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What Happens if it Changes Color when it Moves?: Psychophysical Experiments on the Nature of Chromatic Input to Motion Detectors

KAREN R. DOBKINS,* THOMAS D. ALBRIGHT*

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Several lines of evidence indicate that the processing of motion by the primate visual system continues even when a moving stimulus differs from its surroundings by color alone. To illuminate the mechanisms by which our visual system uses color as a token for motion correspondence, we have developed an "apparent motion" paradigm in which red/green sine-wave gratings undergo reversal of chromatic contrast sign each time they are displaced in a particular direction. Under such conditions, correspondence based upon conservation of chromatic sign conflicts with correspondence based upon chromatically-defined borders. When these heterochromatic stimuli also possess luminance modulation, motion is always perceived in the direction in which the sign of luminance contrast is preserved. At isoluminance, however, two very different chromatic influences on motion detection are revealed. First, when stimuli undergo small spatial displacements, motion is perceived in the direction of the nearest chromatically-defined border even when the sign of chromatic contrast at that border alternates over time. Under these conditions, motion detectors apparently exploit information about image borders defined by color while sacrificing information about the colors that make up those borders. By contrast, when spatial displacement is large, motion is more apt to be perceived in the direction for which sign of chromatic contrast is preserved. In this instance, information about the polarity of chromatic contrast facilitates motion detection. These results suggest that chromatic signals contributing to motion detection are of two distinct types. This conclusion has implications for the degree of crosstalk between magnocellular and parvocellular processing streams in the primate visual system and it reinforces our understanding of how image features affect the way we see things move.

Color Motion correspondence Psychophysics Parvocellular Magnocellular Signed and unsigned chromatic borders

The basic task confronting a motion processor is that of detecting the continuity of objects as they are displaced in time and space. The complexity of this motion correspondence problem increases precipitously with the number of moving objects in a scene. One strategy for reducing correspondence ambiguity involves capitalizing upon the fact that the features comprising an object remain relatively stable over time and space. If a motion detecting system were afforded access to some of these features, it might profit from the ability to detect correspondence between similar features as they undergo displacement.

Of the many image features that might be used as tokens for motion correspondence, color is among the most notable, in view of its tendency for distinct and reliable identification of object boundaries. Despite the appeal of such utilitarian arguments, it is widely believed that the neural representations of image color and motion are largely segregated in the primate visual system. A wealth of anatomical (Hubel & Wiesel, 1972; Lund & Boothe, 1975; Lund, Lund, Hendrickson, Bunt & Fuchs, 1975; Livingstone & Hubel, 1984; DeYoe & Van Essen, 1985; Shipp & Zeki, 1985; Livingstone & Hubel, 1987a) and physiological (Gouras, 1968, 1969; Zeki, 1974; De Monasterio & Gouras, 1975; Schiller & Malpeli, 1978; De Monasterio, 1978; Derrington, Krauskopf & Lennie, 1984; Derrington & Lennie, 1984; Livingstone & Hubel, 1984; Tootell, Silverman, Hamilton, De Valois & Switkes, 1988; Tootell & Hamilton, 1989; Corbetta, Miezen, Dobmeyer, Shulman & Peterson, 1990; Zeki, Watson, Lueck, Friston, Kennard & Frackowiak, 1991) data have provided evidence for two discrete functional subsystems—parvocellular and magnocellular—that are thought to focus on the processing of image color and motion, respectively. Independent magnocellular and parvocellular subpopulations are evident in the retinae and the projections of the two pathways appear to remain segregated through several successive processing stages in the primate visual system.

Many psychophysical studies have been designed to explore functional correlates of this magnocellular/parvocellular dichotomy using moving patterns

*The Salk Institute, P.O. Box 85800, San Diego, CA 92186, U.S.A.

that contain only chromatic cues for form. These "isoluminant" stimuli are contrived with the belief that they selectively activate the parvocellular "stream"; their movement is thus presumed to be undetectable by motion-sensitive neurons in the magnocellular stream. Results, however, have been somewhat equivocal on this point. While the speed at which a pattern is perceived to move is often slowed at isoluminance (Cavanagh, Tyler & Favreau, 1984)—suggesting that motion detectors are truly compromised under most conditions motion is still perceived (Cavanagh & Favreau, 1985; Derrington & Badcock, 1985; Mullen & Baker, 1985; Cavanagh & Anstis, 1988; Simpson, 1990; Cavanagh & Anstis, 1991) and direction can be accurately discriminated (Sato, 1988; Mullen & Boulton, 1989; Lindsey & Teller, 1990).

Attempts to explain the influence of color on motion perception have focused on the properties of neurons in the middle temporal area (MT) of primate visual cortex. Area MT, part of the cortical magnocellular stream, is recognized as a key component of the neural substrate for motion perception. The vast majority of MT neurons are highly selective for direction of motion, but—befitting their status in the magnocellular stream—they show little evidence of selectivity for either the color or form of a visual stimulus (Zeki, 1974; Baker, Petersen, Newsome & Allman, 1981; Maunsell & Van Essen, 1983a; Albright, 1984). While the lack of color selectivity in these direction-selective neurons has been heralded as evidence for the segregation of color and motion processing pathways, relatively little attention has been given to the possibility that chromatically-defined image features may be accessible to motion processing areas of the magnocellular pathway. In support of this possibility, it has recently been shown that many MT neurons continue to signal direction when stimulated with moving patterns that vary only in their chromatic content (Saito, Tanaka, Isono, Yasuda & Mikami, 1989; Charles & Logothetis, 1989; Dobkins & Albright, 1990, 1991a, b; Movshon, Kiper, Beusmans, Gegenfurtner, Zaidi & Carandini, 1991; Charles, Logothetis & Cavanagh, 1991). Whether the residual directional discrimination exhibited by these cells is sufficient to account for perceived motion at isoluminance is a matter of some debate, but the fact remains that some MT neurons have functional access to information that might initially seem within the purview of the parvocellular system.

There are at least two means by which chromatic information might influence motion detection. The simplest possibility is that motion is detected using chromatically-defined image contours as correspondence tokens. This "*unsigned*" *color contrast hypothesis* supposes that chromatic contrast is used to establish a representation of image contours at an early stage of visual processing. Subsequent motion processing areas have access to these chromatically-defined contours but information about the colors themselves is not forwarded through the motion pathway; the sign of chromatic contrast is lost. A more significant role for chromatic information is assumed by our "*signed*" *color contrast hypothesis*. According to this scheme, object color *per se* constitutes a token for motion correspondence.

To a first approximation, the unsigned hypothesis is consistent with the type of chromatic signals known to be carried within early stages of the magnocellular pathway. A salient feature of the response properties of M-type retinal ganglion cells (Lee, Martin & Valberg, 1988, 1989a, b, c; Lee, Pokorny, Smith, Martin & Valberg, 1990) and neurons in the magnocellular laminae of the LGN (Schiller & Colby, 1983; Derrington *et al.*, 1984; Hurlbert, Logothetis, Charles & Schiller, 1987; Logothetis, Schiller, Charles & Hurlbert, 1990) is a phenomenon known as "frequency doubling"—a modulation of firing rate in response to pure chromatic flicker that occurs at twice the flicker frequency. Because these cells respond with equal zeal to the onset of either of the two colors in the flickering stimulus, they signal only a chromatic change in their receptive fields without regard for the *polarity* of the change. This insensitivity to sign of chromatic contrast is also evidenced by studies that have used chromatic stimuli in *spatial* opposition (Gouras & Eggers, 1982; Shapley & Kaplan, 1989; Kaiser, Lee, Martin & Valberg, 1990; Kruger, 1979; Shapley & Kaplan, 1989; Hubel & Livingstone, 1990). By contrast, P cells of the retina (De Monasterio & Gouras, 1975; Gouras & Zrenner, 1979, 1981) and parvocellular LGN neurons (Wiesel & Hubel, 1966; De Valois, Abramov & Jacobs, 1966) are selective for the sign of (spatial and temporal) contrast. Their properties are, in this respect, more in line with the *signed* chromatic contrast hypothesis.

Most prior experiments that have provided evidence for chromatic influence on human motion perception have confounded the differential predictions of the signed and unsigned hypotheses. It is generally the case in the real world and in psychophysical experiments—that both chromatically-defined image contours and the specific colors that define those contours move as one. Using such stimuli it is impossible to discriminate between our two hypotheses. This limitation is illustrated graphically in Fig. 1(A).

We have now developed "apparent motion" stimuli that allow us to distinguish between the predictions of these two hypotheses. Our stimuli consist of heterochromatic sine-wave gratings that undergo repetitive chromatic contrast sign reversal while moving. Under such conditions, motion correspondence based upon conservation of chromatic sign is placed in direct opposition to correspondence based upon chromatically-defined image contours. Psychophysical data obtained using these stimuli confirm the reputed influence of color on the way we see things move and, moreover, suggest the existence of a hybrid mechanism: one in which both signed and unsigned chromatic contrast signals contribute to motion detection.

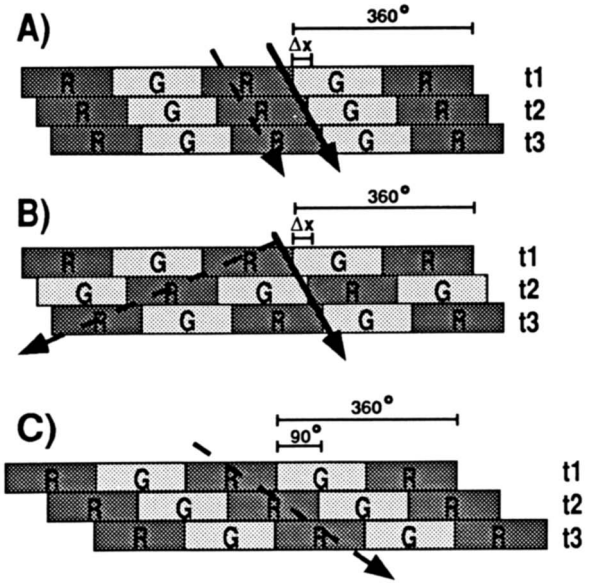

FIGURE 1. Schematic depiction of "apparent motion" stimuli used to characterize chromatic influences on motion processing. Actual stimuli were red/green (R/G) sine-wave gratings (0.45 c/deg). Three temporal frames (t1, t2, t3) are shown. Spatial displacement (Δx) refers to the phase angle (out of 360°) that gratings were displaced on each frame. (A) Conventional drifting heterochromatic grating used in Expt I. Rightward motion is detectable from spatio-temporal correspondence of either "unsigned" chromatically-defined contours (solid arrow) or actual color identity (dashed arrow). (B) Heterochromatic grating that undergoes contrast sign reversal while moving. Motion of proximal "unsigned" chromatically-defined contours is rightward (solid arrow) while motion of the "signed" chromatic cue is leftward (dashed arrow). (C) Heterochromatic grating that undergoes 90° (ambiguous) phase displacement, used in Expts II and III. Unsigned chromatically-defined contours provide ambiguous cues for direction of motion. (A chromatically-defined contour at t1 is equidistant from either of two potential "matches" at t2.) A consistent percept of motion can only occur if information about *sign* of chromatic contrast is utilized as a motion correspondence token.

GENERAL METHOD

Apparatus

All visual stimuli were generated using a high-resolution, high-speed computer video display and digital frame buffer (Pepper SGT, Number Nine Computer Corp: 640 × 480 pixels, analog RGB output, 8 bits/gun). The controller resides in an AT-class (80386) personal computer and it permits 256 simultaneously displayable colors or luminance levels. Stimuli were displayed on a 13 in. analog RGB video monitor (NEC Multisync, 60 Hz, non-interlaced). The voltage/luminance relationship was linearized independently for each of the three guns in the display (Watson, Nielson, Poirson, Fitzhugh, Bilson, Nguyen & Ahumada, 1986). All visual stimuli were confined spatially to the central 50% of the usable portion of the monitor.

Visual stimulation

Chromatic channel activation. The C.I.E. chromaticity coordinates for our stimulus display monitor were: *R* (0.610, 0.350), *G* (0.307, 0.595) and *B* (0. 150, 0.065). All chromatic stimuli were produced by differential modulation of only the monitor's red and green phosphors. The relative activations of the cone photoreceptors caused by these phosphor modulations are illustrated in Fig. 2 using the MacLeod–Boynton chromaticity diagram (MacLeod & Boynton, 1979). Chromatic modulation along the horizontal axis in this space brings about no change in the excitation of short-wavelength-sensitive (S) cones while causing the signals in the long- (L) and medium-wavelength-sensitive (M) cones to covary, so as to keep their sum constant. Cone activations were computed by, first, integrating the spectral radiance distribution for each phosphor with the spectra $\bar{x}$, $\bar{y}$, and $\bar{z}$. The resultant tri-stimulus values were then employed to calculate cone activations using functions provided by Boynton (1986) based upon Smith–Pokorny cone action spectra (Smith & Pokorny, 1972, 1975). Our calculations indicate that the red and green phosphors of our monitor caused little differential activation of S cone photoreceptors but provided about 20% differential activation of L and M cones. Since this modulation was not centered on 0.5 (the point of equal L and M cone modulation), cone contrasts for L and M cones were unequal. Cone contrasts for L and M cones were determined to be 14% and 33%, respectively.

Construction of heterochromatic gratings. Visual stimuli that varied solely in their chromatic content were produced by summing sinusoidal luminance modulations of two different colors (i.e. "mono-phosphor" luminance modulations of both red and green phosphors, for the present experiments), of identical spatial frequency and orientation but of opposite phase. Once summed in this manner the luminance ratio between the two colors is dependent upon the mean luminances and amplitudes (modulation depths) of the composite mono-phosphor sinusoids (Fig. 3). In our experiments luminance contrast amplitude was varied by differentially adjusting the mean luminance of the two mono-phosphor luminance profiles such that the mean luminance of the stimulus was held constant at 20 cd/m^2. Red and green sinusoids were always of equal modulation depth. Luminance contrast (Michaelson) of the resultant

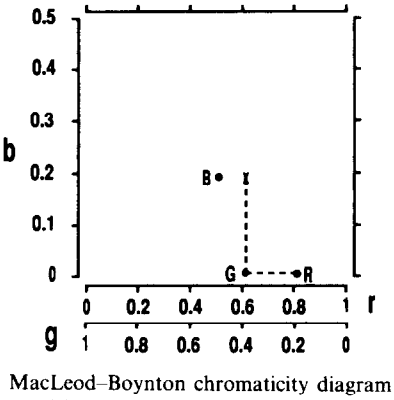

FIGURE 2. MacLeod–Boynton chromaticity diagram showing cone activations caused by isoluminant settings of the three phosphors in our video display (solid circles). Selective L–M and tritan modulation map to horizontal and vertical lines, respectivcly (dashed lines). Conveniently, the R and G phosphors fall very near horizontal, causing little differential activation of S cones. Our calculations indicate that the red and green phosphors of our monitor provide about 20% differential activation of L and M cones. Cone contrasts for L and M cones were determined to be 14 and 33%, respectively.

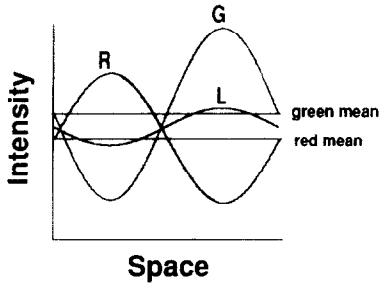

FIGURE 3. Heterochromatic (red/green) gratings were constructed by superimposition of sinusoidal mono-phosphor luminance modulations (of identical spatial frequency and orientation, but of opposite phase). Modulation of luminance contrast amplitude was achieved by differentially adjusting the total luminance of the red and green luminance profiles such that the mean luminance was constant at 20 cd/m^2. Mono-phosphor amplitude modulation depth (MD) was also constant. Luminance contrast (%) = MD $*$ $[(G_{mean} - R_{mean})/(G_{mean} + R_{mean})]$. Using this metric, luminance contrast amplitude could be either positive or negative. In the illustrated example, green (G) is brighter than red (R). The resulting luminance amplitude modulation (L) is shown.

heterochromatic grating is expressed as: modulation depth $*$ $[(G_{mean} - R_{mean})/(G_{mean} + R_{mean})]$. Using this metric, luminance contrast can be either positive or negative, depending upon which of the two phosphor primaries is brighter. That the luminance modulation in these gratings was indeed sinusoidal was verified by measuring luminance as a function of spatial phase using a standard spot photometer (United Detector Technology, Hawthorne, Calif.). By differentially varying the means of the two component sinusoids, it was always possible to find a combination for which luminance was invariant with spatial phase—the photometric isoluminant point. This confirms the linearity of our luminance calibrations for the display monitor. Chromatic contrast amplitude in these stimuli describes the fraction of the potential chromatic modulation between the two primaries and is a function of their individual luminance modulation depths (which were always equal to one another). The point at which the amplitudes of the red and green primaries equalled their respective means was considered 100% chromatic contrast (e.g. Logothetis *et al.*, 1990). [This assignment is arbitrary in the sense that it is the maximum attainable from our particular phosphors. We estimate, however, that this peak level of chromatic contrast causes about 20% differential modulation of M and L cones (Fig. 2).] Because of measurable lability of monitor luminance at low levels, mono-phosphor luminance amplitude modulations, hence chromatic contrast amplitude, never exceeded 75%. To directly examine the effects of chromatic contrast amplitude, we used gratings that were modulated by 75% and, for some experimental conditions, by 37.5%.

Construction of achromatic gratings. Visual stimuli that varied only in their luminance content ("achromatic" gratings) were produced by sinusoidal luminance modulation of the red phosphor alone.

Chromatic aberration. Longitudinal chromatic aberration is a potentially significant source of luminance contamination in heterochromatic stimuli. The "dominant" frequencies of the red (630 nm) and green (525 nm) phosphors in our stimuli differ by about 0.4 D in the human eye (Howarth & Bradley, 1986). Although differential diffraction of this magnitude is potentially troublesome, the effective luminance contrast introduced by chromatic aberration is markedly dependent upon spatial frequency (Flitcroft, 1989). For this reason we have used relatively low spatial frequency (0.45 c/deg) sinusoids in these experiments. Luminance contrast artifacts caused by chromatic aberration are minute ($< 0.5\%$ contrast for maximum 4 mm pupil) for sinusoidal gratings of this low frequency and they are below threshold sensitivity (Robson, 1966; Logothetis *et al.*, 1990; Cavanagh & Anstis, 1991). As an added benefit, this spatial frequency is also known to provide strong activation of motion mechanisms (Watson, Thompson, Murphy & Nachmias, 1980; Newsome, Gizzi & Movshon, 1983; Cavanagh *et al.*, 1984; Graham, 1989).

General. Moving stimuli were of the "apparent motion" type, i.e. gratings were displaced by discrete spatial and temporal intervals, both within a range that normally renders a clear percept of motion (Kolers, 1972). In practice, movement was achieved by spatial phase offset at regular intervals occurring in synchrony with the vertical refresh of the video monitor (i.e. at multiples of 16.67 msec). Stimuli subtended 10° of visual angle (4.5 total cycles), were presented at the center of gaze, and were viewed from a distance of 57 cm. The illuminated background portion of the monitor subtended a rectangular region 25.5° × 19° with a uniform luminance of 1.4 cd/m^2. The mean luminance of the stimulus aperture during the inter-trial interval was 1.4 cd/m^2.

Psychophysical paradigm

The effects of various stimulus parameters on perceived direction of motion were investigated in a two-alternative forced-choice procedure using the method of constant stimuli. Subjects viewed stimuli from a distance of 57 cm with head immobilized using a chin and forehead rest. All stimuli were viewed binocularly with natural pupils. For Expts I and II (but not III), testing began after subjects were adapted to a dimly lit room (approx. 0.5 cd/m^2) for 5 min. Subjects were instructed to fixate a small central spot for the duration of each stimulus exposure (0.267–1.60 sec, depending on the stimulus condition) and to indicate perceived direction of motion (up/down) by a key-press at the end of each trial. Stimulus conditions were varied in a pseudo-random sequence within each block of trials. All stimuli were balanced for direction of motion (up vs down) and all data points are based upon 40 trials. Data collection for each new set of stimulus conditions was preceded by completion of 100 practice trials.

Human subjects

The subjects for Expts I and II were four female undergraduates from the University of California, San Diego. All were inexperienced psychophysical observers naive to the purpose of the experiment. The first author participated as a subject in Expt III. All subjects

possessed normal color vision as assessed by the Farnsworth–Munsell 100 Hue Test and all had either normal or corrected-to-normal visual acuity.

EXPERIMENT I: CHROMATIC CONTRAST SIGN REVERSAL

For this experiment we used heterochromatic gratings that underwent reversal of the sign of chromatic contrast coincident with each spatial displacement. The spatio-temporal profile of this stimulus is illustrated in Fig. 1(B). With each spatial displacement chromatic contrast is inverted (red becomes green, green becomes red, etc.). Under these conditions there are two opposing cues for motion correspondence. The first is a contrast reversing (unsigned) chromatically-defined contour [moving rightward in Fig. 1(B)]. The second is invariant (signed) chromatic contrast [moving leftward in Fig. 1(B)]. It was our objective in using this technique to determine which cue dominates our perceptual experience of motion. If motion detectors are unconcerned with the sign of chromatic contrast motion should be perceived in the direction of the smallest spatial phase displacement, regardless of chromatic sign [in the chromatically "unsigned" direction; solid arrow in Fig. 1(B)], since spatial proximity is itself a potent cue for motion correspondence. If, on the other hand, the sign of chromatic contrast plays a significant role in motion detection, perceived motion should be in the direction that preserves chromatic sign [in the chromatically "signed" direction; dashed arrow in Fig. 1(B)].

Method

We systematically manipulated spatial phase displacement size, luminance contrast amplitude, chromatic contrast amplitude, and temporal frequency to explore the effects of these variables on perceived motion of heterochromatic gratings undergoing repetitive chromatic contrast sign reversal.

Manipulation of spatial displacement size: "weighing" the strength of motion correspondence cues. Because spatial proximity of image features is known to have a strong influence over motion correspondence (e.g. Ullman, 1980), it is useful to consider the behavior of the "proximal" chromatic border, i.e. the one that undergoes the smallest spatial displacement. The novel feature of our stimulus is the fact that the sign of chromatic contrast reverses for this proximal border. One can vary the impact of this proximity effect by adjusting the magnitude of the spatial phase displacement in the unsigned direction. In theory, it should be possible to manipulate phase displacement to find a "displacement balance point" at which the unsigned and signed cues hold equal sway over motion correspondence. In order that we might estimate this balance point, we presented contrast-reversing patterns that were displaced by each of four different spatial phase angles in the unsigned direction (6.4, 12.9 25.7 and 51.4°). (Accordingly, phase angles in the signed direction were 173.6, 167.1, 154.3 and 128.6°.) Within each block of trials, these four conditions were presented in random order.

Manipulation of luminance contrast amplitude in heterochromatic stimuli. A variety of optical and neural factors hold the potential to influence the respective efficacy with which red and green lights can reach motion detectors, and these factors may vary from one individual to another. To account for this variability, we employed a "luminance bracketing procedure", in which we varied the relative luminances of the red and green phases of our heterochromatic gratings. By applying this procedure we felt confident that each subject was presented with at least one red/green pair for which the two chromatic phases provided equally strong inputs to motion detectors (the *psychometric* isoluminance point). Red/green luminance contrast amplitude was thus varied across ten different levels ranging in equal (4%) intervals from −18% (red brightest) to +18% (green brightest) luminance contrast. This range was centered on the photometrically-determined isoluminance point.

When the heterochromatic gratings contained luminance as well as chromatic modulation, luminance modulation was always in phase with chromatic modulation but either the green phase or the red phase could be the brighter of the two. As a result, stimuli possessing non-zero luminance contrast underwent repetitive luminance contrast sign reversal as well as the above-mentioned chromatic contrast sign reversal. For such stimuli, direction of motion of the signed luminance contrast was always coincident with that of the signed chromatic contrast.

Manipulation of chromatic contrast amplitude. In order to examine the effects of chromatic contrast amplitude on signed and unsigned motion correspondence, we used two different chromatic contrasts (75 and 37.5%). Manipulation of chromatic contrast amplitude was achieved by varying the amplitudes (modulation depths) of the red and green sinusoids (Fig. 3).

Manipulation of temporal frequency. Temporal frequency is a somewhat ambiguous (and potentially confusing) term with reference to this contrast reversal stimulus. In these experiments, movement was achieved by spatial phase offset at regular intervals (from 6.4 to 51.4°) occurring in synchrony with every fourth cycle of the 60 Hz video refresh (i.e. frames were updated at 15 frames/sec). If we clock the unsigned chromatic border, we would say that it moves between 0.26 and 2.14 c/sec (depending on spatial displacement). Alternatively, if we clock the signed chromatic border, we would say that it moves between 7.2 and 5.4 c/sec. However, since cells at early stages of visual processing signal light exchange in their receptive fields, we feel that it is most appropriate to refer to temporal frequency of red/green light exchange in a given region of the field. For most of our contrast-reversed experiments, frequency of red/green light exchange was set at 7.5 Hz. This means that, within a given region of visual field, a complete cycle of R/G alteration occurs 7.5 times a second. To study the effects of temporal frequency, we also used a R/G alternation rate of 30 Hz.

Results and discussion

The basic phenomenon: effects of varying spatial displacement and luminance contrast amplitude. The principal results from our chromatic contrast sign reversal experiment are shown in Fig. 4. Within each trial subjects viewed 24 different frames of a heterochromatic grating undergoing (1) repetitive spatial displacement ("apparent motion") and (2) repetitive chromatic contrast sign reversal—for a total duration of 1.6 sec. Luminance contrast between the red and green phases of the grating ranged through ten equal (4%) intervals from −18 to +18%. Chromatic contrast amplitude was 75% of the maximum attainable for our monitor. Temporal frequency of chromatic contrast sign reversal (red/green alternation) was 7.5 c/sec. Subjects' indications of perceived direction have been plotted (arbitrarily) as percent "unsigned border" responses. This percentage identifies the fraction of trials for which subjects reported motion in the direction of the contrast-reversing (unsigned) chromatic border. Hence, a value of 100% indicates that, for the relevant stimulus condition, motion was always perceived in the direction of displacement for the border undergoing chromatic contrast sign reversal. [This unsigned border was always the *proximal* border.] Conversely, a value of 0% indicates that motion was always perceived in the direction that preserved sign of chromatic contrast (and luminance contrast, for non-isoluminant conditions).

There are two important and consistent features to these results. First, all four subjects reported a percept of motion in the direction of the unsigned border for a small range of luminance contrast levels near photometric isoluminance. Away from this isoluminant point, motion was more likely to be seen in the direction that preserved the sign of luminance and color correspondence, i.e. the signed direction. These results suggest that, when stimuli are defined solely by chromatic contrast, motion detectors can utilize information about chromatically-defined image contours while ignoring information about chromatic sign. By contrast, when heterochromatic gratings possess sufficient luminance contrast, luminance polarity is a strong determinant of motion correspondence.

The second important feature concerns the fact that as spatial displacement was increased (thereby lessening the saliency of the proximal, i.e. unsigned border cue), there was a greater tendency to see motion in the signed direction. Consequently, for a 51.4° phase displacement (the largest used in Expt I), motion was always seen in the signed direction for all luminance contrast amplitudes tested. At 51.4° phase shift, unsigned border matches are 2.5 times closer than signed border matches. Signed chromatic border correspondence therefore persists at spatial displacements which clearly favor proximal border matches moving in the opposite direction. These results suggest that when chromatically-defined, unsigned borders provide a relatively weak proximity cue, information about the sign of chromatic contrast dictates motion correspondence.

Finally, each subject's data were fitted with third-order polynomial functions. The resultant peak in these fitted curves provisionally defined the red/green "psychophysical" isoluminant point for a given subject at the spatial and temporal frequency tested.

Effects of varying chromatic contrast amplitude. For visual stimuli near photometric isoluminance, small

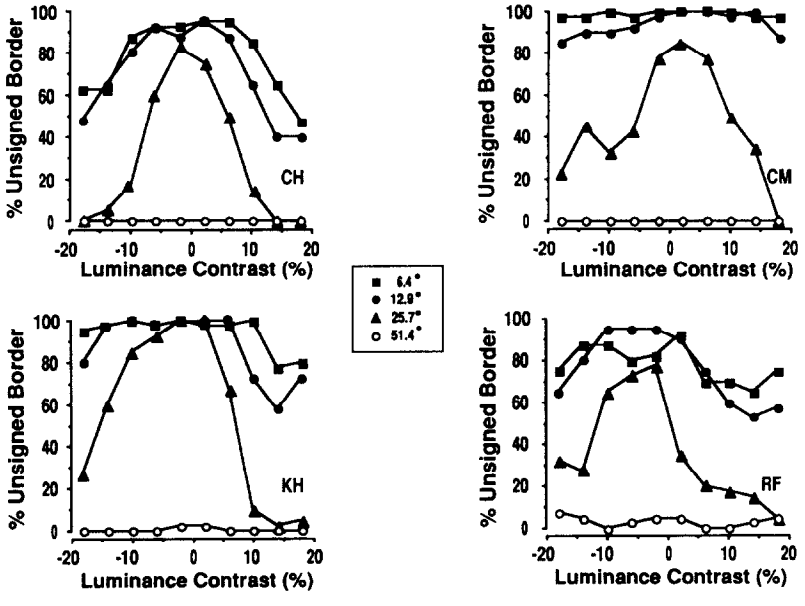

FIGURE 4. Data from four subjects obtained while viewing the heterochromatic contrast-reversing stimulus [Fig. 1(B)] employed in Expt I (75% chromatic contrast amplitude, 7.5 Hz R/G cycle, 24 frames). The percentage of trials for which subjects reported motion in the *unsigned direction* [Fig. 1(B), solid arrow] is plotted as a function of luminance contrast amplitude for each of four different spatial phase displacements: 6.4° (solid squares), 12.9° (solid circles), 25.7° (solid triangles) and 51.4° (open circles). When little or no luminance contrast was present, motion was typically reported in the unsigned direction for small phase shifts, thus defying inversions of chromatic sign. As phase displacement was increased, or when luminance contrast was added, there was greater tendency for subjects to report motion in the signed direction [Fig. 1(B), dashed arrow]. For this and for all subsequent data figures, each data point represents the mean of 40 trials.

spatial displacements nearly always elicited a percept of motion in the unsigned direction. The signal for motion correspondence under these conditions may arise within the magnocellular pathway since neurons at early stages in this pathway signal chromatic contrast without regard for the sign of contrast. This "frequency doubling" response has been shown to wane with chromatic contrast amplitude in M retinal ganglion cells (Lee *et al.*, 1989a, c). Decreasing chromatic contrast amplitude may have correspondingly adverse effects on an unsigned correspondence mechanism. However, since our stimulus configuration, by its very nature, permits only an evaluation of the *relative* effectiveness of signed and unsigned motion correspondence mechanisms, we can not rule out the possibility that decreasing chromatic contrast amplitude may also have adverse effects on a signed correspondence mechanism.

The data presented above (Fig. 4) were collected using heterochromatic gratings that possessed relatively high (75%) chromatic contrast. We repeated these manipulations on all subjects using stimuli that differed only by amplitude of chromatic modulation (37.5%). Results are shown in Fig. 5. The graphs are quite similar to those obtained at 75% chromatic contrast (Fig. 4) except that the curves are more sharply tuned. The slight narrowing of the curves seen for the lower of the two chromatic contrast levels suggests that decreasing chromatic contrast amplitude has adverse effects on an unsigned mechanism, which is consistent with the aforementioned effects of chromatic contrast amplitude on frequency doubling in magnocellular neurons of the retina.

Effects of varying temporal frequency. The data presented in Figs 4 and 5 were obtained using heterochromatic gratings undergoing red/green contrast sign reversal at a frequency of 7.5 Hz We also collected data using a red/green alternation frequency of 30 Hz (Fig. 6). Our reasons for collecting data at this higher temporal frequency were two-fold. First, a number of previous studies have shown that psychophysical estimates of chromatic isoluminance obtained using heterochromatic flicker photometry vary with temporal frequency (Kelly, 1983; Cushman & Levinson, 1983; Swanson, Pokorny & Smith, 1988; Pokorny, Smith & Lutze, 1989). Since the "unsigned peak" that characterizes our motion discrimination curves presumably represents the luminance ratio for which red and green have balanced inputs to motion detectors—and are thus isoluminant for this task—we wanted to determine whether the position of this peak varies with temporal frequency. Second, we wished to determine whether the basic phenomena reported above (Fig. 4) exists at a temporal frequency that is sufficiently high to produce perceptual "fusion" of the red and green (van der Horst, 1969; Varner, Piantanida & Baker, 1977; Wisowaty, 1981; Cushman & Levinson, 1983; Kaiser, Ayama & Vimal, 1986). [It should be noted, however, that the critical flicker frequency for fusion is known to depend greatly on stimulus conditions such as eccentricity (Tyler, 1985; Rovamo & Raninen, 1984), luminance (Wisowaty, 1981) and chromatic contrast (Lindsey, Pokorny & Smith, 1986).] For all four subjects, the 30 Hz red/green alternation frequency (Fig. 6) produced a rightward shift of the unsigned peak relative to that obtained using the 7.5 Hz condition (Fig. 4). Thus, at this higher frequency of red/green light exchange, a smaller red/green luminance ratio was needed to achieve "isoluminance". These results imply that the relative weights of the cone inputs may vary with temporal frequency. Other notable effects of the higher temporal frequency (relative to the 7.5 Hz condition) include a slight overall reduction of the tendency to perceive motion in the unsigned direction and a narrowing of the peaks in the curves. These secondary effects are

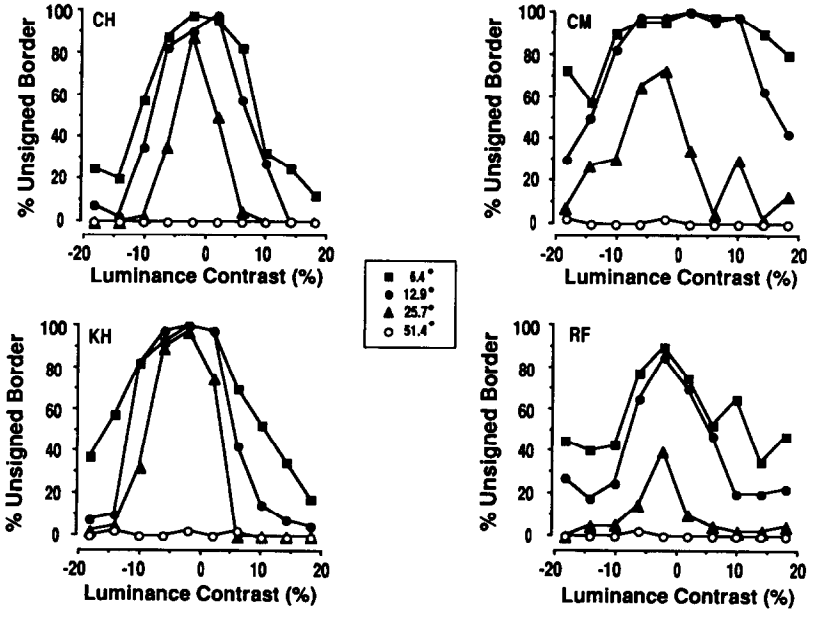

FIGURE 5. Effects of varying amplitude of chromatic contrast. Chromatic contrast amplitude was 37.5% for this condition. All other parameters and symbols are identical to those used for the data illustrated in Fig. 4. The data obtained using 37.5% chromatic contrast are similar to those obtained using 75% (Fig. 4), except that the curves are more finely tuned for the lower contrast. This suggests a relative reduction in the effectiveness of the unsigned mechanism at lower chromatic contrast levels.

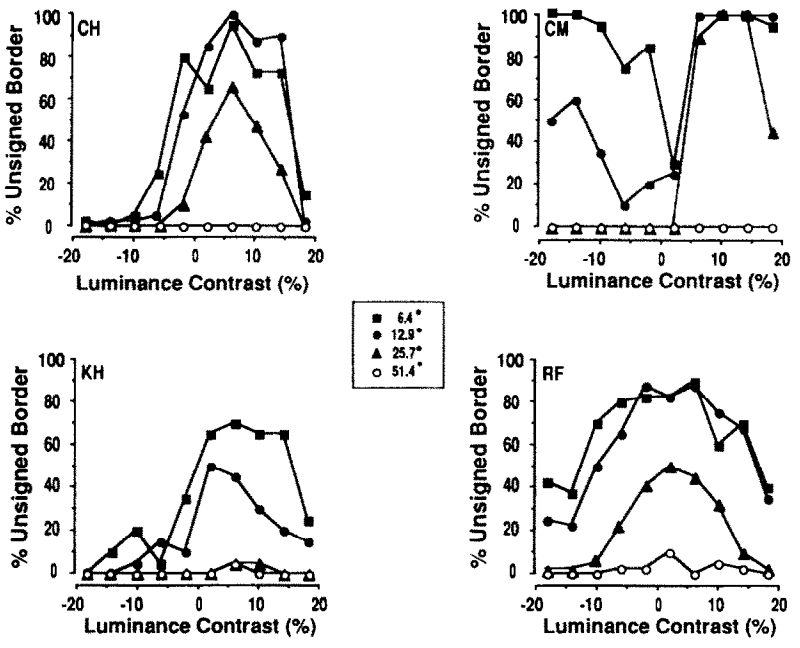

FIGURE 6. Effects of varying temporal frequency. R/G alternation rate was 30 Hz for this condition. All other parameters and symbols are identical to those used for the data illustrated in Fig. 4, which were collected using a temporal frequency of 7.5 Hz. The higher temporal frequency yielded a narrowing of the unsigned peak and a slight overall reduction in the tendency to perceive motion in the unsigned direction, relative to the results obtained for the lower frequency (Fig. 4). These data suggest that increasing temporal frequency reduces the effectiveness of the unsigned mechanism. Furthermore, the rightward shift of the unsigned peak demonstrates that the red/green luminance ratio needed to achieve "isoluminance" is lower at higher temporal frequencies.

reminiscent of those seen using gratings of reduced chromatic contrast amplitude (see above and Fig. 5) and they parallel the reduction of frequency doubling among M retinal ganglion cells, which occurs with similar temporal frequency and chromatic contrast manipulations (Lee *et al.*, 1989a, c).

Chromatic contrast or low levels of luminance contrast? Using heterochromatic sine-wave gratings similar to those used in the present experiments, Cavanagh *et al.* (1984) showed that perceived motion is strikingly slowed at chromatic isoluminance. Even for achromatic gratings, however, motion appears slowed at low luminance contrast levels (Thompson, 1982). As a dramatic demonstration that it is indeed chromatic contrast—and not simply low levels of luminance contrast—that causes the perceived slowing of heterochromatic gratings at isoluminance, Cavanagh *et al.* also showed that an achromatic grating could be made to look like it was moving more slowly by *adding* color to it.

In a similar vein, we entertained the possibility that the tendency to perceive motion in the unsigned direction was due simply to the presence of very low levels of luminance contrast in our heterochromatic gratings and not due to the presence of chromatic contrast *per se*. To test this possibility, we collected data using achromatic gratings that underwent contrast sign reversal with each spatial displacement (7.5 Hz). These stimuli were identical in all respects, save the absence of chromatic contrast, to our heterochromatic gratings. Eight different luminance contrast amplitude levels were used ranging in equal intervals (2.5%) from 2.5 to 20%. The results are shown in Fig. 7. For stimuli at the lowest luminance contrast amplitude tested (2.5%) and for all spatial displacements tested, subjects' reports of motion in the unsigned direction remained significantly below chance (50%). Furthermore, the probability of reporting motion in the unsigned direction was no greater at low luminance contrast levels than it was for high contrast stimuli. On the contrary, subject CM was more apt to see motion in the unsigned direction as luminance contrast amplitude was increased. It should be noted, however, that when compared to the other three subjects, subject CM exhibited a greater overall tendency to report motion in the unsigned direction. Her somewhat atypical performance may explain why under *chromatic* conditions, she frequently reported motion in the unsigned direction even when stimuli deviated from isoluminance (e.g. Fig. 6).

For all subjects, the tendency to report motion of achromatic gratings in the unsigned direction decreased as spatial phase displacement was increased, collapsing to approx. 0% at 51.4′ (Fig. 7). Notably, displacements of 25.7′ also led to a strong signed direction bias at all luminance contrast levels tested (Fig. 7, triangles). By contrast, heterochromatic gratings undergoing identical displacements (25.7′) led to numerous reports of perceived motion in the unsigned direction over a range of luminance contrasts near isoluminance (Fig. 4, triangles). On the basis of these results we conclude that the pronounced tendency to report perceived motion of heterochromatic stimuli in the unsigned direction (Fig. 4)—sometimes for a broad range of a luminance contrast levels—can only be attributable to the presence of chromatic variation in these stimuli.

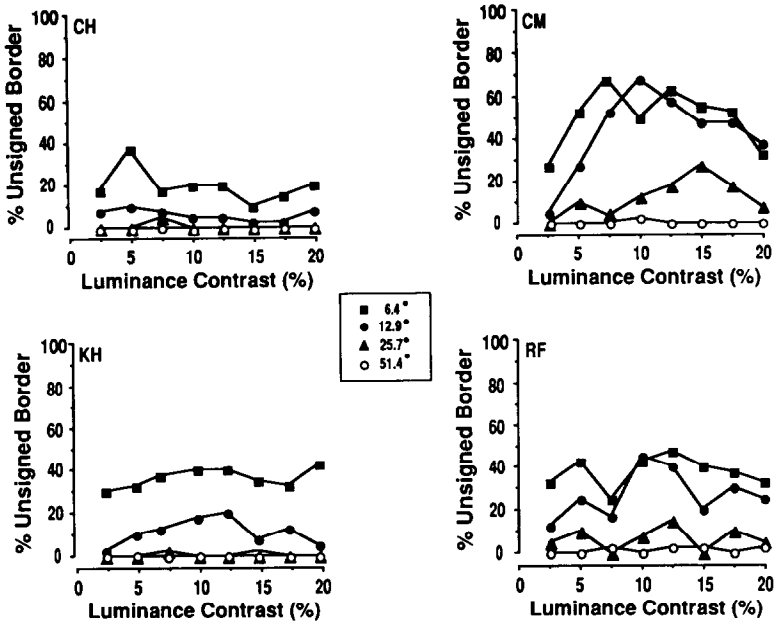

FIGURE 7. Effects of *achromatic* contrast-reversed gratings. Stimulus conditions and symbols are identical to those used for the data presented in Fig. 4, save the absence of chromatic contrast. Motion was rarely reported in the unsigned direction, regardless of luminance contrast amplitude. Furthermore, the tendency to report motion in the unsigned direction was no greater at low than at high luminance contrast levels. The tendency to perceive motion of heterochromatic stimuli in the unsigned direction (Fig. 4) must therefore be attributable to the presence of chromatic variation in these stimuli.

EXPERIMENT II: 90° (AMBIGUOUS) PHASE DISPLACEMENT

In Expt I we found that, at their respective isoluminant points, all four subjects reported motion predominantly in the unsigned direction when presented with a spatial phase displacement of 25.7° (Fig. 4, triangles), and reported motion in the signed direction when presented with a spatial phase displacement of 51.4° (Fig. 4, open circles). The spatial displacement that produces perceived motion in the unsigned direction 50% of the time can be thought of as the point at which signed and unsigned cues provide balanced input for motion correspondence. From the data in Fig. 4 we estimate this signed-unsigned "displacement balance point" to lie somewhere between 25.7 and 51.4°, and we infer that, if the spatial phase angle is sufficiently large (i.e. greater than this displacement balance point), motion will usually be perceived in the signed direction. That a phase angle of 90° should lead to a signed direction bias might seem a foregone conclusion in light of these results obtained with 51.4°. Nonetheless, because this stimulus is completely unconfounded by unsigned chromatic cues for motion correspondence [Fig. 1(C)]—it does, in this respect, represent a singularity in the set of all possible phase displacements—we felt it was the most direct way to verify our signed chromatic contrast hypothesis.

Furthermore, the use of 4% luminance contrast amplitude intervals in Expt I allowed for the "worst case" possibility that we missed a subject's isoluminant point by as much as, but no more than, 2% (occurring when a subject's isoluminant point falls directly in the middle of a luminance contrast interval). It is therefore conceivable that small levels of luminance contrast contributed to the percept of motion in the signed direction for the 51.4° phase shift condition. That this is not an unwarranted concern is evidenced by reports of motion in the signed direction for achromatic gratings which contained luminance contrasts as low as 2.5% (Fig. 7). To address this concern, in Expt II we used smaller luminance contrast amplitude intervals (1.5%), which greatly reduced the potential for residual luminance information in the heterochromatic gratings.

It should be noted that stimuli of this general sort (in which border information provides an ambiguous direction signal) have been previously employed in the "minimum motion" technique for estimating chromatic isoluminance (Anstis & Cavanagh, 1983; Anstis, Cavanagh, Maurer, MacLeod & Mather, 1986).

Method

In Expt II we tested subjects using heterochromatic sine-wave gratings undergoing repetitive 90° phase displacements. The spatial properties of the stimuli were identical, in all other respects, to those used for Expt I. Gratings were moved at 7.5 c/sec (7.5 Hz R/G alternation) so that the results could be directly compared with the results from the contrast-reversed condition (Expt I). As was performed in Expt I, subjects were tested using ten different luminance contrast levels, ranging in equal intervals (4%) from −18 to 18%. We also tested each subject using five additional luminance contrast levels spanning a smaller range (6%) with smaller intervals (1.5%) and centered on our estimate of the subject's isoluminant point. The latter was determined from the location of the "unsigned peak" observed for each subject in Expt I (see Fig. 4).

Results and discussion

The data obtained from these manipulations are shown in Fig. 8. Subjects' indications of perceived

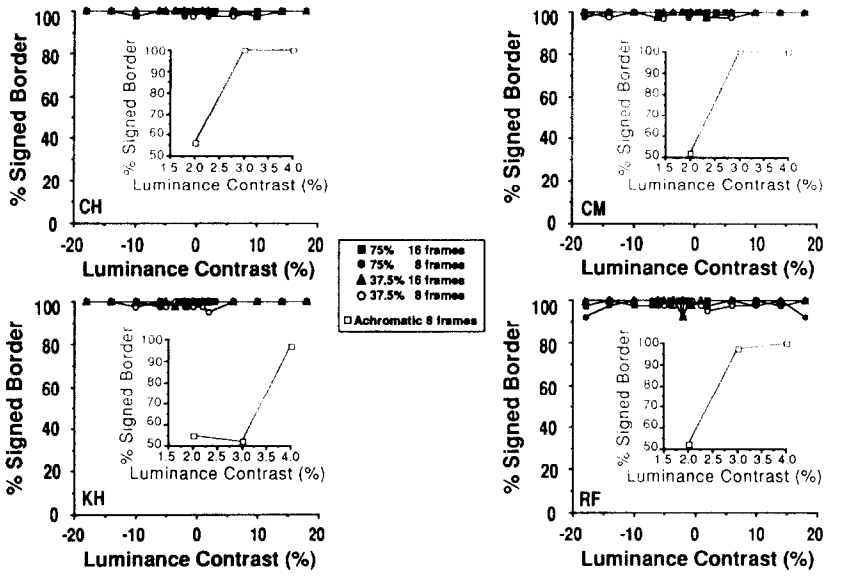

FIGURE 8. Data from four subjects viewing the 90° phase displacement stimulus [Fig. 1(C)] employed in Expt II (7.5 Hz R/G cycle). Each panel contains data obtained under heterochromatic (larger plot) and achromatic (smaller inset) conditions. The percentage of trials for which subjects reported motion in the *signed direction* [Fig. 1(C), dashed arrow] is plotted as a function of luminance contrast amplitude for each of four different heterochromatic conditions: 75% chromatic contrast amplitude, 16 frames (solid squares), 75% chromatic contrast amplitude, 8 frames (solid circles), 37.5% chromatic contrast amplitude, 16 frames (solid triangles) and 37.5% chromatic contrast amplitude, 8 frames (open circles). Fifteen different luminance contrast levels were used, five of which ranged in equal intervals (1.5%) around the isoluminant point determined from Expt I (the "unsigned" peaks of Fig. 4). Subjects reported motion in the signed direction for nearly every trial at all luminance contrast levels tested, and across stimulus conditions. To discount the possibility that small levels of luminance contrast contributed to reports of motion in the signed direction at isoluminance, we repeated the 90° phase displacement experiment (8 frames) using low contrast *achromatic* gratings (inset—open squares). For all four subjects, performance was at chance for 2% contrast gratings. Perceived motion of heterochromatic gratings in the signed direction at isoluminance must therefore be attributable to the presence of chromatic variation in these stimuli.

direction have been plotted as percent "signed border" responses. This percentage identifies the fraction of trials for which subjects reported motion in the direction that preserved the sign of chromatic contrast. Hence, a value of 100% indicates that motion was always perceived in the signed direction. By contrast, a value of 50% indicates that sign of chromatic contrast had no influence over motion correspondence. When presented with heterochromatic gratings having a chromatic contrast amplitude of 75% and displaced at a rate of 7.5 c/sec for a total of 16 frames (0.528 sec exposure), all subjects reported motion in the signed direction on nearly every trial (Fig. 8, solid squares). Because discrimination performance was at ceiling for all luminance contrast amplitude levels tested, we feel secure that sign of chromatic contrast is a viable cue for motion correspondence under these conditions. However, having adequate *a priori* grounds to believe that motion detectors are truly compromised at isoluminance (Ramachandran & Gregory, 1978; Cavanagh *et al.*, 1984; Derrington & Badcock, 1985; Troscianko, 1987; Livingstone & Hubel, 1987b), we included three additional stimulus conditions that progressively increased the difficulty of the discrimination task. Our objective in doing so was to bring performance below ceiling levels in order to "search" for deficits at isoluminance. These manipulations were as follows: (1) 8 frames (0.267 sec exposure) at 75% chromatic contrast (Fig. 8, solid circles), (2) 16 frames at 37.5% chromatic contrast (Fig. 8, solid triangles), and (3) 8 frames at 37.5% chromatic contrast (Fig. 8, open circles). Somewhat surprisingly, increasing task difficulty by these means had little effect: regardless of level of difficulty, all four subjects reported motion in the signed direction on nearly every trial for all luminance contrast amplitude levels tested. These data imply (in rather general terms) that the mechanism reliant upon sign of chromatic contrast for motion correspondence is surprisingly robust.

To further address the possibility that residual luminance contrast could explain perceived motion in the signed direction, we used *achromatic* 90° phase-shifted gratings moving at 7.5 c/sec for 8 frames at three different luminance contrast levels: 2, 3 and 4% (Fig. 8: inset, open squares). All four subjects performed at chance when the achromatic gratings contained only 2% luminance contrast. It is noteworthy that this ineffectual luminance contrast level substantially exceeds the largest residual luminance contrast amplitude that could occur in the heterochromatic condition (0.75%, occurring when a subject's isoluminant point falls directly in the middle of a 1.5% luminance contrast interval). Had subjects relied upon this residual luminance contrast in the heterochromatic condition, signed direction responses would have declined significantly at one or more of the luminance contrast levels tested. We did not, however, observe such a decline under heterochromatic conditions.

EXPERIMENT III: CONTROL FOR CONTRIBUTION FROM ROD PHOTORECEPTORS

The average luminance of our display (20 cd/m^2) is below that required to saturate human rods (Aguilar & Stiles, 1954). The sensitivity of rod photoreceptors varies, as does that of cones, with the wavelength of light (reaching a peak at about 500 nm) but the rod spectral sensitivity profile differs from those of both L and M cones. Moreover, the red/green luminance contrast level yielding *no* differential rod sensitivity for red and green differs from that required to equalize L and M cone outputs. It is therefore probable that the red and green phases of our heterochromatic gratings differentially activate rods. If so, rods could contribute a signal sufficient to account for any residual motion percept that is experienced when moving heterochromatic stimuli are balanced for L and M cone activation. This represents a potentially significant source of artifact that has not generally been addressed satisfactorily in psychophysical and neurophysiological experiments employing isoluminant heterochromatic stimuli.

To discount the possibility that the evidence for a signed mechanism obtained in Expts I and II was contaminated by residual modulation of rods, we repeated the 90° phase displacement experiment during the cone plateau period that occurs following a rod bleach. (During this period, cones have regained their sensitivity to light, whereas rods are still rendered nonfunctional.)

Method

Cone plateau onset and duration were determined prior to the experimental manipulation by adjusting the luminance of a dim green annulus until it was just detectable after a 2 min monocular exposure to bright light, as previously described (Stabell & Stabell, 1976; Nagy, 1980). A conservative estimate of cone plateau onset and duration were 3 and 6 min, respectively. The first author served as a subject for this experiment.

The subject was exposed binocularly to 2 min of the bleaching light. The subject was then presented with the same stimulus used in Expt II (90° phase displacement) and was required to judge direction of motion during the cone plateau period (6 min). Chromatic contrast amplitude was 75%, and the gratings were displaced at 7.5 c/sec for 8 frames. Ten luminance contrast levels were used ranging in equal intervals (1.5%) around the subject's isoluminant point (from −6.75 to 6.75%).

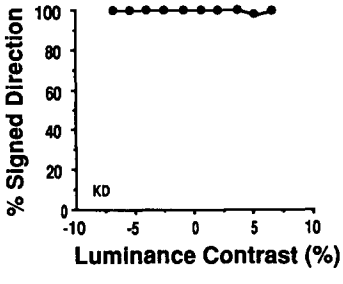

FIGURE 9. Control for rod contribution (Expt III). For a single subject, we conducted a 90° phase displacement manipulation (75% chromatic contrast amplitude, 8 frames) during the cone plateau period following a 2 min rod bleach. Ten different luminance contrast levels ranging in equal intervals (1.5%) from −6.75 to 6.75% were used. Motion was reported in the signed direction on nearly every trial. These results demonstrate that the tendency to perceive motion of heterochromatic gratings in the signed direction at isoluminance cannot be attributed to signals arising from rod photoreceptors.

Results and discussion

Results from this manipulation are shown in Fig. 9. For all luminance contrast levels tested, motion was nearly always reported in the signed direction. We therefore feel confident that, while the heterochromatic stimuli used in these experiments may elicit residual modulation within the rod photoreceptors, this activity does not contribute to the use of signed chromatic contrast for motion correspondence.

GENERAL DISCUSSION

We have presented evidence indicating that the primate motion system exploits one of the most salient features of our visual world—color—as a token for motion correspondence. We have shown, furthermore, that the motion system uses chromatic information of two distinct types. Under certain conditions, direction of perceived motion is determined by spatio-temporal correspondence between chromatically-defined borders in an image, without regard for the sign of chromatic contrast at those borders. However, it is also true that perceived motion may be determined by the sign of chromatic contrast. This occurs when unsigned chromatic borders provide a relatively weak proximal border cue. These findings suggest the existence of both signed and unsigned mechanisms for motion correspondence. In the real world, chromatically-defined image contours and the specific colors that define those contours move as one (i.e. objects do not normally change color when they move). Under environmental conditions, therefore, we should expect unsigned and signed mechanisms to work in unison.

We have found that the respective conditions under which unsigned and signed cues dictate motion correspondence vary as a function of spatial displacement size, luminance contrast amplitude, chromatic contrast amplitude, and temporal frequency. The results of these various manipulations shed light on the neural mechanisms involved, and permit some degree of speculation about the relative contributions of magnocellular and parvocellular pathways to motion detection in the primate visual system.

Before proceeding with the discussion of the results and their functional significance, we will first evaluate potential confounding factors and attempt to discount the possibility that they have contributed to the observed effects of color on motion correspondence.

Potential confounding factors

There are a number of potential sources of artifact associated with heterochromatic stimuli of the sort used

in our experiments. In discussing their potential impact on our results, it is useful to group these into two general classes by factors of origin; we call these "peripheral" and "neural" factors. *Peripheral factors* are those associated with the optics of the eye. *Neural factors* are those associated with variations in the relative strength of red and green within the neural pathway.

Peripheral factors

The techniques we have used to limit luminance artifacts attributable to chromatic aberration of the eye are described in some detail in the Methods. Of principal importance here is the fact that the effective luminance contrast amplitude introduced by chromatic aberration is markedly dependent upon spatial frequency and is minimal (approx. 0.5%) for sinusoidal heterochromatic gratings of the low frequency used in our experiments (0.45 c/deg) and therefore below threshold sensitivity (Robson, 1966; Logothetis, 1990; Cavanagh & Anstis, 1991).

Neural factors

Contribution from rod photoreceptors. The purpose of Expt III (rod inactivation by bleaching) was to determine whether differential activity of rod photoreceptors can account for the use of signed chromatic contrast for motion correspondence that we observed in Expts I and II. On the basis of the results obtained in Expt III, we feel secure in asserting that the differential sensitivity of rods to the red and green phases of our stimuli is not a confounding factor.

Spatial variations in chromatic sensitivity. The potential for variation in the relative sensitivity to red and green as a function of eccentricity underlies a criticism that has been levied against many psychophysical experiments of this general type. Our visual stimuli were confined to a region defined by a 5° radius about the center of gaze. The macular pigment (which decreases rapidly from 0 to 3°) can alter flicker photometry and color matching settings (Hering, 1893), but this appears to be restricted to the S-cone mechanism, leaving the relative spectral sensitivities of the M and L cones unaltered (Wooten, Fuld & Spillman, 1975; Stabell & Stabell, 1980, 1981; Viénot, 1980). It is also possible that small variations in the ratio of M to L cone types exist across the retina. To date, studies which directly address this question are few and far between, mostly due to difficulties associated with distinguishing L from M cones. There has been some suggestion, however, that while the density of S cones varies with eccentricity, L/M cone ratios remain fairly constant out to 40° (Marc & Sperling, 1977). Similar findings have been reported from human psychophysical experiments employing hue discrimination techniques to estimate L/M cone ratios as a function of eccentricity (Nerger & Cicerone, 1992). The results from these experiments indicated that L/M cone ratios were constant across all eccentricities tested (out to 4°). In general, but not without exception (Livingstone & Hubel, 1987b), there exists substantial consensus from psychophysical experiments (of divers types) that the relative contributions of M and L cones remain invariant at least out to 5° eccentricity (Wooten & Wald, 1973; Wooten *et al.*, 1975; Stabell & Stabell, 1980, 1981; Mullen, 1991; Nerger & Cicerone, 1992). On these grounds we think it unlikely that spatial variations in sensitivity to the red and green components of our stimuli are sufficient to account for our results.

To add further weight to this argument, consider the perceptual consequence of a residual luminance signal. Under the achromatic condition of Expt I, when the stimulus *itself* contained a luminance signal, motion was perceived in the direction for which sign of luminance contrast was preserved (Fig. 7). The predicted consequence of a peripheral or a neural luminance signal in our heterochromatic condition is, therefore, a bias toward perceived motion in the signed direction. Since this is in opposition to the "unsigned peak" that we consistently see for small spatial phase displacements (Fig. 4), we feel confident that residual luminance contrast does not contribute to the use of unsigned chromatic borders for motion correspondence. Furthermore, we found in Expt II that small levels of achromatic luminance contrast (2%) could *not* be used for motion correspondence. By contrast, when the stimulus contained only chromatic modulation, the percept of motion was consistent and robust (Fig. 8).

Effects of stimulus speed

The design of the contrast-reversed stimulus used in Expt I ensures that, not only do signed and unsigned cues move in opposite directions, but the signed cue moves at a faster speed than the unsigned cue. Specifically, the ratio of speeds is equal to the ratio of the angles of spatial displacement in the two opposing directions. Thus, for example, if the unsigned phase angle is 25.7°, the unsigned cue moves at 2.4°/sec while the signed cue moves at 14.3°/sec—a six-fold difference in speed between the two cues. Motion is clearly detectable at both speeds since subjects reported motion in the direction of the slower moving (unsigned) cue at isoluminance, while at non-isoluminance motion was generally reported in the direction of the faster (signed) cue. Nonetheless, it is still possible that motion detectors prefer slower speeds when presented with moving contours defined solely by chromatic contrast. Such a tendency could account for perceived motion in one direction at isoluminance and in the opposite direction at non-isoluminance. This explanation lacks credibility, however, since our subjects perceived motion of isoluminant stimuli at both slow speeds *and* high speeds. For example, when the spatial phase displacement was 6.4°, subjects typically reported motion in the unsigned direction (Fig. 4). Under these conditions the unsigned cue moved at 0.6°/sec while the signed cue moved at 16.1°/sec in the opposite direction. Were it the case that subjects perceived motion in the unsigned direction because it was moving more slowly, we might expect that for the 51.4° phase condition subjects would continue to report motion of the slower, unsigned, component. This is contrary to the result obtained (Fig. 4); subjects consistently reported motion

in the faster signed direction (11.9°/sec). Furthermore, in our higher temporal frequency condition (30 Hz R/G alternation) subjects detected motion of isoluminant heterochromatic gratings over a wide range of speeds. For example, when the gratings were displaced by 6.4° of spatial phase, subjects reported motion in the unsigned direction, which moved at 2.4°/sec. By contrast, when the phase displacement equalled 51.4°, subjects reported motion in the signed direction, which moved at 47.7°/sec.

Luminance and color as tokens for motion correspondence

When the luminances of the red and green phases of our stimuli were not "balanced", motion was more likely to be seen in the direction that preserved the sign of both luminance and chromatic contrast. We infer, therefore, that when luminance contrast is sufficiently high, luminance polarity is a stronger cue for motion correspondence than proximity. The influence of luminance contrast on motion correspondence is further revealed using *achromatic* gratings. Here, regardless of the amplitude of luminance contrast, regions of constant luminance polarity were most frequently seen to move in the direction opposite from the proximal border, i.e. in the signed luminance direction. In addition, since the observed unsigned peak for heterochromatic gratings was generally broad enough to encompass a substantial range of luminance contrast amplitudes (see Fig. 4), it can be stated that *the mere addition of color to a low contrast achromatic grating is sufficient to cause a reveral of perceived direction.* These results discredit the possibility that low luminance contrast amplitude is sufficient to explain the unsigned peak and they further imply that unsigned chromatic contrast is a relatively strong cue for motion correspondence.

Magnitude of spatial displacement: relative or fixed?

We have referred to the spatial displacement of our gratings in units of spatial phase angle, i.e. in units that are inherently dependent upon spatial frequency. However, since only one spatial frequency was used in these experiments, each phase angle also refers to a constant angular displacement in visual space. Since the maximum displacement for apparent motion is thought to be dependent upon specific stimulus conditions (e.g. Cavanagh, Boeglin & Favreau, 1985), we felt it of some interest to know whether the displacement balance point for signed vs unsigned cues is relative to spatial frequency (constant phase angle) or a fixed distance in visual space (constant angular displacement).

The most straightforward way to address this issue involves varying grating spatial frequency while keeping spatial phase angle constant. Because of constraints implicit in our specific stimulus configuration, however, we have been unable to accomplish this goal. For one, we are presently obliged to use low spatial frequencies for our heterochromatic gratings in order to limit chromatic aberration (Flitcroft, 1989). A second problem stems from the fact that the speeds of the signed and unsigned cues (speed *a*, speed *b*) that are pitted against each other at one spatial frequency will be different from two speeds (speed *c*, speed *d*) at a second spatial frequency—even though spatial phase displacement remains constant. If the relative sensitivity of motion detectors to one pair of speeds (*a*, *b*) is not the same as the relative sensitivity to the second pair (*c*, *d*), unconfounded comparisons between the two spatial frequencies can not be made. At the present time, therefore, we must consider this issue unresolved.

Neural correlates of perception?

In order for a particular brain region to support the use of chromatic contrast as a token for motion correspondence, it is prerequisite that the neurons in this area (1) are selective for direction of motion and (2) can use chromatic properties of an image to elicit directional selectivity. While it is possible that these two conditions are fulfilled within the parvocellular stream, all lines of evidence suggest that directional selectivity is not a salient property of the cells within this pathway (Zeki, 1978a, b). Moreover, evidence from varied sources indicates that the components of the parvocellular pathway are not directly involved in the analysis of motion (Merigan & Eskin, 1986; Merigan, 1989; Schiller, Logothetis & Charles, 1990; Merigan, Katz & Maunsell, 1991).

Alternatively, might activity within the various cortical components of the magnocellular pathway underlie the use of color for motion correspondence? Directionally selective cells are first found in layer 4B of striate cortex (V1). Layer 4B, which is considered a subdivision of the magnocellular pathway, has been shown to contain some cells that continue to respond to the motion of a stimulus even when that stimulus is defined solely by color (Hubel & Livingstone, 1990). While it is possible that these cells support perceived motion of color-defined stimuli, it remains unknown whether layer 4B neurons use image contours defined by color without regard for the colors themselves (unsigned chromatic correspondence), or use information about the sign of chromatic contrast (signed chromatic correspondence). The magnocellular divisions of area V2 ("thick" stripes), which receive direct input from layer 4B and project to area MT, are also a potential source of contribution to color-facilitated motion correspondence. Appropriate experiments addressing this question have yet to be performed in this area.

Several lines of evidence indicate that cortical visual area MT plays a key role in the processing of visual motion. While MT neurons do not exhibit traditional chromatic selectivity, the results of recent experiments have demonstrated that many MT neurons exhibit directional selectivity for motion of chromatically-defined stimuli (Saito *et al.*, 1989; Charles & Logothetis, 1989; Dobkins & Albright, 1991a, b, 1993; Movshon *et al.*, 1991). In a recent extension of work along these lines, we have found that the directional selectivity of a substantial fraction of MT neurons can be modulated by the same chromatic and luminance manipulations that we have shown to affect perceived direction of motion

(Dobkins & Albright, 1991a, b, 1993). This pattern of neuronal activity rather strikingly parallels the perceptual effects reported herein. Specifically, using isoluminant heterochromatic gratings that were both drifting and undergoing repetitive reversal of chromatic sign [identical to those described above and schematized in Fig. 1(B)] we found that, near photometric isoluminance, MT neurons signaled motion in the direction of the nearest chromatically-defined border even when the sign of chromatic contrast at that border alternated over time. Furthermore, the addition of sufficient luminance contrast to the heterochromatic gratings resulted in a reversal of cellular direction preference; hence MT responses were greatest when regions of corresponding luminance and chromatic sign moved in the preferred direction. In harmony with our psychophysical results, therefore, luminance polarity is a strong determinant of directional selectivity in MT neurons. Finally, we found that increasing the size of the spatial phase displacement also increased the likelihood that, regardless of luminance contrast amplitude, responses would be strongest when regions of consistent chromatic sign moved in the preferred direction. These marked similarities between the perceptual effects reported herein and those seen for directionally selective MT neurons are highly suggestive and make a case for an important contribution from MT.

Building directionally selective units from "early" chromatic signals

The chromatic sensitivities of neurons at early stages of the primate magnocellular and parvocellular pathways are sufficiently well described to permit fruitful speculation about neural origins of the perceptual effects reported herein or, more generally, about the ways in which chromatic signals might enter into motion processing circuits. We will begin by considering the degree to which our results can be accounted for by the properties of magnocellular neurons in the LGN. Later, the evidence for a parvocellular contribution will be examined.

Magnocellular contribution?

Many neurons within the magnocellular populations of both retina and LGN signal temporal alternation between lights of equal luminance, provided that they differ in color. When presented with a non-isoluminant stimulus cycling between red and green, the firing rate of "on-center" magnocellular neurons increases when the brighter of the two colors enters the receptive field (and vice versa for "off-center" cells). When presented with an isoluminant red/green cycling stimulus, however, these cells respond with equal magnitude to each chromatic change, regardless of the direction of change. Since chromatic changes occur twice per red/green cycle, the response occurs at twice the temporal frequency. For this reason the phenomenon has been dubbed "frequency doubling" (Schiller & Colby, 1983; Lee *et al.*, 1988, 1989a, b, c; Logothetis *et al.*, 1990). This property demonstrates that individual neurons within the magnocellular pathway can provide information about the existence of chromatic contrast within an image, although they cannot signal the sign of chromatic contrast.

We suggest that a primary function of the magnocellular system is to provide signals indicating the presence of an image contour —defined by luminance, color, or any of a variety of figural cues— in a form that happens to be computationally efficient for the purpose of detecting motion (Albright, 1992; Stoner & Albright, 1993). In the case of color, information is lost by disregarding sign of chromatic contrast, but that information is of little consequence for motion detection. Rather than acquiescing to the extreme view that color is processed primarily by the parvocellular system, we suggest that the chromatic properties of an image are processed by *both* magnocellular and parvocellular systems, but in a different manner by each as befits their broader functions in visual perception.

Bearing this in mind, we propose a simple mechanism that can explain much of our psychophysical results in terms of activity among a population of magnocellular LGN neurons. The essential characteristics of this mechanism are illustrated in a highly schematic form in Fig. 10. The upper panel depicts the spatial configuration of a red/green grating —the very stimulus we have used in our experiments— at four different moments in time. The grating undergoes chromatic contrast sign reversal with each spatial displacement. In this example, the proximal unsigned cue moves rightward, while the signed cue moves leftward. Below the grating we have shown presumed activation state within a population of contiguous "on-center" magnocellular neurons as a function of the visual stimulation sequence for isoluminant (center panel) and non-isoluminant (bottom panel) stimulus conditions. When the red/green grating is isoluminant, each neuron fires to the onset of either red or green. The resultant neuronal activity (center panel) produces a spatio-temporal "flow" in the direction of the unsigned chromatically-defined contour. Since motion is presumed to be detected on the basis of this spatio-temporal flow using some sort of spatio-temporal comparator (a Reichardt-detector or the equivalent), it becomes possible to explain chromatically-unsigned motion correspondence solely on the basis of magnocellular activation.

The bottom panel in Fig. 10 illustrates the effects that the addition of luminance contrast to the red/green grating should have on the same population of cells. Under these conditions, each "on-center" neuron fires to the onset of the brighter of the two colors. In consequence, the spatio-temporal "flow" among the magnocellular population is now in the opposite direction, i.e. the direction in which sign of luminance and chromatic correspondence are both conserved. Furthermore, in the case of an achromatic grating, the pattern of activity would be expected to be the same as that produced by heterochromatic gratings containing luminance modulation. Under achromatic conditions, therefore, the spatio-temporal flow will also be in the signed direction.

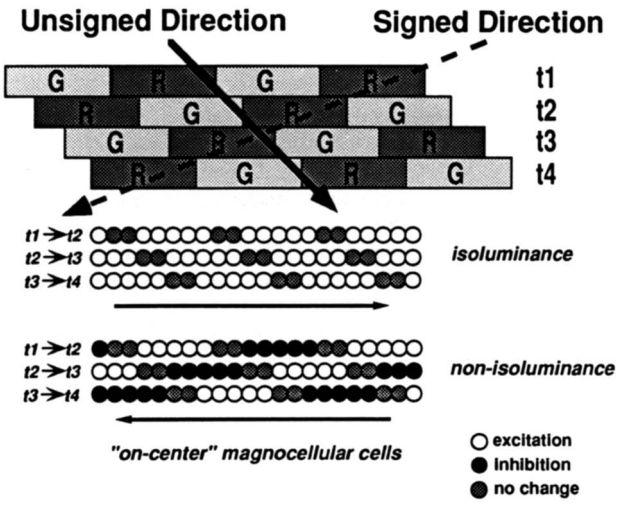

FIGURE 10. Activity among a population of "on-center" magnocellular neurons might signal motion in the *unsigned* direction at isoluminance, and in the *signed* direction away from isoluminance. The upper panel depicts the spatial configuration of our red/green contrast-reversing grating at four different moments in time. The proximal unsigned cue moves rightward (solid arrow), while the signed cue moves leftward, preserving color (and luminance) correspondence over time and space (dashed arrow). Below the grating we have shown presumed activation state within a population of contiguous "on-center" magnocellular neurons as a function of the visual stimulation sequence (e.g. at the transition from t1→t2). When the red/green grating is isoluminant, each neuron fires at the instant a chromatic substitution occurs within its receptive field, regardless of the direction of the substitution (center panel, white circles). Under such conditions, the spatio-temporal "flow" of active neurons is in the direction of the unsigned chromatically-defined contour, which can explain psychophysical reports of motion in the unsigned direction at isoluminance (Fig. 4). The bottom panel illustrates the effects that the addition of luminance contrast to our heterochromatic stimulus should have on the same population of cells. Under this condition, befitting its status as "on-center", a cell is excited whenever the brighter of the two chromatic phases (in this case, green) enters its receptive field (open circles) and inhibited when the dimmer phase enters (solid circles). (Gray circles depict no change in responsivity.) In consequence, the spatio-temporal "flow" is now in the opposite direction, i.e. the direction in which sign of luminance and chromatic correspondence are both conserved. Furthermore, in the case of an achromatic grating, the pattern of activity would be expected to be the same as that produced by heterochromatic gratings containing luminance modulation—i.e. an excitatory response to the brighter of the two luminance phases. Under achromatic conditions, therefore, the spatio-temporal flow will also be in the signed direction. This model thus readily accounts for both our psychophysical data (Fig. 4) and our neurophysiological data (described in the text) obtained from area MT using contrast reversing stimuli undergoing small spatial phase displacements.

This model thus readily accounts for both our psychophysical data (reported herein) and our neurophysiological data (cited above) obtained from area MT using contrast reversing stimuli undergoing small spatial phase displacements. It does not, however, account for chromatically-signed motion correspondence, an important issue that is addressed in the following section.

The use of chromatic sign as a token for motion correspondence

The effect of increasing spatial phase displacement in Expt I was to reveal the existence of a motion detection system that utilizes chromatic sign as a token for motion correspondence. This result was confirmed in Expt II, in which perceived motion could only have resulted from a "chromatically-signed" motion correspondence mechanism. Our psychophysical results obtained using 90° phase-shifted gratings are in agreement with results from previous psychophysical experiments using similar stimulus configurations (Papathomas, Gorea & Julesz, 1989, 1991; Green, 1989; Gorea & Papathomas, 1989; Dobkins & Albright, 1990; Gorea, Lorenceau, Bagot & Papathomas, 1990). Congruent with our psychophysical results, neurophysiological recordings show that, for 90° phase displacements, chromatic sign determines directional selectivity for single neurons in area MT (Dobkins & Albright, 1990, 1993, 1991a, b). What, if anything, can be said about the relative contributions of magnocellular and parvocellular pathways to this signed correspondence mechanism?

Magnocellular neurons of the retina and LGN clearly carry information about chromatic contrast, as evidenced by frequency doubling. Because of the forfeiture of chromatic sign, however, this signal alone would seem insufficient to account for perceived motion of heterochromatic patterns in the signed direction. An alternative explanation rests on the fact that the red/green null point varies among magnocellular neurons of the LGN. This variability assures that, as a population, magnocellular LGN neurons can never be truly silenced (Logothetis *et al.*, 1990). We must, therefore, assume that some magnocellular LGN neurons will have signaled an "imbalance" (i.e. unequal responses) between the red and green phases of our stimuli at any luminance contrast level tested. Were it to have access to such signals, the performance of a luminance-based motion detecting system would never dip to zero (even at a behaviorally defined isoluminant point) because there will always be some magnocellular neurons that continue to respond differentially to the two colors. Whether motion processing areas of the magnocellular pathway actually utilize this information is a matter of some debate, however, since the ability to discriminate motion of isoluminant stimuli cannot be completely accounted for by inter-unit variability in magnocellular LGN (Cavanagh, 1988; Cavanagh & Anstis, 1991).

Alternatively, what is the potential for a parvocellular contribution? There are several sites that may allow some interaction between parvocellular and magnocellular pathways. For example, in area V1 direct connections have been observed linking cortical laminae that contain color-selective neurons with laminae that contain directionally selective neurons (Yoshioka & Lund, 1990). In extrastriate visual cortex, direct connections have been found to exist between areas V4 and MT (Ungerleider & Desimone, 1986; Desimone & Ungerleider, 1986; Maunsell & Van Essen, 1983b). Neurophysiological studies have, furthermore, shown that signals from both parvocellular and magnocellular layers of the LGN converge onto cells in the superficial layers of V1 (Malpeli, Schiller & Colby, 1981; Nealey & Maunsell, 1991). While similar experiments have demonstrated only a weak parvocellular input to MT (Nealey, DePriest

& Maunsell, 1989; Maunsell, Nealey & DePriest, 1990), our results imply that a greater parvocellular contribution may be revealed if appropriate heterochromatic stimuli are employed. In any event, it seems that there are numerous means by which parvocellular signals might mingle with magnocellular. Interactions of this sort could influence motion processing by creating motion detectors that are not themselves selective for color, yet can use information about the sign of chromatic contrast to detect direction of motion.

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