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THE CONTRIBUTION OF COLOR TO MOTION IN NORMAL AND COLOR-DEFICIENT OBSERVERS

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Abstract—By opposing drifting luminance and color gratings, we have measured the "equivalent luminance contrast" of color, the contribution that color makes to motion. We found that this equivalent contrast was highest (> 10%) for low spatial and temporal frequencies and was higher for red/green than for blue/yellow stimuli. Equivalent luminance contrast was about 4% for a green/purple stimulus that fell along the tritan confusion line, indicating a modest input to the motion pathway from the short wavelength-sensitive cones (B-cones). Contrast thresholds for the discrimination of the direction of motion showed that the contribution of color to motion was about the same (within a factor of 2) as that for luminance in terms of multiples of threshold contrast. These responses to moving, chromatic gratings could be mediated by any of several factors that can create a residual response in a luminance pathway: temporal phase lag between the responses to the colors of the stimuli, second harmonic distortion in the response and variability in equiluminance points across units. Each of these factors was evaluated experimentally and their combined effect could account for only a small portion of the contribution of color to motion. As a result, we attribute the perception of the motion of equiluminous stimuli to an opponent-color input to directionally selective cortical units. Chromatic stimuli had little or no equivalent contrast for color-deficient observers, whether the stimulus was red/green, which they discriminate less well than normals, or blue/yellow, which they discriminate almost as well as normals. The equivalent contrast measure provided an excellent basis for classifying normal, protan and deutan observers.

Motion Color Colorblindness

It has often been claimed that color and motion are analyzed independently in the visual cortex (Zeki, 1978, 1980; Livingstone & Hubel, 1987, 1988) and that the pathway that analyzes motion responds only to luminance information (Ramachandran & Gregory, 1978). However, there is a motion response to equiluminous, colored stimuli (Cavanagh & Favreau, 1985; Cavanagh, Boeglin & Favreau, 1985; Cavanagh, Tyler & Favreau, 1984; Derrington & Badcock, 1985; Gorea & Pappathomas, 1989; Mullen & Baker, 1985) and in this paper we examine whether the contribution of color to the motion system is a residual response of a luminance pathway or a true opponent-color contribution. We used two approaches to compare these alternatives. First, we measured the spatial and temporal frequency properties of the contribution of color to motion in order to determine whether they were characteristic of chromatic or luminance mechanisms and second, we examined various optical and neural factors that might cause a color stimulus to produce a response in a luminance pathway.

One explanation of the observations of motion response to equiluminous stimuli is that the luminance pathway is not capable of completely ignoring color signals. In the traditional model (Hurvich & Jameson, 1957), the three cone signals are transformed into an achromatic, or luminance signal and two chromatic signals. The luminance pathway responds to a particular sum of the signals from the different cone classes and does not distinguish between colors in any way: the responses to any two colors can be made identical by adjusting their relative intensities. At this equiluminance point, the luminance pathway will have no response to spatial or temporal alternation between the two colors. However, this null response only occurs if the luminance pathway meets several criteria including a perfectly matched, linear response to both colors. Any deviation between the phase of the response to each color or any nonlinearity in the response will produce a residual luminance signal that cannot be canceled by readjusting the relative luminances of the colors in the stimulus.

Differences in response properties for different color stimuli have been frequently reported in both psychophysical and pysiological studies. Using human observers, Cushman and Levinson (1983), deLange (1958), von Grünau (1977), Lindsey, Pokorny and Smith (1986) and Swanson, Pokorny and Smith (1988) have found a temporal phase difference between the response to red and green stimuli such that minimum flicker matches were best at phase differences other than 180° for red vs green stimuli.

The properties of the luminance pathway measured psychophysically have their counterparts in the broadband or nonopponent units of the magnocellular and parvocellular pathways (De Valois & De Valois, 1975; Logothetis, Schiller, Charles & Hurlbert, 1989). Of these, the units in the magnocellular stream may be most relevant for mediating motion responses since they provide a major projection to area MT, a structure that is specialized in the analysis of motion (De Yoe & van Essen, 1988; Maunsell & Newsome, 1987). Physiological studies have shown that despite the generally nonopponent nature of units of the magnocellular pathway, several factors contribute to ensure a response to a chromatic stimulus. Smith, Lee, Pokorny, Martin and Valberg (1989) recorded from units in the magnocellular stream at the level of the retina and found large phase lags for the response minimums to flickering chromatic stimuli. Second harmonic distortion (frequency doubling) in response to chromatic stimuli has been reported in the phasic cells of the monkey retina (Lee, Martin & Valberg, 1989) and the magnocellular units of the LGN to which they project (Derrington, Krauskopf & Lennie, 1984). These factors of phase lag and nonlinearity may be the source of responses to chromatic stimuli that have been reported for nonopponent cells both in the retina (Gouras & Eggers, 1982) and in the magnocellular layers of the LGN (Krueger, 1979; Schiller & Colby, 1983; Derrington, Krauskopf & Lennie 1984). For example, Schiller and Colby (1983) demonstrated that magnocellular units will always respond to the exchange of two differently colored lights no matter what the relative luminance of the lights.

In addition to inter-color response differences, variation from cell to cell in the relative sensitivity to the two colors of the stimulus will ensure that some cells in the luminance pathway will respond to a stimulus no matter what the luminance ratio of the two colors presented. Several studies (Derrington *et al.*, 1984; Lee, Martin & Valberg, 1988; Logothetis *et al.*, 1990; Shapley & Kaplan, 1989) have reported variations in the null luminance ratios for units in the magnocellular stream that are presumed to project to motion analysis centers. This variation in null points means that, no matter what the luminance balance of the colors in the stimulus, some units will always be responding. For example, Logothetis *et al.* (1989) evaluated the summed response of a group of 41 magnocellular units to a flickering red/green spot. When the luminance ratio was set at the mean of the individual equiluminance points, the summed response was still 40% of the response measured at the highest luminance contrasts.

These factors suggest that a moving, equiluminous stimulus produces a robust response in a luminance pathway. In theory, appropriate gain, phase and harmonic content adjustments in the stimulus could compensate for the imbalance in response properties for the different stimulus colors. However, the cell-to-cell scatter in equiluminance points of nonopponent units in the magnocellular stream (Derrington *et al.*, 1984; Logothetis *et al.*, 1989; Lee *et al.*, 1988; Shapley & Kaplan, 1989) is a potential source of a response to equiluminous stimuli in a luminance pathway that cannot be eliminated by any adjustment of the stimulus. The goal of our experiments was to determine whether the residual responses in a luminance pathway accounted for the motion response to equiluminous colored stimuli or whether opponent-color pathways were responsible.

In Experiments 1 and 2, we measured the spatiotemporal properties of the contribution of color to motion for normal and color-deficient observers. No adjustments were made to compensate for possible phase differences or harmonic distortion in the visual system's responses to the stimuli in these first two experiments. The color-deficient group was included for two reasons. First, the color-deficient observers serve as a control group whose data indicate the level of display and optical artifacts that produce responses to color in the absence of chromatic mechanisms. Second, we wished to evaluate whether the strength of the contribution of color to motion is a useful test for diagnosing color-deficiencies. We are interested in motion tests of color-deficiencies because motion can often drive eye movements

producing optokinetic nystagmus that we can easily measure in preverbal and nonverbal populations (Cavanagh, Anstis & Mather, 1984; Maurer, Lewis, Cavanagh & Anstis, 1989; Anstis, Cavanagh, Maurer, Lewis, MacLeod & Mather, 1986; Teller & Lindsey, 1988; Logothetis & Charles, 1990).

In Experiments 3 and 4, we examined the factors of phase, harmonic distortion and inter-unit variability and showed that they do not contribute significantly to motion perception. We discuss factors that may attenuate these effects that are so evident in the responses of individual magnocellular units. Our conclusion is that although there is a response to chromatic stimuli in a luminance pathway, this factor only accounted for a small portion of the motion response to color stimuli that we measured. Our data indicate a relatively strong and direct contribution of opponent-color signals to cortical, directionally selective units.

To examine the contribution of color to motion we developed a motion nulling paradigm. If two luminance gratings drifting in opposite directions (Fig. 1) are superimposed, the net direction of motion depends on the relative contrasts of the gratings (Levinson & Sekuler, 1975). If the components have equal contrasts then neither direction is perceived and counterphase flicker is seen instead. To measure the contrast of a rightward moving grating (see Fig. 1) we could adjust the contrast of a calibrated grating that drifts to the left. The contrast setting that gives a motion null would then be equal to the contrast of the rightward moving grating, 10% in Fig. 1. We used this technique to evaluate the contribution of color to motion by superimposing a colored grating and a luminance grating drifting in opposite directions.

Since it is difficult to be sure that a color grating is truly equiluminous, we used a color grating that contained both color and luminance contrast—a grating of light green bars and dark red bars, for example (Fig. 2)—in a procedure that allowed us to determine the luminance contrast in the color grating. A luminance pathway should "see" only this luminance contrast in the color grating and in our opposing motion paradigm, the motion null would occur when the contrast of the oppositely drifting luminance grating reached this value. However, if color contributes to the motion system, the motion null would occur when the contrast of the luminance component in the color grating was *less* than the contrast of the opposing luminance grating. The contribution of color to the grating's effectiveness in this motion nulling task will be defined as the "equivalent luminance contrast" of the color.

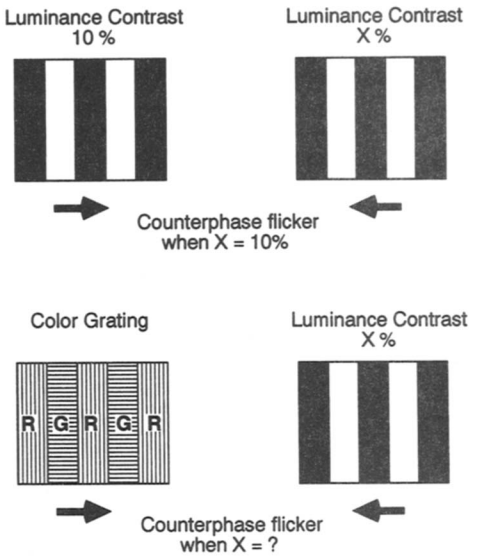


Fig. 1. Two superimposed luminance gratings moving in opposite directions produce counterphase flicker when they have equal contrasts (as well as equal spatial and temporal frequencies). When they have unequal contrasts, motion is seen in the direction of the grating with the higher contrast. Adjusting the contrast of one grating to null the motion therefore measures the contrast of the other grating (the contrasts are equal at the motion null). The same technique can be used to measure the equivalent contrast of an equiluminous color grating. The contrast of a luminance grating necessary to null the motion of the color grating is taken as the "equivalent" luminance contrast of the color grating. A significant problem with this technique is assuring that the color grating is equiluminous. Any deviation from equiluminance will increase the luminance contrast necessary to null the motion. Although square waves are shown here, sine wave stimuli were used in the experiments.

EXPERIMENT 1: EQUIVALENT LUMINANCE CONTRAST

We investigated red/green, blue/yellow and green/purple gratings with normal and color-deficient observers. Since we were interested in possible clinical applications of this test we used free viewing and did not correct for chromatic aberration. To avoid chromatic aberration effects we used low spatial frequency stimuli (see Appendix). Control conditions at higher spatial frequencies were run to determine the extent to which chromatic aberration affected the data. The green/purple stimuli were chosen to fall along the observer's tritan confusion line and so stimulated only their short wavelength-sensitive cones (B-cones). These stimuli were also viewed

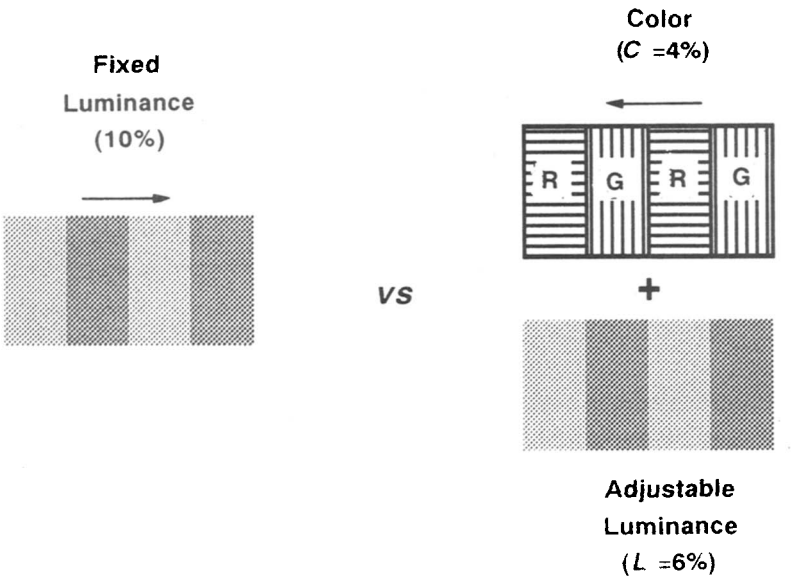


Fig. 2. A fixed contrast luminance grating drifting to the right is superimposed on a color grating, varying in both color and luminance, drifting to the left. The observer adjusts the relative luminance of the red and green (L) in the color grating over a range around equiluminance to locate two motion nulls: one when red is more luminous than green, as shown here, and another when green is more luminous than red (not shown). The motion null occurs when the effective contrast of the color grating equals that of the oppositely drifting luminance grating (10% here). The total effective contrast, T, of the color grating is given by the sum of its luminance contrast, L (say 6%) and the equivalent contrast, C, of the color in the grating (4%). Sine wave stimuli were used in the experiments.

following a bleach of the B-cones (Brindley, 1953) to verify that only B-cones were involved.

Description of the stimulus

The contribution of red/green stimuli to motion was studied using a red/green grating drifting in one direction, superimposed on a light yellow/dark yellow luminance grating drifting in the opposite direction. Although it might seem straightforward to fix the red/green contrast at equiluminance and vary the luminance contrast of the luminance grating drifting in the opposite direction to find a motion null, this requires that the equiluminance of the red/green grating be preset with great accuracy. Any deviation from equiluminance in the red/green grating will increase the luminance contrast necessary to null its motion. We must be able, therefore, to determine the luminance contrast, if any, of the color grating in order to evaluate if there is any additional contribution to motion that is specific to color.

To do so, we used the stimulus shown in Fig. 2. The rightward moving luminance grating is made by summing red and green sine waves in phase to produce a yellow grating that varies in luminance but not chromaticity. The leftward moving color grating is made by adding red and green sine waves 180° out of phase to produce a grating that varies in chromaticity and also in luminance if the red and green sine waves do not have the same luminance amplitudes. These oppositely moving gratings are displayed, superimposed, at the same spatial location.

The contrast of the rightward moving luminance grating is fixed at, say, 10% and the red-to-green luminance balance of the leftward moving colored grating is varied by the observer through a range that includes equiluminance. The leftward moving color grating is the sum of color and luminance components—the luminance contrast arising from the imbalance of the red and green luminances. The observer adjusts the red-to-green luminance balance of the leftward combined stimulus (by adjusting the gain of the red component—see Methods), until its motion just nulls the rightward motion of the 10% contrast luminance grating (this contrast remains fixed). As the observer adjusts the red-to-green luminance balance of the combined stimulus, he is varying its luminance contrast while leaving its chromatic contrast relatively constant.

In modeling the effectiveness of the color grating as a motion stimulus, we assume that the total effective contrast, T, is the sum of two components: (1) its luminance contrast, L, due to the imbalance, if any, of the red and green

luminance amplitudes; and (2) a color contribution to motion which produces an increase in the total effective contrast that we label the "equivalent luminance contrast", C, of the color,

$$T = L + C. \quad (1)$$

There may, of course, be a more complex relation between the contributions of color and luminance but this simple additive model will serve as a convenient starting point and, in fact, performs reasonably well in direct tests (Experiment 4).

The motion null will occur when the total effective contrast of the color grating, T, equals the fixed luminance contrast of the oppositely moving luminance grating, in this case 10% and, therefore

$$T = 10.$$

If color makes no contribution to motion ($C = 0$) we can simply consider the luminance contrasts of the rightward and leftward stimuli and predict that the two gratings must have equal luminance contrasts for their motions to cancel [Fig. 3(a)]. The motion null will therefore occur when the red-to-green luminance contrast, L, of the color grating is 10%. On the other hand, if the color is making a contribution equivalent to, say, 4% luminance contrast ($C = 4$), then only 6% imbalance of red and green in the leftward stimulus is necessary to cancel the opposing motion. Thus, if we know the red vs green luminance contrast at the null point (6% here), we can subtract it from the known 10% rightward luminance contrast to derive the equivalent luminance contrast of the color (4%).

We refer to the red vs green luminance imbalance, L, as the luminance contrast of the color grating, but this contrast cannot be measured directly by a photometer. It is the individual's luminance contrast and has a value of zero at the observer's equiluminance setting and increases as one or the other color changes its luminance away from that setting (see Kaiser, 1988). To determine the value of L, we exploit the fact that there are two null points, one with red more luminous than green and one with green more luminous than red, where the luminance contrast of the color stimulus has the same value (Fig. 3). The separation between the two null points allows us to calculate the luminance contrast, L, of the color grating at the motion null [see equation (3) of the Methods section] and the equiluminance point which falls halfway between these null points. We then have two of the three terms of equation (1), T and L, and can derive the equivalent luminance contrast, C, of the color in the grating. Note that in Fig. 3(b), the contribution of color to motion has been shown as a constant amount at all luminance contrasts of the color grating—the effective contrast functions for Fig. 3(b) have simply been translated upwards by 4% from those in Fig. 3(a). In Experiment 4, we obtain data that give partial support for this assumption of linear summation between color and luminance contributions.

Methods

The display was presented on a 19″ Conrac 5411 RGB monitor controlled by a Grinnell 270 color graphics system having 512 × 480 pixel spatial resolution, 256 intensity levels per color and a 30 Hz interlaced raster. Internal look-up tables in the Grinnell were used to linearize the luminance output of each phosphor independently. Following calibration, the maximum luminances available from the red, green and blue phosphors were 40, 40, and 10 cd/m^2, respectively. The phosphors of the monitor were determined by spectroradiometry to have CIE x and y coordinates of 0.596 and 0.346 for red, 0.293 and 0.604 for green and 0.149 and 0.069 for blue (Fig. 4). The yellow of the blue/yellow gratings was the mixture of equiluminant red and green (equiluminant for the CIE observer, $x,y = 0.485, 0.441$). The purple of the green/purple gratings was set individually for each observer to fall along his tritan confusion line so that the green and purple appeared to have identical hue following a 1 min bleach of the B-cones (see below).

The stimuli covered 27 × 27 cm on the screen and were viewed from a distance of 1.94 m subtending a visual angle of 8°. Observers viewed the display binocularly, with natural pupil, no head restraints and no correction for chromatic aberration. There was a central fixation bull's-eye 0.5° in dia for the red/green stimulus but 2.0° in dia for the blue/yellow and the green/purple stimuli in order to mask the macular region. The display was surrounded by a gray border 0.125° in width having the same mean luminance as the rest of the display and the room was otherwise dark.

The stimuli were vertically oriented sine wave gratings. Their spatial frequency was either 0.5 or 1.0 c/deg for the red/green and blue/yellow

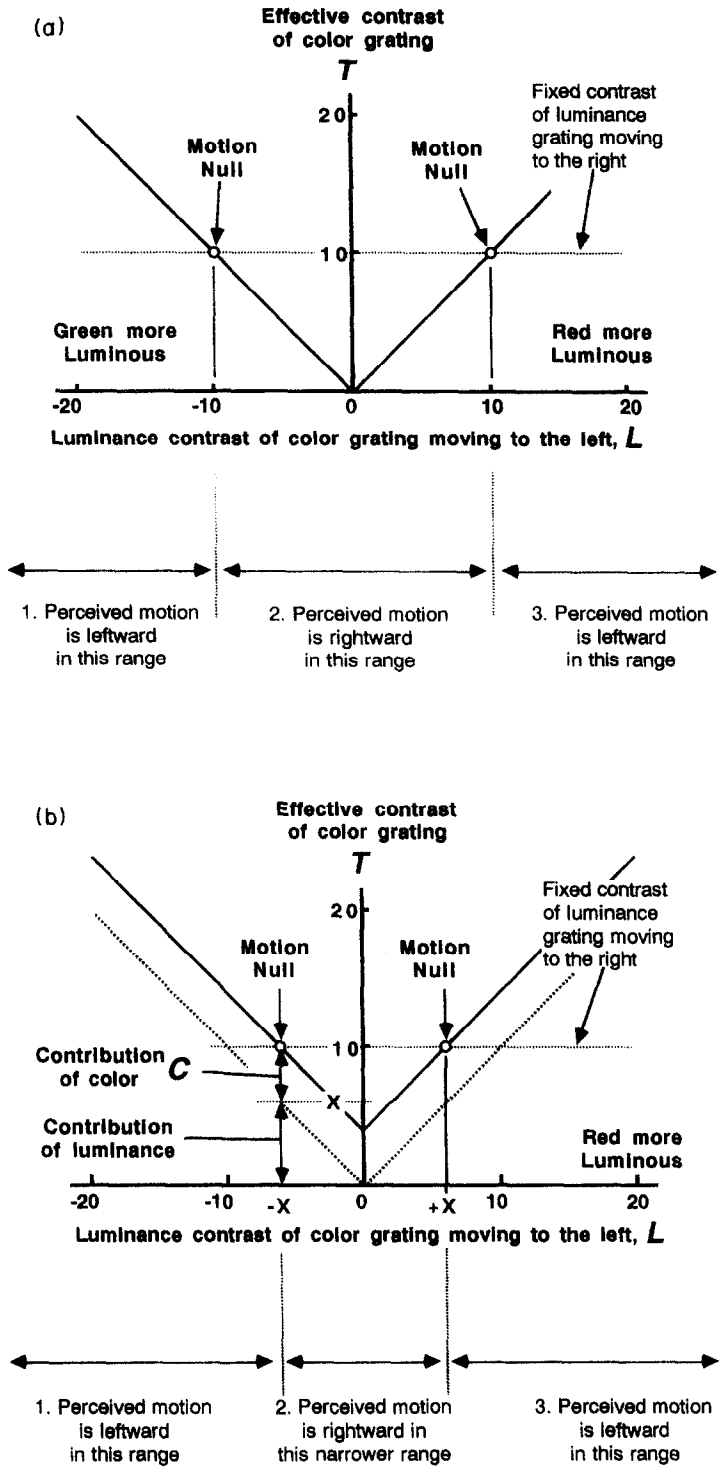


Fig. 3. Total effective contrast, T, and direction of motion in the opposing motion stimulus as a function of the luminance contrast, L, between the red and green in the color grating. The color grating is drifting to the left and the superimposed luminance grating to the right. The luminance grating has a fixed contrast, 10% in this case, and the observer adjusts the luminance contrast of the color grating to find the motion null points. The two null points are assumed to be equally spaced about the unknown equiluminance point ($R = G$). The equivalent contrast, C, of the color in the grating is the difference between the luminance contrast in the color grating and its total effective contrast, T. At the motion null points, T is equal to the fixed contrast of the superimposed luminance grating moving in the opposite direction. In (a) color is assumed to make no contribution to motion and the effective contrast of the color grating is equal to the *absolute value* of luminance contrast between the red and green. In (b), color is assumed to make a contribution equivalent to 4% luminance contrast ($C = 4$) and the effective contrast is raised everywhere by 4%

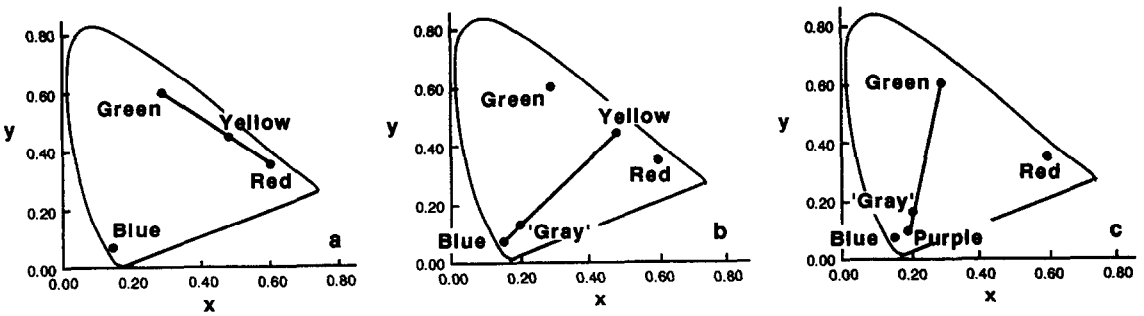


Fig. 4. CIE x and y chromaticities of the stimuli. The red, green and blue points show the chromaticities of the monitor's phosphors. (a) The red/green stimulus is modulated along the line joining the red and green points with a mean chromaticity approximately at the yellow point produced by the mixture of equiluminant red and green (the actual position is given by the mixture of the red and green of the color grating and varies as the observer adjusts their relative amplitudes). The oppositely drifting, luminance grating that is superimposed on the color grating is light and dark yellow and the yellow has the same chromaticity as the mixture of the red and green of the grating. (b) The blue/yellow stimulus is modulated along the line joining the blue and yellow points with a mean chromaticity approximately at the bluish "gray" point produced by the mixture of equiluminant blue and yellow. The opposing luminance grating is a spatial luminance modulation of the same bluish gray. (c) The green/purple stimulus is modulated between the green point and a purple chosen so that the modulation falls along the tritan confusion line for the observer. The mean chromaticity is approximately at the bluish "gray" point produced by the mixture of equiluminant green and purple. The opposing luminance grating is a spatial luminance modulation of this bluish gray.

stimuli. Tests were also run at 2.0 and 4.0 c/deg for the red/green stimulus to examine the effects of chromatic aberration. The temporal frequency of the drifting gratings was set at 2.0, 4.0 or 8.0 Hz. The green/purple stimulus was tested only at 0.5 c/deg and 2 Hz, once with the unbleached left eye and once with the bleached right eye.

The color grating was produced by superimposing two sine waves, one for the first color and one for the second, 180° out of phase, both drifting leftward at the same rate. In the superimposed rightward drifting luminance grating, the two colored sine waves were added together in phase producing a variation in luminance but not chromaticity. The ratio of mean luminance between the two colors in the luminance grating was the same as in the color grating but their contrast was set to a lower value. The luminance grating therefore always had the same mean chromaticity and mean luminance as the color grating. As a result, whenever the observer altered the relative luminances of the two colors during the procedure, the mean chromaticity and mean luminance of the luminance grating varied accordingly. Its contrast, however, always remained fixed. The luminance grating was yellow (CIE x,y of 0.485, 0.441 whenever red and green were at photometric equiluminance) for the red/green condition but a very bluish "gray" (CIE $x,y = 0.193, 0.119$ whenever blue and yellow were at photometric equiluminance) for the blue/yellow condition. Note that the mixture of equiluminant blue and yellow requires a great deal of blue since it contributes much less to luminance than does yellow; this moves the chromaticity of the mixture closer to the chromaticity of the blue phosphor. The luminance grating was a similar bluish gray for the green/purple condition (different for each observer, see below).

The luminance contrast of a grating was defined in the usual way as the difference between the maximum and minimum luminances of the grating divided by their sum. The chromatic contrast of a grating was defined in terms of the percentage of the maximum chrominance modulation obtainable with the phosphors involved. Modulating both the red and green phosphors at 100% contrast, for example, and adding them in antiphase was therefore arbitrarily defined as 100% chromatic contrast.

The chromatic contrast of the color grating was set at a nominal value of 100% while the luminance contrast of the luminance grating was set to one of three nominal values m: 0.05, 0.10, or 0.15 (5%, 10%, or 15%). For each contrast of the luminance grating, m, both the chromatic contrast of the color grating as well as the luminance contrast of the luminance grating were reduced by dividing by $1 + m$ (i.e. 1.05, 1.10 or 1.15, respectively) so that the summed waveforms always remained positive. Since both gratings were changed by the same factor, their

effectiveness relative to each other remained unchanged and we refer to their stimulus contrasts by their nominal values of 100% chromatic contrast and luminance contrast of m.

When the color and luminance variations were combined, the waveforms of the two colors in the red/green grating were given as follows (the other gratings were defined similarly): x is horizontal position, t is time, R is the maximum luminance of the red phosphor in the stimulus (varied by the observer), G is the maximum luminance of the green phosphor (fixed by the experimenter), m is the nominal contrast of the rightward drifting luminance grating, f_S and f_T are the spatial and temporal frequencies of the gratings.

$$\text{Red } (x,t) = R \cdot \left\{1 + \left[\frac{m \cdot \sin(2\pi f_S x - 2\pi f_T t) + \sin(2\pi f_S x + 2\pi f_T t)}{1+m}\right]\right\}$$

$$\text{green } (x,t) = G \cdot \left\{1 + \left[\frac{m \cdot \sin(2\pi f_S x - 2\pi f_T t) - \sin(2\pi f_S x + 2\pi f_T t)}{1+m}\right]\right\}.$$

To make the measurements for the red/green conditions, we fixed the maximum green luminance of the waveform, G, and the observer varied the maximum red luminance, R, to find two null points, the upper null R_U (whose contrast with the fixed green is shown as $+X$ in Fig. 3) and the lower null R_L ($-X$ in Fig. 3). Since in both cases the contrast of the oppositely moving yellow grating is the same (varying R changes the mean chromaticity but not the luminance contrast of the yellow grating), we assume that the two nulls represent equal luminance contrast of the red about its unknown point of equiluminance, R_E, with the green (shown at 0% luminance contrast in Fig. 3). That is,

$$(R_E - R_L)/(R_E + R_L) = (R_U - R_E)/(R_U + R_E)$$

and therefore,

$$R_E = \sqrt{R_U R_L}. \quad (2)$$

The luminance contrast of the color grating, L, at either motion null point is then the Michelson contrast between either the upper or lower null luminance and the equiluminance point,

$$L = (R_U - R_E)/(R_U + R_E)$$

substituting for R_E.

$$L = (\sqrt{R_U} - \sqrt{R_L})/(\sqrt{R_U} + \sqrt{R_L}). \quad (3)$$

The equivalent contrast, C, of the color in the grating is now given from equation (1) by the difference between the fixed contrast of the oppositely moving luminance grating, m, which, at motion null, equals the total effective contrast of the color grating, T, and the luminance contrast of the color grating at the motion null, L,

$$C = T - L. \quad (4)$$

The maximum green luminance of the waveform, G, that we used depended on the subject group. In each case, we chose a value for green such that red was equiluminous with the green for the observer when the maximum red luminance of the waveform, R, fell near 25 cd/m^2, a value which allowed a range of luminance contrast for the color grating of at least 20% about the equiluminance point. The values we used ranged from 35 to 40 cd/m^2 for the normal observers, 40 cd/m^2 for all the deutans and from 12 to 17 cd/m^2 for the protans.

Three levels of fixed contrast, m, of the luminance grating were used: 5, 10 and 15%. For each contrast level of the luminance grating the observer made four motion null settings at the lower null point and four at the upper null point (see Fig. 3) and from these we calculate two values: the equiluminance point, expressed as the logarithm of the ratio of the red and green luminances at equiluminance, $\log(R_E/G)$, and the equivalent luminance contrast of the color, C. The final values for the equivalent contrast and the equiluminance point were the averages of the values across the three fixed luminance contrast conditions ($m = 5$, 10 and 15%).

If at a given contrast level, m, there was no motion reversal, then the total effective contrast of the color grating was always equal to or greater than that of the luminance grating. In this case, the separation between the null points (and therefore the value of L) was taken to be zero. The equivalent contrast of the color for that condition was then given by the luminance grating's contrast ($C = m$) and lower luminance contrast conditions were not included in the averages. The equiluminance setting was taken as the value determined at higher luminance contrasts.

The procedure for the blue/yellow and green/purple stimuli was identical to that described here for the red/green stimuli with the following exceptions: in the blue/yellow

conditions, the maximum blue luminance was held constant (at 10 cd/m^2, the maximum value available on the monitor) and yellow varied; in the green/purple conditions, the maximum purple luminance was held constant (with blue fixed at 10 cd/m^2 and red adjusted for each observer to make a tritanopic match between the green and purple as described below) and green varied.

The observer completed the upper and lower null settings of all the combinations of spatial and temporal frequencies for a single luminance contrast and a single color pair in one session. There were twelve combinations for red/green, six for blue/yellow, and two (bleached/unbleached) for green/purple. Two more sessions then followed at the remaining fixed luminance contrast levels. The order of the luminance levels was random for each observer.

In order to bleach the B-cones for the green/purple stimuli, the observers exposed their eye to be tested to approx. 4800 td of violet light for 1 min. The light was produced by focusing the beam of a 300 W Kodak Carousel with reflector type lamp through an $f/2.8$, 35 mm lens with the outer lens against the carousel. The light exiting the lens then passed through a 435 nm interference filter having a 7 nm half-bandwidth at half-amplitude. The resulting beam was viewed through a natural pupil measured at approx. 3 mm. The CIE x and y coordinates of the light, measured with a Minolta Chromameter were 0.16 and 0.01. The effectiveness of the bleach was evaluated by viewing a drifting green/purple squarewave under conditions chosen to optimize chromatic sensitivity (2 Hz, 0.5 c/deg, Kelly, 1983). The observer adjusted the luminance and the red/blue balance of the purple until the green and purple bars appeared to have identical hue and luminance (at this setting, they appeared approximately achromatic following the bleach). The observer also reported the time course of the return of chromatic sensations. The bleach produced approx. 1 min during which no chromatic variation could be seen in the tritanopic stimulus.

For the experimental conditions, the observer first exposed himself to the bleaching light for 1 min and then moved immediately to the motion nulling display and made settings for up to 1 min or until he observed a change of the chrominance in the display. Following the bleach, the stimulus appeared nearly achromatic. As the bleach wore off, a very noticeable yellow filled alternate stripes, turning finally to green. Simultaneous with this shift through yellow to green, the remaining stripes shifted to purple. If the observers noticed any chromatic changes before the minute had elapsed, they stopped making readings. At least four settings were made in each condition. To generate the purple used in the procedure the blue phosphor was set at its maximum value of 10 cd/m^2 and the red phosphor luminance was adjusted to the proportion, relative to the blue, that produced the tritanopic match described above. The purple had CIE x,y coordinates of 0.209, 0.116 with a maximum luminance of 15.5 cd/m^2 for observer PC, 0.229, 0.127 with a maximum luminance of 18.0 cd/m^2 for DV, and 0.149, 0.069 with a maximum luminance of 10.0 cd/m^2 for CM, a protanomalous observer. The "bluish-gray" of the luminance grating for these three observers whenever the green and the respective purples were at photometric equiluminance had CIE x,y coordinates of 0.224, 0.194 for observer PC, 0.242, 0.211 for DV, and 0.173, 0.148 for CM.

For the red/green conditions there were four observers, including the two authors, with normal color vision (no errors on the Ishihara plates) and normal or corrected-to-normal acuity, and nine color-defective observers with 14 or more errors on the Ishihara test (see Table 1). Five of these observers were classified as deutans by our tests and four as protans. All had normal or corrected acuity. We also collected Nagel II Anomaloscope readings for the four normals, four protans and two of the deutans (as well as for eight other normals, Table 1). For the blue/yellow conditions, two normal (PC, DV), two deutan (BA, RD) and two protan (CB, JP) observers participated and for the green/purple condition two normal observers (PC, DV) and one protan (CM) participated.

Results

Derivation of the data. In Fig. 5, we have taken two examples of our data to indicate how the equivalent luminance contrast, C, of the color was determined. Observers nulled the motion of a drifting luminance grating having either 5, 10 or 15% contrast by varying the luminance contrast of a color grating that drifted in the opposite direction. In Fig. 5, the luminance contrasts of the color gratings at the null points [equation (3)] are shown for a normal observer, SA, and a deutan observer, BA, for red/green gratings at 0.5 c/deg and

Table 1. Comparison of anomaloscope, Ishihara and motion tests. The observers were initially classified as normal or color deficient based on the number of errors on the Ishihara plates. The average Nagel *II* anomaloscope setting for twelve normals (eight in addition to the four shown here) was 41.6 (minimum of 37.5 and a maximum of 43.0) while the mean range of acceptable settings was 1.9 (minimum of 0 and a maximum of 5). Classification of the color deficits was based on both the setting and the acceptance range. For the Ishihara plates, the classification of the color deficit was based on the errors for plates 22–26. For the opposing motion task, the classification of normal vs color deficient was based on the equivalent contrast measure for red/green stimuli at 2 Hz and 0.5 c/deg (Experiment 1, Fig. 14) and the classification of the color deficit was based on the equiluminance settings in the same conditions

	Observer												
Test	DV	SA	PC	JL	BA	FB	AC	DL	RD	GS	CM	JP	YL
Anomaloscope	42.5	42.0	37.5	43.0	6.5	—	17.0	—	—	43.0	45.5	42.0	40.0
Range	0.5	2.0	3.0	2.0	13.0	—	46.0	—	—	4.0	3.0	2.0	6.0
Deficit*	N	N	N	N	D	—	D	—	—	N	P	N	D/P
Ishihara	0	0	0	1	15	18	16	13	18	22	24	24	22
Deficit*	N	N	N	N	D	D	D	D	D	D	P	P	D/P
Equiluminance†	−0.16	−0.08	−0.21	−0.09	−0.18	−0.18	−0.23	−0.21	−0.22	0.24	0.28	0.27	0.27
Equiv. contrast†	0.15	0.07	0.15	0.10	0.01	0.02	0.00	0.01	0.00	0.00	0.01	0.00	0.00
Deficit*	N	N	N	N	D	D	D	D	D	P	P	P	P

*N, normal; D, deuteranomalous; P, protanomalous; D/P, unspecified red/green deficit.
†Data from red/green stimuli at 2.0 Hz and 0.5 c/deg.

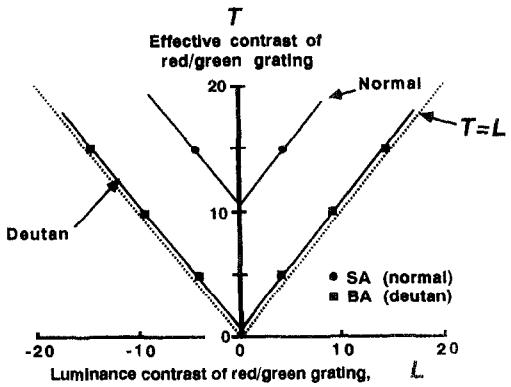


Fig. 5. Total effective contrast, T, as a function of the luminance contrast, L, between the red and green in the color grating. Sample data for two observers, SA and BA, for 2 Hz, 0.5 c/deg red/green stimuli. Measurements were taken for 5, 10 and 15% contrast of the luminance grating. The observer adjusted the luminance contrast of the color grating to find the motion null points. The normal observer reported motion nulls only when the luminance grating had 15% contrast (the one datum point shown). At lower contrasts of the luminance grating, the motion of the color grating always dominated, even at equiluminance. The equivalent contrast of the color in the grating, the difference between the luminance contrast of the color grating (the dotted V rising from the origin) and the total effective contrast, is therefore >10% for the normal observer in this condition. It is <1% for the color-deficient observer. The luminance contrasts of the color gratings are shown here aligned, for convenience, on a common equiluminance point for both observers.

2 Hz. The V-shaped dotted lines of unit slope rising from the origin indicate the effective contrast that the color grating would have if color made no contribution. If this were so, the effective contrast of the color grating would be equal to its luminance contrast. The lines plotted through the data points indicate the observed effective contrasts in these two examples. The shift of these lines from the dotted lines indicates an increase in the effective contrast and the amount of the shift, is the equivalent luminance contrast of the color in the color grating. Note that the equivalent luminance contrast is substantial, more than 10%, for the normal observer, but very small, less than 1%, for the color-deficient observer. Averages of these equivalent contrasts are plotted in the graphs to follow.

Normal observers. In color-normal adults, the equivalent luminance contrast of the color in the red/green grating was about 12% for 0.5 c/deg gratings moving at 2 Hz [Fig. 6(a)]. It dropped with temporal frequency to about 7% at 8 Hz. At 1.0 c/deg, the equivalent contrast was less and also dropped with temporal frequency. There was substantial individual variability in

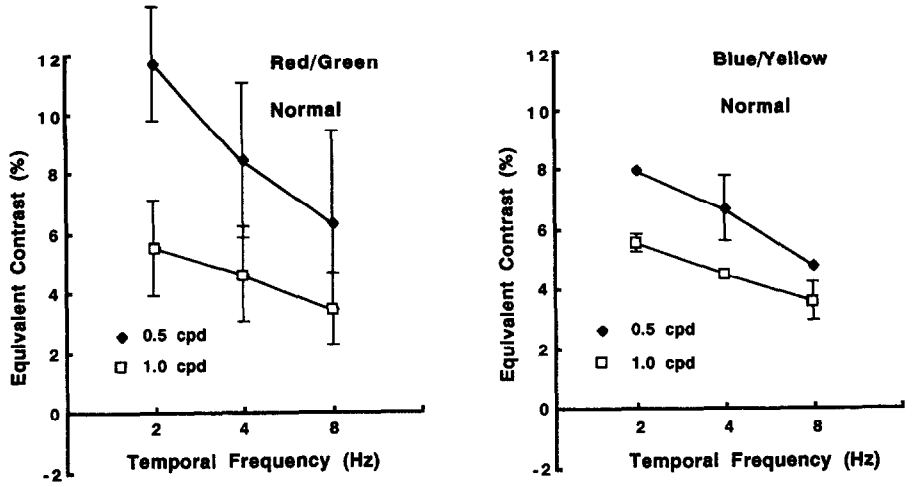


Fig. 6. Equivalent contrast of color for red/green and blue/yellow gratings for four normal observers as a function of spatial and temporal frequency. Vertical bars show standard errors (±1 SE).

these settings (the individual values can be seen on the vertical axes of Fig. 14).

The color in the 0.5 c/deg, blue/yellow gratings had an equivalent luminance contrast of about 8% at 2 Hz and dropped to 5% at 8 Hz [Fig. 7(b)]. At 1.0 c/deg, the equivalent contrast values were somewhat less and again dropped with increasing temporal frequency.

The color in the green/purple gratings at 0.5 c/deg and 2.0 Hz had about 4% equivalent contrast (Fig. 7). Since this dropped very close to zero following the bleaching of the B-cones, we conclude that the motion contribution for the green/purple grating was mediated principally by the B-cones.

Color-deficient observers. The results were very different for color-deficient observers (4 protans and 5 deutans). Unlike the normals, the

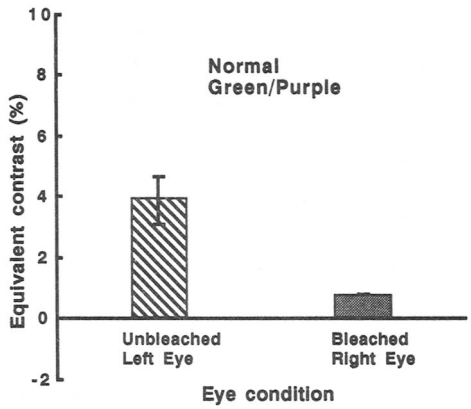


Fig. 7. Equivalent contrast of color in green/purple gratings for two normal observers. The gratings differentially stimulate only the B-cones. The right eye was tested following bleaching of the B-cones and the left eye was tested unbleached. Vertical bars show standard errors (±1 SE) where larger than the data symbols.

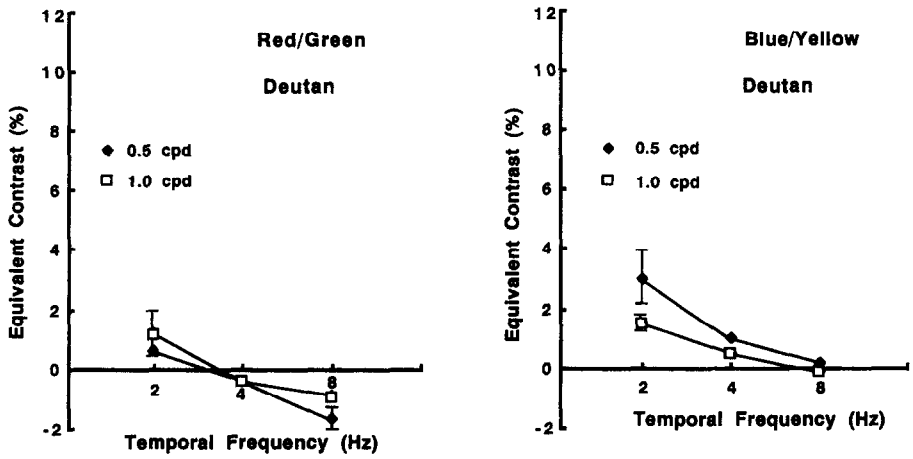


Fig. 8. Equivalent contrast of color for red/green and blue/yellow gratings for five deutan observers as a function of spatial and temporal frequency. Vertical bars show standard errors (±1 SE) where larger than the data symbols.

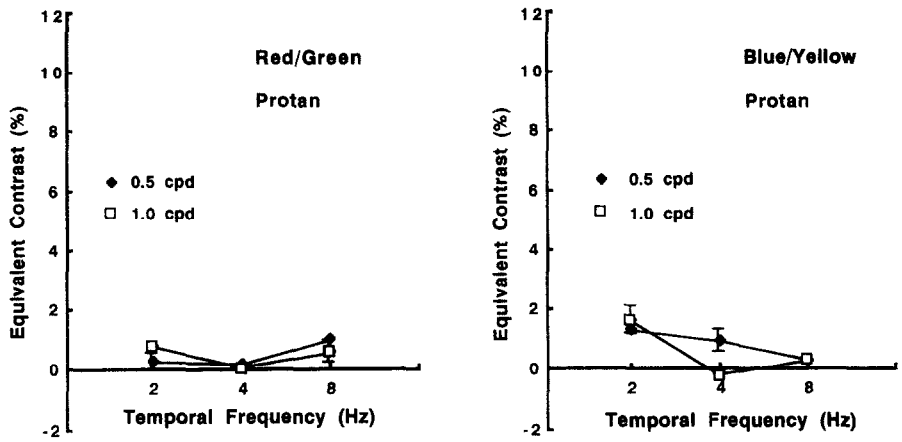


Fig. 9. Equivalent contrast of color for red/green and blue/yellow gratings for four protan observers as a function of spatial and temporal frequency. Vertical bars show standard errors (±1 SE) where larger than the data symbols.

color-deficient observers, whether deutans or protans, showed little or no contribution of color to motion for red/green gratings (Figs 8 and 9). Not surprisingly, Experiment 2 will show that the color-deficient observers could not see these red-green gratings very well; they were visible but much less so than for the normal observers. However, the color-deficient observers also showed little or no contribution of the blue/yellow stimuli to motion (Figs 8 and 9), even though they could detect these blue/yellow gratings almost as well as normals (as we show in Experiment 2). This finding will be discussed in more detail later.

One protan observer was also run with a green/purple stimulus that fell along his tritanopic confusion line. For this observer, the equivalent contrast of the color with this grating (4.1%) was similar to the value for the normal observers. The equivalent contrast dropped to near zero (0.6%) following bleaching of the B-cones showing that the contribution was mediated by the B-cones for this observer.

Summary graph. The sparing of the motion response to the tritanopic stimulus for the protan observer suggests that the loss in motion sensitivity for the color-defective observers might be limited to the red/green opponent signal (R − G, the difference in the R-cone and G-cone signals produced by the stimulus). The poor performance on the blue/yellow stimulus for these observers may be a result of the large R − G signal in this stimulus (see Table 2). Figure 10 shows a summary of data from normal and color-defective observers as a function of the stimulus colors. Only data for 2 Hz, 0.5 c/deg conditions are included and there are data from four normals and nine color-defectives in the red/green condition, two normals and two color-defectives in the blue/yellow condition and, finally, two normals and one protan in the green/purple condition. Because of the variation in observers across these conditions, this comparison is only informal.

For normal subjects, the contribution of color to motion for the red/green stimulus is approx.

Table 2. Cone modulations for red/green, blue/yellow and green/purple stimuli. The amplitudes of cone modulation for the three stimuli of Experiment 1 are given based on the Smith and Pokorny (1975) and Boynton (1979) cone fundamentals for the CIE observer. The percent modulation about the mean values are shown in parentheses. Note that since each stimulus is equiluminous, the amplitudes of the middle (G) and long (R) wavelength-sensitive cone modulations are equal and opposite. These cone fundamentals are only appropriate when the eye is adapted to white. Since that was not the case in our experiments (see Fig. 4 for the mean chromaticities of each stimulus), these values can only be considered as first-order approximations

	Cone					
Stimulus	R		G		B	
R/G	5.09	(13.7)	−5.09	(−34.1)	−0.01	(−8.3)
B/Y	−4.68	(−14.5)	4.68	(23.9)	3.71	(97.1)
G/P	0.00	(0.0)	0.00	(0.0)	2.60	(95.9)

three times that for the green/purple and the equivalent contrast for the blue/yellow falls midway between the two. The contribution from the red/green stimulus is near zero for the color defectives and rises to match that of the normals for green/purple. Again, the equivalent contrast for the blue/yellow falls midway between the other two.

It appears that the contribution of color to motion measured in our motion nulling paradigm can be modeled as a sum of two components (Fig. 11): one, a R – G component and the other a blue/yellow opponent signal (B – Y, the difference between the B-cone signal and the sum of the R- and G-cone signals produced by the stimulus). The B – Y component is isolated by tritanopic stimuli that vary only along the B-cone axis (like our green/purple stimulus) because neither the R – G nor luminance mechanisms (R + G) respond to these stumuli (MacLeod & Boynton, 1979; Krauskopf *et al.*, 1982; Derrington *et al.*, 1984). The B – Y component appears to produce significantly less "equivalent luminance contrast" for motion in our nulling paradigm than does the R – G component. The color-defective observers have lost the R – G signal but preserved the weaker B – Y. Because of its greater effectiveness as an input to motion, the R – G component in our blue/yellow stimulus predominates in determining the equivalent contrast settings for normal observers in this condition. For the color-defective observers, the absence of the stronger R – G component in the blue/yellow stimulus accounts for the unexpectedly large drop in contribution to motion for this stimulus, a stimulus which they see quite well.

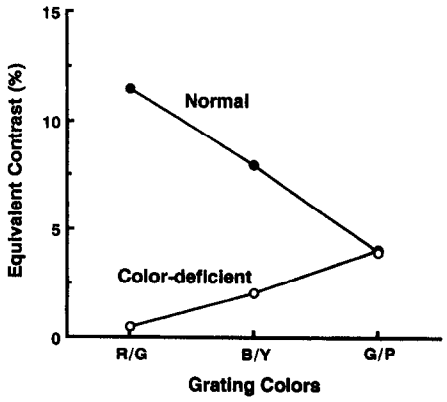
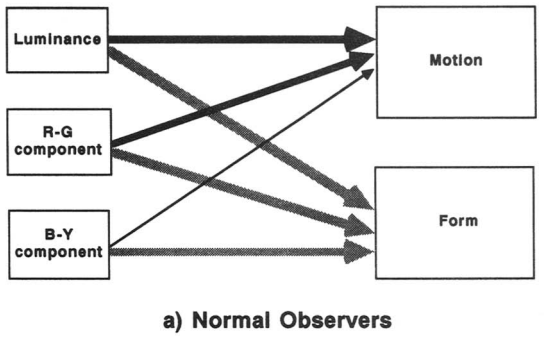
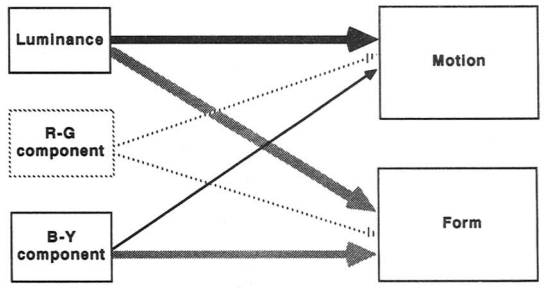


Fig. 10. Equivalent contrast as a function of stimulus colors for normal and color-deficient observers. The stimulus colors: R/G, red/green; B/Y, blue/yellow; G/P, green/purple. Only data for 2 Hz and 0.5 c/deg conditions are included.



a) Normal Observers



b) Protan and Deutan Observers

Fig. 11. Contributions of luminance, R – G and B – Y components to motion and form analysis. (a) For normal observers, luminance has the strongest contribution to motion followed by the R – G opponent-color component. The B – Y component contributes very little to motion. All components are assumed to contribute strongly to form vision. (b) For color-deficient observers, the contribution of the R – G opponent-color component is extremely weak or absent, both for motion and form vision. Since the B – Y contribution to motion is weak as well, the color-deficient observers effectively have little or no motion response to any equiluminous color stimulus in the motion nulling task. On the other hand, their B – Y response in form vision is at normal levels.

For form vision, we assume that the R – G and the B – Y components are less imbalanced in their contribution so that protan and deutan observers retain a robust form perception for equiluminous green/purple as well as red/green stimuli.

Luminance artifacts and rod intrusion. Luminance artifacts can be produced by misalignment or nonlinearities in the monitor or by chromatic aberration in the eye. Any luminance artifact in an equiluminous color stimulus will add directly to its effective contrast, inflating the equivalent contrast measures. This artifact sets a lowest possible value for the equivalent contrast that will be present in all the measurements and, for the color-deficient observers, it will be the main or only contributor to the measured equivalent contrast. Since the color-defective

observers had little or no equivalent contrast for the color stimuli (<1% at 0.5 and 1.0 c/deg, averaged over the three temporal frequencies), we can conclude that the stimuli at these low spatial frequencies produce luminance artifacts of less than 1% and that our readings for the normal viewers are true readings of color contribution to motion.

To determine if chromatic aberration was the principal source of the results for the color-deficient observers, we derived the theoretical value of the luminance contrast generated by chromatic aberration. The contrast of this artifact increases with the square of the spatial frequency (see Appendix) and the data from spatial frequencies covering the range of 0.5–4 c/deg (for red/green stimuli averaged over the three temporal frequencies) show this squared increase for the color-defective observers (Fig. 12), evidence that their performance was determined principally by chromatic aberration. The data of Fig. 12 also indicate that chromatic aberration effects are negligible at 0.5 and 1.0 c/deg but become substantial above 1 c/deg and that these frequencies should be avoided for uncorrected, free-viewing situations. Indeed, they perhaps should be avoided altogether since the alignment requirements of an achromatizing lens introduce as many problems as it solves at higher spatial frequencies (Bradley *et al.*, 1989).

In Fig. 12, the normal observers show a U-shaped curve resulting from two factors:

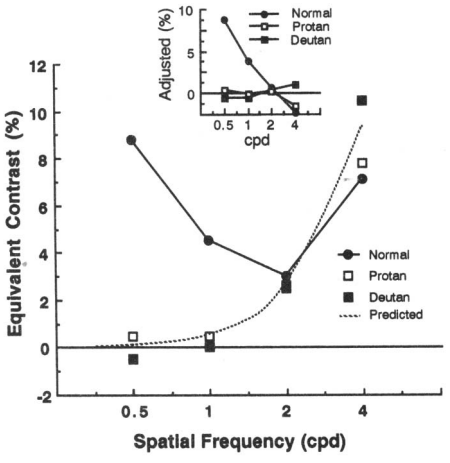


Fig. 12. Equivalent contrast of color for red/green gratings as a function of spatial frequency for normal, deutan and protan observers. The curved line is the predicted luminance artifact produced by chromatic aberration (see Appendix). The inset shows the contribution of color to motion with the predicted luminance artifact subtracted from the measured equivalent contrasts.

(1) the color contribution to motion that decreases with spatial frequency; and (2) the chromatic aberration artifact that increases with spatial frequency. We can estimate the contribution of color to motion at spatial frequencies where chromatic aberration is significant by taking the difference between the values for normal and color-defective observers (see inset, Fig. 12). It is evident that the contribution estimated this way drops rapidly toward zero at spatial frequencies above 1.0 c/deg.

Chromatic aberration therefore creates a substantial luminance signal in response to color stimuli above 1.0 c/deg, guaranteeing that a motion system that relies on luminance signals will never be motion-blind for stimuli above that value. Equiluminous stimuli at and below 1.0 c/deg produce negligible luminance artifacts of this type however, and, if the visual system responds to these stimuli at all, it must rely on other mechanisms.

Our results place an upper limit of 1% contrast not only on luminance artifacts but also on the contribution of rods. The color-deficient observers have normal rod function, so the rod contribution for equiluminous stimuli must again be less than the total effective contrast for these observers, about 1% for the low spatial frequencies. Moreover, since we can assume that rod function is the same for normals and color-deficient observers, we conclude that there is little or no rod intrusion affecting our measurements for normals.

Equiluminance results. The technique we have developed to measure the equivalent luminance contrast of color for stimuli composed of two colors also gives the equiluminance setting for these two colors [equation (2)] and these settings are very useful in diagnosing color defects. The equiluminance results for red/green and blue/yellow (Fig. 13) gratings show the expected large difference between the protan observers and the deutans. In fact, we used these data to classify the color-deficient observers as protan or deutan (Table 1). Previous studies have reported similar large shifts in equiluminance settings for protans (Cavanagh *et al.*, 1984; Crone, 1959; De Vries, 1948; Pokorny & Smith, 1972; Verriest, 1971). The deutans and the normals differed in their equiluminance settings in the expected direction but there was significant overlap between the readings in the two groups (see Table 1).

Combined graph. Equiluminance settings on their own would not be sufficient to separate

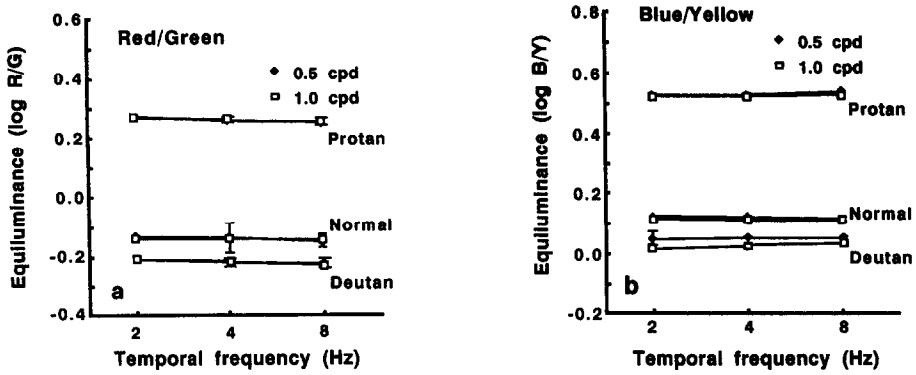


Fig. 13. Equiluminance points of red/green and blue/yellow gratings for normal, deutan and protan observers as a function of spatial and temporal frequency. Vertical bars show standard errors (±1 SE) where larger than the data symbols.

normals from deutans reliably. However, the equivalent contrast settings for normals and deutans were very different (Fig. 6 vs Figs 8 and 9). Combining both equiluminance values and equivalent contrast values therefore allows us to discriminate all three groups. Plotting the equiluminance settings for the red/green stimuli on the horizontal axis in Fig. 14 and the equivalent contrast setting for the corresponding stimuli on the vertical axis separates these three vision groups: normals, protans and deutans. The separation is best at 0.5 c/deg and 2.0 Hz and becomes progressively poorer at higher spatial and temporal frequencies. Note that neither equiluminance nor equivalent contrast measures alone could separate all three groups and that classification of the deficits by the Ishihara plates was inconsistent as well (Table 1). The anomaloscope settings clearly distinguished the normals from the deutans that were tested. For the protans, however, both the settings and the acceptance ranges overlapped the values for the normals.

EXPERIMENT 2: CONTRAST THRESHOLD FOR MOTION

In this experiment, we measured the contrast threshold for direction discrimination for red/green, blue/yellow and yellow/black stimuli and compared these thresholds to the contributions to motion for the same stimuli, measured in Experiment 1. At the same time, we measured detection thresholds for these moving stimuli in order to compare the contrast required to see the grating and the contrast required to see it

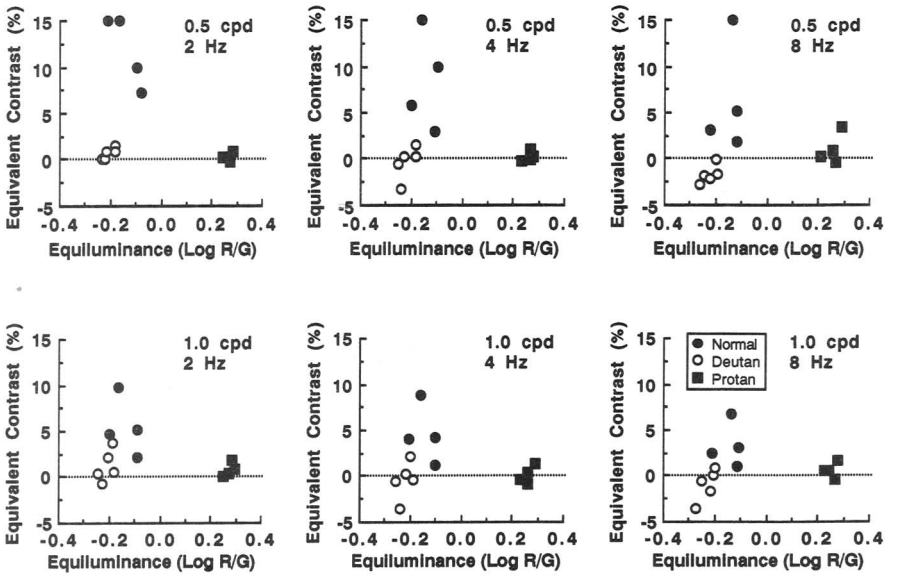


Fig. 14. Combined plots of equivalent contrast on the vertical axes and equiluminance point on the horizontal axes for individual normal, protan and deutan observers. All data are for red/green gratings and each of the six combinations of two spatial and three temporal frequencies is plotted separately.

move. We expected that for the colored gratings there should be a range of contrast above the detection threshold but below the motion threshold where the moving gratings would be seen as stationary (Cavanagh *et al.*, 1984).

Our first experiment showed that color stimuli produced a moderate contribution to the motion system, requiring up to 12% luminance contrast to null their motion. By measuring contrast thresholds for motion discrimination, we can examine whether the relative contribution of color and luminance are equal in strength in terms of threshold multiples. That is, the motion of a red/green grating of maximum saturation on our monitor was just nulled by the opposing motion of a luminance grating of about 12% luminance contrast (Fig. 6). Did this null occur when both of these gratings were equal multiples of their contrast threshold?

Finally, the previous experiment indicated that the color-deficient observers received little contribution of color to motion. We might therefore expect that they cannot see equiluminous color gratings, in particular red/green ones, move at all. In fact, the equivalent contrasts for these observers for red/green gratings were small but still greater than zero (except for deutans in some conditions). We therefore felt that they should be able to see the motion of a chromatic stimulus but only at much higher contrasts.

Method

The stimuli were sinusoidal gratings modulated in color (red/green and blue/yellow) or luminance (yellow/black). The luminance contrast of the yellow/black grating was defined in the usual way as the difference between the maximum and minimum luminances of the grating divided by their sum. The red/green gratings were produced by adding red and green sine wave gratings 180° out of phase. Their chromaticity was centered at the equiluminant mixture (CIE coordinates were $x = 0.485$, $y = 0.441$) of the red and green points specified above, and the chromatic contrast of these gratings was defined in terms of the percentage of the maximum chrominance modulation obtainable with the red and green phosphors. Modulating both the red and green phosphors at 100% contrast and adding them in antiphase was therefore arbitrarily defined as 100% chromatic contrast. Using this convention, a grating of 2% luminance contrast is composed of a red and a green grating, each at 2% contrast, added in phase. A 2% chromatic contrast grating is composed of the same two gratings added in antiphase. The blue/yellow gratings were modulated about the equiluminant mixture of blue and yellow (CIE x and y coordinates were 0.193 and 0.119, respectively) specified previously, and the chromatic contrast of these gratings was defined in terms of the percentage of the maximum chrominance modulation obtainable between these points.

All gratings appeared within a square frame which subtended 8 deg^2 of visual angle at the 1.93 m viewing distance. The display had a mean luminance of 26 cd/m^2 and a dark surround. The monitor contrast range was reduced so that the maximum variation of luminance produced by video signal was from 10 to 30% (depending on condition and observer) of the mean value of 26 cd/m^2. The linearization of screen luminance was adjusted to be appropriate for each contrast range. The gratings were vertical and had spatial frequencies of 0.5 or 1.0 c/deg. The fixation bull's-eye (0.5° for red/green and luminance stimuli, 2.0° for the blue/yellow stimulus to mask the macular region) at the center of the display provided a stimulus for accommodation. The gratings moved at a rate of 2, 4 or 8 Hz either left or right.

Observers were one normal, PC, one deutan, BA, and one protan, CM. They had normal or corrected-to-normal acuity and no measurable astigmatism.

The testing was done binocularly using natural pupils. First luminance, then chromatic contrast thresholds were obtained for each of the six combinations of the three temporal and two spatial frequencies. The psychophysical procedure was a revised ascending method of limits in which a computer-implemented algorithm allowed the contrast to increase more slowly through the anticipated threshold region (Brussell & Cavanagh, 1984). The observer's task was to initiate the trial, and, with the contrast increasing continuously, to signal with a joystick when the grating was visible in the detection task and to signal the direction of motion by moving the joystick left or right, in the motion discrimination task. The grating disappeared once the response was made and the average duration of the grating presentation was 0.7 sec. The direction of grating motion was randomized in every trial. Each luminance threshold was the mean of six measurements. To find the chromatic contrast threshold at 0% luminance modulation, thresholds at each of five different red/green contrast ratios (contrast

of the red grating divided by the contrast of the green grating; both contrasts increased continuously during the presentation so as to maintain a constant ratio between them) in the equiluminance region were obtained and the threshold for red/green equiluminance was defined as the peak of this range. This procedure is based on the finding that, within the spatiotemporal region represented here, a color grating is least visible when it contains no luminance contrast (Kelly, 1983; Mullen, 1985). The threshold at each red/green contrast ratio was the mean of six measurements. A similar procedure was followed for the blue/yellow measurements.

Results

Figure 15 shows the sensitivity (the reciprocal of the contrast thresholds) for detection and for direction discrimination as a function of spatial and temporal frequency for the normal, deutan and protan observers. As expected, the sensitivity for red/green stimuli for the protan and deutan observers was much lower (about one-sixth) than that measured for the normal observer. The sensitivities for luminance and blue/yellow stimuli, however, were similar for the normal, protan and deutan observers.

As has been reported previously for comparable stimuli, there was no difference between detection and motion thresholds for the achromatic stimuli and sensitivity increased with temporal frequency between 2.0 and 8.0 Hz (Kelly, 1979; Watson *et al.*, 1980). For the normal observer, the red/green detection sensitivity dropped with increasing temporal frequency, as expected (Kelly, 1983—note that the vertical axes of the graphs cover 3 log units so that substantial effects appear as gradual slopes). The motion sensitivity dropped with temporal frequency as well, suggesting that the motion threshold was based on chromatic mechanisms. The sensitivity for direction discrimination was lower than that for detection and between these two thresholds, in the shaded area on the graphs, the normal observer reported that the color bars could be seen but did not appear to move. For the protan and deutan observers, both detection and motion sensitivity rose with temporal frequency and there was very little difference between the two functions.

The detection sensitivity for the blue/yellow gratings decreased with increasing temporal frequency for the normal and protan observers but stayed fairly constant for the deutan. The

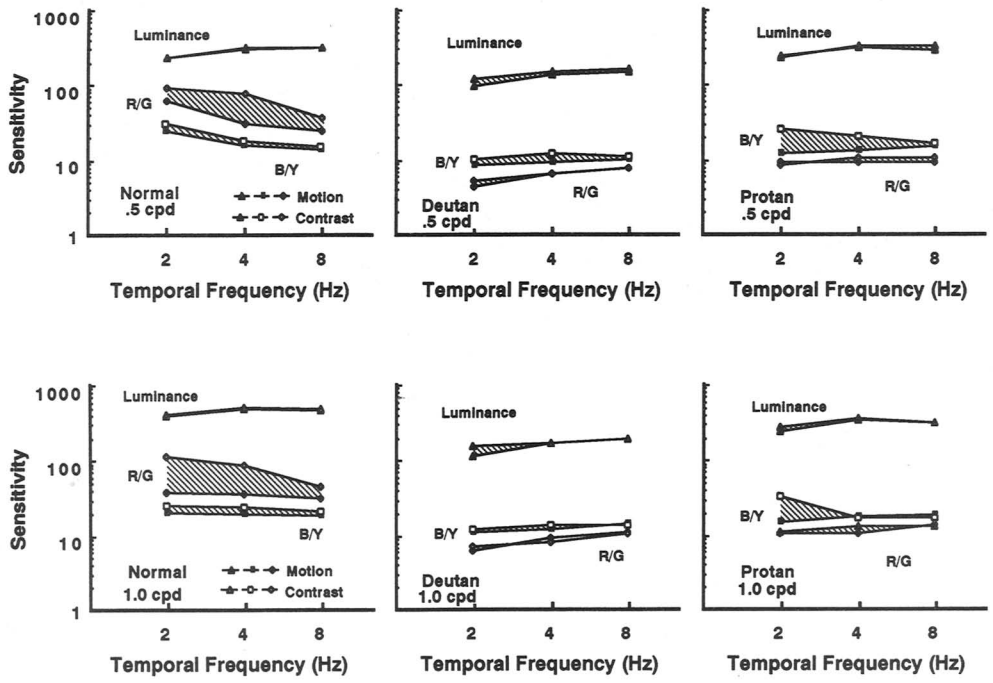


Fig. 15. Contrast sensitivity for direction discrimination (solid symbols) and detection (open symbols) for luminance, red/green and blue/yellow gratings as a function of temporal frequency. The data for each observer—normal, deutan and protan—are shown separately for the two spatial frequencies. Within the shaded regions that are above contrast threshold but below motion threshold, the gratings can be seen but do not appear to move. Note that comparisons of absolute sensitivities between chromatic and luminance stimuli are not meaningful for the contrast scales used here.

direction discrimination sensitivity decreased with temporal frequency for the normal observer, again indicating a chromatic mechanism, but stayed constant or even increased with temporal frequency for the protan and deutan observers. A threshold difference between detection and discrimination was evident with the blue/yellow stimuli for the protan observer but less so for the normal and deutan.

For the color-deficient observers, many of the chromatic sensitivity functions increased with temporal frequency rather than dropped as would be expected for the response of a chromatic pathway. The increase in sensitivity was as much as a factor of 2 between 2 and 8 Hz—about the same as the increase in achromatic sensitivity over the same range (both increases produce a very slight slope on a 3 log unit vertical axis). This implies that these detection and discrimination tasks may have been mediated by luminance for these observers. If this was the case, the luminance signal could arise either from experimental, monitor, optical, or neural sources. One possibility is that the five red/green contrast ratios that were tested sampled the equiluminance region too sparsely and the ratio chosen as "equiluminous" deviated slightly from equiluminance. However, the change of threshold setting with red/green ratio was typically too shallow for this factor to have had much effect. A second possibility is a nonlinear response characteristic in the monitor, eye (chromatic aberration) or neural response to the stimulus. With the chromatic contrast in the 10–25% range at threshold for these observers, it would take a 2–5% deviation from linearity to produce a threshold level of response in the luminance pathway (approx. 0.5% luminance contrast necessary for detection and discrimination in the luminance pathway). This level of nonlinearity is greater than that present in our monitor and greater than that produced by chromatic aberration (see Appendix). This leaves a neural source as the most likely origin for the nonlinearity, suggesting that our color stimuli started to produce a threshold level of activation in a luminance pathway once they reach 10–25% chromatic contrast, at least for the color-deficient observers.

An alternate explanation is that a different motion system (Anstis, 1980; Braddick 1980; Cavanagh & Mather, 1989) mediated the motion perception of the color-deficient observers in the threshold task. Although low-level, directionally selective detectors presumably mediate the response for the normal observers, the threshold of these mechanisms may be so elevated for the color-deficient observers that the task reveals the properties of a higher-level or second-order motion system instead. This possibility is discussed in more detail in the next section.

To summarize, the color-deficient observers appeared to rely on a very weak luminance-mediated, or perhaps higher-order, signal to perceive the motion of isolated color gratings. The normal observer, on the other hand, must have relied on color-sensitive mechanisms since the sensitivity functions were unlike those of the achromatic stimuli and were well above the possibly luminance-influenced functions of the color-deficient observers. The following section presents a comparison of performance in this threshold task with that in the motion nulling task. This comparison supports the idea that a single, chromatically based process mediated the performance in both tasks for the normal observer while two different processes were involved for the color-deficient observers, in particular, for blue/yellow stimuli.

Threshold multiples. The stimuli in Experiment 1 were presented at 100% chromatic contrast, whereas in this second experiment, the stimuli were at threshold contrast. To examine whether performance was mediated by the same mechanisms in both tasks, we reanalyzed the data of the first experiment in terms of threshold multiples. For example, the motion threshold was 1.6% for a red/green grating and 0.5% for a luminance grating for observer PC (0.5 c/deg, 2 Hz, Fig. 15). Therefore, the 100% red/green grating in Experiment 1 was at 60 times its motion threshold, and the 15% contrast luminance grating that would null its motion for this observer was at 30 times its threshold.

Table 3 shows the relative strengths of the opposing color and luminance gratings at motion null in Experiment 1 in terms of threshold multiples. The color threshold

Table 3. Threshold multiples. The chromatic contrast of a color grating and the contrast of the luminance grating that will just null its motion (from Experiment 1) are expressed here in terms of multiples of their respective thresholds (from Experiment 2)

	R/G vs luminance (threshold multiples)		B/Y vs luminance (threshold multiples)	
Observers	R/G	Luminance	B/Y	Luminance
Normal (PC)	32.9	16.8	16.4	12.6
Deutan (BA)	7.7	−0.2	11.1	1.9
Protan (CM)	10.6	3.4	15.5	2.7

multiple is the contrast of the color grating in Experiment 1 (always 100%) divided by its motion discrimination threshold from Experiment 2. The luminance threshold multiple is the equivalent luminance contrast measured in Experiment 1 (the contrast of the luminance grating that would null the motion of the color grating at equiluminance) divided by the motion discrimination threshold for a luminance grating of the same spatial and temporal frequency from Experiment 2. These threshold multiples were derived individually from the data for each observer but averaged over the different spatial and temporal frequencies.

For the red/green stimuli, the color and luminance gratings that produced a motion null were both high in terms of threshold multiples for the normal observer, and both low for the deutan and protan observers. Whatever mechanism mediates the motion response for the normal is simply weak or absent for the color-deficient observers.

The blue/yellow results were quite different. The *chromatic* threshold multiples for the color-deficient observers are very similar to those of the normal (these observers could discriminate the direction of motion of blue/yellow stimuli at almost the same contrasts as the normal), but the *luminance* threshold multiples are much lower than those of the normal (very little luminance contrast was required to null the motion of the blue/yellow stimulus).

These results suggest that the color-deficient observers relied on different mechanisms in the threshold and suprathreshold tasks for blue/yellow stimuli. The improved performance of the color-deficient observers for these stimuli in the threshold task may be due to the involvement of a second motion process, one that responds to any moving contour including not only those defined by luminance or color but also those defined by texture, stereo or relative motion (Anstis, 1980; Cavanagh & Mather, 1989; Cavanagh *et al.*, 1989). This higher-level process should therefore have a robust response to isolated, drifting blue/yellow stimuli. We assume that the higher-level process is less able to participate in the opposed motion task because the superposition of the two gratings defeats the form extraction process necessary to track either of them.

For the normal observer, on the other hand, there was no evident dissociation between the performance in the two tasks. This observer appears to detect motion in both tasks by a more sensitive process whose performance in both cases decreases with temporal frequency (Figs 6 and 15)—the signature of a chromatic mechanism.

Before we can conclude that the contribution of color to motion is mediated by chromatic mechanisms for the normal observer, however, we must rule out all other possible sources. In the following two experiments we examine phase lag, harmonic distortion and interunit variability.

EXPERIMENT 3: PHASE LAG AND HARMONIC DISTORTION

In this experiment, we measured two neural sources that could produce residual activity in luminance-based units in response to our color gratings: temporal phase lag between the responses to the two colored components of the stimuli and spatiotemporal second harmonic distortion. Cushman and Levinson (1983), deLange (1958), Lindsey *et al.* (1986), Swanson *et al.* (1988) and von Grünau (1977) have reported phase lags of 20° and more between red and green in minimum flicker studies. Smith *et al.* (1989) report similarly large phase lags for the response minimums in the nonopponent, phasic units of the monkey retina. A temporal offset of 20° will produce a significant luminance component (equivalent to about 17% contrast) in a drifting red/green grating. Second harmonic distortion is a likely source of the frequency-doubled response of magnocellular units to exchanges of color lights (Schiller & Colby, 1983) and Derrington *et al.* (1984) and Lee *et al.* (1989) report that many units in the magnocellular stream show a second harmonic response to chromatic sinusoidal stimuli.

We measured these two possible sources of residual response using quadrature motion techniques (Cavanagh, Antis & MacLeod 1987; Shadlen & Carney, 1986; Stromeyer, Kronauer, Madsen & Stein 1984). In this technique, a stationary chromatic stimulus (e.g. a red/green sine wave) is set in counterphase flicker. For luminance-based units which add together responses to the red and the green components in a nonopponent fashion, any phase lag between the response to the two colors or second harmonic distortion will produce a residual activity (Fig. 16) that is itself flickering in counterphase. We then introduce a stationary, counterphasing luminance stimulus positioned as a lure so that it will combine with the counterphasing neural

response to generate a moving stimulus. The observer then alters the stimulus phase lag or introduces a real second harmonic component to null the neural response and so measure its strength. The underlying assumption is that the two counterphasing components can only produce motion if both stimulate the same units. Since the lure varies only in luminance, motion can only arise when the color stimulus also creates some residual response in luminance-based units. Because of the spatiotemporal phase of the lure, we can isolate the luminance-based responses being probed to those due to phase lag or second harmonic distortion.

The quadrature stimulus is based on the geometric equality between a drifting grating and the sum of two counterphasing sinusoidal stimuli, 90° out of phase with each other in both space and time (quadrature phase):

$$\cos(2\pi f_S x)\cos(2\pi f_T t) + \sin(2\pi f_S x)\sin(2\pi f_T t) = \cos(2\pi f_S x - 2\pi f_T t).$$

This relationship allows us to test for the presence of one counterphasing component (product of cosines) by introducing a second component (product of sines) to produce motion (right hand sine term) even though neither component in isolation has any net motion. We have previously used this technique (Cavanagh *et al.*, 1987) to set the equiluminance of two colors: the color stimulus is counterphased and combined with a luminance counterphasing stimulus in quadrature phase. Any inequality in the luminance balance of the two color sine waves produces a net luminance counterphase grating [Fig. 16(a)] which then combines with the luminance lure in quadrature phase to produce motion. Therefore, to determine the equiluminance setting for the two colors, the observer simply adjusts the luminance ratio until no motion is seen. This technique has been shown to produce the same settings as minimum flicker when the tests have the same spatial and temporal frequencies (Cavanagh *et al.*, 1987). For example, if the red phosphor and green phosphor of the display monitor are modulated in phase to produce the luminance lure with a contrast of m, and

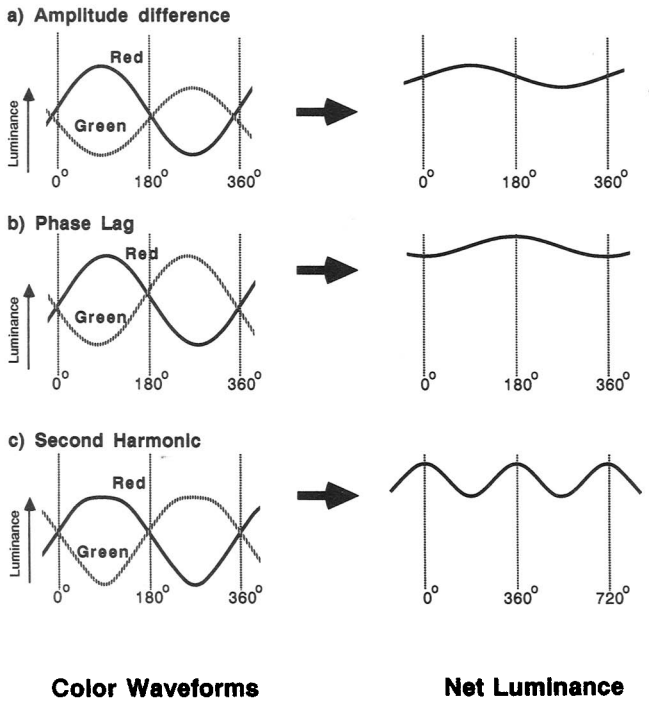


Fig. 16. (a) The sum of red and green sine waves, 180° out of phase, produces a net luminance modulation if the amplitudes of the two sine waves differ. The luminance waveform is also a sine wave with the same frequency as the color waveforms and in phase with the color waveform that has the higher amplitude. (b) The sum of red and green sine waves having the same amplitude also produces a net luminance modulation if their phase difference is not exactly 180°. The luminance waveform is a sine wave with the same frequency as the color waveforms and its phase is the mean of the phases of the two color waveforms, 90° as shown here. (c) A second harmonic distortion in the red and green waveforms produces a net luminance modulation that is a sine wave at the second harmonic.

out of phase to produce the chromatic counterphasing grating, we have (ignoring constant terms)

$$R(x, t) = m\cos(2\pi f_S x)\cos(2\pi f_T t) + \sin(2\pi f_S x)\sin(2\pi f_T t) \quad (5)$$

$$G(x, t) = m\cos(2\pi f_S x)\cos(2\pi f_T t - \sin(2\pi f_S x)\sin(2\pi f_T t). \quad (6)$$

We can use the same approach to measure the temporal phase lag between the motion system's response to the red and green stimuli. Ignoring constant terms,

$$R(x, t) = m\cos(2\pi f_S x)\cos[2\pi f_T(t + \theta)] + \sin(2\pi f_S x)\cos[2\pi f_T(t + \theta)] \quad (7)$$

$$G(x, t) = m\cos(2\pi f_S x)\cos(2\pi f_T t) - \sin(2\pi f_S x)\cos(2\pi f_T t). \quad (8)$$

A stationary red/green stimulus of spatial frequency f_S is set in counterphase temporal modulation at frequency f_T [the sin · cos terms of equations (7) and (8)]. A stationary luminance lure is introduced (the cos · cos terms) having the same spatial and temporal frequencies but 90° out of phase with the chromatic stimulus in space *only*. Since it is not in quadrature spatiotemporal phase with the red/green stimulus, it does not produce any motion. However, any phase lag between the response to the red and to the green waveforms in the red/green stimulus will upset the inverse relation of the two waves and produce a response shifted 90° temporally from the peaks and troughs of the red and green waveforms [Fig. 16(b)]. This residual neural response will then be in quadrature phase with the response to the luminance lure and the combination of the two will produce motion. If at some point there is a phase lag between the neural responses to the two stimulus colors, it can be canceled by introducing the opposite phase lag in the stimulus [the value θ in equation (7)]. When it has been exactly canceled, no motion will be visible and when it has been overcompensated, the motion will reverse direction. The motion reversal point can therefore be used to accurately measure phase lag in the pathways responding to counterphasing gratings.

In the experiment, observers adjusted the temporal phase lag [the value θ in equation (7)] to determine the reversal point. Spatial phase was accurately set by proper alignment of the color images on the monitor. Average misalignment on our monitor was zero and the maximum less than 0.5 mm (equivalent to 5° of phase of the 1 c/deg stimulus) in the corner areas.

We measured second harmonic distortion (at twice the spatial and temporal frequencies) in a similar manner. A 180° phase difference between the waveforms of the two colors, red and green in equations (9) and (10), is necessary to create a chromatic waveform at the fundamental frequency. If a second harmonic distortion is present in the response to both colors, however, this 180° phase offset for the fundamental is a 360° phase offset for the second harmonic. The second harmonic components for the two colors are therefore in phase and produce a residual response that could have carried motion information in our first experiment. To measure the second harmonic distortion [Fig. 16(c)], we again started with a stationary, counterphasing color grating [second term on the right-hand side of equations (9) and (10)] and added a stationary, counterphasing luminance lure that had twice the spatial frequency and twice the temporal frequency and could be aligned to any temporal phase ϕ [first term in equations (9) and (10)]. This procedure indicated whether or not a second harmonic distortion was present in the response of luminance-based units at any temporal phase ω by producing visible motion when $\phi = \omega + 90°$. However, the procedure did not measure the amplitude of the second harmonic but only indicated whether or not it was strong enough to generate visible motion (this required about 1% contrast). In this first procedure, the amplitude, a, of the third term in equations (9) and (10) is set to 0.0. The function of this third term is described next.

Although second harmonic distortion might occur at any phase, it is most likely at peaks-add or peaks-subtract phase (relative to the chromatic waveform) since that is where it will occur due to a compressive or expansive response function, respectively. In order to test not only the presence of a second harmonic component but also its amplitude, we performed a second test. With the luminance lure fixed at 90° spatiotemporal offset from peaks-add phase [$\phi = 0°$ in the sine terms of equations (9) and (10)], we inserted an additional second harmonic component with variable amplitude, a, to the color grating in peaks-add phase with the chromatic waveform [third term on the right-hand side in equations (9) and (10)]. This term, since it is in quadrature phase with the luminance lure,

generated visible motion that was then eliminated by adjusting the amplitude a. When the motion was nulled, the value of a indicated the amplitude of the second harmonic distortion at the peaks-add or peaks-subtract phase. If a was zero, then the second harmonic present in the chromatic stimulus at that phase had zero amplitude. This test can measure the amplitude of harmonic components that might not be visible in the first test (< 1% contrast).

$$R(x,t) = m\sin(4\pi f_S x)\sin[4\pi f_T(t+\phi)] + \cos(2\pi f_S x)\cos[2\pi f_T] + a\cos(4\pi f_S x)\cos[4\pi f_T] \quad (9)$$

$$G(x,t) = m\sin(4\pi f_S x)\sin(4\pi f_T(t+\phi) - \cos(2\pi f_S x)\cos(2\pi f_T t) + a\cos(4\pi f_S x)\cos[4\pi f_T]. \quad (10)$$

In the experiment, the observers adjusted first the relative temporal phase of the luminance lure (ϕ) while the added second harmonic component was set to zero ($a = 0$). Any second harmonic distortion in the response of the motion system would then become visible as a leftward or rightward motion when the adjustable phase differed from the distortion product phase by 90°. No adjustments of spatial phase were made because a response nonlinearity in the visual system produces second harmonic components only at peaks-add or peaks-subtract spatial phase relative to the fundamental. These were the spatial phase values tested by our procedure: a second harmonic component in peaks-add phase would produce motion in one direction whereas one in peaks-subtract phase would produce motion in the opposite direction.

In the final condition, the observers adjusted the amplitude, a, of the added second harmonic waveforms while the temporal phase of the lure was set to 0° ($\phi = 0$). This is the most likely temporal phase for the second harmonic distortion, the position produced by a compressive or expansive response function, assuming that the first phase lag test [equations (7) and (8)] shows little or no temporal lag.

The harmonics of a counterphasing grating are defined by two frequencies: one spatial and one temporal. The procedure represented by equations (9) and (10) evaluates the harmonic distortion at the second spatial and temporal harmonics. We could also evaluate the distortion for the second temporal harmonic at the fundamental spatial frequency or for the second spatial harmonic at the fundamental temporal frequency. However, the effect of our basic equiluminance procedure is to null any luminance-based response at the fundamental spatial and temporal frequencies so that all harmonics combined with either fundamental have zero energy. Since the harmonic that combines the second spatial and second temporal harmonics is the first that can have any power following the equiluminance setting, it is the component most likely to reveal significant nonlinearities.

Methods

The display was identical to those of Experiment 1. Red/green and blue/yellow stimuli were presented at the six combinations of two spatial frequencies (0.5 and 1.0 c/deg) and three temporal frequencies (2, 4 and 8 Hz) for the phase lag tests and two (2 and 4 Hz) for the second harmonic tests (8 Hz could not be used because the minimum four samples per cycle of its second harmonic that are required for the quadrature technique cannot be generated by our 30 Hz system). The green/purple stimulus was presented only at 0.5 c/deg and 2 Hz and the purple was adjusted to produce a tritan color pair with the green for each observer. The luminances for the red/green, blue/yellow and green/purple displays were set as in Experiment 1. Observers first set equiluminance for the displays with the stimulus described by equations (5) and (6). They then made four adjustments of relative phase lag to achieve a motion null with the stimuli described by equations (7) and (8).

In a separate session, observers searched the phase space (ϕ) of the second harmonic component in steps of 22.5° with the stimuli described by equations (9) and (10) with the added second harmonic component set to zero ($a = 0$) reporting the direction of motion, if any was visible. Finally, they made four settings of the amplitude, a of the added second harmonic while the temporal phase of the lure was set to 0° ($\phi = 0$) to find the amplitude setting that produced neither motion to the left nor to the right.

Two normal observers participated, PC and SS.

Results

Figure 17 shows the results for phase lag for the three different stimuli. These phase lags appear to be much smaller than those reported for minimum flicker settings by Cushman and

Levinson (1983), deLange (1958), Lindsey *et al.* (1986), Swanson *et al.* (1988), and von Grünau (1977). This may be due to the direct measurement technique that involves only the response of the motion pathway. There may be additional phase lags that contribute to flicker judgements especially at low temporal frequencies.

In physiological recordings, Smith *et al.* (1989) found extremely large phase lags (up to 90°) for units in the magnocellular stream at the spatial and temporal frequencies that we have used in our experiments. For units in the parvocellular stream they found smaller phase lags, similar to those we have measured here. Their physiological results suggest that the large phase lags observed in psychophysical minimum flicker judgments may involve principally magnocellular responses whereas the smaller phase lags we measure for color gratings in our motion task may be mediated only by parvocellular input.

The phase lags we measured indicate that luminance-based units do have some response to the chromatic gratings due to imperfect phase cancellation. The luminance contrast of the sum of two otherwise identical gratings that depart from perfect antiphase by a phase lag of θ is given by

$$L = \sin(\theta/2). \tag{11}$$

The maximum measured phase lag was 3° for the blue/yellow stimulus at 8 Hz. This implies a response in luminance-based units that is equivalent to the response to a 2.6% contrast luminance grating. This is an appreciable part of the blue/yellow contribution to motion at this temporal frequency [Fig. 7(b)] and indicates that the remaining contribution of color to motion drops more rapidly with temporal frequency than Fig. 7(b) shows. The phase lag in other conditions does not appear to contribute significantly to the motion response.

The results for the green/purple stimulus showed phase lags similar to those for the blue/yellow stimuli ($2.46 \pm 0.54°$ for PC and $1.52 \pm 0.22°$ for SS).

The results for the second harmonic distortion were straightforward (Fig. 18). The observers could detect no consistent motion as they moved the phase of the second harmonic motion from 0 to 360° for any of the stimuli. Adding a real second harmonic component ($a > 0$) at peaks-add phase did produce motion and the observers adjusted the amplitude of this component to null the motion. The amplitude of this add second harmonic component at motion nulled never differed significantly from zero. Similar results were found for the green/purple stimulus ($0.46 \pm 0.33\%$ second harmonic amplitude at peaks-add phase for PC and $0.07 \pm 0.49\%$ for SS). We conclude that there was no appreciable second harmonic distortion in the response to our stimuli. This distortion may appear under more extreme stimulation

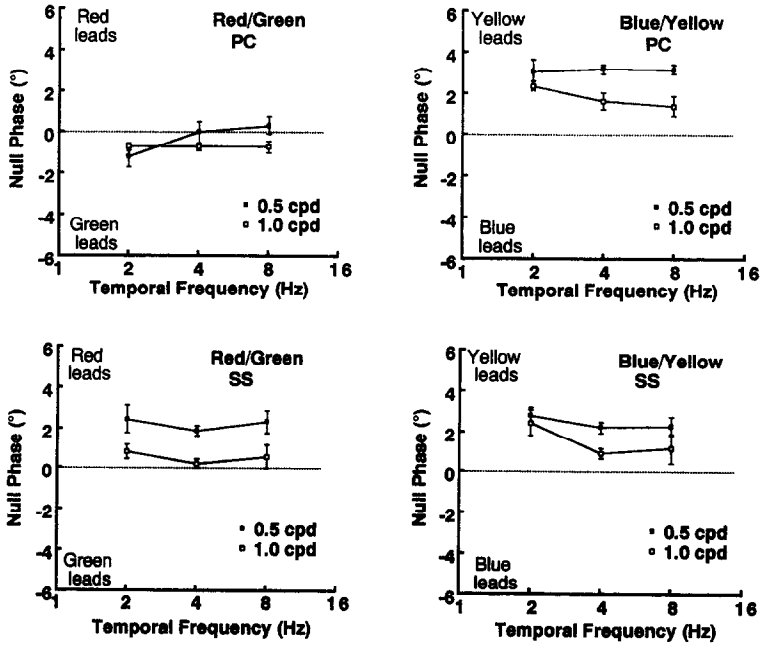


Fig. 17. Temporal phase lag for red/green and blue/yellow stimuli as a function of spatial and temporal frequency. Vertical bars show standard errors (±1 SE).

conditions such as the light exchange stimuli of Schiller and Colby (1983) where higher chromatic contrasts of saturated monochromatic lights and sharp temporal transients were used. A logarithmic nonlinearity at the receptors would produce a second harmonic whose amplitude is invariant with spatial and temporal frequency of the stimulus. Since we measured negligible second harmonic distortion in this experiment and since the color contribution to motion that we measured in Experiment 1 varied with spatial and temporal frequencies, we conclude that there is no appreciable logarithmic distortion at the receptor for our stimuli.

In summary, it appears that there were no significant effects due to unequal tracking of the two color stimuli by the motion system at least for the stimuli used in our experiments. There are two possible reasons for these unexpectedly small phase shifts and harmonic distortions.

First, magnocellular units clearly do show large phase shifts and second harmonic distortion in response to chromatic gratings. However, combinations of magnocellular responses may reduce these effects substantially. In particular, magnocellular units come in two types: ON-center and OFF-center (Wiesel & Hubel, 1966). If the original signal is reconstructed from these two signals by taking their difference *prior* to motion detection, then both phase shifts and second harmonic distortions will cancel in the combined signal. It is unlikely that the cancellation would be total but it certainly may account for some of the unexpectedly low measurements of phase shift and second harmonic distortion in our motion tasks.

On the other hand, if the signals are combined *following* motion detection, it can be shown that the ON- and OFF-dependent motion responses (whether generated by phase shifts or second harmonic distortion) to our luminance lure stimuli will be in opposite directions and the motion signals will cancel each other in our test *even though they would not do so in response to a drifting chromatic grating*. In other words, our results with chromatic gratings using a luminance lure would be meaningless for purely chromatic stimuli. However, it is evident from the literature that ON and OFF responses are combined prior to motion detection implying that our test is valid. This can be seen in the results of Schiller (1982) who blocked ON pathways in monkeys with injections of APB. If ON and OFF signals were analyzed separately, he would have found that half of the directionally selective cortical cells stopped responding. Instead he found that cortical cells retained their direction selectivity to the trailing edge of a light bar but stopped responding to the leading edge, indicating that both ON and OFF signals were driving each cell. We also know that the combination is a difference, not a sum. If it

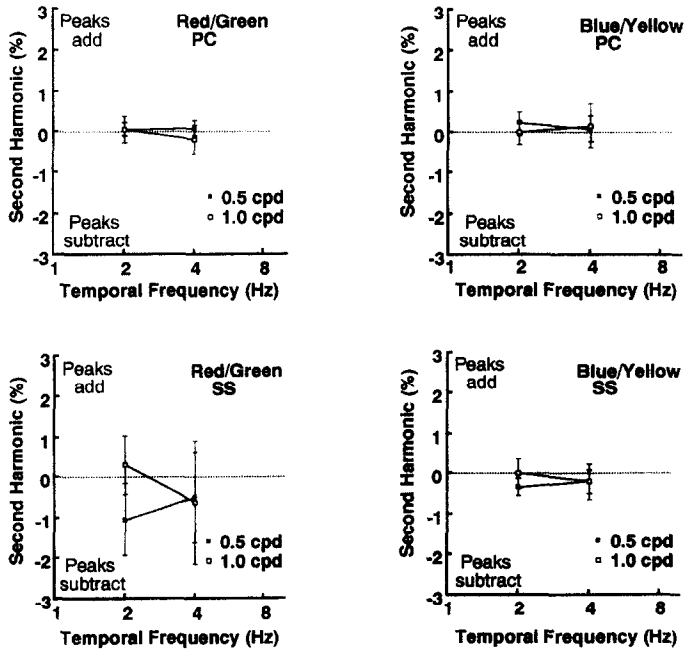


Fig. 18. Spatiotemporal second harmonic amplitude at cosine phase for red/green and blue/yellow stimuli as a function of spatial and temporal frequency. Vertical bars show standard errors (±1 SE).

were a sum, cortical units would respond as full wave rectifiers with frequency doubling. A sine wave grating that jumped by 90° in phase would then be making a 180° jump in its full wave rectified version and its direction of motion would be ambiguous to detectors that summed ON and OFF responses. This prediction is clearly wrong. Nakayama and Silverman (1985) showed that a 90° jump is the *optimal* displacement for luminance-defined gratings and this could only occur if the motion detectors that combine ON and OFF signals use the difference (thus recovering the fundamental) not the sum of ON and OFF signals. Baker *et al.* (1989) report that the optimal jump size of luminance defined sine waves was somewhat less than 90° (between 54 and 72°) but that motion direction was nevertheless clearly discriminated for 90° jumps. We also verified that equiluminous, chromatic gratings jumping through 90° steps produced appropriate, unambiguous impressions of motion. We conclude that the differencing of ON and OFF responses prior to motion detection may explain why our measurements show less phase shift and second harmonic distortion than is seen in the physiological results.

A second reason is that our stimuli produced only modest modulations of long wavelength-sensitive R-cones and medium wavelength-sensitive G-cones (Table 2). Even very nonlinear systems may respond linearly to small signals so that our stimuli may have fallen in this linear, small-signal operating range. On the other hand, B-cones, which received substantial modulation from our blue/yellow and tritanopic stimuli, contribute little to luminance (Cavanagh *et al.*, 1987; Eisner & MacLeod, 1980; Lee & Stromeyer, 1989) so that phase shifts and distortions involving B-cone signals would produce little effects in a luminance pathway. Perhaps if we had used higher contrasts and square wave stimuli rather than sine wave stimuli (thus introducing higher temporal frequency and accentuating phase lags), we would have measured significant phase shifts or distortion products like those demonstrated by several previous experiments (Cushman & Levinson, 1983; de-Lange, 1958; Derrington *et al.*, 1984; Lee *et al.*, 1989; Lindsey *et al.*, 1986; Schiller & Colby, 1983; Smith *et al.*, 1989; Swanson *et al.*, 1988; von Grünau, 1977). However, in our experiment, these effects had small amplitudes and could not have accounted for the contribution of color to motion that we measured (Experiment 1).

Having eliminated phase lag and second harmonic distortion as possible sources for the main motion responses to the chromatic stimuli in Experiment 1, the remaining factor to examine is the scatter of equiluminance points across units in a luminance-based pathway. This factor allows color to contribute to motion without involving opponent-color pathways.

EXPERIMENT 4: INTERUNIT VARIABILITY IN EQUILUMINANCE

If the perception of motion depends only on responses in a luminance pathway, an "equiluminous" stimulus will still produce a response if the null or equiluminance point varies across units since there will always be some units responding no matter what the relative luminances of the two colors. The strength of the additional response in the luminance pathway produced by the variability depends in a straightforward way on the relative luminances of the two colors—the effect is largest at equiluminance when the luminance pathway should have no response and drops rapidly as the luminance contrast between the two colors increases. The purpose of this experiment is to model the additional response in the luminance pathway due to interunit variability and test for its presence in the motion response to colored gratings.

Physiological studies have revealed a variation in the equiluminance points of units in the magnocellular stream that project to the directionally selective cells in the cortex. Lee *et al.* (1988), Logothetis *et al.* (1989), and Shapley and Kaplan (1989) have shown that individual units in the magnocellular stream do show a null activity point at a particular luminance ratio between the two colors of their stimulus and that this null ratio varies somewhat from unit to unit. In particular, Logothetis *et al.* (1989) showed that because of this variability in "equiluminance" points across units, the minimum in the combined responses of 41 magnocellular units (the group "equiluminance" point) was only a factor of 2.6 smaller than the maximum combined response. This represents a very robust response.

In addition to the interunit variability within local regions, equiluminance settings may vary with retinal position as well (Livingstone & Hubel, 1987; Mullen, 1991; White & Muermans, 1990; variations in the spectral sensitivity of individual cones due to changes in the optical

density of the photopigment may contribute to this effect, Burns & Elsner, 1985) so that an extended stimulus cannot be equiluminous simultaneously over its full extent. In this final experiment, we determine the effect that inter-unit variability—whether due to local variations or retinal inhomogeneity—should have on the response of a luminance pathway to colored stimuli and we test the prediction against data from our opposing motion paradigm. The results show that although the effect of inter-unit variability in equiluminance is present, it accounts for only a small portion of the overall contribution of color to motion.

Response of achromatic pathway to color stimuli

In this section, we compute the effective contrast of a drifting red/green grating in a luminance pathway as a function of the relative luminance contrast between the two colors. We assume that the net contrast is simply the sum of the contrasts sensed by all the directionally selective luminance units.

The left panel of Fig. 19 shows the response of a single unit in a luminance pathway to a drifting red/green grating as a function of its luminance contrast. The response function is given by the grating's absolute luminance contrast. At the center of the horizontal scale, the red and green have equal luminance as measured by a photometer and the unit "sees" a uniform field with no contrast. At the right end of the horizontal scale, the grating is bright red and dark green while at the other end it is bright green and dark red. In both cases, however, the unit merely detects an identical light and dark grating.

We assume that the contrast sensed by individual units are summed to produce the net contrast. If all units had the same null point, there would be a single, true response null in the luminance pathway and the overall function would look like that of the single unit shown on the left in Fig. 19. On the other hand, in right-hand panel of Fig. 19, we have the more likely situation of variable null points for individual units and overlapping functions. If we take the response to be the sum of the activity of the individual units (thick, curved line on the right in Fig. 19 shows the average value for graphical convenience), we see that there is no longer a true null. The mean functions dips to a minimum at photometric equiluminance but this minimum response is not zero. The shape of the actual function depends on the response characteristic of the individual units (shown as linear in Fig. 19) and the distribution of equiluminance points. We do not know either of these factors, but we can determine the effect of scatter for a range of response characteristics and distributions and this will be sufficient to test the scatter hypothesis.

We examined compressive, linear and expansive response functions. We also considered the distribution of equiluminance points; in particular, we examined uniform, singly and doubly peaked distributions.

Figure 20 shows examples of responses for units with linear and nonlinear response functions with the scatter of equiluminance points distributed uniformly between $\pm 5\%$ (similar to the range reported by Lee *et al.*, 1988); a broader range would widen the predicted functions in Fig. 20 without changing the nature of the predictions. The response functions of the individual units are shown by the set of medium-weight curves in the upper panels. A linear function of luminance contrast is shown

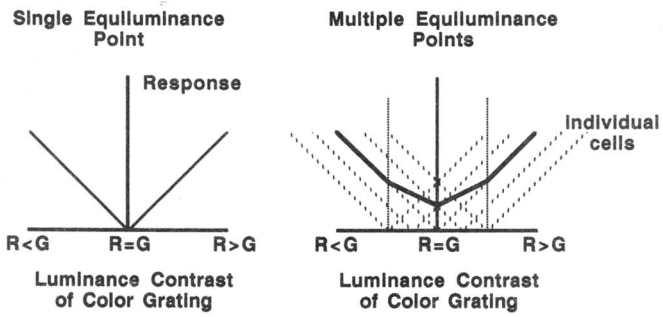


Fig. 19. The response of luminance-based units to a color grating as a function of the luminance contrast between the two colors in the grating. On the left, the response for a single unit is shown and the response function follows the absolute value of the luminance contrast. On the right, different units have different equiluminance points. The net response is shown, for graphical convenience, as the average of the individual responses and indicated by the heavy curve. The curve has a minimum but the response is greater than zero at the minimum value.

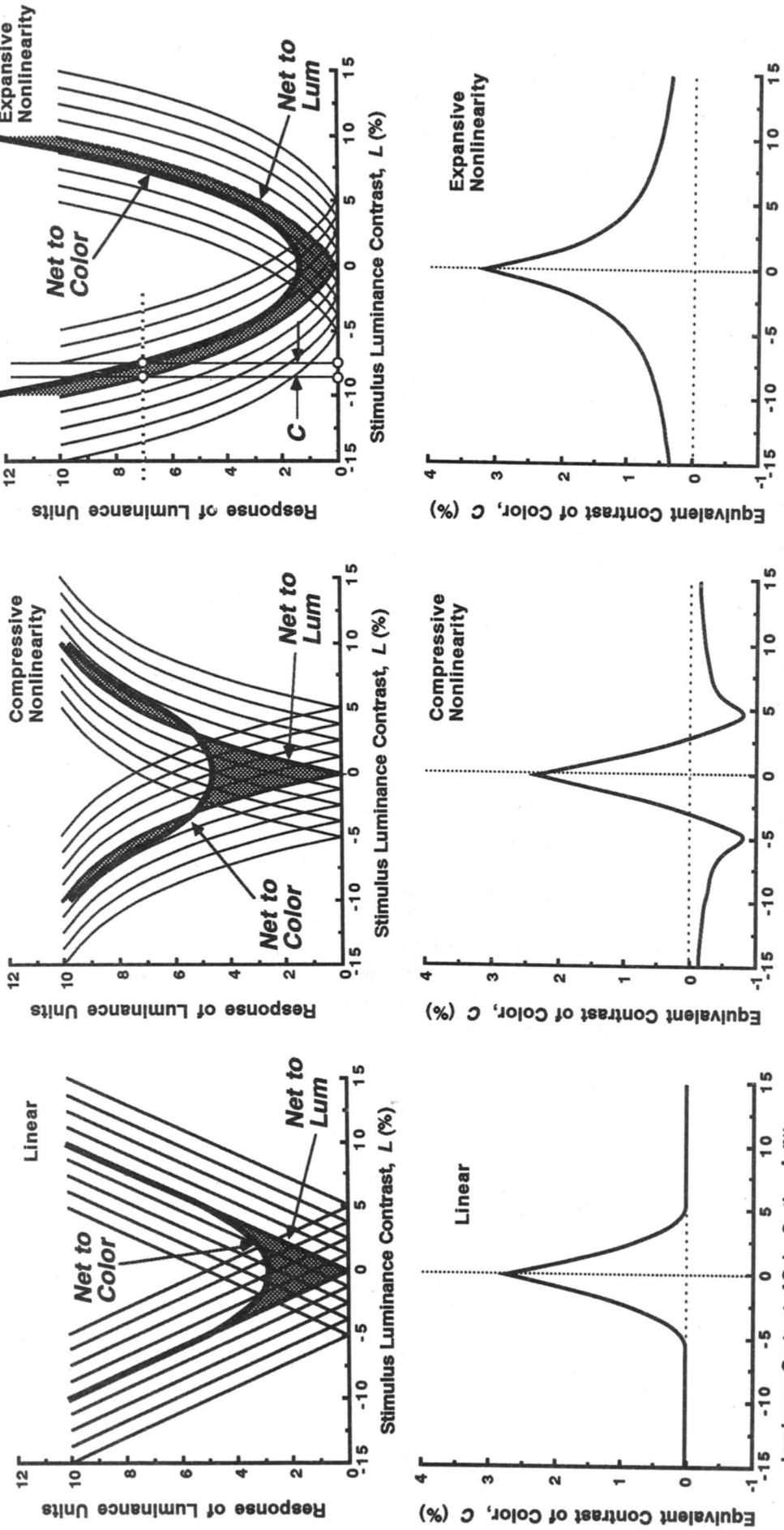


Fig. 20. The response of luminance-based units to a color and to a luminance grating as a function of luminance contrast. Three contrast response functions: a linear function (left), a compressive square-root nonlinearity (center), and an expansive squared nonlinearity (right). In the upper panels, responses of individual units to the color grating are shown as medium-weight curves with a uniform distribution of equiluminance (null) points. The net responses to color and to luminance (heavy curves) are shown as the average responses of the individual units. The shaded areas indicate the differences between the net responses to the color and luminance gratings that result from the scatter of individual equiluminance points. The lower panels show this difference directly as the equivalent luminance contrast produced by the presence of the color in the gratings.

in the left panel, the square root of contrast in the center panel, and the square of the contrast in the right panel. The net response of all these units (shown as the average of the individual functions) to a luminance grating as a function of its contrast is shown by the heavy, V-shaped curves labeled "net to lum". Since there is no variation across units in the null point to a luminance grating, the response to a luminance grating with luminance contrast L is just $f(|L|)$ where f is the response function of the unit. This is the central function of the individual units with its null at photometric equiluminance.

The net response of these same units to a color grating as a function of the luminance contrast between the two colors of the grating is shown by the thick U-shaped curves labeled "net to color"

Figure 20 shows the net response of the luminance-based units, a variable which we cannot measure directly. We can, however, simulate our opposing motion paradigm and determine the contrast a luminance grating needs in order to match the net response produced by a color grating with a particular luminance contrast. These two gratings should have the same strength and therefore should exactly null each other's motion. The equivalent contrast of the color in the stimulus (as defined in Experiment 1 but now considering *only* the response in a luminance pathway) is then given by the difference between the color grating's luminance contrast and the contrast of a luminance grating that produces the same net response. This is demonstrated in the upper right-hand panel by a dotted line for a response level of 7.0 (in arbitrary units). A color grating requires about 7.5% luminance contrast to produce this response level but a luminance grating needs about 8.2% contrast. The difference between the two is 0.7% and this is the extra response, the equivalent contrast, contributed by color to a luminance pathway due to interunit variability. The difference between the net response to color and the net response to luminance is shown by the shaded areas in the upper panels and plotted directly in the bottom panels.

The bottom panels show that as a result of the interunit variability of null points, the presence of color in the grating adds a significant response in the luminance pathway, particularly at equiluminance. However, this additional response drops rapidly to zero once the luminance contrast of the color grating is outside the range of the equiluminance point scatter of individual units.

Next we consider the effect of nonlinear response characteristic of the individual units. With a compressive nonlinearity (Fig. 20, center panels, a square root nonlinearity), the effect of the presence of color is to decrease the response (compared to a luminance grating of the same contrast) over a substantial range. For an expansive nonlinearity (Fig. 20, right-hand panels, a squared nonlinearity), the equivalent contrast of the color again has a peak at equiluminance, and drops toward zero, remaining positive.

The predictions shown in Fig. 20 are for a uniform distribution of equiluminance points over a $\pm 5\%$ range. We also tested single and double peaked triangular distributions and obtained very similar predictions (not shown). In summary, for any response function and for uniform, peaked, or bimodal distribution of equiluminance points of individual units, the equivalent contrast of a color grating in a luminance pathway should have a peak at equiluminance and drop away quickly on either side of equiluminance. The width and height of the inverted V functions in the bottom panels of Fig. 20 would vary directly with the SD of the distribution of individual equiluminance points but the shapes of the functions are not otherwise greatly affected by the shape of the distribution.

What would the equivalent contrast function look like if color made a contribution to motion through an opponent-color pathway and not through residual activation of a luminance pathway (i.e. if there were no interunit variation in equiluminance points)? We can assume that a contribution from an opponent-color pathway would be a function of the chromatic contrast of the stimulus and this is fairly independent of its luminance contrast, at least over the range we are looking at here (maximum of $\pm 30\%$). Assuming a simple linear model in which the color contribution sums with the luminance contrast to produce the total effective contrast, the function would just be a V-shaped curve that is raised everywhere by the same amount (Fig. 21). The difference between this raised V and the luminance contrast gives us a constant equivalent contrast at all values of luminance contrast (Fig. 21, central panel).

We can now compare these functions to the actual data of the equivalent contrast of color in a motion task. Our calculation of equivalent contrast in Experiment 1 assumed that the

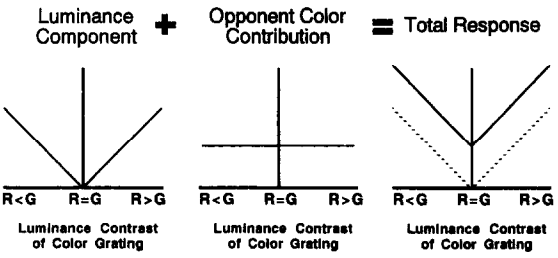


Fig. 21. The total response to a color grating as the sum of luminance and opponent color contributions. In this case, the equivalent luminance contrast, the difference of the total effective contrast of the color grating and its luminance contrast, measures the opponent-color contribution. Since the chromatic contrast and, therefore, the opponent-color response, is fairly constant over the moderate range of luminance contrasts of the color grating that were tested, the equivalent contrast should be fairly constant as well.

contribution of color to motion was fairly constant as a function of physical contrast (see Fig. 3). We presented luminance gratings of 5, 10 and 15% luminance contrast and found the physical luminance contrast of the opposing color grating that would just null the motion at each of those contrasts. The contrast of the opposing luminance grating measures the total effective contrast, T, of the color grating and the luminance contrast of the color grating is L. The equivalent luminance contrast of the color, C, in the grating is just the difference of these two as in equation (4) but when we averaged the three values for equivalent contrast based on three different values of L in Experiment 1, we discarded the information about their differences and are predicted here. The differences between the equivalent contrasts for the three different opposing luminance contrasts that we observed were neither large nor systematic but the data from Experiment 1 are not ideal for evaluating the possible differences in equivalent contrast with changes in grating luminance contrast. First, the range of effective contrasts examined was only 10% (i.e. from 5 to 15%), and second, we did not determine the minimum effective contrast for the color grating when it was at experimental equiluminance, $L = 0$.

To evaluate the scatter hypothesis, we therefore measured equivalent contrast for a broader range of opposing luminance contrasts that included the equiluminance point. We used only one spatial and one temporal frequency for red/green and blue/yellow gratings. We chose 1 c/deg and 8 Hz for technical reasons: we needed to keep the contrast of the opposing luminance grating as small as possible ($\pm 25\%$, to maintain color contrasts) while examining the largest possible range of luminance contrasts for the color grating (about $\pm 20\%$). These conditions are met when the equivalent contrast is lowest as it is for 1 c/deg and 8 Hz (Fig. 6).

Method

The procedure was identical to that of Experiment 1 with the following exceptions. First, only red/green and blue/yellow gratings at 1 c/deg and 8 Hz were used. Second, the contrast of the opposing luminance grating was set at 10, 15, 20 and 25%. At the motion nulls, the effective contrast of the color grating, T, was equal to the contrast of the opposing luminance grating and the luminance contrast of the color grating, L, was determined from the separation of the two motion nulls using equation (3) (one, for red/green gratings, with red more luminous than green and the other with green more luminous than red). The equivalent contrast of the color in the color grating, C, was given by the difference between its effective contrast and its luminance contrast.

Finally, to measure the effective contrast at equiluminance, $L = 0$, additional readings were taken to find the highest value of opposing luminance contrast for which there was no reversal of motion (luminance never overcame color) as the observer adjusted the luminance contrast of the color grating. This measures the minimum effective contrast of the color grating, equal to the contrast of the luminance grating that will just null the motion of the color grating when it is equiluminous. Adjustments were made for several closely spaced values of opposing luminance contrast—1% steps of contrast between 3 and 9%—until the highest value that produce a single motion null point was found. Motion was ambiguous at this setting but if the luminance contrast of the color grating was changed in either direction, the same direction of motion was seen.

Two observers participated. Both had normal or corrected-to-normal acuity and normal color vision.

Results

Figure 22 shows the measured equivalent contrast of the color in the color gratings as a function of their luminance contrast for both subjects. The equivalent contrasts measured here appear higher than those measured in the 1 c/deg, 8 Hz condition of Experiment 1 (Fig. 6) but most of the difference is due to procedure and observer effects. Experiment 1 sampled only

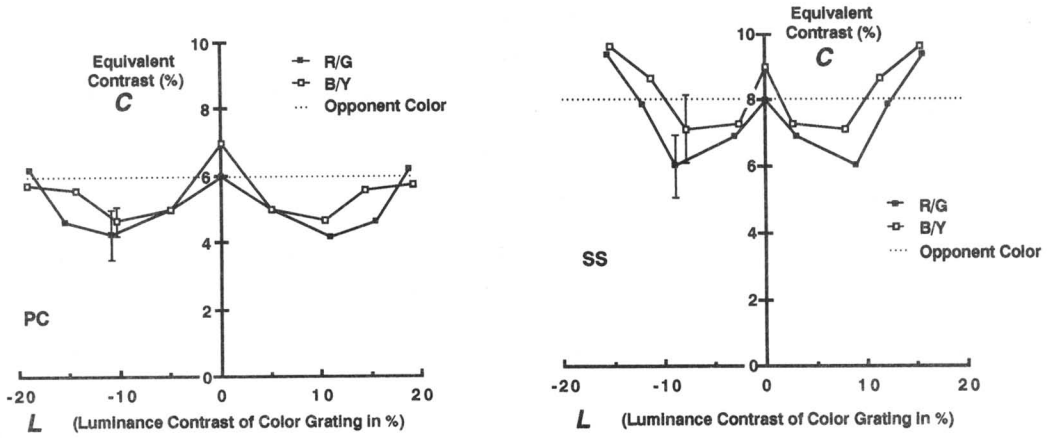


Fig. 22. Equivalent contrast of color measured for red/green and blue/yellow gratings at 1.0 c/deg and 8 Hz as a function of the luminance contrast of the gratings. The dotted line shows the predicted contribution of an opponent-color mechanism. Vertical bars show typical standard errors (±1 SE).

the contrast conditions that gave the lowest values seen in Fig. 22 (those near 5 and 10% luminance contrast in the color grating) and observer SS, who participated in Experiment 4 but not Experiment 1, made higher settings than the group averages from Experiment 1 (but still within the observed range of values for that experiment).

The equivalent contrast does not decrease to zero on both sides of equiluminance as predicted by the scatter hypothesis (Fig. 20). Although there is an initial drop, the equivalent contrast then rises again as the color grating reaches higher values of luminance contrast. The overall trend of these results is neither a continuous drop nor rise but is fairly level with a local variation superimposed. The flat, overall trend is compatible with an opponent-color input to motion, where chromatic contrast directly activates directionally selective units (Fig. 21). However, the equivalent contrast does not remain completely constant. There is a rise of about 2% in the equivalent contrast values from the lowest values adjacent to equiluminance up to the local maximum of equiluminance. There may be, therefore, a small contribution of scatter to the motion response that produces the central 2% peak in the observed functions. This local maximum has about the same value as the equivalent contrasts in Experiment 1 (3.5–3.8%) but this is only a coincidence. The local maximum is the difference between the peak at equiluminance and the adjacent minimum values in Fig. 22 whereas the equivalent contrasts reported in Experiment 1 are based on the average of these values adjacent to the equiluminance point.

The size of this contribution from interunit variablity is unexpectedly low given the variability of equiluminance points seen for magnocellular units (Lee *et al.*, 1988; Logothetis *et al.*, 1989; Shapley & Kaplan, 1989). If the motion response were based directly on the responses of the magnocellular units recorded by Logothetis *et al.* (1989), the central peak should have had a value of 30–40%, not the 7 or 8% seen in Fig. 23 nor the 2% amplitude of the local maximum.

There are two possible reasons for our unexpectedly low estimate for the contribution of interunit variability. First, our model, as well as the simulated total response of several magnocellular units reported by Logothetis *et al.* (1989), assumed that the responses of all the units are summed. If on the other hand, we consider two groups of cells, ON-center and OFF-center whose responses are summed within each group and then differenced, it is easily shown that a more stable and more pronounced equiluminance null emerges. Each cortical motion detector receives input from several ON and OFF LGN units in order to construct an oriented receptive field and we described previously the evidence suggesting that ON and OFF signals are differenced prior to motion detection (p. 2132). The greater the number of ON and OFF cells combined in this fashion, the greater the stability and depth of the equiluminance null and the less the expected effect of interunit variability.

Second, although interunit variability ensures a motion response in the luminance pathway at "equiluminance", it has the opposite effect within the motion detector itself. In our prediction of the effects of interunit variability, we assumed that a directionally selective unit had a single equiluminance point. However

a directionally selective unit requires, in its simplest form, input from a pair of detectors, or subunits, that are spatially offset and combined with a temporal delay (Barlow & Levick, 1965; Reichart, 1961). If the spectral sensitivities of *subunits* are not matched within each pair, a chromatic grating drifting, say, leftward may actually activate some motion detectors that prefer the opposite direction of motion (Derrington & Badcock, 1985). As a result of these reverse responses, the total motion response may be reduced. If the equiluminance points of the subunits are randomly sampled from the distribution of possible values (no pairwise correlation), equal motion responses in both directions are generated at "equiluminance" and no net motion is produced in the luminance pathway. Therefore, mismatching of the equiluminance points within subunit pairs may also have reduced the peak effect of interunit variability that we observed in Fig. 22.

In summary, the small effect of interunit variability observed at equiluminance in Fig. 22 may have resulted both from response differencing across ON and OFF units and from mismatching of subunit equiluminance points within motion detectors. However, neither of these two factors nor the basic effect of interunit variability can explain the maintained advantage of colored gratings over luminance gratings (e.g. equivalent contrast > 0) when the color grating has a high luminance contrast. An opponent-color input to motion detectors is the most likely explanation of this result.

DISCUSSION

Our experiments have demonstrated that color makes an important contribution to the perception of motion. In this final section, we claim that this contribution is mediated by an opponent-color response and that it combines with a luminance response to form a common motion pathway. We discuss the possible physiological mechanisms mediating the contribution of color to motion and we present a model for the phenomenon of slowed motion based on velocity miscalibration. Lastly, we discuss the usefulness of our new test for diagnosing color deficits, especially in nonverbal populations.

Opponent-color input to motion

Our results have shown that the contribution of color to motion in normal observers could not be explained by the combination of display or chromatic aberration artifacts nor by phase lag, second harmonic distortion, or interunit variability in a luminance pathway. Chromatic aberration and display artifacts were shown to produce less than 1% luminance contrast (Fig. 12); the second harmonic components arising in the motion pathway were all less than 1% (Fig. 18); and the phase lag produced at most 3% contrast (Fig. 17). Finally, interunit scatter in equiluminance points may have accounted for 2% luminance contrast in response to equiluminous stimuli (Experiment 4) but less than that for the color stimuli of Experiment 1 which were not tested at equiluminance. The combined effect of all these factors cannot exceed 4–5%, well below the equivalent contrasts of up to 15% that we measured for red/green stimuli (Fig. 14, top left panel), although perhaps sufficient to explain the motion response to tritanopic color stimuli. We conclude that the major contribution of color to motion for normal observers in our opposing motion paradigm is not mediated by a luminance pathway.

On the other hand, our data do suggest that the contribution of color to motion is mediated by opponent-color pathways. In particular, the contribution of color to motion in Experiment 1 decreased with both temporal and spatial frequency for normal observers. Both of these decreases are consistent with the behavior of the chromatic mechanisms and opposite to the behavior of luminance mechanisms in the frequency ranges tested (deLange, 1958; Kelly, 1983).

Interestingly, our data indicate that opponent-color signals contribute to the motion system only for very low spatial frequencies, up to about 1.0 or 2.0 c/deg (Fig. 12). The contrast sensitivity function for color is low pass (Kelly, 1983), but the response to color extends to 12.0 c/deg (Mullen, 1985), well beyond 1.0 c/deg. If opponent-color signals contribute to directionally selective units, why would they contribute over only part of the available range? One possibility is that they do not need to above 1.0 c/deg. Our data on chromatic aberration (Fig. 12) showed that above 1.0 c/deg, luminance artifacts in the eye produced substantial contribution to motion for color stimuli even in color-deficient observers. Therefore, in the range above 1.0 c/deg, optical artifacts ensure a response to chromatic stimuli no matter what the relative luminances of the colors; below

2.0 c/deg, however, the visual system must find other mechanisms to respond to the motion of equiluminous color stimuli. In other words, opponent-color mechanisms contribute to the motion system only over the range of stimulus parameters for which the visual system would otherwise be motion-blind. The contribution may be a functional addition to the visual system that improves the motion response to equiluminous stimuli.

How significant is the 10 or 15% equivalent contrast (at the most effective settings) that color contributes to motion? Is it a lot or a little? A contribution equivalent to 10 to 15% luminance contrast must be considered substantial since it is 20–30 times the level of luminance threshold. In addition, the results of Experiment 2 showed that the contribution of color to motion was similar to that of luminance for the normal observer in terms of contrast threshold multiples. Those results were based on the contrast thresholds for direction discrimination, however, and perhaps the most striking observation about the motion of chromatic stimuli is that the threshold for direction discrimination is typically much higher than the threshold for detection (Fig. 15, observer PC, R/G stimuli, also see Lindsey & Teller, 1990). Evidently, the visual system is more sensitive to the presence of color patterns than to their motion and this, as well as the perhaps related phenomenon of slowed motion discussed later, gives the impression that the motion response to chromatic stimuli is weak.

Recent work by Stromeyer, Eskew and Kronauer (1990) shows that this is not the case, at least not for stimuli modulating the R- and G-cone classes. The motion discrimination thresholds for chromatic stimuli (R- and G-cones modulated out of phase) are in fact about four times *lower* than those for luminance stimuli (R- and G-cones modulated in phase) when both thresholds are expressed in terms of the cone contrasts (this is true of our results for red/green and luminance stimuli in Experiment 2 as well). Counteracting this greater sensitivity for out-of-phase (chromatic) than in-phase (luminance) modulation is the great overlap in spectral sensitivity of the R- and G-cone classes. The effect of this overlap is that the maximum out-of-phase (chromatic) cone modulation is fairly low (about 30% with the red and green phosphors of our monitor) whereas the in-phase (luminance) modulation can easily reach 100%. Chromatic stimuli modulating R- and G-cones out of phase produce weaker motion responses at least in part because they can produce only moderate levels of cone contrast, not because the motion system is less sensitive to them. Chromatic stimuli that modulate the B-cone axis can produce much higher levels of cone contrast, but modulation of this cone class may not produce much response in the motion system.

Srinivasan (1985) has argued that that motion detection should be color-blind since optimum performance requires that the two subunits of each motion detector have similar spectral sensitivity functions. However, optimal performance requires only that spectral sensitivity be matched within detectors, not across detectors. This condition can be met even if some detectors receive opponent-color input as long as for any given detector both subunits receive similar input. More to the point, an optimal motion system should not be blind to the motion of any contour that the visual system can detect, whether defined by luminance, color, texture, or depth.

Contribution of B-cones to motion

Our data suggest that the opponent-color input to motion may be organized along the cardinal axes of color space proposed by MacLeod and Boynton (1979). The equivalent contrast of the color in the green/purple stimulus falling along the tritanopic confusion line in Experiment 1 was similar for normal and color-deficient observers while the advantage of the color normal over color-deficient observers increased as a function of the R − G component in the stimulus.

Lee and Stromeyer (1989) have examined the perception of motion for stimuli differentially stimulating only the B-cones. They attributed the perception of motion for these stimuli to the contribution of B-cones to a luminance pathway. They estimate the contribution of B-cones to be about 1 or 2% of that of the long wavelength-sensitive, R-cones or medium wavelength-sensitive, G-cones to the luminance pathway. On the other hand, in Experiment 1 here, we measured an equivalent contrast of 4% for the B-cone contribution to motion. We obtained our estimate at temporal frequencies well below those used by Lee and Stromeyer (1989). We attribute the difference in estimates not just to the difference in stimulus conditions but to the evaluation of different systems at these different temporal frequencies: at low temporal

frequencies, we claim to have measured a chromatic response whereas at higher frequencies, they claim to have measured a luminance-based response.

Their value for a luminance-based contribution of the B-cones to motion is similar to the upper limit of B-cone contribution to luminance that we have measured in a previous experiment (Cavanagh *et al.*, 1987). Using the motion technique described by equations (5) and (6), a blue/green stimulus in counterphase modulation was added in quadrature phase to a counterphasing luminance sine wave and the blue/green luminance ratio was adjusted until no motion was seen. This gives the equiluminance setting between blue and green. We then bleached the B-cones of the observers and found that the settings for equiluminance changed by no more than 1 or 2%.

Although the color-specific motion response for stimuli sensed only by the B-cones was about 4% in Experiment 1 here, some or all of that amount may be accounted for by phase lag, second harmonic distortion and interunit variability factors. Our data do not determine unequivocally whether the contribution to motion from tritanopic stimuli is greater than zero, but it is clear that this contribution is much weaker than that of the R − G opponent-color mechanism.

Common motion pathway for luminance and color

Even though the data suggest an independent contribution to motion from opponent-color pathways, they do not imply an independent analysis of motion in these pathways. The fact that the motion of a drifting color grating can be nulled by that of a drifting luminance grating, rather than producing a perception of transparency where both are seen simultaneously (Adelson & Movshon, 1982), argues that the two signals contribute to a common pathway. We claim that the main contribution of color to this common pathway is not due to the imperfections of a luminance-based response but to an opponent-color response.

Our results therefore suggest that there should be directionally selective units, and perhaps precursors to these units, that respond to both luminance and chromatic contrast. One structure in visual cortex that appears to meet these requirements is area MT. Albright (1987), Saito, Tanaka, Isono, Yasuda and Mikami (1989), and Charles and Logothetis (1989) have reported cells in area MT that do respond to equiluminous color and to luminance.

Slowed motion

Previous work has shown that the perceived velocity of drifting colored gratings slowed down or even stopped as the colors approached equiluminance (Cavanagh *et al.*, 1984; Moreland, 1982). We attribute this slowed velocity perception not to a weak motion response but to a miscalibration in the decoding of velocity, or velocity normalization, for these stimuli. The response of a directionally selective unit in visual cortex does not unambiguously signal stimulus velocity but increases both with stimulus velocity (up to some maximum) and with stimulus contrast (e.g. Holub & Morton-Gibson, 1981). To recover velocity independently of contrast, the visual system needs a second class of cells that provides a separate measure of contrast and we suggest that the second class is made up of nondirectional units.

If these two types of cells respond in a similar way to contrast, then the velocity may be recovered* by using the response of the nondirectional units to correct the response of the directional units. However, if the two types of cells respond differently to contrast, the recovered velocities will be inaccurate. In particular, if the nondirectional units are more sensitive to stimulus contrast than are the directional units, then the estimate of the contribution of contrast to the directional response will be too high and the recovered velocity will be too low. We claim that this is what happens for chromatic gratings and a comparison of direction discrimination thresholds and detection thresholds shows that nondirectional

*We assume in this model that the response of the directional unit is some separable combination of a function of velocity, $h(v)$, and a function of contrast, $g(c)$, and that the response of the nondirectional unit provides an estimate of this same $g(c)$. This estimate is used to recover $h(v)$ from the directional response and v is then recovered from $h(v)$. If the same function, $g(c)$, is not involved in both types of units then recovery will lead to errors as described in the text.

A more general model would invert the contrast function of the nondirectional response to recover the contrast itself. This estimate would then allow an accurate recovery of velocity even if the directional and nondirectional contrast functions differed as long as the contrast is above the thresholds of both types of units. Since human performance does not show this accurate recovery we have favored the response estimation model rather than a contrast estimation model.

units are more sensitive for chromatic stimuli (Fig. 15, here; also Lindsey & Teller, 1990). As we saw in Fig. 15 for moving red/green gratings, there is a fairly broad range of contrasts for which the grating is visible but its motion is not (the shaded regions for the normal observer). We assume that higher sensitivity of the non-directional units seen at threshold levels is maintained at suprathreshold contrasts and thus creates an overestimate of the effect of contrast and an underestimate of velocity. Moreover, we claim that whenever a difference between detection threshold and direction discrimination threshold is observed, velocity miscalibration will also occur at suprathreshold levels. This miscalibration is not limited to chromatic stimuli. Campbell and Maffei (1981) report that when luminance stimuli are presented in the periphery they may also appear to slow down or stop. In support of our conjecture, the threshold for detection for their stimuli is indeed lower than the threshold for direction discrimination.

Troscianko and Fahle (1988) have presented an alternate model for the slowing of chromatic gratings. Their model has three components: first, perceived velocity increases directly with contrast (i.e. no velocity constancy) up to some asymptotic value; second, the motion of chromatic gratings and luminance gratings is sensed by the same mechanisms; and third, chromatic gratings appear slowed because they have a low effective contrast. However, their proposal fails to account for several features of velocity judgments. First of all judgements for luminance gratings do show quite reasonable velocity constancy, producing veridical settings for contrasts as low as 1–5% (Campbell & Maffei, 1981; Cavanagh *et al.*, 1984). Second, when the opposing motions of a chromatic grating and a luminance grating just null each other, they must be considered to have equal effective contrast and, according to Troscianko and Fahle, they should appear to move at the same velocity when presented individually. However, the equiluminous color grating appears slowed when viewed alone whereas the luminance grating of about 12% contrast that will null its motion (Fig. 6) appears to move at its true speed (Cavanagh *et al.*, 1984). Finally, the perceived speed of a moving equiluminous grating increases with spatial frequency (Cavanagh *et al.*, 1984) but its equivalent contrast decreases (Fig. 6).

Derrington and Badcock (1985) presented a model of motion detection in which the subunits of each detector were randomly connected to color-opponent units having either R-cone centers or G-cone centers. As mentioned previously, they showed how this mismatch in subunit spectral characteristics leads to responses from some units that prefer the direction of motion opposite to the actual motion of the stimulus. They argued that these reverse motion responses at and near equiluminance could explain the slowed motion seen in these conditions. However, their model deals only with the contribution of color to motion that passes through the luminance pathway. The mismatch in subunit spectral characteristics may therefore contribute something to the overall slowing but our data argue that the opponent-color pathways are the major contributor to the motion response for chromatic grating and thus that the principal source of slowing is the miscalibration of velocity normalization.

Physiological pathways for motion analysis

We have argued that the contribution of color motion is carried by color-opponent pathways in the visual system and we have done so despite clear evidence that the early non-opponent (magnocellular) pathway is quite capable of responding strongly to chromatic stimuli.

Units in the magnocellular stream are typically nonopponent or broadband in their response but often retain some response to chromatic stimuli (Derrington *et al.*, 1984; Gouras & Eggers, 1982; Krueger, 1979; Schiller & Colby, 1983; Wiesel & Hubel, 1966). Schiller and Colby (1983), for example, demonstrated that magnocellular units will always respond to the exchange of two differently colored lights no matter what the relative luminance of the lights, showing frequency doubling (a transient response at each color exchange) in the range near "equiluminance". Lee *et al.* (1989) also showed strong frequency doubling in the responses to sinusoidal chromatic flicker. Logothetis *et al.* (1989) demonstrated that because of the variability of the null points of individual magnocellular units, the combined response of several units never drops to much less than half of its maximum as the ratio of luminances between the two colors in the stimulus are varied over a large range. Finally, magnocellular units do have an inherent spectral opponency in their structure since their surrounds are dominated by long wavelength-sensitive R-cones (Wiesel & Hubel, 1966). In

particular, their response is typically shut off for large red fields (Livingstone & Hubel, 1984). Since the centers of the magnocellular units receive input from both R- and G-cones, low spatial frequency stimuli with individual bars large enough to cover the receptive field surrounds should produce an opponent-color response from the magnocellular units.

Given these results, we would expect that magnocellular units would make a substantial contribution to the motion response for chromatic stimuli. However, we have argued that this is not the case for two reasons: (1) our data for chromatic stimuli did not show the properties expected from a magnocellular contribution; and (2) the magnocellular response to chromatic stimuli may be greatly attenuated by the time it reaches cortical motion detectors. Here are these arguments restated in more detail.

First, the results of our experiments do not support the participation of magnocellular units in the motion response to chromatic stimuli at the low spatial and temporal frequencies we used. The spatiotemporal properties in Experiments 1 and 2 were distinctly chromatic but more important, the phase lags in response measured between red and green, yellow and blue and green and purple stimuli in Experiment 3 were never larger than 3°. Smith *et al.* (1989) have measured phase lags in retinal ganglia that project to magnocellular and parvocellular units and found extremely large values (up to 90°) for those projecting to magnocellular units at the temporal frequencies that we have used in our experiments but fairly small values for those in projecting to parvocellular units. These results strongly suggest that the phase lags we measure in our motion task are mediated by parvocellular input.

Second, how can the robust response of the magnocellular units to chromatic stimuli appear to have so little impact at the level of the motion detectors? In the discussion of Experiments 3 and 4, we suggested that interactions between ON- and OFF-center magnocellular units could greatly reduce the net response to chromatic stimuli. If ON- and OFF-center responses are independently pooled and then differenced prior to motion detection, the effects of phase lag, second harmonic distortion (frequency doubling) and interunit variability will be much attenuated (and the linearity of the response improved). In addition, differences in spectral sensitivity between the subunits of individual motion detectors will also blunt a luminance-based motion response. Do these "improved" response properties imply that cortical motion detectors should show deep null responses at equiluminance points that vary little from unit to unit? Our answer is no since we argue that opponent-color, parvocellular signals also contribute to the motion detectors to provide a response through the equiluminance region. There is, nevertheless, a significant change in performance at or near equiluminance in that velocity becomes noticeably underestimated. It is clear that no change in performance should have occurred if the robust magnocellular response to chromatic gratings were passed on to motion detectors. For example, the summed group response of magnocellular units at "equiluminance" of 30–40% of their maximum response (Logothetis *et al.*, 1990) would support a strong motion response in the luminance pathway that should not suffer any loss in apparent velocity. Clearly, something must act to reduce the magnocellular response to chromatic gratings at higher levels or none of the performance losses observed at equiluminance could possibly occur.

Can the parvocellular stream contribute to the perception of motion? Schiller, Logothetis and Charles (1990) and Merigan and Maunsell (1990) used small lesions of magnocellular and parvocellular layers of the lateral geniculate to test the impairment that each caused for motion perception. Following magnocellular lesions, the deficits at high temporal frequencies and low contrasts were pronounced. However, at low temporal frequencies and high contrasts (such as those used in our Experiments 1, 3 and 4) the deficits were small, suggesting that in this range, information in the parvocellular stream does support the perception of motion.

Recent studies show that high-level cells in the motion system do respond to equiluminous color stimuli. Albright (1987), Saito *et al.* (1989), and Charles and Logothetis (1989) have all reported that equiluminous, colored gratings can drive the directionally selective cells of area MT. None of these studies has been able to definitively link these responses to either the magnocellular or parvocellular streams.

Color-deficient observers

The color-deficient observers showed little or no contribution of color to motion in the nulling experiment either for red/green stimuli which they discriminated poorly or for blue/yellow

stimuli which they saw almost as well as normals. The one protan tested for stimuli along his tritanopic confusion line showed approximately the same equivalent contrast as the normal observer, so this loss of opponent-color input to motion appears to be specific to the red/green opponent mechanism. The color deficient observers were able to see equiluminous color stimuli move when presented alone in the threshold task, a response that might be mediated by a higher-level motion system.

The measurement of color's contribution to motion was very effective for identifying color-deficient observers and classifying them as protans and deutans as well. Since the task involves identifying the direction of the stimulus motion, it lends itself easily to optokinetic nystagmus measures on preverbal or nonverbal populations (Anstis *et al.*, 1986; Cavanagh *et al.*, 1984; Logothetis & Charles, 1990; Maurer *et al.*, 1989; Teller & Lindsey, 1988). The loss of chromatic input to motion was substantially the same for all the color-deficient observers even though they were a heterogeneous group including very mild anomalous trichromats (both protans and deutans) and at least one dichromat (deuteranope). Therefore, this test is not very sensitive to the degree of color deficiency but it is extremely sensitive to mild losses and is able to classify the type of loss better than other techniques. On the other hand, the wide range of equivalent contrasts measured for the four normals (see Fig. 14, top left panel, for example) suggests that there may be substantial variations in the strength of normal color vision.

Our results in Experiment 2 show that the contrast thresholds for detection and direction discrimination of chromatic gratings also show losses for color-deficient observers that are similar in magnitude to those we measured with the opposed motion test. Even though these threshold measures could be used to screen for color deficiencies, there are three reasons why we favor the opposed motion test. First, threshold settings are relatively difficult to make and require either trained observers or large numbers of measurements. The opposing motion task, on the other hand, is very simple and can even be done without instructions or training if OKN measures are used (Teller & Lindsey, 1988). Second, the opposing motion task does not require a search through a range of luminance ratios to find the equiluminance point; only two values need to be measured (the two null points of Fig. 3) and from these both the equivalent contrast and the equiluminance point are derived. Third, the opposing motion task was less sensitive to the colors being tested as long as tritanopic colors were avoided. In particular, the color-deficient observers showed large losses for blue/yellow gratings in the opposing motion task but only moderate losses for these same colors in the threshold tasks.

Although the opposing motion task screens for color deficiencies quite well, it is not meant to replace the isochromatic plates as a basic test of color vision. Isochromatic plates evaluate the primary aspects of color vision—the ability to see forms defined by color—and they do this very well, using inexpensive equipment in a test that takes only a few minutes to administer. The opposing motion task offers more diagnostic power but at the expense of more elaborate equipment. On the other hand, the opposing motion task has the ability to drive OKN making it the best choice to measure color deficiencies in nonverbal and preverbal populations (Teller & Lindsey, 1988).

In conclusion, we have presented evidence that opponent-color mechanisms contribute directly to the motion responses of the visual system. In fact, the motion system appeared to be very sensitive to red/green chromatic stimuli, more so than to luminance stimuli when both are scaled in terms of cone contrast (Stromeyer *et al.*, 1990). The weak motion responses typically reported for red/green chromatic stimuli do not arise because the motion system is less sensitive to them—the responses are weak at least in part because even the most saturated red/green stimulus produces only moderate levels of cone contrast at equiluminance compared to the 100% contrast that is easily attainable for luminance stimuli.

We argued that the opponent-color contribution is carried by parvocellular units, at least within the range of spatial and temporal frequencies that we have studied. Since both parvocellular and magnocellular streams must be contributing to motion analyses at some point, the division between these two streams which is clear at low levels in the visual system (van Essen, 1985; Livingstone & Hubel, 1984, 1987, 1988) may be less so at higher levels. Finally, we have demonstrated that our technique of measuring the contribution of color to motion offers important advantages for the screening of color deficits, especially among nonverbal populations.

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REFERENCES

Adelson, E. H. & Movshon, J. A. (1982). Phenomenal coherence of moving gratings. *Nature, 300*, 523–525.

Albright, T. D. (1987). Isoluminant motion processing in macaque visual area MT. *Society for Neurosciences Abstracts, 13*, 1626.

Anstis, S. M. (1980). The perception of apparent movement. *Philosophical Transactions of the Royal Society of London B, 290*, 153–168.

Anstis, S. M., Cavanagh, P., Maurer, D., Lewis, T., MacLeod, D. I. A. & Mather, G. (1986). Computer-generated test for colorblindness. *Color Research and Applications, 11*, S63–S66.

Baker Jr, C. L., Baydala, A. & Zeitouni, N. (1989). Optimal displacement in apparent motion. *Vision Research, 29*, 849–859.

Barlow, H. B. & Levick, W. R. (1965). The mechanism of directionally selective units in the rabbit retina. *Journal of Physiology, 178*, 477–504.

Boynton, R. M. (1979). *Human colour vision*. New York: Holt, Rinehart & Winston.

Braddick, O. (1980). Low-level and high-level processes in apparent motion. *Transactions of the Royal Society of London B, 290*, 137–151.

Bradley, A., Thibos, L. & Zhang, X. (1989). Luminance artifacts in the retinal images of isoluminant color-modulated stimuli: Effect of correcting axial chromatic aberration. *Investigative Ophthalmology and Visual Science (Suppl.), 28*, 92.

Brindley, G. S. (1953). The effects on colour vision of adaptation to very bright lights. *Journal of Physiology, 122*, 332–350.

Brussell, E. M. & Cavanagh, P. (1984). An anticipated threshold technique for measuring contrast sensitivity. *American Journal of Optometry and Physiological Optics, 61*, 125–126.

Burns, S. A. & Elsner, A. E. (1985). Color matching at high illuminances: The color-matching-area effect and photopigment bleaching. *Journal of the Optical Society of America A, 2*, 698–712.

Campbell, F. W. & Maffei, L. (1981). The influence of spatial frequency and contrast on the perception of moving patterns. *Vision Research, 21*, 713–721.

Cavanagh, P. & Favreau, O. E. (1985). Color and luminance share a common motion pathway. *Vision Research, 25*, 1595–1601.

Cavanagh, P. & Mather, G. (1989) Motion: The long and short of it. *Spatial Vision, 4*, 103–129.

Cavanagh, P., Anstis, S. M. & MacLeod, D. I. A. (1987). Equiluminance: Spatial and temporal factors and the contribution of blue-sensitive cones. *Journal of the Optical Society of America A, 4*, 1428–1438.

Cavanagh, P., Anstis, S. M. & Mather, G. (1984). Screening for color blindness using optokinetic nystagmus. *Investigative Ophthalmology and Visual Sciences, 25*, 463–466.

Cavanagh, P., Arguin, M. & von Grünau, M. (1989). Interattribute apparent motion. *Vision Research, 29*, 1197–1204.

Cavanagh, P., Boeglin, J. & Favreau, O. E. (1985). Perception of motion in equiluminous kinematograms. *Perception, 14*, 151–162.

Cavanagh, P., Tyler, C. W. & Favreau, O. E. (1984). Perceived velocity of moving chromatic gratings. *Journal of the Optical Society of America A, 1*, 893–899.

Charles, E. R. & Logothetis, N. K. (1989). The responses of middle temporal (MT) neurons to isoluminant stimuli. *Investigative Ophthalmology and Visual Sciences (Suppl.), 30*, 427.

Crone, R. A. (1959). Spectral sensitivity in color-defective subjects and heterozygous carriers. *American Journal of Ophthalmology, 48*, 231–235.

Cushman, W. B. & Levinson, J. Z. (1983). Phase shift in red and green counterphase flicker at high frequencies. *Journal of the Optical Society of America, 73*, 1557–1561.

Derrington, A. M. & Badcock, D. R. (1985). The low level motion system has both chromatic and luminance inputs. *Vision Research, 25*, 1874–1884.

Derrington, A. M., Krauskopf, J. & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *Journal of Physiology, 357*, 241–265.

DeYoe, E. A. & Van Essen, D. C. (1988). Concurrent processing streams in monkey visual cortex. *Trends in the Neurosciences, 11*, 219–226.

Eisner, A. & MacLeod, D. I. A. (1980). Blue sensitive cones do not contribute to luminance. *Journal of the Optical Society of America, 70*, 121–123.

van Essen, D. C. (1985). Functional organization of primate visual cortex 3. In Peters, A. & Jones, E. G. (Eds), *Cerebral cortex* (pp. 259–329). New York: Plenum Press.

Gorea, A. & Papathomas, T. V. (1989). Motion processing by chromatic and achromatic visual pathways. *Journal of the Optical Society of America A, 6*, 590–602.

Gouras, P. & Eggers, H. M. (1982). Retinal responses to color contrast. *Investigative Ophthalmology and Visual Science (Suppl.), 22*, 176.

von Grünau, M. (1977). Lateral interactions and rod intrusion in color flicker. *Vision Research, 17*, 911–916.

Holub, R. A. & Morton-Gibson, M. (1981). Response of visual cortical neurons of the cat to moving sinusoidal gratings: Response–contrast functions and spatio temporal interactions. *Journal of Neurophysiology, 46*, 1244–1259

Howarth, P. A. & Bradley, A. (1986). The longitudinal chromatic aberration of the human eye and its correction. *Vision Research, 26*, 361–366.

Hubel, D. H. & Livingstone, M. S. (1987). Segregation of form, color and stereopsis in primate area 18. *Journal of the Neurosciences, 7*, 3378–3415.

Hurvich, L. M. & Jameson, D. (1957). An opponent-process theory of color vision. *Psychological Review, 64*, 384–404.

Kaiser, P. K. (1988). Sensation luminance: A new name to distinguish CIE luminance from luminance dependent on an individual's spectral sensitivity. *Vision Research, 28*, 455–456.

Kelly, D. H. (1979). Motion and vision II: Stabilized spatiotemporal threshold surface. *Journal of the Optical Society of America, 69*, 1340–1349.

Kelly, D. H. (1983). Spatiotemporal variation of chromatic and achromatic contrast thresholds. *Journal of the Optical Society of America, 73*, 742–750.

Krauskopf, J., Williams, D. R. & Heeley, D. W. (1982). Cardinal directions of color space. *Vision Research, 22*, 1123–1131.

Krueger, J. (1979). Responses to wavelength contrast in the afferent visual system of the cat and the rhesus monkey. *Vision Research, 19*, 1351–1358.

deLange, H. (1958). Research into the dynamic nature of the human fovea-cortex systems with intermittent and modulated light. II. Phase shift in brightness and delay in color perception. *Journal of the Optical Society of America, 48*, 784–789.

Lee, J. & Stromeyer, C. F. III (1989). Contribution of human short wave cones to luminance and motion detection. *Journal of Physiology, 413*, 563–593.

Lee, B. B., Martin, P. R. & Valberg, A. (1988). The physiological basis of heterochromatic flicker photometry demonstrated in the ganglion cells of the macaque retina. *Journal of Physiology, 404*, 323–347.

Lee, B. B., Martin, P. R. & Valberg, A. (1989). Non-linear summation of M- and L-cone inputs to phasic retinal ganglion cells of the macaque. *Journal of the Neurosciences, 9*, 1433–1442.

Levinson, E. & Sekuler, R. (1975). The independence of channels in human vision selective for direction of movement. *Journal of Physiology, 250*, 347–366.

Lindsey, D. T. & Teller, D. Y. (1990). Motion at isoluminance: Discrimination/detection ratios for moving isoluminant gratings. *Vision Research, 30*, 1751–1762.

Lindsey, D. T., Pokorny, J. & Smith, V. C. (1986). Phase-dependent sensitivity to heterochromatic flicker. *Journal of the Optical Society of America A, 3*, 921–927.

Livingstone, M. S. & Hubel, D. H. (1984). Anatomy and physiology of a color system in the primate visual cortex. *Journal of the Neurosciences, 4*, 309–356.

Livingstone, M. S. & Hubel, D. H. (1987). Psychophysical evidence for separate channels for perception of form, color, movement and depth. *Journal of the Neurosciences, 7*, 3416–3468.

Livingstone, M. S. & Hubel, D. H. (1988). Segregation of form, color, movement and depth: Anatomy, physiology and perception. *Science, 240*, 740–749.

Logothetis, N. K. & Charles, E. R. (1990). The minimum motion technique applied to determine isoluminance in psychophysical experiments with monkeys. *Vision Research, 30*, 829–838.

Logothetis, N. K., Schiller, P. H., Charles, E. R. & Hurlbert, A. C. (1989). Perceptual deficits and the role of color-opponent and broad-band channels in vision. *Science, 247*, 214–217.

MacLeod, D. I. A. & Boynton, R. M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America, 69*, 1183–1186.

Maunsell, J. H. R. & Newsome, W. T. (1987). Visual processing in monkey extrastriate cortex. *Annual Review of Neuroscience, 10*, 363–401.

Maurer, D., Lewis, T., Cavanagh, P. & Anstis, S. M. (1989). Testing the luminous efficiency of colors in babies. *Investigative Ophthalmology and Visual Science, 30*, 297–303.

Merigan, W. H. & Maunsell, J. H. R. (1990). Macaque vision after magnocellular lateral geniculate lesions. *Visual Neuroscience, 5*, 347–352.

Moreland, J. D. (1982). Spectral sensitivity measured by motion photometry. In Verriest, J. G. (Ed.), *Colour deficiencies VI* (pp. 61–66). The Hague: Junk.

Mullen, K. T. (1985). The contrast sensitivity of human color vision to red-green and blue-yellow chromatic gratings. *Journal of Physiology, 359*, 381–400.

Mullen, K. T. (1991). Colour vision as a post-receptoral specialization of the central visual field. *Vision Research 31*, 119–130.

Mullen, K. T. & Baker, C. L. (1985). A motion aftereffect from an isoluminant stimulus. *Vision Research, 25*, 685–688.

Nakayama, K. & Silverman, G. H. (1985). Detection and discrimination of sinusoidal grating displacements. *Journal of the Optical Society of America A, 2*, 267–274.

Pokorny, J. & Smith, V. C. (1972). Luminosity and CFF in deuteranopes and protanopes. *Journal of the Optical Society of America, 60*, 562–569.

Ramachandran, V. S. & Gregory, R. (1978). Does colour provide an input to human motion perception? *Nature, 275*, 55–56.

Reichardt, W. (1961). Autocorrelation, a principle for the evaluation of sensory information by the central nervous system. In Rosenblith, W. A. (Ed.), *Sensory communication* (pp. 303–317). New York: Wiley.

Saito, H., Tanaka, K., Isono, H., Yasuda, M. & Mikami, A. (1989). Directionally selective response of cells in the middle temporal area (MT) of the macaque monkey to the movement of equiluminous opponent color stimuli. *Experimental Brain Research, 75*, 1–14.

Schiller, P. H. (1982). Central connections of the retinal ON and OFF pathways. *Nature, 297*, 580–583.

Schiller, P. H. & Colby, C. L. (1983). The responses of single cells in the lateral geniculate nucleus of the rhesus monkey to color and luminance contrast. *Vision Research, 23*, 1631–1641.

Schiller, P. H., Logothetis, N. K. & Charles, E. R. (1990). The role of color-opponent and broad-band channels in vision. *Visual Neuroscience, 5*, 321–346.

Shadlen, M. & Carney, T. (1986). Mechanisms of human motion perception revealed by a new cyclopean illusion. *Science, 232*, 95–97.

Shapley, R. & Kaplan, E. (1989). Responses of magnocellular LGN neurons and M retinal ganglion cells to drifting heterochromatic gratings. *Investigative Ophthalmology and Visual Science. (Suppl.), 30*, 323.

Smith, V. C. & Pokorny, J. (1975). Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm. *Vision Research, 15*, 161–172.

Smith, V. C., Lee, B. B., Pokorny, J., Martin, P. R. & Valberg, A. (1989). Response of macaque ganglion cells to changes in the phase of two flickering lights. *Investigative Ophthalmology and Visual Science (Suppl.), 30*, 323.

Srinivasan, M. V. (1985). Shouldn't directional movement detection necessarily be "colour-blind"? *Vision Research, 25*, 997–1000.

Stromeyer, C. F. III, Eskew, R. T. Jr & Kronauer, R. E. (1990). The most sensitive motion detectors in humans are spectrally opponent. *Investigative Ophthalmology and Visual Science (Suppl.), 31*, 240.

Stromeyer, C. F. III, Kronauer, R. E., Madsen, J. C. & Klein, S. A. (1984). Opponent-movement mechanisms in human vision. *Journal of the Optical Society of America A, 1*, 876–884.

Swanson, W. H., Pokorny, J. & Smith, V. C. (1988). Effects of temporal frequency on phase-dependent sensitivity to heterochromatic flicker. *Journal of Optical Society of America A, 4*, 2266–2273.

Teller, D. Y. & Lindsey, D. T. (1988). Quantitative characteristics of infant isoluminance measures with moving gratings. *Investigative Ophthalmology and Visual Science (Suppl.), 29*, 60.

Troscianko, T. & Fahle, M. (1988). Why do isoluminant stimuli appear slower. *Journal of the Optical Society of America A, 5*, 871–880.

Verriest, G. (1971). Les courbes spectrales photopiques d'efficacité lumineuse dans les déficiences congénitales de la vision des couleurs. *Vision Research, 11*, 1407–1434.

de Vries, H. L. (1948). The luminosity curve of the eye as determined by measurements with the flicker photometer. *Physica, 14*, 319–348.

Ware, C. (1982). Human axial chromatic aberration found not to decline with age. *Graefe's Archives of Clinical and Experimental Ophthalmology, 218*, 39–41.

Watson, A. B., Thompson, P. G., Murphy, B. J. & Nachmias, J. (1980). Summation and discrimination of gratings moving in opposite directions. *Vision Research, 20*, 341–347.

White, C. W. & Muermans, M. (1990). Chromatic isoluminance in the visual field obtained by flicker photometry. *Investigative Ophthalmology and Visual Science (Suppl.), 31*, 263.

Wiesel, T. N. & Hubel, D. H. (1966). Spatial and chromatic interactions in the lateral geniculate body of the rhesus monkey. *Journal of Neurophysiology, 29*, 1115–1156.

Wolfe, J. M. & Owens, D. A. (1981). Is accommodation colorblind? Focusing chromatic contours. *Perception, 10*, 53–62.

Zeki, S. M. (1978). Functional specialization in the visual cortex of the rhesus monkey. *Nature, 274*, 423–428.

Zeki, S. M. (1980). The representation of colours in the cerebral cortex. *Nature, 284*, 412–418.

APPENDIX

Luminance Artifact Introduced in a Chromatic Sinusoidal Target by Chromatic Aberration

A grating that varies in chromaticity but not in luminance can be produced by the superposition of two sine waves of different colors each at the same spatial frequency but 180° out of phase. A potential luminance artifact arises due to the axial chromatic aberration of the lens which prevents both wavelengths from being in focus simultaneously. An out-of-focus sine wave is simply the same sine wave at a slightly lower contrast. The problem arises because the observer can control the relative contrast of the two colors by reaccommodating. We assume that whenever the experimenter adjusts the two colors to be equiluminous, the observer will attempt to reaccommodate to bring back luminance contrast (Wolfe & Owens, 1981).

In order to determine at what point it is necessary to control for axial chromatic aberration we first calculate the blur circle resulting from chromatic aberration, then the resulting loss of contrast and finally the maximum luminance artifact that this can produce.

Blur circle

The blur circle, b, in meters, for a chromatic aberration of c dioptres (a difference of c dioptres between the lens power at the two wavelengths making up the chromatic grating), a lens power at the first wavelength of D dioptres, and a pupil diameter of p meters is

$$\frac{b}{\frac{1}{D}-\frac{1}{D+c}}=\frac{p}{\frac{1}{D+c}}.$$

Solving for b

$$b = cp/D$$

or in degrees of visual angle

$$b = 57.3[cp/D]/[1/D]$$

$$b = 57.3cp. \tag{1}$$

Contrast reduction

The convolution of the blur circle with the sine wave is given by the product of their Fourier transforms. Since the transform of the sine wave is two delta functions at f and $-f$, the amplitude of the convolution, also a sine wave, is given by the value of the Fourier transform of the blur circle at f and $-f$. Since the blur circle is circularly symmetric, we can use the Fourier Bessel transform. The circle function representing the blur circle has a radius of $b/2$ and a height of $4/\pi b^2$ (constant energy in the stimulus). For radius r in spatial coordinates and radius ρ in frequency coordinates where $J_1(\rho)$ is the first order Bessel function and circ(r) is 1 for $r \leqslant 1$ and 0 otherwise,

$$\begin{aligned}&\mathrm{B}[(4/\pi b^2) \times \mathrm{circ}(2r/b)]\\ &\quad = (4/\pi b^2) \times (b^2/4) \times J_1(2\pi b\rho/2)/(b\rho/2)\\ &\quad = J_1(\pi b\rho)/(\pi b\rho/2).\end{aligned} \tag{2}$$

The amplitude, a, of the resulting sine wave is given by the product of the transform in equation (2) and the transform of the original sine wave at frequency f.

$$a = J_1(\pi bf)/(\pi bf/2).$$

Expanding J_1 and dropping higher terms,

$$\begin{aligned}a &= 2[\pi bf/2 - (\pi bf)^3/16 + (\pi bf)^5/384 - \cdots]/(\pi bf)\\ &= 1 - (\pi bf)^2/8\end{aligned} \tag{3}$$

substituting from equation (1),

$$\begin{aligned}a &= 1 - (57.3\pi c\rho f)^2/8\\ &= 1 - 4050(cpf)^2\end{aligned}$$

or, for pupil diameter in mm,

$$a = 1 - 0.00405(cpf)^2. \tag{4}$$

Worst case artifact

The largest luminance artifact occurs if equiluminance is set while the observer focuses on one color and then, after it is set, switches focus to the other color. When equiluminance is first set, the first color, which is in focus, will have amplitude a_1, and the second, out of focus by c dioptres, has amplitude a_2 in the stimulus but its amplitude on the retina where it is out of focus is $a_2[1 - 0.00405(cpf)^2]$. Since these two sine waves are set to equiluminance,

$$a_1 = a_2[1 - 0.00405(cpf)^2]. \tag{5}$$

When the observer reaccommodates after the setting is made, he or she can generate the highest luminance contrast by focusing on the second color. This brings the amplitude of this color back to a_2 and reduces the contrast of the

first color to $a_1[1 - 0.00405(cpf)^2]$. The two waveforms no longer have the same amplitude and the resulting luminance artifact has an amplitude of the difference of the two and a mean luminance given by the sum of the two (assuming that they are both present at 100% contrast), producing an artifact with a Michelson contrast, c_a, of

$$c_a = \frac{\{a_2 - a_1[1 - 0.00405(cpf)^2]\}}{\{a_2 + a_1[1 - 0.00405(cpf)^2]\}}.$$

Substituting for a_1 for equation (5),

$$c_a = \frac{\{a_2 - a_2[1 - 0.00405(cpf)^2]^2\}}{\{a_2 + a_2[1 - 0.00405(cpf)^2]^2\}}$$

$$= \frac{\{1 - [1 - 0.00405(cpf)^2]^2\}}{\{1 + [1 - 0.00405(cpf)^2]^2\}}.$$

Ignoring higher order terms,

$$c_a = 0.00405(cpf)^2$$

or, expressed in percent contrast, for chromatic aberration, c, in diopters, pupil dia, p, in mm and spatial frequency, f, in c/deg,

$$c_a = 0.405(cpf)^2.$$

If the chromatic grating is at less than 100% modulation, then the contrast of the artifact is reduced by the same amount.

In our first experiment, there was no initial equiluminance setting that could then be undone by reaccommodating later on but observers could be reaccommodating as they adjusted red/green luminance ratio so as to maintain a maximum luminance contrast. Since the measured null points occur when one color is physically more luminous than the other, the observers need only adopt the strategy of focusing on the more luminous color to artificially increase the effective contrast of the two colors. They will therefore need less physical contrast in the color grating to overcome the motion of the oppositely moving luminance grating at one null point, and similarly less contrast at the other null point where they focus on the other color. This corresponds to the worst case artifact so that if green is in focus at 0 D from the fixation then red, at −0.4 D [chromatic aberration estimated from Howarth and Bradley (1986) and Ware (1982) for the dominant wavelengths of our phosphors] is focused behind the retina and can be brought into focus by accommodating in front of the fixation plane. For a pupil dia of 3 mm, the artifact as a function of spatial frequency should be

$$c_a = 0.405(cpf)^2$$

$$= 0.58f^2.$$

This function is plotted as the curved, dotted line in Fig. 12.

The chromatic aberration would be greater than 1.0 D for blue/yellow and green/purple gratings. To produce the artifact with blue in the stimulus the observer must refocus to beyond infinity. Little or no accommodative control of relative contrast was possible with blue stimuli.