Perceptual, oculomotor, and neural responses to moving color plaids

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Abstract. Moving plaids constructed from two achromatic gratings of identical luminance contrast are known to yield a percept of coherent pattern motion, as are plaids constructed from two identical chromatic (eg isoluminant red/green) gratings. To examine the interactive influences of chromatic and luminance contrast on the integration of visual motion signals, we constructed plaids with gratings that possessed both forms of contrast. We used plaids of two basic types, which differed with respect to the phase relationship between chromatic and luminance modulations (after Kooi et al, 1992 *Perception* **21** 583 – 598). One plaid type ('symmetric') was made from component gratings that had identical chromatic/luminance phase relationships (eg both components were red-bright/green-dark modulation). The second plaid type ('asymmetric') was made from components that had complimentary phase relationships (ie one red-bright/green-dark grating and one green-bright/red-dark grating). Human subjects reported that the motion of symmetric plaids was perceptually coherent, while the components of asymmetric plaids failed to cohere. We also recorded eye movements elicited by both types of plaids to determine if they are similarly affected by these image cues for motion coherence. Results demonstrate that, under many conditions, eye movements elicited by perceptually coherent vs noncoherent plaids are distinguishable from one another. To reveal the neural bases of these perceptual and oculomotor phenomena, we also recorded the responses of neurons in the middle temporal visual area (area MT) of macaque visual cortex. Here we found that individual neurons exhibited differential tuning to symmetric vs asymmetric plaids. These neurophysiological results demonstrate that the neural mechanism for motion coherence is sensitive to the phase relationship between chromatic and luminance contrast, a finding which has implications for interactions between 'color' and 'motion' processing streams in the primate visual system.

1 Introduction
Moving objects frequently overlap in their projection upon the retinae. Perceptual reconstruction of the visual scene requires that the resulting compound image features be properly decomposed into the constituent object motions. The study of motion coherence in plaid patterns has been instrumental in understanding how the visual system accomplishes this task. Psychophysical studies employing these stimuli suggest that similarity of the overlapping image features plays a key role. When the component gratings of a plaid pattern are identical along a particular stimulus dimension, a coherently moving plaid pattern is perceived. Conversely, when the gratings differ sufficiently along a particular stimulus dimension, the two component gratings are frequently seen to slide noncoherently across one another. Thus, depending on component grating similarity, either 'pattern' or 'component' motion may dominate motion perception (figure 1a).

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(a) Bi-kinetic (conventional) plaid stimulus

(b) Uni-kinetic plaid stimulus
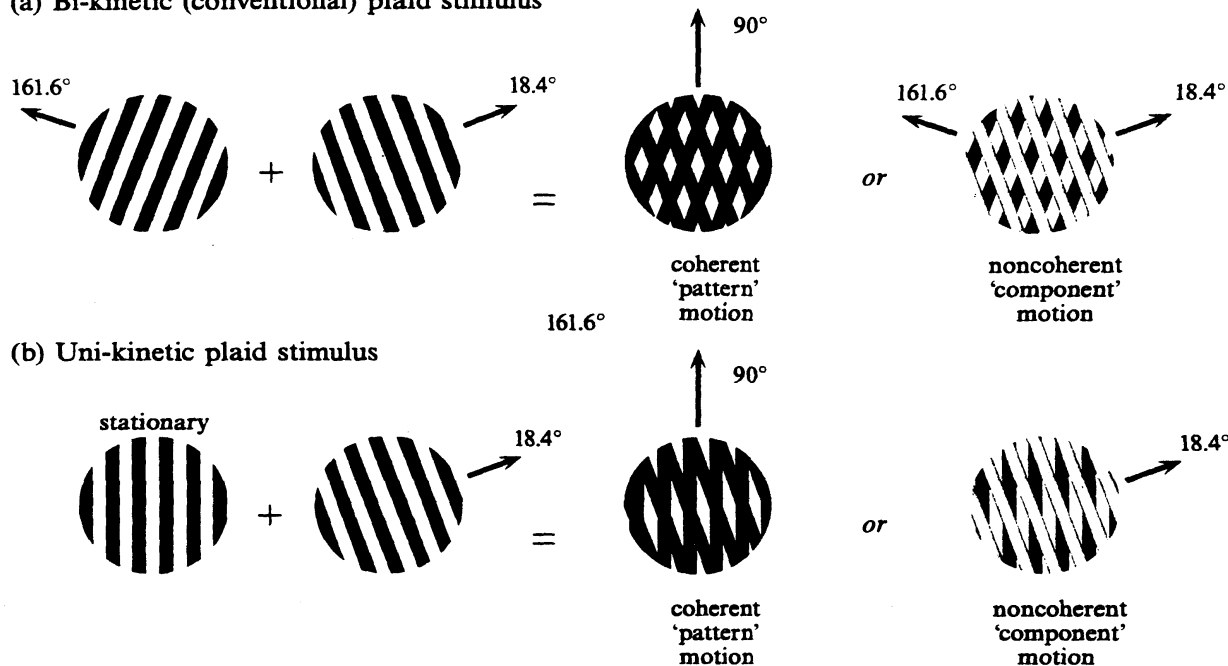
Figure 1. Coherent and noncoherent moving plaid patterns.

(a) 'Bi-kinetic' plaids are constructed by superimposition of two moving component gratings. When the components are identical, a coherently moving plaid pattern is commonly perceived (upwards in this case). Conversely, when the components differ sufficiently along one or more stimulus dimensions, they are frequently seen to slide noncoherently across one another.

(b) 'Uni-kinetic' plaid patterns are constructed from one moving and one stationary component. Pattern motion is upward, in this example, parallel to the orientation of the stationary component. Component motion is simply the motion of the single moving component, which appears to slide across the stationary component. Pattern and component motion are thus each associated with a single direction of motion.

Anticipating the many recent explorations of the role of component similarity in motion coherence, Wallach (1935) observed that differently oriented overlapping stripes possessing either different line spacing or different colors tended to be perceived as moving independently more frequently than when the stripes were of identical appearance. In contemporary studies on moving plaid patterns, Adelson and Movshon observed that noncoherent motion was perceived if the two gratings of a plaid pattern differed sufficiently along the dimensions of spatial frequency (see also Smith 1992), luminance contrast (Adelson and Movshon 1982), or horizontal binocular disparity (Adelson 1984). A simple explanation for such component similarity effects is the *'channel model'*, originally advanced by Adelson and Movshon (1982) to account for the influence of spatial frequency on motion coherence. This model supposes that moving gratings differing along a particular featural dimension are processed within separate channels. In this scenario, noncoherence occurs for dissimilar gratings because the neural mechanisms responsible for encoding pattern motion are feature-selective, and thus respond to one, but not both, of the component gratings. Conversely, perceptual coherence occurs when both components activate the same neural mechanism.

Wallach's early demonstration of the impact of color similarity on motion coherence has been confirmed by a number of recent studies (Krauskopf and Farell 1990; Dobkins et al 1992; Kooi and De Valois 1992; Kooi et al 1992; Farell 1995; Cropper et al 1996; Krauskopf et al 1996). In one of the earlier studies, Krauskopf and Farell (1990) employed moving plaid patterns composed of grating components modulated along different axes of 3-D color space (Derrington et al 1984). These investigators found that when both component gratings were modulated along the same cardinal axis, plaids were perceived

to move coherently. By contrast, when gratings were modulated along *different* cardinal axes, they appeared to slide noncoherently across one another. These results suggested that color-selective neurons are predominantly selective for modulation along the cardinal axes of color space.

More recent findings have forced this view of color selectivity to be amended: plaids composed of gratings modulated along different *noncardinal* directions of color space can also produce noncoherent motion, although perhaps not as strongly as those modulated along different cardinal axes (Kooi et al 1992; Farell 1995; Krauskopf et al 1996; but cf Krauskopf and Farell 1990). Of special interest here is the finding that plaids composed of gratings that each activate both the chromatic (eg red/green) and luminance (ie bright/dark or 'achromatic') cardinal axes can be configured to be noncoherent if the chromatic/luminance phase relationships of the two gratings are complementary (eg when one grating is red-bright/green-dark and the other is green-bright/red-dark— referred to as *asymmetric*). Conversely, plaids made from component gratings with the same chromatic/luminance phase relationships (ie when both gratings are either red-bright/green-dark or green-bright/red-dark—referred to as *symmetric*) are perceptually coherent. The noncoherence of aysmmetric plaids is consistent with the existence of neural mechanisms selective for modulation along noncardinal, as well as cardinal, directions in color space.

Regardless of whether the underlying neural mechanisms are tuned for cardinal or noncardinal directions, if we wish to extend Adelson and Movshon's channel model to account for the influence of color on motion coherence, we would have to assume that the neural mechanisms underlying motion coherence are selective for different color dimensions. Although appealing in its simplicity, application of the channel model to the effects of color similarity are difficult to reconcile with the much-heralded view that motion-sensitive neurons in the primate visual system are not color selective (eg Zeki 1974, 1978; Baker et al 1981; Van Essen et al 1981; Maunsell and Van Essen 1983; Albright 1984).

To elucidate the mechanisms underlying the influence of color on motion coherence, we studied perceptual, oculomotor, and neurophysiological responses to moving color plaids. We employed asymmetric and symmetric plaids (composed of various combinations of red-bright/green-dark and green-bright/red-dark gratings), modeled after previous psychophysical experiments (Krauskopf and Farell 1990; Kooi et al 1992; Farell 1995; Krauskopf et al 1996). We first present, briefly, the results of *psychophysical* experiments, which confirm and extend those previous experiments and identify optimal stimulus parameters for subsequent oculomotor and neurophysiological experiments.

Second, we present the results of *oculomotor* experiments designed to ask whether *oculomotor* responses are sensitive to the same color manipulations that affect perception. An answer in the affirmative would be consistent with other evidence suggesting that motion perception and oculomotor tracking are subserved by a common neural substrate. On a more practical note, the degree of correspondence between these two behavioral measures—oculomotor and psychophysical—bears on the utility of oculomotor tracking as a means to infer perceptual state in animals—an issue of great importance for related neurophysiological experiments.

Last, we present the results of a small number of *neurophysiological* recordings from individual neurons in the middle temporal visual area (area MT) of visual cortex in an alert rhesus monkey. We are led to an interest in MT responses to color plaids for several reasons. First, we wished to investigate whether directional responses in MT neurons are influenced by color plaids in a fashion similar to that observed perceptually. In a previous study in which perceptual transparency cues were used as a way of manipulating motion coherence in moving plaid patterns, Stoner and Albright (1992) demonstrated a correlation between the responses of MT neurons and human perceptual judgments, suggesting a potential neural substrate for the perceptual phenomenon. The strength of the claim

that MT neurons underlie the perceptual integration of visual motion signals will depend upon demonstrating that the neuronal effects generalize across the various stimulus parameters known to influence perceptual motion coherence.

A second motivation for these neurophysiological experiments concerns the long-standing controversy regarding the extent to which 'motion' and 'color' areas interact in the primate visual system. Although several studies have demonstrated chromatic input to area MT, as evidenced by the finding that area MT neurons can signal the direction of motion of red/green isoluminant stimuli (Charles and Logothetis 1989; Saito et al 1989; Dobkins and Albright 1990, 1994; Gegenfurtner et al 1994), MT neurons appear *not* to be selective for the phase relationship between chromatic and luminance modulations. In other words, MT neurons respond equally well to red-bright/green-dark as to green-bright/red-dark stimuli, and thus canot be considered to constitute chromatic/luminance channels of the type that might explain the noncoherence of asymmetric color plaids. If area MT neurons were found to respond differentially to symmetric vs asymmetric color plaids without responding differentially to the component gratings when presented individually, this would argue against the channel-based hypothesis. Such a result might instead be explained by color-selective mechanisms (possibly parvocellular in nature) that modulate input to area MT under certain conditions.

The results from our experiments demonstrate a significant influence of color on the integration of motion signals in all three domains tested: psychophysical, oculomotor, and neurophysiological. These findings add to the growing body of literature demonstrating that the motion system has far more access to color information than previously believed.

2 General methods
In this section we identify methods that apply generally to our psychophysical, oculomotor, and neurophysiological experiments. Methods specific to each experiment are presented separately.

2.1 *Apparatus*
Visual stimuli were generated with a computer video display and digital frame buffer (Pepper SGT, Number Nine Computer Corp: 640×480 pixels, analog RGB output, 8 bits/gun, 60 Hz frame rate). The controller resided in an AT-class personal computer and permitted 256 simultaneously displayable colors or luminance levels (selected from a palette of 16 million). Stimuli were displayed on a 20-inch Phillips C2064-AS RGB video monitor. The CIE chromaticity coordinates for our stimulus display monitor were: Red (0.618, 0.350), Green (0.280, 0.605), and Blue (0.152, 0.067). [For four naive subjects tested psychophysically on a newer apparatus, we used a 21-inch F2-21 Nanao monitor with the following CIE coordinates: Red (0.625, 0.340), Green (0.290, 0.605), and Blue (0.150, 0.070)]. The voltage/luminance relationship was linearized independently for each of the three guns in the display (Watson et al 1986b). Stimulus generation operated under the charge of a PDP 11/73, which provided coded instructions for selection and timing of visual stimuli produced by the graphics device. The PDP 11/73 was also used for data acquisition, analysis, and behavioral control.

2.2 *Visual stimulation*
2.2.1 *Construction of red/green gratings.* The components of all plaid patterns were 1.0 cycle deg^{-1} sinusoidal gratings, which contained both chromatic (red/green) and luminance contrast. Gratings were produced by summing sinusoidal luminance modulations of the red and green phosphors, of identical spatial frequency and orientation but 180° out of phase with each other. Rendered in this manner, luminance contrast of the resultant red/green grating is dependent upon the mean luminances and modulation depths of the red and green sinusoids (see figure 2). In our experiments, modulation depth was kept constant (at 90%) and was identical for the red and green sinusoids.

In order to vary the luminance contrast in the grating, the mean luminances of the red and green sinusoids were differentially adjusted such that the mean luminance of the resultant red/green grating was 10 cd m^{-2}. Luminance contrast of the red/green grating is expressed as: modulation depth $\times [(G_{mean} - R_{mean})/(G_{mean} + R_{mean})]$. With this metric, luminance contrast can be either positive or negative, depending upon which of the two colors is brighter. By our convention, positive (+) contrast refers to the case where the green phase of the grating is brighter than the red. Likewise, negative (−) contrast refers to the case where red is brighter than green.
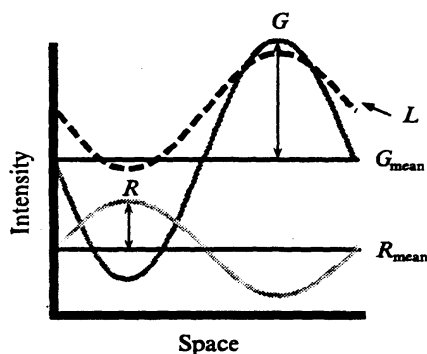
Figure 2. Spatial profile of luminance contrast in red/green gratings. Red/green gratings were produced by sinusoidal modulation of red and green phosphors in opposite spatial phase. In the illustrated example, green (G) is brighter than red (R), which we provisionally define as '+' luminance contrast. The resulting luminance modulation (L) is shown. (See text for details.)

2.2.2 *Modulation in 3-D color space.* It is important to note that the color components of our plaid stimuli differ somewhat from those employed in previous experiments (eg Kooi et al 1992; Farell 1995; Krauskopf et al 1996), and were not crafted to selectively activate axes in Derrington, Krauskopf, and Lennie (DKL) 3-D color space (Derrington et al 1984). These differences result from the fact that the neurons we studied were part of another experiment that required specific methods/parameters to produce significant neural responses near isoluminance (see Dobkins and Albright 1994). First, because of the method used for varying luminance contrast in our gratings (see above), red/green gratings possessing different levels of luminance contrast were necessarily of different mean chromaticities. That is, positive (+) contrast gratings had a mean chromaticity that was more green than the mean chromaticity for negative (−) contrast gratings. Second, we did not attempt to precisely isolate the L − M/L + M plane, ie the plane that produces no variation in S-cone activity. Nonetheless, we estimate [on the basis of Smith−Pokorny cone fundamentals (Smith and Pokorny 1972) and the conversion equations provided in Boynton (1986)] that the red and green phosphors of our monitor produced negligible activation of S-cone photoreceptors [R = 0.002, G = 0.003 units in MacLeod and Boynton (1979) chromaticity space], and thus S cones should not contribute to our results.

2.2.3 *Construction of moving plaid patterns.* Chromatic plaid patterns were created by interlacing two component gratings at 60 Hz (each grating was presented on every other vertical refresh, ie at 30 Hz). Motion of the grating components was achieved by spatial phase offset (between 60.0° and 63.3° phase shift, depending on the grating orientation), coincident with every other vertical refresh of the video monitor (ie every 33.33 ms, or 30 Hz frame rate). These discrete spatial and temporal intervals are known to be within a range that renders a clear percept of motion (eg Burr et al 1986; Watson et al 1986a) and elicits responses in MT neurons (Mikami et al 1986; Newsome et al 1986). For both component grating motion and the resulting pattern motion, we refer

to direction-of-motion in polar coordinates, with 0° motion denoting motion rightward, 90° denoting motion upward, etc.

2.2.4 *Uni-kinetic vs bi-kinetic plaids*. For these experiments, we employed moving plaid patterns in which only one of the two component gratings moved, while the other remained stationary (Dobkins et al 1992; Duncan et al 1994). We refer to these as '*uni-kinetic*' plaids, similar to those described by Gorea and Lorenceau (1991). In contrast to conventional '*bi-kinetic*' plaids (ie plaids composed of two moving gratings, figure 1a) the uni-kinetic plaid design yields a single component motion. Thus, for the uni-kinetic plaid, *both* coherent and noncoherent motion percepts are each associated with a single motion (see figure 1b). This uni-kinetic design was essential for the purpose of our oculomotor experiments (see section 4). Component motion corresponds to the motion of the single moving grating. The 'intersection of constraints' (IOC) (Adelson and Movshon 1982) yields the velocity consistent with a single rigidly translating surface, ie pattern motion. The stationary grating component is consistent with motion parallel to its orientation at any one of an infinite number of speeds. The real motion of the moving component is likewise constrained to be one of a subset of possible velocities, only one of which is consistent with that of the stationary grating. The velocity satisfying the constraints offered by both components is thus parallel to the orientation of the stationary component. It is worth noting that uni-kinetic plaids can be considered a special case of 'type II' plaids for which, unlike 'type I' plaids, pattern direction does *not* lie between the two component directions (eg Ferrera and Wilson 1990).[1]

On half of the trials, the stationary grating of the plaid was oriented vertically, while the other grating moved in a direction of 18.4° at 5.4 deg s^{-1} (see figure 1b). Here, the computed (IOC) pattern motion was 90.0° (upward) at 17.0 deg s^{-1}. The predicted component motion (ie the velocity orthogonal to the orientation of the moving grating) was 18.4° at 5.4 deg s^{-1}—this corresponds to the perceived direction of the grating when presented alone. We refer to this plaid configuration as '*pattern-up*'. On the other half of the trials, the plaid configuration was such that these component and pattern directions of motion were reversed. Here, the stationary component of the plaid was oriented 18.4° counterclockwise from horizontal, while the moving component drifted in a 90.0° direction at 5.1 deg s^{-1}. Thus, component motion was 90.0° at 5.1 deg s^{-1}, whereas resulting pattern motion was 18.4° at 16.1 deg s^{-1}. We refer to this plaid configuration as '*component-up*'. For both pattern-up and component-up plaids, pattern and component motions differed from each other in direction by 71.6° and by a factor of 3.2 in speed.

For comparison with our uni-kinetic procedure, bi-kinetic color plaid patterns were also employed for one subject (GS). Here, the two component gratings moved at 18.4° and 161.6°, at 5.4 deg s^{-1}. Resultant pattern motion was 90.0° (upward) at 17.0 deg s^{-1}. All other stimulus parameters and color configurations were identical to those employed for uni-kinetic plaids.

2.2.5 *Symmetric vs asymmetric plaids*. Two types of plaids were used, which differed with respect to the phase relationship between chromatic and luminance modulations. One type of plaid ('symmetric') was made from components that possessed identical chromatic/luminance phase relationships. In other words, both gratings were either

[1] The distinction between type I and type II plaids has been argued to be important because vector averaging and IOC computations yield appreciably different directional solutions for type II, but not for type I, plaids. The perceptions accompanying the two types of plaids may, it is suggested, provide insight into which type of computation the visual system employs (but see Stoner and Albright 1994). Because our uni-kinetic plaids possess only a single motion vector (ie that of the moving component), the vector average solution for coherent motion is the same as that predicted for noncoherent motion. This prediction, however, is inconsistent with the findings presented herein.

green-bright/red-dark [ie positive (+) luminance contrast] or both red-bright/green-dark [ie negative (−) luminance contrast]. We refer to these configurations as '+/+' and ' − /−', respectively. The second plaid type ('asymmetric') was made from components that had complementary phase relationships between chromatic and luminance modulations. That is, one grating was green-bright/red-dark and the other was red-bright/green-dark, or vice versa. We refer to these configurations as '+/−' and '−/+'. For our psychophysical and oculomotor experiments, the positive (+) and negative (−) contrast components of the plaids were set to be +30% and −30% luminance contrast, with respect to photometric (V_λ) isoluminance.

3 Experiment 1: psychophysics

The goal of our psychophysical experiments was to ascertain whether the previously demonstrated effects of color on motion coherence in bi-kinetic plaids extended to our *uni-kinetic* plaid design (see figure 1b and section 2). In addition, we wished to obtain psychophysical data for the purpose of comparison with oculomotor and neurophysiological data.

3.1 Methods

3.1.1 *Subjects.* Authors KD and GS participated in these psychophysical experiments. They also provided oculomotor data, which were obtained simultaneously with the perceptual data (see section 4.1). In addition, four naive subjects, blind to the purpose of the experiment, also provided psychophysical data. All subjects had normal or corrected-to-normal acuity and normal color vision, as assessed by the Ishihara Hue Test.

3.1.2 *Stimuli.* Uni-kinetic color plaids were presented foveally through a circular aperture subtending 22 deg in diameter. They were viewed from a distance of 60 cm through a darkened tunnel (60 cm long × 23.3 cm diameter), which was used to conceal stationary contours in the field of view. Stimuli consisted of both pattern-up and component-up plaids, under four different chromatic/luminance phase configurations (symmetric: +/+ and −/−; asymmetric: +/− and −/+). This resulted in eight different stimulus conditions, which were presented randomly across trials. For each condition 40 trials of data were collected (total trials = 320).

3.1.3 *Paradigm.* Each trial began with the appearance of a small spot (0.3 deg diameter) in the center of the screen, which the subject was instructed to fixate. Naive viewers were instructed to report *coherent* motion when a single plaid pattern appeared to move across the screen, and to report *noncoherent* motion when one grating appeared to slide across a second grating (subjects first received 160 trials of practice). Naive subjects began each trial with a key press, viewed the plaid stimulus for 1500 ms, and provided their perceptual report with a key press when the stimulus was extinguished.

For subjects GS and KD, for whom eye-movement data were also obtained, fixation was confirmed by magnetic-search-coil oculography (see section 4.1). When the subject had
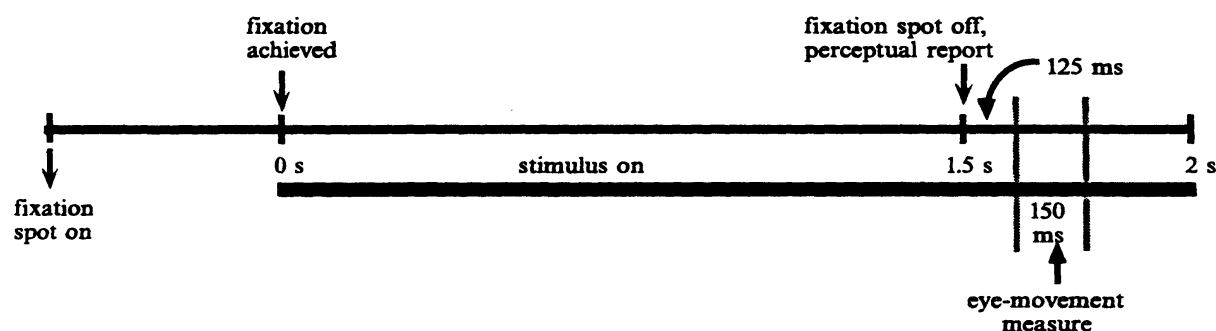
Figure 3. Temporal sequence of events during each trial. Perceptual reports were coincident with 'fixation spot off'. Eye movements were analyzed over a 150 ms epoch beginning 125 ms subsequent to 'fixation spot off'. (See text for details.)

fixated the spot for 666 ms, the plaid stimulus was presented for a duration of 2000 ms. The fixation spot was extinguished 1500 ms after stimulus onset at which point the subject provided a perceptual report by key press. Subjects based their decision on the period just prior to fixation off. During the last 500 ms of stimulus presentation, when fixation was unrestrained, the moving stimulus elicited tracking eye movements, which were analyzed off-line. A timeline depicting these events is shown in figure 3.

3.2 Results and discussion

For the purpose of comparison, subject GS was tested with bi-kinetic plaids. As expected, he consistently reported coherent motion for symmetric plaids (100% of trials, data not shown), and noncoherent motion for asymmetric plaids (100% of trials), confirming earlier reports that combined chromatic and luminance information influences perceptual motion coherence in bi-kinetic plaids (Kooi et al 1992; Farell 1995; Krauskopf et al 1996).

Six subjects were tested with uni-kinetic plaids, and their perceptual reports were similarly affected by the color configuration of the moving plaid. Psychophysical data obtained from the uni-kinetic condition are presented in table 1, separately for each subject as well as separately for each of the eight different plaid conditions. For all subjects, including naive viewers unaware of the purpose of the experiment, symmetric and asymmetric uni-kinetic color plaids produced predominantly coherent and noncoherent motion percepts, respectively.

Table 1. Percentage of trials judged to be perceptually coherent, for pattern-up and component-up moving color plaids. For all subjects, data are shown separately for the two types of *symmetric* plaids (+/+ and −/−) and the two types of *asymmetric* plaids (+/− and −/+). The symbol +/− refers to the case when the 'green brighter than red' component ('+' luminance contrast) moved, while the other component ('red brighter than green', ie '−' luminance contrast) was stationary. The symbol −/+ refers to the converse. Symmetric and asymmetric plaids elicited percepts of predominantly coherent and noncoherent motion, respectively.

Stimulus	Symmetric		Asymmetric		Symmetric		Asymmetric	
	+/+	−/−	+/−	−/+	+/+	−/−	+/−	−/+
	Subject KD				Subject GS			
Pattern-up	100	92.5	17.5	0	100	87.5	0	0
Component-up	100	100	2.5	0	100	100	0	0
	Subject CA (naive)				Subject DP (naive)			
Pattern-up	100	100	2.5	0	100	100	20	0
Component-up	97.5	100	7.5	7.5	95	97.5	2.5	0
	Subject AL (naive)				Subject KG (naive)			
Pattern-up	95	95	12.5	10	100	95	0	0
Component-up	95	100	77.5	0	100	95	15	0

3.2.1 *Luminance control.* It is known that achromatic gratings of sufficiently different luminance contrasts fail to cohere (Adelson and Movshon 1982). If the two selected red/green gratings of which our asymmetric plaid pattern was comprised did not contain equivalent luminance contrasts *perceptually*, the effects we observed could be due simply to differences in perceptual luminance contrast, rather than to the asymmetry of chromatic/luminance phase relationship between the two component gratings, as we have hypothesized.

To determine whether an error of this sort could account for the data obtained under asymmetric conditions, two subjects (GS and KD) were tested with a control in which plaid patterns consisted of achromatic (yellow/black) luminance-modulated gratings. The contrasts of the two luminance gratings were varied so as to simulate a range of possible luminance-contrast mismatches between the two components in our asymmetric red/green plaids. For both subjects, a difference of contrast greater than 40% between the two gratings (eg when one grating possessed 10% contrast and the

other grating possessed 50% contrast) was needed to produce the degree of noncoherence observed for asymmetric red/green plaids. In fact, differences as large as 10% still consistently produced a *coherent* motion percept. Because any misestimation of perceptual luminance equivalence for our subjects was extremely unlikely to have exceeded this amount, we feel confident that the noncoherent percept observed for asymmetric plaids was due to the different chromatic/luminance phase relationships of the two components, rather than luminance-contrast differences.

4 Experiment 2: oculomotor responses

Tracking eye movements and perceptual reports are very different types of behaviors. By looking for correlations between these two behaviors when engaged by common visual stimulation, we sought evidence for a common neural substrate. Previous studies of eye movement responses to moving plaids have employed *coherent* plaid patterns, with results suggesting a correspondence between oculomotor and perceptual responses (Manny and Fern 1990; Yo and Demer 1992; Harris et al 1993; Beutter and Stone 1996).

Here, we report oculomotor responses elicited by *noncoherent* moving plaids. In previous experiments, we have examined oculomotor responses using noncoherent bi-kinetic plaids, under a variety of conditions known to influence perceptual motion coherence, including variation along the dimensions of spatial frequency and luminance contrast, as well as manipulation of perceptual transparency. The results of these experiments suggested that eye movements are generally made in the pattern direction irrespective of the perceptual status of the moving plaid (Stoner, unpublished observations; see also Kooi et al 1992). However, because *two* component motions accompany the noncoherence of bi-kinetic plaids (figure 1a), the interpretation of eye movements elicited by these stimuli is problematic. At least two confounding possibilities exist: (i) the eyes, attempting to track both components, will move in an intermediate direction; or (ii) the eyes will alternate relatively rapidly between tracking one component and the other. If this switching occurs within the span of a single eye-movement measurement, the resulting measurement will also tend to an intermediate direction. Because, for bi-kinetic type I plaids, pattern direction is intermediate to the motion of both components, either of these possibilities could lead erroneously to the conclusion that perception and oculomotor tracking are differentially sensitive to manipulations of motion coherence. The uni-kinetic plaid, in which only one component grating moves, avoids these complications because both coherent motion and noncoherent motion are each associated with a *single* motion (see figure 1b).

4.1 *Methods*

4.1.1 *Magnetic-search-coil oculography.* As previously described, eye-movement data were collected coincidentally with the acquisition of perceptual data for two subjects (authors KD and GS), thus allowing for a comparison between the two behavioral responses. Eye movements were monitored by the technique of magnetic-search-coil oculography (Robinson 1963). Briefly, a search coil implanted within a soft annular contact was placed in the left eye, which had been anesthetized with Proparacaine HCl (0.5%) (see Collewijn et al 1975 for details).

Prior to data collection, eye-movement gain and position were calibrated with the use of software implemented on a PDP 11/73. For this purpose, fixation targets (0.3 deg diameter) were placed in five positions: at a central location, 5 deg above and below center, and 5 deg to the left and right of center. Eye position was continuously monitored while the subject fixated each of the five spots, and hardware controls (ie gain and offset) were adjusted to achieve calibration (error margin = ~0.5 deg).

4.1.2 *Paradigm.* Methods were as described for experiment 1, with the addition of the recording of the spontaneous eye movements elicited at the offset of fixation. Because

subjects based their perceptual judgments on the period just prior to fixation off, ie at the point just before the eyes moved, perceptual reports and oculomotor tracking were deemed to be based upon the same period of visual stimulation.

4.1.3 *Single moving gratings.* For reference, eye movements elicited by the single moving components of the uni-kinetic plaid were also obtained. Red/green gratings of +30% and −30% luminance contrast, moving in directions corresponding to 18.4° or 90.0° were employed (ie a total of four conditions, which correspond precisely to the moving components used to produce our uni-kinetic plaid stimuli). Grating speed was 5.4 deg s^{-1} and 5.1 deg s^{-1} for the 18.4° and 90.0° motion directions, respectively.

4.1.4 *Oculomotor data analysis.* At the end of the experiment, the direction and speed of tracking eye movements were computed for each trial. Eye movements were measured during the initial (ie open-loop) phase of oculomotor pursuit. This measurement interval, which began 125 ms after the offset of fixation and lasted 150 ms (see figure 3), was chosen to allow comparison of oculomotor and perceptual responses elicited by as near the same period of visual stimulation as possible. During this open-loop phase of pursuit, the eyes accelerate from a velocity of zero (ie fixation) and only approach target speed near the end of this phase. An unavoidable negative consequence is that measurements made over this period are somewhat noisy and yield a low speed relative to that of the moving target.

Individual eye-movement traces were visually inspected to exclude trials that contained saccades within this window of time (10.2% of the total trials for GS, 13.5% for subject KD). Eye-movement speed and direction were calculated separately for each trial. This was accomplished by software on the PDP 11/73 that calculated the horizontal and vertical components of the ocular displacements per unit time, and then computed the eye-movement speed in the direction of the eye movement.

While there did exist for subjects KD and GS a few trials on which asymmetric plaids were reported as 'coherent' and symmetric plaids were reported as 'noncoherent' (ie 0% for the bi-kinetic plaid condition and < 2.5% for the uni-kinetic plaid condition), these anomalous trials were too rare to permit any statistically useful conclusion. For that reason, we present the oculomotor data in terms of the *stimulus* type, ie symmetric and asymmetric, keeping in mind that these categories correspond, with few exceptions, to perceptual reports of coherent and noncoherent motion, respectively. In addition, because the percentage of trials judged to be perceptually coherent by subjects GS and KD was found to be nearly identical for the two types of symmetric plaids (+/+ and −/−), as well as for the two types of asymmetric plaids (+/− and −/+, see table 1), data obtained for the two conditions in each group have been pooled.

4.2 Results and discussion

4.2.1 *Oculomotor responses to single moving gratings.* Tracking-eye-movement responses elicited by single moving red/green gratings are shown in figure 4. Each data point represents the eye-movement vector (direction and speed) elicited from a single trial. Eye-movement data obtained for single red/green gratings were pooled across the two (+30% and −30%) luminance contrasts tested, for each of the two directions of motion. For both subjects, 18.4° gratings moving at 5.4 deg s^{-1} (filled circles) and 90.0° gratings moving at 5.1 deg s^{-1} (open squares) elicited distinctly different distributions of eye direction and speed.

Mean velocity vectors (GS: 60 trials/direction; KD: 40 trials/direction) are represented by the large open icons. For subject GS, mean eye-movement directions (2.6° and 111.5°) were displaced somewhat from stimulus directions (by 15.8° and 21.5° for the 18.4° and 90.0° conditions, respectively). This pattern of displacement was highly consistent for this subject and becomes relevant when interpreting eye movements
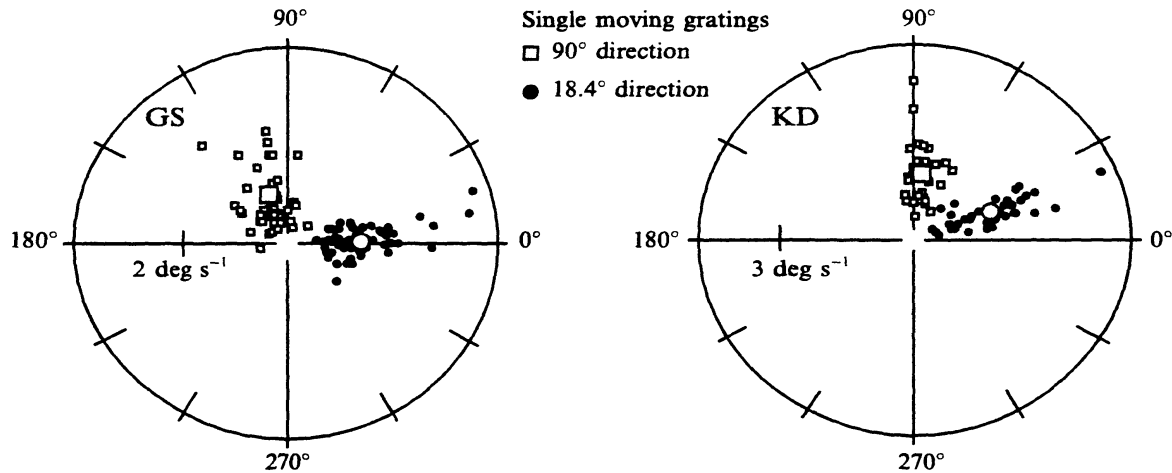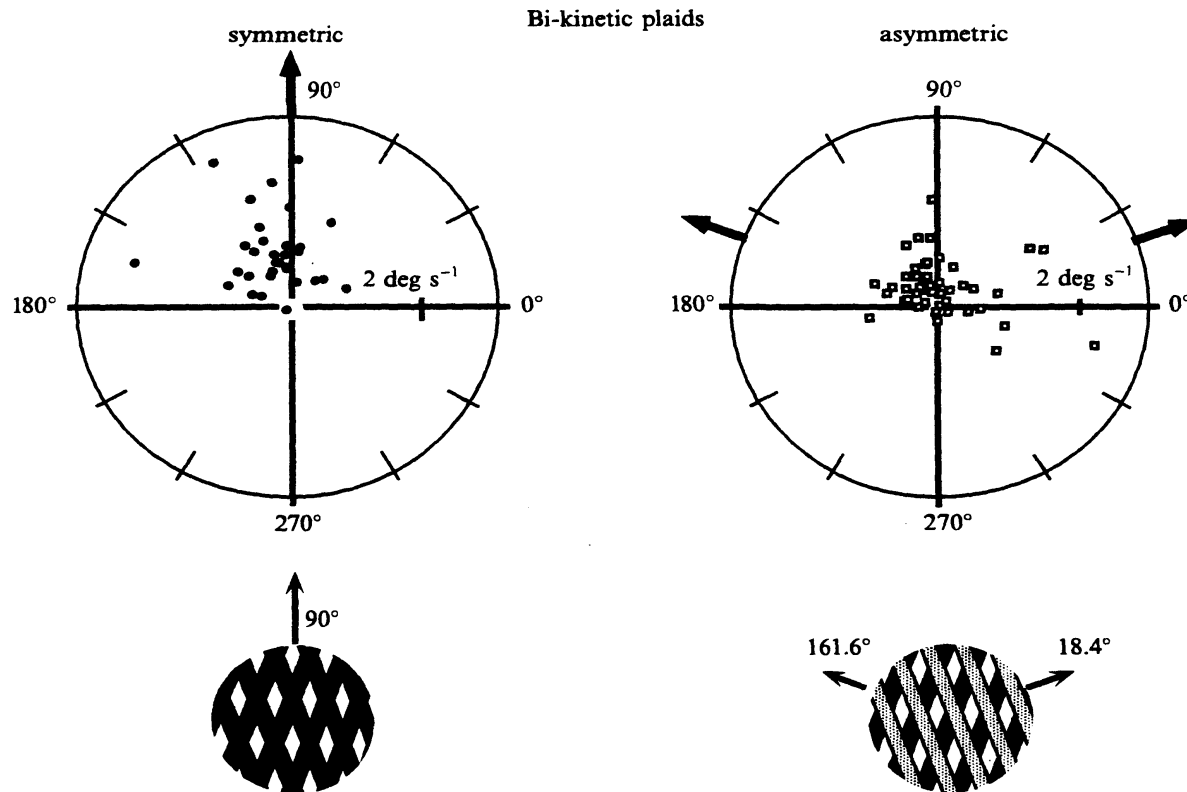
Figure 4. Oculomotor responses elicited by single red/green gratings. Gratings were either 'green brighter than red' (+30% luminance contrast) or 'red brighter than green' (−30% luminance contrast), moving in directions of 18.4° or 90.0°. Grating speed was 5.4 deg s^{-1} and 5.1 deg s^{-1} for the 18.4° and 90.0° conditions, respectively. Each data point represents the eye-movement vector (direction and speed) from a single trial (GS: 60 trials/direction; KD: 40 trials/direction). Mean vectors are represented by the large open icons. For subject GS, mean eye-movement directions (2.6° and 111.5°) elicited by the two gratings were displaced somewhat from the stimulus directions. For subject KD, mean directions (21.9° and 83.3°) were close to stimulus directions for the 18.4° and 90.0° conditions, respectively. For both subjects, 18.4° (filled circles) and 90.0° (open squares) gratings elicited distinctly different distributions of tracking eye movements, with virtually no overlap.

elicited by plaid patterns. Eye-movement speeds for subject GS were 1.5 deg s^{-1} and 1.0 deg s^{-1} for the 18.4° and 90.0° conditions, respectively. For subject KD, mean tracking directions (21.9° and 83.3°) were close to stimulus motion directions, and speeds were 1.9 deg s^{-1} and 1.7 deg s^{-1} for the 18.4° and 90.0° conditions, respectively. Note that, as described in section 4.1, these speeds are predictably low relative to that of the grating owing to their being measured during the open-loop phase of pursuit.

4.2.2 *Oculomotor responses to bi-kinetic plaids.* Noncoherent motion of bi-kinetic plaids yields a percept of two gratings sliding across one another. One might expect, therefore, that the associated eye movements would be bimodal. In previous experiments, however, this result was not observed. Rather, eye movements were typically observed in the pattern direction (Stoner, unpublished observations; see also Kooi et al 1992). Figure 5, which illustrates this pattern of results, shows eye movements evoked by symmetric and asymmetric bi-kinetic plaids for subject GS. Each point represents the eye-movement velocity from a single trial (total trials = 80). No obvious bimodality can be seen for asymmetric plaids. Thus, while GS's perceptual reports indicated two gratings sliding noncoherently across one another, his oculomotor responses did not. For reasons outlined above, however, the fact that there are two motions associated with noncoherent bi-kinetic plaids makes the apparent dissociation between perceptual and oculomotor responses difficult to interpret.

4.2.3 *Oculomotor responses to uni-kinetic plaids.* Tracking eye movements elicited by symmetric and asymmetric uni-kinetic plaids are shown for pattern-up plaids in figure 6a. Here, the stationary grating was vertically oriented, while the other grating moved in a 18.4° direction at 5.4 deg s^{-1}, resulting in 90.0° pattern motion at 17.0 deg s^{-1}. Bold arrows in the figure indicate predicted pattern (based on IOC) and component directions. For subject GS tested with symmetric plaids, the mean eye-movement vector was 71.7°, 1.6 deg s^{-1} (large open circle, left). For asymmetric plaids, subject GS's mean vector was 9.1°, 0.6 deg s^{-1} (large open square, right). For subject KD tested with symmetric plaids, the mean eye-movement vector was 71.3°, 2.1 deg s^{-1}. For asymmetric

Figure 5. Oculomotor responses elicited by conventional bi-kinetic plaids for one subject (GS). These data were collected coincidentally with the acquisition of psychophysical data. The two component gratings moved in directions of 18.4° and 161.6°, each at 5.4 deg s^{-1}, yielding upward (90.0°) pattern motion at 17.0 deg s^{-1}. Predicted pattern direction (based on intersection of constraints, IOC) and component direction (based on velocity of moving component) are marked by arrows on polar plots. As was the case for psychophysical data, we pooled the oculomotor data associated with the two types of symmetric plaids ($+/+$ and $-/-$) and the two types of asymmetric plaids ($+/-$ and $-/+$).

Each data point represents the eye-movement vector (direction and speed) from a single trial (total trials = 80). Despite the fact that the subject reported noncoherent motion for asymmetric plaids, his eyes moved in a direction close to the pattern direction (ie mostly upward). Because this result may be an unavoidable consequence of tracking bidirectional stimulus, we adapted unidirectional ('uni-kinetic') plaids for the remainder of our analyses.

plaids, her mean vector was 55.2°, 1.9 deg s^{-1}. For both subjects, eye movements elicited by symmetric vs asymmetric plaids yielded clearly separate distributions as demonstrated by Hotelling's two-sample test ($p < 0.001$; see Batschelet 1980).

For component-up plaids (figure 6b), the stationary grating was oriented 18.4° counterclockwise from horizontal, while the other grating moved in a 90.0° direction at 5.1 deg s^{-1}, resulting in 18.4° pattern motion at 16.1 deg s^{-1}. For subject GS, the mean eye-movement vector for symmetric plaids was 23.0°, 2.6 deg s^{-1}. For asymmetric plaids, subject GS's mean vector was 30.9°, 0.6 deg s^{-1}. For subject KD, the mean vector for symmetric plaids was 50.8°, 1.8 deg s^{-1}. For asymmetric plaids, the mean vector was 60.8°, 1.6 deg s^{-1}. Thus, for both subjects, the directional differences associated with coherence/noncoherence were reduced for the component-up plaids as compared to the pattern-up plaids. Nevertheless, the distributions of eye movements elicited by symmetric vs asymmetric component-up plaids were found to have distinctly different centers for both subjects (Hotteling's two-sample test, $p < 0.001$).

These findings demonstrate a correlation between smooth tracking eye movements and perceptual state and hence imply that one might be used to infer the other. The strength and potential utility of such inferences, however, depends both upon the

subject and the stimulus. The distinct eye-movement clusters formed when subject GS viewed pattern-up plaid patterns, for example, suggest that stimulus type (and hence percept) could fairly reliably be predicted from a single eye movement. The reliability of classifying individual eye movements, while potentially still useful, would be less for subject GS viewing component-up plaids. For subject KD viewing component-up plaids, individual trials have little predictive value. The likelihood of a particular perceptual state might nonetheless be inferred from population statistics.

It is noteworthy that neither subject exhibited eye movements in the directions corresponding to the predicted (IOC) pattern direction or the predicted component direction (bold arrows in figure 6). Table 2 presents the mean eye-movement directions in comparison to predicted directions for uni-kinetic plaids, as well as for single moving gratings. For subject GS, this discrepancy might partially be accounted for by differential pursuit gain along the horizontal and vertical axes, as can be witnessed in his single-moving-grating data (see table 2 and figure 4). This explanation is not generally applicable as evidenced by the observation that the eye movements elicited by single moving gratings were nearly veridical for subject KD (average misalignment ~5°, see figure 4). Other possibilities are addressed further in section 6.

In sum, our observation that both oculomotor and perceptual responses differentiate for coherent vs noncoherent conditions suggests that they may arise from common neural mechanisms. On a more practical note, our oculomotor technique may allow us to infer perceptual motion coherence from eye movements in laboratory animals, as obtaining a measure of perceptual motion coherence from monkeys via operant conditioning is an onerous task.

Table 2. Predicted directions (D_{pred}), mean eye-movement directions (D_{eye}), and the difference between the two ($D_{pred} - D_{eye}$), for subjects GS and KD. Predicted stimulus direction for *symmetric* conditions, which elicit coherent pattern motion, is determined from the 'intersection of constraints' (IOC). Predicted direction for *asymmetric* conditions, which elicit noncoherent component motion, is the direction of the moving component. Data have been pooled for the two types of symmetric (+/+ and −/−) and the two types of asymmetric (+/− and −/+) conditions.

Stimulus	$D_{pred}/°$	Subject KD		Subject GS	
		$D_{eye}/°$	$(D_{pred} - D_{eye})/°$	$D_{eye}/°$	$(D_{pred} - D_{eye})/°$
Grating 18.4°	18.4	21.9	−3.5	2.6	15.8
Grating 90°	90.0	83.3	6.7	111.5	−21.5
Pattern-up					
symmetric	90.0	71.3	18.7	71.7	18.3
asymmetric	18.4	55.2	−36.8	9.1	9.3
Component-up					
symmetric	18.4	50.8	−32.4	23.0	−4.6
asymmetric	90.0	60.8	29.2	30.9	59.1

5 Experiment 3: responses of MT neurons

It has previously been shown that a subset of MT neurons respond selectively to the motion of plaid patterns (Movshon et al 1985; Rodman and Albright 1989), and that this selectivity is affected by stimulus manipulations that influence perceptual motion coherence (Stoner and Albright 1992). In order to investigate whether MT neurons are influenced by color plaids in a fashion that mirrors the perceptual and oculomotor results presented above, we recorded the responses of MT neurons elicited by symmetric and asymmetric moving plaid patterns, in an awake fixating monkey. Although neither perceptual nor oculomotor responses were obtained from this monkey (spontaneous

(a) Uni-kinetic ('pattern-up') plaids
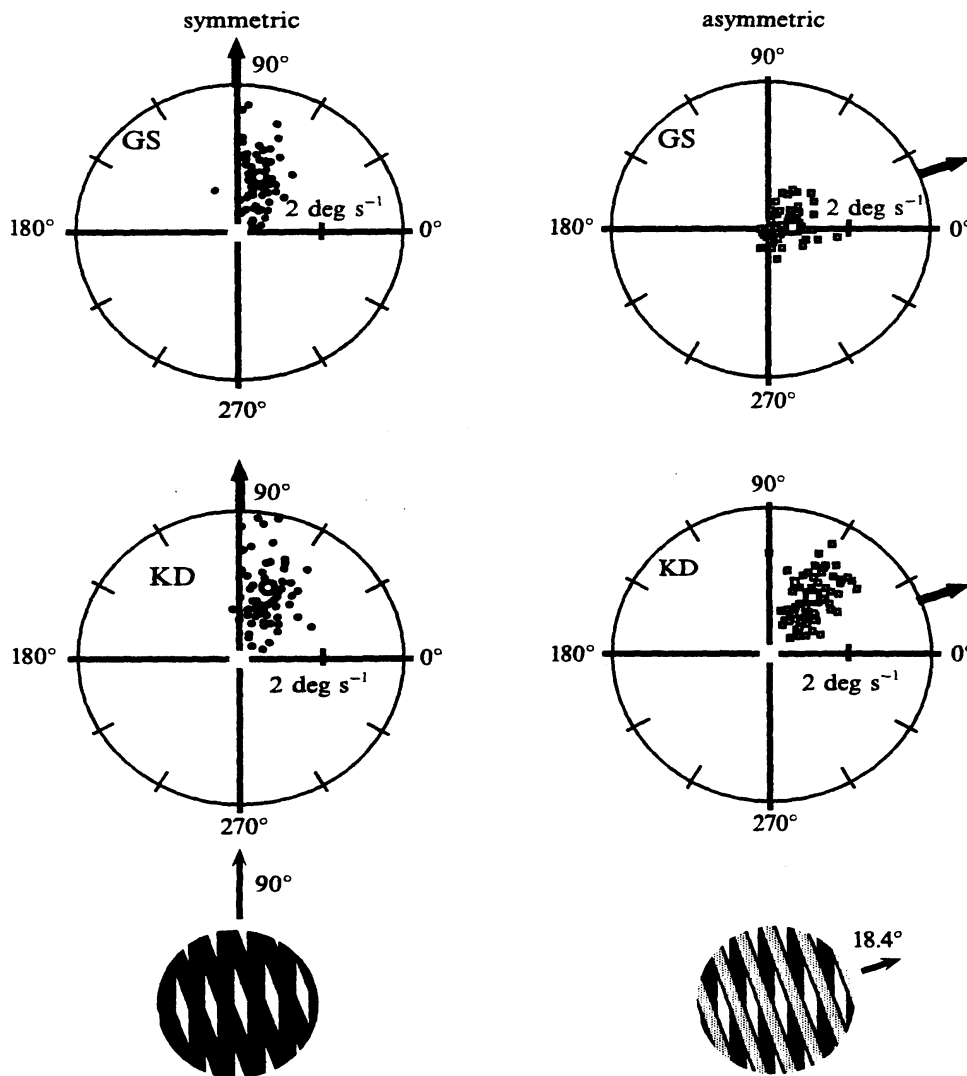
Figure 6. Oculomotor responses elicited by symmetric and asymmetric uni-kinetic plaids.

(a) 'Pattern-up' plaids. For subject GS, the mean eye-movement vector was 71.7°, 1.6 deg s^{-1} for symmetric plaids (large open circle, left) and 9.1°, 0.6 deg s^{-1} for asymmetric plaids (large open square, right). For subject KD, the mean eye-movement vector was 71.3°, 2.1 deg s^{-1} for symmetric plaids and 55.2°, 1.9 deg s^{-1} for asymmetric plaids. For both subjects, tracking eye movements elicited by symmetric vs asymmetric plaids yielded clearly separate distributions (Hotelling's two-sample test; $p < 0.001$). Predicted pattern and component directions are marked by arrows on polar plots.

eye movements could not be elicited owing to the fact that stimuli were not foveally placed, see section 5.1.5), we predicted that symmetric and asymmetric plaids would have differential effects on the responses of MT neurons, as the two stimulus types are highly correlated with coherent and noncoherent motion reports, respectively, in humans. Specifically, we expected to find that neuronal responses to component motion in the preferred direction would be greater for asymmetric plaids than for symmetric plaids. Conversely, we predicted that neuronal responses to pattern motion in the preferred direction would be greater for symmetric plaids than for asymmetric plaids.

(b) Uni-kinetic ('component-up') plaids
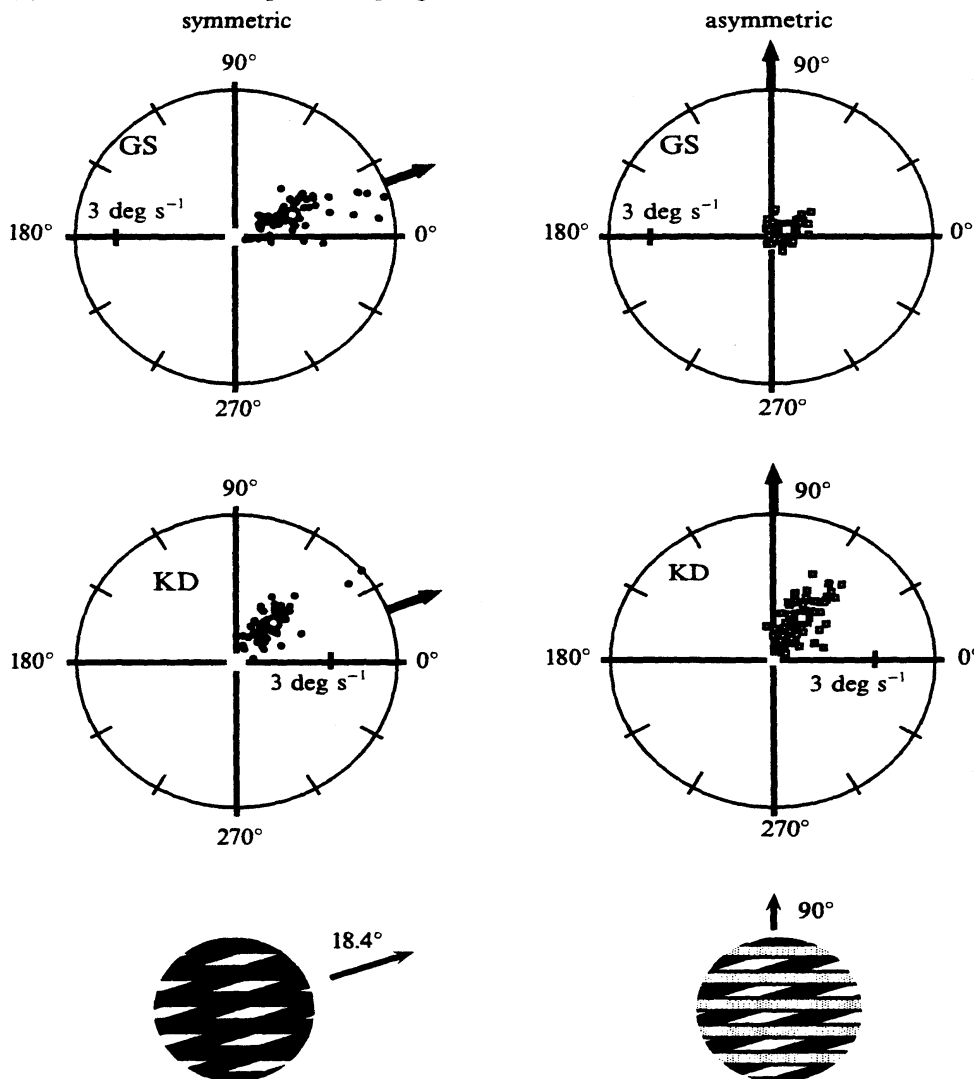
Figure 6 (continued)

(b) 'Component-up' plaids. For subject GS, the mean vector was 23.0°, 2.6 deg s⁻¹ for symmetric plaids and 30.9°, 0.6 deg s⁻¹ for asymmetric plaids. For subject KD, the mean vector was 50.8°, 1.8 deg s⁻¹ for symmetric plaids and 60.8°, 1.6 deg s⁻¹ for asymmetric plaids. Thus, for both subjects, the directional differences associated with coherence/noncoherence were much reduced for the component-up plaids as compared to the pattern-up plaids. Nevertheless, symmetric and asymmetric plaids yielded clearly separate clusters for subject GS. Furthermore, despite the lack of clear separation for subject KD, the eye movements elicited by symmetric vs asymmetric component-up plaids were found to have distinctly different centers (Hotelling's two-sample test; $p < 0.001$).

5.1 Methods

Detailed methods for animal preparation and electrophysiology have been described previously (Dobkins and Albright 1994) and are briefly summarized below.

5.1.1 *Subjects.* One female rhesus monkey (*Macaca mulatta*) was used for this study. The neurons from which we recorded were studied during the course of another experiment. Our protocols have been approved by the Salk Institute Animal Care and Use Committee and they conform to USDA regulations and NIH guidelines for the humane care and use of laboratory animals.

5.1.2 *Surgical preparation.* The monkey was surgically prepared by conventional techniques for training and physiological recording. Two stainless-steel recording cylinders and a post for head restraint were affixed to the skull with dental acrylic and stainless-steel screws. Cylinders were positioned bilaterally over parietal lobe regions (centered at approximately AP: −4 mm, ML: 17 mm). A search coil for measuring eye position (Cooner Wire Co) was surgically implanted in one eye by the method described by Judge et al (1980). The leads of the coil were soldered to a 2-pin miniconnector (Powell Electronics) and affixed to the cranial implant with dental acrylic. One week prior to the first neurophysiological recording session, one of the recording cylinders was opened and an 8 mm diameter hole was drilled through the skull to allow electrode passage into area MT.

5.1.3 *Behavioral training.* The monkey was trained to fixate a small (0.3 deg diameter) spot of light on the video display in the presence of moving visual stimuli for the duration of each trial (up to 3 s). Head movements were prevented by bolting the implanted post to the frame of the primate chair. Performance on the fixation task was monitored by continuously recording eye position by the magnetic-search-coil technique (Robinson 1963). Upon successful completion of a trial, the animal was given a small (approximately 0.15 ml) juice reward.

5.1.4 *Electrophysiological recordings.* Paralyene-coated tungsten microelectrodes with exposed tips of 10 μm or less were used to record extracellular potentials from single isolated neurons. Electrodes were lowered into the brain through a stainless-steel guide-tube by way of a hydraulic microdrive. Level of spontaneous activity, receptive field size, position relative to sulci, and degree of selectivity for direction of motion were all criteria used to establish that our recordings were from area MT.

Once an MT neuron was isolated, its receptive field was mapped and directional selectivity assessed with the aid of a high-contrast luminance-defined bar (85 cd m^{-2} on a background of <1 cd m^{-2}). The neuron was then presented with different color stimuli, each for a total duration of 1.5 s.

5.1.5 *Stimuli.* We adapted the stimuli used in the psychophysical and oculomotor experiments for use in our neurophysiological experiments. Stimuli that subtended 10 deg of visual angle were aligned with the geometric center of the receptive field for each neuron studied. The stimuli were configured so that either pattern or component motion was in the neuron's preferred direction. The luminance contrasts of the two types of color gratings (red-bright/green-dark and green-bright/red-dark) were chosen to elicit equivalent neuronal responses (see below). All neurons were tested both with single moving gratings and with uni-kinetic plaid patterns.

5.1.6 *Finding gratings with equal and opposite luminance contrast.* We predicted differential tuning for symmetric vs asymmetric plaids. Such a result could be obtained if the two different components of the asymmetric plaid were to elicit (when presented individually) different levels of response from the neuron under study. This pattern of results is, in fact, implied by the *channel model*. As part of our strategy to exclude this as a possible explanation, we attempted to equate the components used to test each neuron. Thus, asymmetric plaids were tailored for each neuron, composed of two red/green gratings of equal and opposite luminance contrast that individually yielded the same neuronal response. To this end, each neuron was first presented with a single red/green grating moving in its preferred direction. Responses from the neuron were collected for eight different red/green luminance contrasts of the grating, varied in equal (8%) intervals from −32% (red brighter than green) to +24% (green brighter than red).

A smooth curve was fit to the response of the neuron as a function of red/green luminance contrast (by linearly interpolating between data points and convolving the interpolated curve with a Gaussian, sd = 2.3%), and the luminance contrast yielding the minimum in the curve was provisionally defined as the *neural* isoluminance point (see Dobkins and Albright 1994). From this, luminance contrasts that were neuronally 'equivalent' but of opposite polarity were selected by adding to and subtracting from neural isoluminance a specified amount of luminance contrast (eg if the isoluminance point was determined to be −8%, adding and subtracting 24% luminance contrast would yield +16% and −32% luminance-contrast red/green gratings).

In some cases, however, it was difficult to obtain a clear estimate of the neural isoluminance point by this procedure (ie in cases where a neuron did not exhibit a clear minimum). In these cases, we used luminance-contrast values closer to those used in our psychophysical and oculomotor experiments, and our only criterion was that the two different red/green gratings (of + and − luminance contrast) elicited equal responses from the neuron (see below).

5.1.7 Directional tuning curves for the equal and opposite red/green gratings.

Once the two red/green gratings were chosen, we collected neural responses elicited by motion of each of the two gratings in three different directions: the neuron's preferred direction, and +71.6° and −71.6° away from the preferred direction. This manipulation allowed us to confirm that the two selected red/green gratings elicited equivalent directional tuning and overall responsiveness. In addition, the directions in which these single gratings moved correspond to those of the component and pattern motions elicited under the uni-kinetic plaid condition (see below).

5.1.8 Responses to uni-kinetic color plaid patterns.

Neurons were next presented with uni-kinetic plaids, composed of the two selected red/green gratings. Plaids were moved such that either the pattern or the component direction corresponded with the neuron's preferred direction. When the plaid was oriented such that the pattern moved in a neuron's preferred direction, component motion was 71.6° away. Likewise, when the component moved in the preferred direction, pattern motion was 71.6° away from the preferred direction. Component and pattern speeds were identical to those employed in the psychophysical and oculomotor experiments (component motion = 5.1 or 5.4 deg s⁻¹; pattern motion = 16.1 or 17.0 deg s⁻¹). Each neuron was tested under four different color configurations of the uni-kinetic plaid (+/+, −/−, +/−, and −/+), at two different orientations of the plaid. Note that the two plaid orientations employed are analogous to the pattern-up and component-up plaids employed in our psychophysical and oculomotor experiments, although they did not necessarily correspond to component motion at 18.4° and 90.0° (because of the added constraint of alignment of directions with neuronal direction preferences).

5.1.9 Data analysis.

The measure of response was the mean firing rate (spikes s⁻¹) averaged over 5 trials of stimulus presentation (stimulus duration = 1.5 s). As was the case for our psychophysical and oculomotor experiments, data were analyzed by combining the responses to the two types of symmetric plaids (+/+ and −/−) and the two types of asymmetric plaids (+/− and −/+).

In order to quantify how well each neuron responded to pattern vs component motion in its preferred direction, a pattern/component ratio, P/C, was calculated (P/C = mean response elicited by motion of the *pattern* in the preferred direction/mean response elicited by motion of the *component* in the preferred direction), separately for symmetric vs asymmetric plaids. P/C ratios greater than 1.0 indicate that pattern motion responses were greater than component motion responses, while ratios lower than 1.0 indicate the converse.
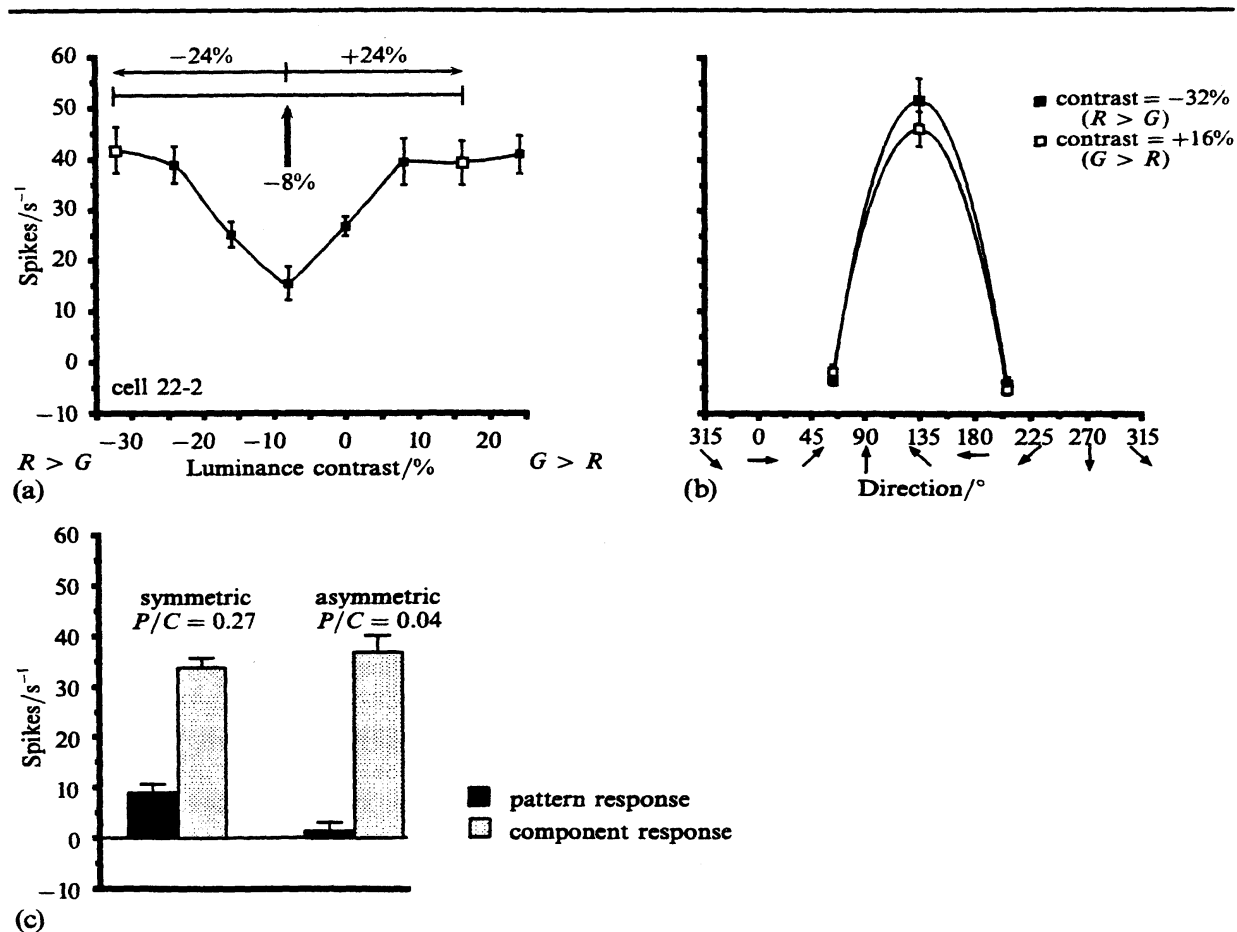
Figure 7. Data from an MT neuron presented with symmetric and asymmetric color plaids. The neuron's receptive field was centered 10° from the center of the gaze in the upper contralateral quadrant. Direction preference was up and to the left (135°, by our convention).

(a) Responses of the neuron to single gratings moving in the preferred direction, at eight different red/green luminance contrasts. Error bars denote standard errors of the means. The contrast yielding a minimal response, in this case −8% contrast, was considered to be the neural iso-luminance point. Thus, −32% and +16% were considered to be equivalent (each 24% away from the neural isoluminance point), and were selected to make up the components of the plaid.

(b) Responses of the neuron tested with both −32% and +16% red/green gratings moving in the preferred direction (135°) and at 71.6° away (at 63.4° and 206.6°). The tuning and overall responsiveness were essentially identical for the two red/green gratings, demonstrating that, on the basis of these criteria, the neuron could not distinguish between the two (paired t-tests: 63.4°: $t = 0.7$, ns; 135°: $t = 1.0$, ns; 206.6°: $t = 0.9$, ns).

(c) Responses of the neuron to uni-kinetic color plaids constructed such that pattern and component motions moved at 135° and 202.6°, or vice versa. As for psychophysical and oculomotor data, we pooled the neural responses elicited by the two types of symmetric plaids (+/+ and −/−) and the two types of asymmetric plaids (+/− and −/+). Dark bars illustrate the response of the neuron to pattern motion in the preferred direction, whereas gray bars show the response to component motion in the preferred direction. Standard errors are shown for all conditions. For symmetric plaids, the neuron responded better to component than to pattern motion, resulting in a P/C ratio of 0.27. When the plaid was asymmetric, the neuron's response to pattern motion diminished, while its response to component motion increased, resulting in a shift in the P/C ratio to 0.04. Thus, in comparison to the symmetric condition, under the asymmetric condition the neuron became more responsive to component motion in its preferred direction.

5.2 Results and discussion

We tested a total of seven MT neurons. Data from one MT neuron are shown in figure 7. The receptive field center of the neuron was 10° eccentric to fixation, in the upper contralateral field. Direction preference was up to the left (135°, by our convention). When tested with a moving (5.1 deg s^{-1}) red/green grating ranging in luminance contrast from −32% to 24%, a minimal response was observed at −8% contrast, which we provisionally defined as the neural isoluminance point (figure 7a). Thus, the two gratings selected to make up the components of the plaid were −32% and +16%. These two values are each 24% away from the neuronal isoluminance point, and elicited indistinguishable responses ($t = 0.45$, ns) from the neuron (figure 7a, open squares).

The same neuron was then tested with both −32% and +16% red/green gratings moving in the preferred direction (135°) and at 71.6° away (ie at 63.4° and 206.6°). This neuron demonstrated sharp directional tuning (figure 7b). Moreover, the tuning and overall responsiveness were essentially identical for the −32% and +16% red/green gratings, demonstrating that, on the basis of these criteria, the neuron could not distinguish between the two (paired t-tests—63.4°: $t = 0.7$, ns; 135°: $t = 1.0$, ns; 206.6°: $t = 0.9$, ns). These two red/green gratings thus made up the components of the plaid pattern.

Plaids were constructed such that pattern and component motions occurred at 135° and 202.6°, or vice versa. The responses of the neurons to motion of the uni-kinetic plaid under symmetric (+/+, −/−) and asymmetric (+/−, −/+) conditions are shown in figure 7c. Dark bars illustrate the response of the neuron to pattern motion in the preferred direction, whereas gray bars show the response to component motion in the preferred direction. For symmetric plaids, the neuron responded better to component than pattern motion, resulting in a P/C ratio of 0.27, and could thus be loosely classified as a 'component' neuron. When the plaid was asymmetric, however, the neuron's response to pattern motion diminished significantly ($t = 3.02$, $p < 0.005$), while its response to component motion increased slightly, resulting in a large shift in the P/C ratio to 0.04. Thus, in comparison to the symmetric condition, under the asymmetric condition the neuron became more responsive to component motion in its preferred direction, a result which mirrors the noncoherence of asymmetric plaids observed perceptually.

Data from another MT neuron are shown in figure 8. The receptive field center of this neuron was 8.5° eccentric to fixation, in the upper contralateral field. Preferred direction of motion was leftward (ie 180°). Red/green gratings of −32% and +10% luminance contrast were chosen for this neuron, as they elicited equal responses from the neuron ($t = 0.9$, ns). This is demonstrated in figure 8a, which presents the responses to motion of the −32% and +10% contrast gratings in the preferred direction (180°) and at 71.6° away (108.4° and 251.6°). These two chromatic gratings (−32% and 10%) thus made up the components of the plaid pattern for this neuron.

When tested with uni-kinetic plaids, directions were 180° and 108.4°, or vice versa. The responses to the motion of the plaid under symmetric and asymmetric conditions are shown in figure 8b. For symmetric plaids, the neuron responded better to pattern than to component motion, resulting in a P/C ratio of 1.31, and could thus be loosely classified as a 'pattern' neuron. When the plaid pattern was asymmetric, however, the response to pattern motion diminished dramatically ($t = 3.47$, $p < 0.005$), and the P/C ratio fell to 0.71. This neuron was also re-tested with the use of a larger luminance-contrast difference between the two gratings (−32% and +32%). In this case, the effect was even stronger: the P/C ratio was 1.63 for symmetric plaids and 0.64 for asymmetric plaids. Thus, the responses of this neuron were remarkably similar to those observed in psychophysical and oculomotor experiments, ie pattern motion dominated under symmetric conditions, while component motion dominated under asymmetric conditions.
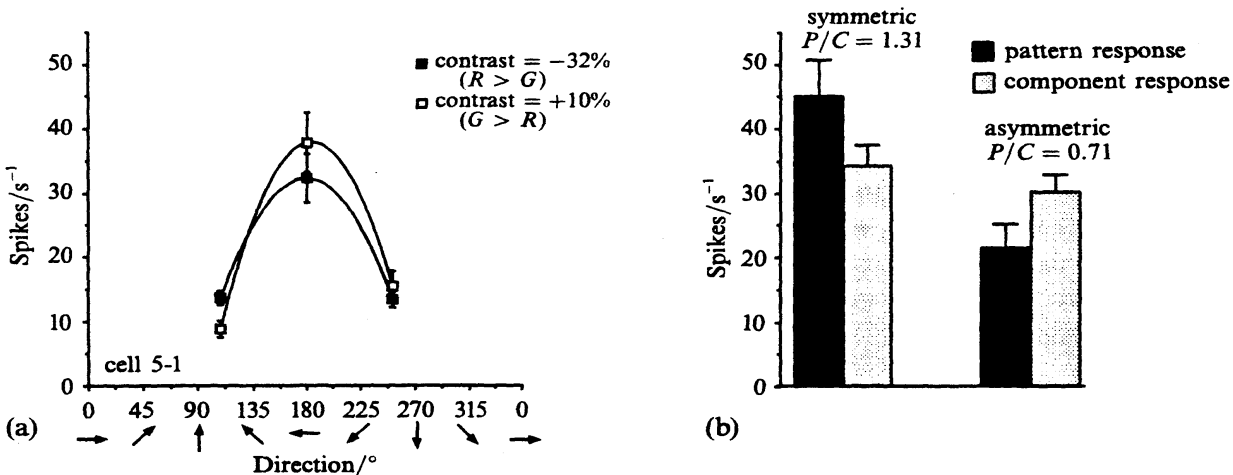
Figure 8. Data from another representative MT neuron. This neuron's receptive field center was 8.5° eccentric to fixation, in the upper contralateral field. Preferred direction of motion was leftward (180°, by our convention).

(a) Chromatic red/green gratings of −32% and +10% luminance contrast were chosen for this neuron, as they elicited equal responses from the neuron when presented in the preferred direction, ie at 180° ($t = 0.9$, ns). Directional tuning was determined by testing in the preferred direction and at 71.6° away (at 108.4° and 251.6°). As for motion in the preferred direction, equal responses for −32% and +10% gratings were observed in the 251.6° direction ($t = 0.8$, ns). At 108.4°, a significant difference was found only if a Bonferonni adjustment was not applied ($t = 2.9$, $p = 0.025$). These two red/green gratings (−32% and 10%) made up the components of the plaid pattern for this neuron.

(b) Responses of the neuron to uni-kinetic color plaids, constructed such that pattern and component motions occurred at 180° and 108.4°, or vice versa. For symmetric plaids, the neuron responded better to pattern than to component motion, resulting in a P/C ratio of 1.31. When the plaid pattern was asymmetric, however, the response to pattern motion diminished dramatically, and the P/C ratio fell to 0.71.

Figure 9a presents the P/C ratios for the seven neurons tested, under both symmetric and asymmetric conditions. P/C ratios greater than 1.0 indicate that neural responses were greatest for pattern motion in the preferred direction. Likewise, P/C ratios less than 1.0 indicate that responses were greatest for component motion. Negative P/C ratios indicate that pattern motion in the preferred direction actually *inhibited* the neuron.

Five out of the seven neurons tested exhibited lower P/C ratios under asymmetric (+/−, −/+) compared to symmetric (+/+, −/−) conditions. The two remaining neurons (11-4 and 14-7, see figure 9a) did not show such an effect as they exhibited no response to pattern motion. It is interesting to point out that some neurons became inhibited by pattern motion under asymmetric conditions (eg neuron 10-3), while others, which were inhibited by pattern motion in their preferred direction under symmetric conditions, became even *more* inhibited by pattern motion under asymmetric conditions (eg neuron 10-1).

In order to directly examine the influence of color configuration on pattern vs component responses, the P/C ratio obtained for asymmetric plaids has been plotted against the P/C ratio obtained for symmetric plaids, separately for each of the seven neurons, in figure 9b. If neurons were unaffected by the color configuration of the plaid, data points would fall along the diagonal line. The fact that our data points fall largely on one side of the diagonal demonstrates that symmetric vs asymmetric plaid patterns differentially affect neural responses ($t = 2.96$, $p < 0.05$).

In sum, regardless of whether a neuron responded better to pattern or component motion in the symmetric condition, on the whole neurons became relatively more responsive to component motion under asymmetric conditions. These neurophysiological
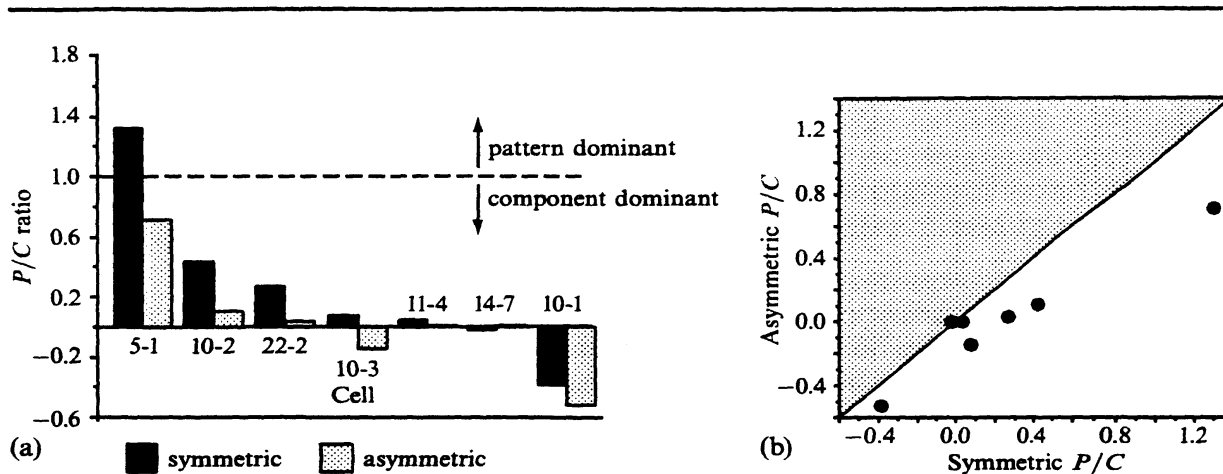
Figure 9. (a) P/C ratios for both the symmetric and asymmetric conditions tested in seven MT neurons. P/C ratios greater than 1.0 indicate that neural responses were greatest for pattern motion in the preferred direction. Likewise, P/C ratios less than 1.0 indicate that responses were greatest for component motion. Negative P/C ratios indicate that pattern motion in the preferred direction inhibited the neuron. In general, P/C ratios were smaller for asymmetric than for symmetric plaids.

(b) The P/C ratio obtained for symmetric plaids plotted against the P/C ratio obtained for asymmetric plaids, separately for each of the seven neurons. If neurons are unaffected by the color configuration of the plaid, data points would fall along the diagonal line. The fact that our data points fall largely on one side of the diagonal demonstrates that symmetric vs asymmetric plaid patterns differentially affect neural responses ($t = 2.96$, $p < 0.05$). In sum, regardless of whether a neuron responded better to pattern or component motion in the symmetric condition, on the whole neurons became relatively more responsive to component motion in the asymmetric condition.

data thus mirror the perceptual as well as oculomotor phenomena reported above. While the scope of our conclusion regarding MT neurons is limited by the small sample size, our results are nonetheless robust and statistically significant, indicating that the specific way in which chromatic and luminance contrast are combined can affect the neural integration of motion signals.

6 General discussion

Our results demonstrate the influence of color on motion coherence in three domains: perceptual, oculomotor, and neurophysiological responses. In psychophysical experiments, we found that symmetric plaids produce a percept of coherent motion. By contrast, we found that asymmetric plaids produce a percept of noncoherent motion. These findings are in line with previous observations regarding the role of component similarity in motion coherence, and further confirm more recent findings that stimuli modulated along the noncardinal axes of color space can be configured to produce noncoherent motion (eg Kooi et al 1992; Farell 1995; Krauskopf et al 1996). The results from our oculomotor experiments demonstrate that, under many conditions, smooth tracking eye movements elicited by symmetric vs asymmetric plaids are distinguishable from one another. The general similarity of these results to those obtained from our psychophysical studies suggests the existence of common neural mechanisms underlying the perceptual and oculomotor responses. In addition, this finding has implications for the feasibility of inferring perceptual states in animal subjects via eye movements. Finally, in our neurophysiological experiments we found that symmetric and asymmetric plaids elicit differential responses in individual MT neurons. These results are consistent with our earlier findings implicating area MT in the selective integration of moving image features (Stoner and Albright 1992; Duncan et al 1995) and further demonstrate that MT neurons have access to information about stimulus color.

In the remainder of this discussion we address three aspects of these results. First, we discuss the relationship between the observed perceptual and oculomotor responses. Second, we address the hypothesized role of area MT in motion signal integration. Finally, we discuss potential neural mechanisms underlying the noncoherence of color plaids and the implications for interactions between 'color' and 'motion' processing streams in the primate visual system.

6.1 Do oculomotor responses reflect perception?

Several previous studies have used plaid patterns to investigate the concordance between direction of smooth tracking eye movements and perceived direction in moving plaid patterns (Manny and Fern 1990; Yo and Demer 1992; Harris et al 1993; Beutter and Stone 1996). All of these studies employed bi-kinetic luminance-modulated plaids, for which conditions were set to yield a *coherent* plaid pattern percept. For type I plaids (ie where the pattern direction lies in between the two component directions), eye movements reliably follow the predicted pattern direction (Manny and Fern 1990; Yo and Demer 1992; see Beutter and Stone 1997 for use of a related diamond stimulus). For type II plaids (ie where the pattern direction does *not* lie in between the two component directions), however, eye movements are not precisely in the direction predicted by the IOC solution (Yo and Demer 1992; Harris et al 1993).

We wished to extend the search for a correlation between eye movements and perception to include *noncoherently* moving plaids. In our combined psychophysical/oculomotor experiments, in which subjects were asked to report only coherence vs noncoherence, we discovered that eye movements were not precisely aligned with the directions predicted for either component or pattern motions (see figures 6a and 6b, and table 2). The discrepancy between the predicted and oculomotor directions does not, by itself, imply that *perception* and eye movements are incongruent, however. Indeed, it is well-documented that the perceived direction of motion for coherently moving plaids can deviate from the IOC prediction (Ferrera and Wilson 1990; Yo and Wilson 1992; Harris et al 1993; Bowns 1996; Alais et al 1997). Similarly, the perceived directions associated with noncoherent motion have also been shown to depart from the predicted direction of component motion (Kim and Wilson 1996). Moreover, because motion coherence judgments are categorical and criterion-dependent, perceived direction cannot be precisely inferred from them. Hence, determining whether eye movements and perception exhibit more than the qualitative agreement indicated by the results presented herein requires that subjects be made to report not simply motion coherence, but perceived direction. Preliminary experiments in our laboratory in which we did just that reveal that eye movements are indeed more closely aligned with the perceived directions of symmetric and asymmetric uni-kinetic plaids than with the predicted directions. Thus, similar to the oculomotor responses, the perceived directions corresponding to symmetric and asymmetric plaids exhibit less angular separation than do the predicted component and pattern motions. These results suggest that neither perception nor eye movements are subserved by neural circuitry that precisely recovers component and pattern motions. Clearly, more experiments are needed to determine both the precise relationship between oculomotor and perceptual responses and the neural computations underlying each.

6.2 MT contribution to perception of moving plaid patterns

The vast majority of neurons in area MT are highly selective for direction of motion. This response property, in conjunction with results from microstimulation and lesion studies, has implicated area MT as a key component of the neural substrate for motion perception (see Albright 1993 for review). When observers are presented with bi-kinetic plaids made from identical components, it has been shown that many MT neurons ('component type') respond predominantly to motion of the components, whereas a

minority of MT neurons ('pattern type') respond predominantly to motion of the pattern (eg Movshon et al 1985; Rodman and Albright 1989). Because human observers typically report coherent motion when viewing plaids of this construction, only neurons of the pattern type behave in a way that is consistent with what is perceived.

More recently Stoner and Albright (1992) extended these findings by demonstrating that the tendency of individual MT neurons to respond to pattern vs component motions covaried with stimulus configuration. Employing perceptual transparency cues as a way of manipulating motion coherence, they showed that plaids configured to elicit a percept of coherent pattern motion were more likely to elicit a pattern-type response from a neuron, whereas plaids configured to elicit a percept of component motion were more likely to elicit a component-type response from the same neuron.

The results from the present neurophysiological experiments employing uni-kinetic color plaid patterns similarly demonstrate a correlation between the behavior of MT neurons and motion coherence judgments in human observers. Although we cannot rule out a potential contribution from cortical areas other than MT (eg areas V2 and V3), our results, in conjunction with those of Stoner and Albright, provide evidence that MT contributes to the perceptual phenomenon. Moreover, the fact that the neuronal effect generalizes across two very different stimulus manipulations (the transparency manipulations used by Stoner and Albright, as well as the chromatic/luminance cues used in the present experiments) indicates that it is the perceptual coherence, rather than any specific aspect of the stimulus, that is most highly correlated with the neuronal response.

6.3 Potential neural mechanisms for noncoherence of color plaids

6.3.1 *Channel-based theories.* Several psychophysical studies have demonstrated the influence of color on visual motion coherence (Wallach 1935; Krauskopf and Farell 1990; Dobkins et al 1992; Kooi and De Valois 1992; Kooi et al 1992; Farell 1995; Cropper et al 1996; Krauskopf et al 1996). Specifically, if one component of a moving plaid is isoluminant red/green and the other is achromatic, moving plaid patterns tend not to cohere (Krauskopf and Farell 1990). Although such results were originally taken to imply the existence of color channels tuned to cardinal axes of color space, this conclusion has recently been called into question by the finding that plaids composed of gratings modulated along *noncardinal* directions of color space can also produce noncoherent motion; plaids composed of gratings with complementary chromatic/luminance phase relationships, ie when one component is red-bright/green-dark and the other is green-bright/red-dark, also tend not to cohere (Dobkins et al 1992; Kooi et al 1992; Farell 1995; Krauskopf et al 1996; and see table 1 of current study).

In order for these latter findings to fit into a channel model of motion coherence, one need only propose that the color channels that feed into motion integration mechanisms are 'higher-order', ie that they respond selectively to specific *combinations* of cardinal axis excitation (see Krauskopf et al 1986; Lennie et al 1990; Webster and Mollon 1991, 1994 for discussions of higher-order color channels *unrelated* to motion). Regardless of the exact nature of these color channels, channel-based explanations for noncoherence of color plaids imply the existence of neurons selective for modulation along different directions in color space and sensitive to pattern motion. One population of such directionally selective neurons would be expected to respond vigorously to moving red-bright/green-dark gratings yet give little response to moving red-dark/green-bright gratings. A complementary second population would presumably respond in an opposite fashion. Noncoherence of asymmetric color plaids, according to the channel model, thus results from the independent activation of two sets of neurons each signaling the motion of one grating but blind to the other.

Although our neurophysiological results in MT are somewhat preliminary, they appear to directly refute a simple channel model: MT neurons were found to be differ-

entially affected by symmetric vs asymmetric plaids, despite the fact that they did not respond differentially to 'red-bright/green-dark' vs 'green-bright/red-dark' gratings when presented individually. It should be pointed out, however, that our results do not preclude the possibility of a channel-based explanation in other areas of the primate visual system. In fact, area V3 has been shown to contain color-selective neurons as well as neurons sensitive to pattern motion (Gegenfurtner et al 1997). Whether, as required by the channel model, neurons with both properties exist within area V3 remains unknown.

6.3.2 *Depth from occlusion cues.* An alternative 'depth-from-occlusion' explanation supposes that the 'blobs' or intersections of plaid patterns with dissimilar components are interpreted as regions of overlap between two surfaces. As a consequence, the pattern-direction motion signals arising from these 'extrinsic' features (Shimojo et al 1989) are suppressed and/or decomposed into constituent motions (Stoner and Albright 1993, 1994, 1996, 1998), leading to a percept in which component motion dominates. The involvement of depth-from-occlusion mechanisms in the perception of moving *achromatic* stimuli is well-documented, both by psychophysical (eg Shimojo et al 1989; Stoner et al 1990; Vallortigara and Bressan 1991; Trueswell and Hayhoe 1993; Lindsey and Todd 1996; Stoner and Albright 1996) and neurophysiological (eg Stoner and Albright 1992; Duncan et al 1995; Duncan and Stoner 1997; Stoner et al 1997) studies. More to the point, Stoner and Albright (1998) have provided evidence that depth-from-occlusion processes, rather than channel mechanisms, are responsible for the noncoherence of plaids with components of different luminance contrasts. Accordingly, components of different contrasts are perceptually segmented into different depth planes owing to the existence of luminance-defined *X-junctions* at the regions of grating overlap. Chromatic variation along X-junctions is also known to be an important cue for transparent occlusion (D'Zmura et al 1997). The noncoherence of asymmetric plaids may be due to the activation of neural mechanisms sensitive to chromatic variation along X-junctions—variation lacking in symmetric plaids. Evaluation of this hypothesis awaits future experimentation and might be accomplished via the introduction of stimulus manipulations that influence depth assignment and figural interpretation [eg relative size (Stoner and Albright 1996) and binocular disparity (Duncan and Stoner 1997; Stoner et al 1997)] but leave chromatic differences unaffected.

6.3.3 *Implications for interactions between 'color' and 'motion' pathways in the primate visual system.* Whatever the neural mechanism underlying the perceptual phenomenon, it must be one that is (i) involved in motion processing and (ii) sensitive to the phase relationship between luminance and chromatic contrast. Such a mechanism would appear to be precluded, however, by evidence for parallel processing of 'motion' and 'color' in the primate visual system. Considerable data document the existence of two distinct subcortical pathways—parvocellular (P) and magnocellular (M)—which originate in the retina and remain segregated up through layer 4C of area V1. [There also exists a third pathway, the 'koniocellular' (K) pathway, which is less studied and appears to respond selectively to stimuli that modulate the S cones (eg Irvin et al 1993; Martin et al 1997).] The suggestion has been made, largely on the basis of physiological response properties, that the P division subserves color and form vision, while the M division subserves motion perception (see Van Essen 1985; DeYoe and Van Essen 1988; but cf Merigan and Maunsell 1993). At the cortical level, the segregation between P and M is less than complete. Although dorsal areas, such as area MT, appear to receive predominantly M input, ventral areas, such as area V4, receive almost equal contributions from M-channels and P-channels (Maunsell et al 1990; Ferrera et al 1994).

Particularly relevant to this discussion are the different types of chromatic responses observed within subcortical M and P divisions. M neurons are not selective for the phase relationship between chromatic and luminance contrast, responding equally

well to red-bright/green-dark stimuli as to green-bright/red-dark stimuli. In addition, M neurons exhibit 'frequency doubling' in response to isoluminant red/green flicker, ie they respond with equal amplitude to the onset of red as to the onset of green (eg Schiller and Colby 1983; Lee et al 1988; Shapley and Kaplan 1989). Because M neurons do not respond differentially to red vs green, they are unable to convey information about color *identity*.

By contrast, P neurons of the retina and LGN exhibit chromatically-opponent responses (eg De Valois et al 1966; Wiesel and Hubel 1966; Gouras and Zrenner 1979; Derrington et al 1984; Reid and Shapley 1992). For example, a given P neuron may be more responsive to red than green, and in this sense can signal color identity (ie 'red'). In the case of our stimuli, this neuron would respond more strongly to a red-bright/green-dark grating than to a green-bright/red-dark grating. A P neuron selective for 'green' would respond in a complementary fashion. In this way, P neurons clearly do convey information about the phase relationship between chromatic and luminance modulation.

How these M and P chromatic signals influence cortical motion processing has recently been addressed by studies investigating the response properties of neurons in area MT, which is part of the dorsal cortical stream. In contradiction to a strict color/motion dichotomy, many MT neurons can signal the direction of motion of isoluminant red/green stimuli (Charles and Logothetis 1989; Saito et al 1989; Dobkins and Albright 1990, 1994; Gegenfurtner et al 1994). Although the limited P input to MT (Maunsell et al 1990) might be thought responsible for the observed chromatic responses in MT, recent experiments suggest that this phenomenon can be supported by frequency-doubled chromatic responses originating in magnocellular neurons (Dobkins and Albright 1994, 1998).

Nonetheless, the (albeit small) P input to area MT leaves open the possibility that, under certain conditions, MT may have functional access to color information encoded by P neurons or regions of cortex that receive P input (for example V4). In line with this possibility, recent neurophysiological studies demonstrate that responses of MT neurons to stochastic motion displays are significantly enhanced when the signal and noise dots differ in color, compared to when they are of identical color (Croner and Albright 1997). This ability relies on access to color identity information, which is within the purview of the parvocellular, but not the *magnocellular*, pathway.

The remarkable finding in our color plaid study is that MT neurons are differentially affected by symmetric vs asymmetric color configurations, despite the fact that they do not respond differentially to the component gratings that comprise the plaid. Because selectivity for the phase relationship between chromatic and luminance contrast is clearly not a property of MT neurons (see figure 7b or 8a) or of the magnocellular neurons that supply the major input to area MT, these results suggest that (color-selective) P input to MT may contribute by exerting a modulatory influence on the integration of motion signals. Perhaps the most direct way to evaluate this possibility would be to deactivate the parvocellular laminae of the LGN and test for selective disruptions of color-influenced motion integration in MT.

In conclusion, our neurophysiological experiments demonstrate a unique influence of color on motion integration, suggesting a functional interaction between 'color' and 'motion' pathways in the primate visual system. Moreover, the striking similarity between our MT and psychophysical results provides a potential neural substrate for the perceptual noncoherence of moving plaids, and further suggests that the 'channel model' of motion noncoherence needs to be re-evaluated.

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