al., 1993). The calibrations were repeated periodically throughout the data collection period, but no significant changes in the system were observed.

With this display system, 1024 luminance levels could be produced for each color channel. This level of quantization provides enough contrast resolution to measure signals near detection threshold. The experiments were controlled using custom Matlab code with the extensions provided by the high level Psychophysics Toolbox (Brainard, 1997) and low level VideoToolbox (Pelli, 1997).

Stimuli
Subjects made speed comparisons between a test contrast pattern and a standard. The stimulus arrangement is shown in Figure 7. The test and standard were radial harmonic contrast patterns (spatial frequency, 0.5 cpd) presented on a uniform gray background (26° vertical × 35° horizontal). The background luminance was 50 cd/m², and its chromaticity was CIE x, y = 0.320, 0.329. Each contrast pattern was shown inside a circular aperture (4° radius) centered 6° horizontally on either side of a small fixation mark. The stimulus contrast was windowed temporally with a 0.25 s Gaussian envelope (full-width, half-maximum). The test could have one of many colors and contrasts, while for most of the experiments the standard contrast pattern was seen only by the L cones and had a contrast of 2.5%. Control experiments to test transitivity were performed using an S cone standard, but with other parameters the same. Control experiments to test for S cone isolation were performed by superimposing light from a slide projector with a yellow filter (Kodak Wratten 12). This added 60 cd/m² of yellow light to the background. The spectral power distribution of the added light (Figure 4 in Wandell et al., 1999) was confined almost entirely to wavelengths above 500 nm.

Procedure
Speed matches were made using a two-alternative, forced choice design. On each trial, the test and standard were presented randomly on either side of fixation. The test stimulus color and contrast were varied across conditions, but the test stimulus always moved at 8.2°/s. The speed of the L cone standard stimulus was varied. In each trial, the observer indicated which stimulus appeared faster. Based on the response, the speed of the standard was adjusted using a simple staircase rule. If the standard was judged faster, its speed was decreased; if it was judged slower, its speed was increased. The initial speed of the standard was selected randomly, and the velocity adjustment step began at 0.8°/s and was reduced to 0.1°/s by the fifth staircase reversal. Five staircases were interleaved within a block, corresponding to the five levels of contrasts tested for a given color stimulus. The stimulus color was varied across blocks, and the block order was counterbalanced across observers. Each staircase continued until at least 16 staircase reversals were tallied. The data were inspected to ensure that each staircase had converged to a stable estimate. Speed match values and their associated variances were estimated by taking the mean and standard error of the last 8 reversals.

Contrast detection thresholds were also measured using a two–spatial alternatives, forced choice staircase. In the threshold task, observers indicated on which side of fixation the stimulus appeared. The target contrast began well above threshold and was adjusted in logarithmic steps using a "3 down, 1 up" procedure. The step size was initially 0.6 log units and was reduced to 0.1 log units by the fourth reversal. The staircase ran until at least 16 reversals were tallied. Detection thresholds were estimated by a maximum likelihood fit of the Weibull function (Watson, 1979).

A chin and forehead rest was used to maintain head position and the stimuli were viewed with both eyes. Observers were asked to maintain fixation on the central fixation mark, which flickered 100 ms before stimulus onset to alert the observer. The brief stimulus presentation time prohibited serial fixation of both stimulus positions on any one trial. The tasks were quite easy to do while maintaining fixation.

Data Analysis
The measurements we report include the contrast and color of the test stimulus as the independent variable and the velocity of the standard as the dependent variable. We summarize the functional relationship between contrast and speed by the conventional form

$$S = \left(\frac{c^p}{c^p + \sigma^p}\right) M$$

where S is the perceived speed, c is the stimulus contrast, M is the maximum speed, and p and σ are parameters that determine the

slope and semisaturation points of the curve. This function was fit to the data by a maximum likelihood procedure. For each subject, preliminary fits with three free parameters (M, p, and σ) were used to find the best slope and maximum speed. The parameters M and p were then fixed for that subject, and in the figures presented only the semisaturation point, σ, was free to vary.

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