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Color and luminance in the perception of 1- and 2-dimensional motion

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Abstract

An isoluminant color grating usually appears to move more slowly than a luminance grating that has the same physical speed. Yet a grating defined by both color and luminance is seen as perceptually unified and moving at a single intermediate speed. In experiments measuring perceived speed and direction, it was found that color- and luminance-based motion signals are combined differently in the perception of 1-D motion than they are in the perception of 2-D motion. Adding color to a moving 1-D luminance pattern, a grating, slows its perceived speed. Adding color to a moving 2-D luminance pattern, a plaid made of orthogonal gratings, leaves its perceived speed unchanged. Analogous results occur for the perception of the direction of 2-D motion. The visual system appears to discount color when analyzing the motion of luminance-bearing 2-D patterns. This strategy has adaptive advantages, making the sensing of object motion more veridical without sacrificing the ability to see motion at isoluminance. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The physical speed and direction of a stimulus do not always predict perceived motion accurately. Perceived motion is influenced by such non-motion parameters as spatial frequency (Diener, Wist, Dichgans & Brandt, 1976; Campbell & Maffei, 1981; Smith & Edgar, 1991), contrast (Thompson, 1982; Stone & Thompson, 1992; Agonie & Gorea, 1993), retinal eccentricity (Campbell & Maffei, 1981), and color (Moreland, 1982; Cavanagh, Tyler & Favreau, 1984; Cavanagh & Favreau, 1985), and by the perceptual segmentation and grouping of stimulus components within a scene (Brown, 1931a,b; Duncker, 1939; Adelson & Movshon, 1982; Farell, 1995; Bex & Makous, 1997). These multiple influences raise questions about how many distinct motion pathways the visual system contains and how motion signals from different sources are combined. These questions have been a major testbed for studying functional segregation of cortical processing (e.g. see Gegenfurtner & Hawken, 1996 for a review of effects of color). Two of the variables affecting perceived speed—color versus luminance and 1-D versus 2-D motion—are examined here. Their interaction provides evidence of specialized processing of 2-D motion of luminance-bearing patterns.

1.1. Color's contribution to motion

Stimuli defined solely by chromatic modulation can contribute robustly to the perception of motion. This has been shown in a variety of motion tasks at suprathreshold contrasts (Cavanagh & Favreau, 1985; Krauskopf & Farell, 1990; Cavanagh & Anstis, 1991; Chichilnisky, Heeger & Wandell, 1993; Dobkins & Albright, 1993; Metha, Vingrys & Badcock, 1994; Cavanagh, 1995; Gegenfurtner & Hawken, 1995; Cropper & Derrington, 1996a; Gegenfurtner & Hawken, 1996) and at threshold, where cone contrasts for direction discrimination can be considerably lower for color stimuli than for luminance stimuli (Stromeyer, Eskew & Kronauer, 1990; Derrington & Henning, 1993; Palmer, Mobley & Teller, 1993; Gegenfurtner & Hawken, 1995; Stromeyer, Kronauer, Ryu, Chaparro & Eskew, 1995). Compared to luminance contrast, however, color con-

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trast often appears to be less effective as a source of motion signals, even under those conditions where motion mechanisms are most sensitive to color. Under some stimulus conditions, motion discriminations might fail entirely at isoluminance, even though the moving stimulus is visible (Ramachandran & Gregory, 1978; Lindsey & Teller, 1990; Cavanagh & Anstis, 1991; Derrington & Henning, 1993; Palmer, Mobley & Teller, 1993; Teller & Lindsey, 1993). This occurs particularly at contrasts equal to and somewhat above the threshold for pattern detection. Thus, the threshold contrast for pattern detection is lower, by as much as a factor of 4 or 5 for some observers in some conditions (Lindsey & Teller, 1990; Palmer et al., 1993), than the threshold contrast for discriminating direction of motion. Between these two thresholds motion pathways are functionally color blind and contrast detection pathways are functionally motion blind.

My interest here, however, is in suprathreshold vision, where the motion of isoluminant stimuli is perceived, but often appears as slower and less smooth than the motion of luminance stimuli having the same physical speed (Moreland, 1982; Cavanagh et al., 1984; Livingstone & Hubel, 1987; Mullen & Boulton, 1992; Teller & Lindsey, 1993). The difference in perceived speed is most prominent at low speeds, low spatial frequencies, and low chromatic contrasts (Cavanagh et al., 1984; Burr, Fiorentini & Morrone, 1998b). It is under these conditions that one also finds the largest difference between chromatic and luminance stimuli in the contrast gain of perceived speed (Hawken, Gegenfurtner & Tang, 1994; Gegenfurtner & Hawken, 1996; see also Cropper & Derrington, 1996b), in direction discrimination thresholds (Stromeyer et al., 1995), and in the response latency to motion onset (Burr et al., 1998b). As stimulus speed increases, these differences gradually diminish.

The comparative disadvantage of color as a medium for velocity perception seems to be linked specifically to a deficit in motion processing. It has no parallel in the processing of spatial position, which is conveyed as accurately by color as by luminance when their contrasts are equated (Krauskopf & Farell, 1991), nor in the processing of spatial phase, for which sensitivity is similar for color, luminance, and combinations of luminance and color (Martini, Girard, Morrone & Burr, 1996), nor even in the processing of flicker (Henning & Derrington, 1994).

What, then, is the relationship between the contributions of color and luminance to motion perception? Both color and luminance can support the perception of different speeds and directions at the same time and location and thus can act as independent sources of motion signals (Krauskopf & Farell, 1990; Cropper, Mullen & Badcock, 1996; Krauskopf, Wu & Farell, 1996). More frequently, however, color and luminance are found to interact. Drifting color and luminance gratings show cross-adaptation: Adapting to the motion of a luminance grating causes a subsequently viewed static chromatic grating to appear to move in the opposite direction (and vice versa) (Derrington & Badcock, 1985; Mullen & Baker, 1985; Webster, Day & Cassell, 1992). A drifting color grating can also null a motion aftereffect induced by a luminance grating (Cavanagh & Favreau, 1985). When chromatic and luminance contrasts are combined in a single moving grating, both color and luminance contribute to the cancellation of the motion of a superimposed luminance grating moving in the opposite direction (Cavanagh & Anstis, 1991). Color can determine the perceived direction of a display whose luminance content is directionally ambiguous (Papathomas, Gorea & Julesz, 1991). Motion signals from luminance and color summate more efficiently than predicted by probability summation (Palmer et al., 1993). And, as a final example, dichoptically viewed counter-phase flickering gratings, defined by luminance in one eye and by color in the other, can combine to yield the perception of directional motion (Carney, Shadlen & Switkes, 1987).

Taken at face value, these results might be most easily explained by the notion that motion analyzers treat color as equivalent to a low-contrast luminance signal. This can be tested by measuring perceived speed. When their physical speeds are equal, a luminance grating of higher contrast will appear to drift faster than one with a lower contrast, at least at low speeds (Thompson, 1982; Stone & Thompson, 1992). If color and luminance contrast are interchangeable, we would expect the motion response to be a function of the sum of color and luminance contrast. So, by adding chromatic contrast to a low-contrast luminance grating we should be able to increase its apparent speeds to match that of a higher-contrast luminance grating. However, instead of adding to effective contrast and therefore to perceived speed, chromatic contrast "dilutes" the motion derived from luminance, lowering the perceived speed (Cavanagh et al., 1984; Mullen & Boulton, 1992) and reducing the power of the stimulus to generate and null motion aftereffects (Cavanagh & Favreau, 1985). The implication is that color and luminance give rise to separate motion signals that are subsequently combined.

Other theories of the slowness of color have thus far faired better. It might be due to a contrast miscalibration by color-sensitive motion units (Cavanagh & Anstis, 1991), to differing temporal filtering within color and luminance pathways (Metha & Mullen, 1997; Burr, Fiorentini & Morrone, 1998a), or to mismatching color sensitivities within or between motion detectors (Derrington & Badcock, 1985). Not being incompatible (or even independent), all these factors could contribute to the effect. None of them, as they stand, can explain the results for 2-D motion presented below. But, after all, doing so isn't their raison d'être.

1.2. 1-D versus 2-D motion

The luminance-color interactions mentioned above come from studies of the influence of color on grating motion. A 1-D spatial pattern (such as a drifting grating or line of visually unlimited extent or viewed through an isotropic aperture) is seen as moving in a direction perpendicular to its orientation. This is because motion parallel to the orientation of a 1-D pattern leaves the pattern unchanged. This axis of undetectable motion makes a drifting 1-D pattern consistent with an infinite number of 2-D motion vectors within ± 90° of the perceived drift direction. Thus a 1-D pattern has an underdetermined trajectory in a 2-D space, such as the retinal surface.

The motion of a rigid 2-D pattern, by comparison, has an unambiguous 2-D motion. The simplest 2-D pattern in the Fourier domain contains two 1-D components with differing orientations. In general, the motion of such a 2-D pattern, described by the intersection-of-constraints (IOC) formulation (Adelson & Movshon, 1982; Farell, 1998, Eqns. 1 and 2), differs in both direction and speed from that of the pattern's 1-D components. Whether 2-D object motion is derived perceptually from 1-D motion signals (Adelson & Movshon, 1982; Welch, 1989) or more directly from motion signals with the direction of the moving 2-D features (Gorea & Lorenceau, 1991; Derrington & Badcock, 1992; Wilson, Ferrera & Yo, 1992; Rubin & Hochstein, 1993) is the subject of on-going controversy.

Suppose one superimposes two differently-oriented drifting isoluminant gratings that have the same chromaticities. Then, depending on the gratings' spatial and temporal similarities, they will display either the coherent motion of a rigid plaid pattern or the transparent motion of independently moving gratings. In this respect, isoluminant gratings act, qualitatively at least, like luminance gratings. (The two differ quantitatively: Chromatic gratings are more likely than luminance gratings to cohere [Kooi, De Valois, Switkes & Grosof 1992b] and are less accurate as predictors of perceived plaid direction [Gegenfurtner, 1998]). However, if one superimposes drifting gratings modulated in *different* color-space directions, then the outcome depends on the specific modulation directions. Krauskopf and Farell (1990) showed that superimposed gratings do not interact if they are modulated along different cardinal directions (Krauskopf, Williams & Heeley, 1982). Rather than moving coherently, cardinal-axis gratings retain their separate motion trajectories and are seen to drift transparently across each other. Similar results have been obtained by Cropper et al. (1996). However, superimposed gratings modulated *between* cardinal directions tend to be seen as moving coherently. These results imply that motion is analyzed by three independent mechanisms whose sensitivities are selective to modulations along the luminance axis and the two opponent-color axes. Gratings with differing cardinal-axis color-space directions will stimulate different motion mechanisms and so will separately contribute to independent motion percepts; gratings with differing intercardinal color-space directions will stimulate the same motion mechanisms and so will jointly contribute to a single motion percept.

Using a more sensitive technique (2-afc relative coherence judgments) Krauskopf et al. (1996) found that within the isoluminant plane motion coherence was minimal when the component gratings were modulated along color-space directions separated by 90°. This result held whether the 90° difference was between cardinal or non-cardinal directions. These data point to the existence of motion pathways selective to intercardinal directions in the isoluminant plane, though these pathways appear to be somewhat less effective than the cardinal-axis pathways (Farell, 1995; Cropper et al., 1996). However, when Krauskopf et al. looked outside the isoluminant plane, within planes containing the luminance axis, they found a different result. Outside the isoluminant plane, coherence was minimal when the component gratings were modulated along different cardinal axes. There was, in other words, no evidence of non-cardinal-axis mechanisms. Thus, intercardinal mechanisms are found only in the isoluminant plane; outside this plane there appears to be only one motion mechanism and it is tuned to luminance. By a motion-coherence criterion, then, there are separate motion mechanisms sensitive to modulations of luminance and to modulations of color, but not to modulations of luminance-color combinations. We will later see this conclusion echoed and reinterpreted by results of experiments presented below, which examine perceived speed and direction, rather than motion coherence.

The evidence on color-luminance interactions in motion perception, then, is split. A number of studies, mentioned above, have shown interactions between luminance and color in the perception of grating motion. The sparser evidence from studies of the perception of plaid motion shows no sign of such interactions (Krauskopf & Farell, 1990; Cropper et al., 1996; Krauskopf et al., 1996). The experiments described next show that these two sets of findings are not contradictory; their difference comes about because color and luminance combine differently in the perception of 1-D motion than in the perception of 2-D motion.

2. Experiment 1: perceived speed

In this experiment we compare the perceived speed of stimuli defined by luminance contrast, color contrast, and luminance-plus-color contrast. The stimuli were drifting 1-D patterns (gratings) and drifting 2-D patterns (plaids).

2.1. Method

Two patterns, a test pattern and a spatially identical comparison pattern, were presented sequentially and in random order on each two-interval trial. The test pattern was defined by a modulation of color (red/green) or an in-phase modulation of color and luminance. The comparison pattern was defined by a modulation of luminance only. During a block of trials the speed of the test was fixed and the speed of the comparison was varied. The perceived speed of the test pattern was specified by the physical speed of the comparison pattern that had the same perceived speed as the test.

The speed of the comparison was varied in either of two ways. A constant-stimulus procedure, in which the comparison speed was randomly selected on each trial from seven linearly spaced values, was used for three of the four observers. Each stimulus interval lasted 1 s; the two intervals of a trial were separated by a blank period of 0.9 s. The beginning of each stimulus interval was announced to the ear, by a short beep. The second interval was followed after 0.75 s by a display of a response panel consisting of two on-screen buttons; observers clicked on the appropriate button to select the interval (first or second) that contained the faster-moving of the two patterns shown on that trial. Observers were provided no feedback about their performance or the true speed of the comparison stimulus until the end of the run of trials.

The remaining observer (the author) used an adjustment method. The test and comparison patterns appeared simultaneously, the test to the left of the fixation point and the comparison to the right, and remained in view indefinitely. Moving the mouse to the right increased the speed of the comparison pattern, while moving the mouse to the left decreased it. When the observer was satisfied that the speeds appeared equal, he clicked the mouse button to end the trial. Another mouse click began the next trial. This latter click was effective only after the observer had erased the last setting by moving the mouse leftward or rightward beyond a critical distance. The range of adjustable speeds was set in accordance with pilot data to substantially exceed the range of equivalent-speed settings likely to be selected during experimental trials.

The patterns were gratings or plaids that appeared within a circular aperture. The gratings were sinusoidal modulations along the $L+M+S$ (luminance) axis or the $L-M$ (red/green) axis of an elaboration of the color space of MacLeod and Boynton (1978) (Derrington, Krauskopf & Lennie, 1984). The orientation of the test gratings was 45° for two observers and 135° for the other two. The plaids were the superposition of two gratings oriented at 45 and 135°. The plaids' veridical drift direction was vertical. Minimum-motion measurements (Anstis & Cavanagh, 1983) were used to set the chromatic modulations to isoluminance for each subject. Mean display luminance was 31 cd m^{-2}. The gray background had the same luminance and chromaticity as the space-averaged patterns.

Grating spatial frequencies spanned a three-octave range, from 0.125 to 1.0 c deg^{-1}, though not all observers judged all frequencies. The luminance and color contrasts of the test and comparison patterns were equal multiples (10 × or 20 ×) of the threshold contrast for detecting those patterns, based on prior measurements of each subject's detection thresholds. The comparison pattern was a luminance-only pattern. Its contrast was equal to the contrast of the luminance component of the luminance-plus-color test pattern it was paired with. Because a plaid containing gratings of equal contrasts has twice the contrast as the components, the inclusion of contrast levels differing by a factor of 2 facilitates comparisons of data for 1- and 2-D motion. Luminance-plus-color gratings were generally constructed with light and red phases coincident.

The patterns appearing within a trial were identical in their static spatial parameters; test gratings were paired with comparison gratings, and test plaids were paired with comparison plaids, with no spatial frequency or orientation differences between them. There were four parameters on which test and comparison patterns might differ: speed (the variable speed of the comparison pattern could be greater or less than the constant speed of the test pattern), chromatic contrast (always positive in the test and zero in the comparison), luminance contrast (always positive in the comparison and either the same or zero in the test), and direction (randomized across trials separately for the test and comparison patterns).

The stimuli were displayed on a calibrated monitor controlled by a Macintosh computer. Single gratings were displayed on alternate pixel rows; plaids were displayed by using all pixel rows. Subjects viewed the monitor from a distance of 57 cm with natural pupils. At this distance, the diameter of the aperture was 10.7°. A black square 6′ on a side, appeared in the center of the aperture, as a fixation point.

Observers were instructed to fixate the central square and to base their judgments on perceived speed.

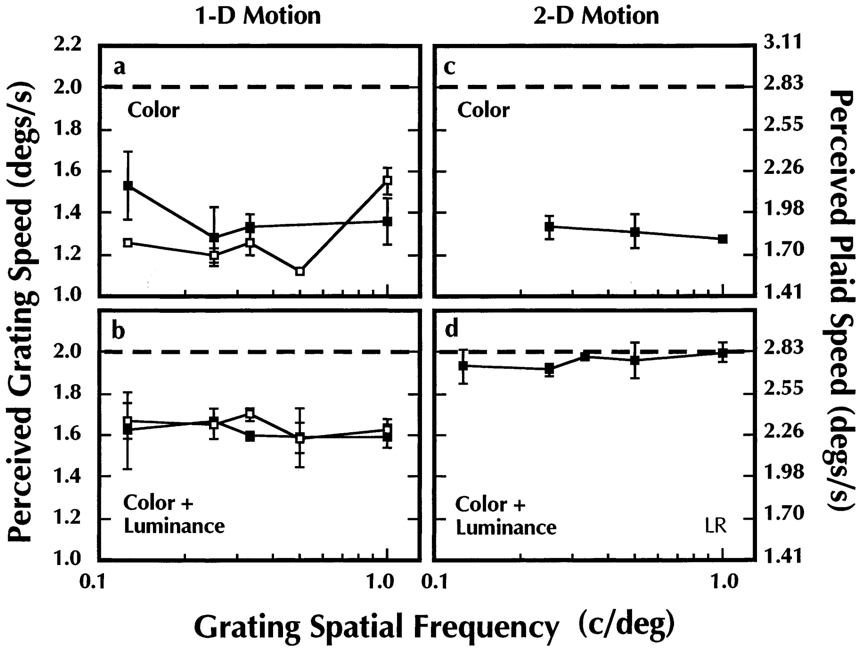

Fig. 1. Perceived speeds of gratings and plaids modulated in color only or in both luminance and color; Experiment 1, observer LR. Physical speed is shown by the dashed line. A test pattern's perceived speed is defined as the physical speed of a spatially identical luminance modulation with the same perceived speed as the test pattern. Test grating speed was 2 deg s^{-1}; test plaids, composed of orthogonal 2 deg s^{-1} gratings, had a coherent speed of $2\sqrt{2}$ deg s^{-1}. Perceived speed of (a) color gratings; (b) color-plus-luminance gratings; (c) color plaids; and (d) color-plus-luminance plaids as a function of grating spatial frequency and contrast. Contrasts of luminance and color gratings were equal multiples (10 ×, filled symbols, or 20 ×, open symbols) of detection threshold. Error bars are ± 1 S.E.

2.2. Results

The data gathered by the constant-stimulus method were the proportions of trials on which the comparison pattern was seen as moving faster than the test pattern. These proportions, expressed as a function of comparison speed, were fit with a Weibull function. The speed yielding the 50% point was determined and taken as the perceived speed of the test stimulus. Fig. 1 shows the perceived speeds of color and luminance-plus-color gratings and plaids for the observer (LR) tested on the largest number of spatial frequencies and Fig. 2 shows data for all four observers.

Fig. 1a shows that for observer LR a 2 deg s^{-1} isoluminant red–green grating appeared to move on average at the same speed as a 1.33 deg s^{-1} achromatic comparison grating of the same spatial frequency. This result, which is consistent with previous research (e.g. Cavanagh et al., 1984), was found for all spatial frequencies tested and was little affected by a doubling of test and comparison contrasts.

Data for test gratings with both luminance and chromatic contrast appear in Fig. 1b. The 2 deg s^{-1} luminance-plus-color test gratings had the same average perceived speed as a 1.66 deg s^{-1} luminance grating. This value is similar (in fact, fortuitously identical) to the average of the perceived speeds of the test gratings' luminance and color components, as has also been found in earlier studies (Cavanagh et al., 1984; Cavanagh & Favreau, 1985).

Data for isoluminant red/green plaids appear in Fig. 1c. The component orthogonally oriented gratings each drifted at 2 deg s^{-1}, giving the plaid a speed of 2.83 deg s^{-1} in the vertical direction. The average perceived speed of this plaid was 1.86 deg s^{-1}. This value corresponds to a component 1-D speed of 1.31 deg s^{-1}, the

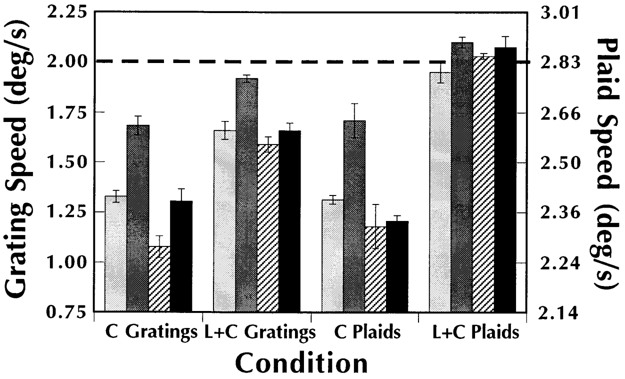

Fig. 2. Perceived speed of gratings and plaids for the four observers of Experiment 1, averaged over spatial frequency and contrast. Data for observer LR, from Fig. 1, are given by the left-most bar in each condition. Physical speed is shown by the dashed line. Relative to luminance-defined comparison patterns, test patterns with chromatic contrast have reduced perceived speeds, except for 2-D patterns containing luminance contrast.

same as the perceived speed of individual isoluminant gratings (Fig. 1a). Thus, the observer sees isoluminant plaids as moving at the speed predicted from the perceived speed of the plaids' 1-D components.

Data for luminance-plus-color plaids are shown in Fig. 1d. These plaids were made from orthogonally oriented luminance-plus-color gratings, each of which was identical to those yielding the data of Fig. 1b. The plaids appeared to move at the same speed as a comparison plaid drifting at 2.76 deg s^{-1} (vs. a veridical speed of 2.83 deg s^{-1}). At this speed the plaids 1-D components drift at 1.95 deg s^{-1}. This is faster than the perceived speed of component luminance-plus-color gratings (1.66 deg s^{-1}) and well within measurement error of the physical speed of the 1-D components of the comparison luminance plaid (2 deg s^{-1}). Thus, while adding color to a luminance grating substantially reduces its perceived speed, adding color to the component luminance gratings of a plaid leaves perceived speed unchanged.

The general indifference of LR's perceived speed data to spatial frequency and contrast was characteristic of the data of all observers, so results were averaged over these variables in Fig. 2 for each of the four observers. For all observers luminance-plus-color gratings had a perceived speed intermediate between those of color gratings and luminance gratings, while luminance-plus-color plaids had perceived speeds that equaled those of the luminance plaid comparison patterns. Thus, the presence of color contrast slowed the motion of luminance-bearing 1-D patterns but did not affect the perceived speed of luminance-bearing 2-D patterns.

The contrast of a plaid is twice that of each of its equal-contrast components. However, this contrast difference is not important for the effects shown in Figs. 1 and 2, for a doubling of contrast had little effect on the perceived relative speeds of test and comparison patterns. In addition, the perceived speeds of isoluminant gratings and plaids were commensurate (e.g. Fig. 1a, c) despite the contrast difference between them. The lack of contrast effects does not show that a doubling of contrast does not influence perceived speed, but rather that in this experiment it influences the perceived speeds of test and comparison stimuli equally (cf. Hawken et al., 1994).

Another difference between the gratings and plaids of this experiment is speed. The speed of test gratings was 2 deg s^{-1}, while that of test plaids was 2.83 deg s^{-1}. The results, however, do not depend on these values. Observer LR ran additional conditions at higher and lower comparison grating speeds, 1 and 4 deg s^{-1}, yielding plaid speeds of 1.4 and 5. 7 deg s^{-1}, respectively. Perceived speed was proportional to the new comparison speeds and the contribution of color to perceived speed again depended on the presence of luminance contrast and on pattern dimensionality, as in Fig. 1. For the faster speeds, however, there was a diminution of the perceived speed difference between color and luminance patterns, as found by others (Burr et al., 1998b). Results were also qualitatively unchanged by changing grating orientations to yield drift direction differences of 60° or 120°, instead of 90°, while increasing or decreasing grating speeds, respectively, to maintain constant plaid speed.

To determine whether the dominance of luminance in 2-D motion depended on spatial registration between luminance and color modulations, observer LR reran the experiment (at one spatial frequency) with a 90° phase shift between the chromatic and luminance grating components. This manipulation had no effect on her perceived speed data for either 1-D or 2-D patterns.

3. Experiment 2: perceived direction

Color exerted no influence on the perceived speeds of 2-D luminance-plus-color patterns in Experiment 1. Color's influence on the perceived direction of these patterns is examined in Experiment 2. The patterns used in this experiment were plaids produced by combining a color-plus-luminance grating with either a color grating or a luminance grating. One plaid type ($C/L+C$ plaids), consisting of a color-only grating and a color-plus-luminance grating, can be thought of as a color plaid plus a luminance grating. The other type ($L/L+C$ plaids), consisting of a luminance-only grating and a color-plus-luminance grating, can be thought of as a luminance plaid plus a color grating. Unlike the plaids used in Experiment 1, these plaids have an asymmetrical distribution of color and luminance modulations across component orientations.

The results of Experiment 1 lead us to predict that the two types of asymmetrical plaids will have different perceived directions of motion. When equal in physical speeds, the two component gratings of each plaid type will have unequal perceived speeds, i.e. $L+C>C$ and $L+C<L$. This is because of their differing ratios of luminance and chromatic contrast. The IOC prediction is that the plaid will appear to veer toward the direction of motion of the component with the faster perceived speed (Stone, Watson & Mulligan, 1990; Kooi, De Valois, Grosof & De Valois, 1992a). On the basis of Experiment 1, however, we expect that this IOC prediction will be observed in $C/L+C$ plaids, but not in $L/L+C$ plaids. The latter type of pattern is equivalent to a luminance plaid plus a color grating; the 2-D (plaid) motion of the luminance pattern should be unaffected by the presence of color contrast. The plaid should be seen to move in its veridical direction, unperturbed by the asymmetry of its components' perceived speeds. The data of Kooi and De Valois (1992) are consistent with this prediction.

Measuring perceived direction, then, allows us to compare chromatic and luminance 2-D patterns, to see whether the perceived motion of each type of pattern is influenced by the addition of the other type of contrast. This comparison is not possible with the symmetrical plaids used to measure perceived speed. However, we run into a problem when we try to implement the perceived direction experiment: The components of asymmetrical plaids are usually seen as moving independently, not coherently (Farell, 1995). The problem, in other words, is that the 2-D motion we wish to measure is usually not observed with these patterns. As a rule, one sees a symmetric plaid, composed of two luminance or two color gratings, moving in the IOC direction, and the unpaired grating—color or luminance, respectively—moving in a direction perpendicular to its orientation, sliding across the plaid. The only exception to this rule, at the contrasts examined in the Farell (1995) study, occurs in $L/L+C$ plaids when the luminance and color gratings had unequal spatial frequencies. If luminance has the higher frequency, then the luminance plaid and the chromatic grating move coherently, in a single direction.

Hence, we can obtain coherent motion from $L/L+C$ plaids by manipulating spatial frequency. However, getting coherent motion from $L+C/C$ plaids requires another strategy. One strategy was found to work: Keeping the luminance contrast very low, near the detection threshold for luminance when combined with chromatic contrast in $L+C$ gratings.

3.1. Methods

The experiment required two sets of measures. The relative perceived speeds of the three types of component grating (luminance gratings, color gratings, and luminance-plus-color gratings) were measured by the constant-stimulus method of Experiment 1. The two types of asymmetrical plaids were then made from these gratings and measures of their perceived directions were taken, using either of two methods. With one method we measured the direction of a comparison plaid that is perceived as moving in same direction as the test plaid. With the other method we measure the ratio of the component gratings' physical speeds required for the test plaids to be perceived as moving in the veridical direction. These data were compared with predictions based on the perceived speeds of the component gratings. Two observers ran under each of the two plaid conditions, one each under the two perceived-direction methods.

3.1.1. $L/L+C$ plaids

$L/L+C$ plaids yield consistently coherent motion when the spatial frequency of the luminance components exceeds that of the chromatic component by a factor of 2 or more (Farell, 1995). To generate such plaids, I displayed the luminance components as missing-fundamental squarewaves and the color component as a sinewave grating at the fundamental frequency. The spatial frequencies and contrasts of the plaids' two missing-fundamental luminance squarewaves were the same. Initially this frequency was either 0.25 or 0.5 c deg^{-1}, but in order to verify the results over a larger range of frequencies this set was expanded to cover 0.125–1 c deg^{-1}. The sinusoidal color grating, with frequency and phase of the missing fundamental, was added to one of the two luminance gratings. The orientations of the plaids' components were 45 and 135°, with drift directions of 135 and 45°, respectively, giving the plaid a veridical 90° (vertical) direction of coherent motion when the components' physical speeds were equal.

The contrasts of the luminance and chromatic components were either 10 × or 20 × detection threshold, and all four combinations of luminance and chromatic contrasts (10 × and 10 ×; 10 × and 20 ×; 20 × and 10 ×; 20 × and 20 ×) were used in separate runs of trials. As it turned out, all these contrast conditions resulted in coherent displays and yielded similar data, and so were pooled.

The relative perceived speeds of the differently-oriented 1-D components (luminance-plus-color grating and luminance-only grating) were measured for each observer by the constant stimulus method used in Experiment 1. As expected, the components differed in perceived speed; the luminance-plus-color grating appeared slower. The resulting IOC prediction has the perceived direction of the plaid deviating, on average for the two observers, by 11° from vertical when the physical speeds of the components are equal.

3.1.2. $C/L+C$ plaids

The $C/L+C$ plaids were formed out of sinusoidal luminance and color gratings. The spatial frequencies of both the plaid's luminance and its color components were the same (0.5 or 0.25 c deg^{-1} for one observer, 0.25 c deg^{-1} for the other). Luminance contrast was added, in phase, to one of the component color gratings, with the light and red phases of the two gratings in register. The components' orientations and drift directions, and the plaids' drift direction (vertical), were the same as for $L/L+C$ plaids. The contrast of the color component was 20 × detection threshold and that of the luminance component was 5 ×. At this contrast the luminance component was near threshold when combined in phase with the color component.

The relative perceived speeds of the differently-oriented 1-D components (color-only grating and luminance-plus-color grating) were again measured by the method of Experiment 1. The speed of the color-only grating was fixed at 2 deg s^{-1} and the speed of the luminance-plus-color grating was varied from trial to trial to determine the speed required for a match. The color grating had by far the slower perceived speed. The resulting IOC prediction is that the perceived direction of the plaid should differ, on average for the two observers, by 15° from the vertical when the physical speeds of the components are equal.

3.1.3. *Perceived direction measurements*

Two methods were used to measure perceived direction. One, a two-interval method, kept the physical speeds of the test plaid's two motion components equal and varied the relative speeds of the components of a comparison plaid. The comparison plaids were symmetric, with modulations of luminance or color only: For the $L/L+C$ condition, the comparison plaid differed from the test plaid in that it had no color contrast; and for the $C/L+C$ condition, the comparison plaid differed from the test plaid in that it had no luminance contrast. The first interval contained the test plaid and the second contained the comparison plaid. The components of the test plaid drifted at 2 deg s^{-1}. The fixed-motion component of the comparison plaid also drifted at 2 deg s^{-1}, while the variable-motion component had a speed selected from seven linearly spaced values, one of which was randomly selected on each trial. The variable component of the comparison plaid had the same drift direction as the apparently faster component of the test plaid, i.e. the luminance-only component of the $L/L+C$ plaid and the luminance-plus-color component of the $C/L+C$ plaid. Thus, the effect on perceived direction of the test plaid's asymmetrical distribution of component color and luminance was measured using a comparison plaid with asymmetrical component speeds. Observers indicated whether the comparison plaid drifted in a more leftward or a more rightward direction than the test plaid. The resulting psychometric function gave the comparison plaid's component speed ratio required for the perception of matching plaid directions.

The other, one-interval, method varied the relative speeds of the test plaid's two motion components. The perceptually slower of the two motion components had a fixed speed and the faster had a variable speed. In the $L/L+C$ condition, the luminance-plus-color component drifted at 2 deg s^{-1} in all trials, while the speed of the luminance-only component was varied from trial to trial by the method of constant stimuli. In the $C/L+C$ condition, the color-only component drifted at 2 deg s^{-1} in all trials while the speed of the luminance-plus-color component was varied from trial to trial. Observers judged whether the plaid drifted leftward or rightward with respect to vertical. The component speed required for the perception of vertical drift was determined from the resulting psychometric function.

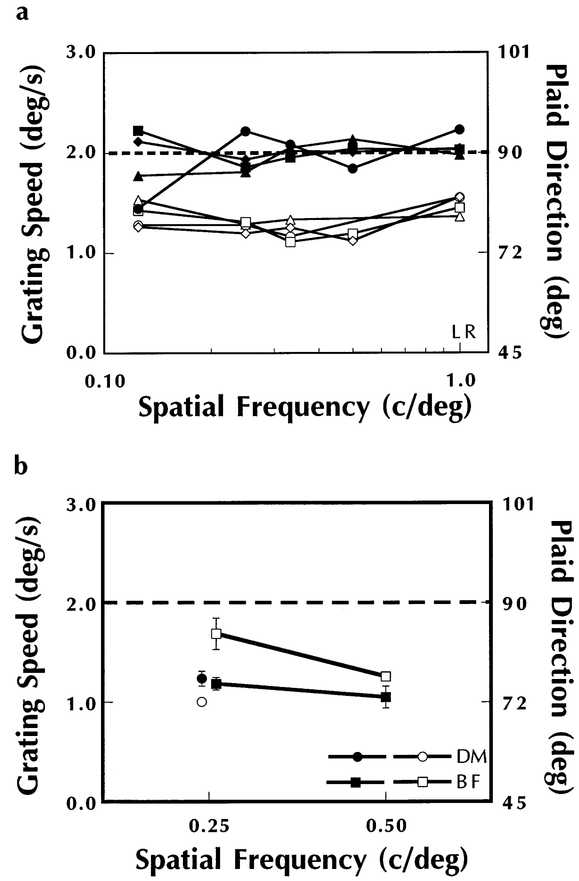

Fig. 3. Perceived direction of asymmetric plaids and perceived speed of their components; Experiment 2. Open symbols give the perceived speed of one of the component gratings, indicated on the left ordinate, relative to that of the other grating, moving nominally at 2 deg s^{-1} (dashed line). They also give the perceived plaid direction (right ordinate) given by the intersection of constraints. Filled symbols give the perceived direction (right ordinate) of the plaid obtained by superimposing the two gratings and the corresponding relative perceived grating speeds (left ordinate). (a) Data for $L/L+C$ plaids, each comprised of a luminance grating and a luminance-plus-color grating; observer LR. Luminance components were missing-fundamental square-waves and the color components were sine-wave gratings at the fundamental frequency. The perceived speed of $L+C$ components is below that of L components, but each component contributes equally to plaid direction. (b) Data for $C/L+C$ plaids, each comprised of a color grating and a luminance-plus-color grating, for two observers. All component gratings were sinusoids. The perceived speed of C components is below that of $L+C$ components and the perceived plaid direction deviates accordingly from 90°. Error bars are ± 1 S.E.

Two observers were used in each method. The two methods appear to give equivalent results.

3.2. *Results*

Plaid direction was manipulated experimentally by varying component speed. We can interchangeably express the data in terms of either of these variables, direction or speed. Fig. 3a shows data for the $L/L+C$ condition for observer LR; data for the other observer were very similar. Open symbols give data from gratings and show the perceived speed of luminance-plus-color gratings (left ordinate), relative to luminance-only gratings. Filled symbols give data from plaids and show the direction of $L/L+C$ plaids (right ordinate) and the corresponding speed of the luminance-plus-color component (left ordinate). The IOC prediction is that the plaid's direction should be determined by the grating's perceived speed; the plaid direction data (filled symbols) should be at the level of the grating speed data (open symbols). Instead, the plaid directions and the grating speeds form two distinct, nearly non-overlapping, distributions, with plaid direction at the level of the dashed line, indicating veridical perception of plaid direction. In general there is no tendency to see a $L/L+C$ plaid as veering away from the direction of the luminance-plus-color component, despite the perceived sluggishness of this component when it is viewed as an isolated grating. The only exceptions are two points at the lowest spatial frequency and luminance contrast. Here the number of visible pattern cycles is small, the displacement phase angle is small, and the perceived speed is slow; consequently, estimates of direction are error-prone.

Data for the $C/L+C$ condition, in Fig. 3b, show a very different pattern. Perceived plaid direction (filled symbols) deviates from the veridical (dashed line) and is in the vicinity predicted by the perceived speed of the component luminance-plus-color grating (open symbols). For one observer the plaid was further from the veridical than predicted by the component speed and for the other the plaid was closer to the veridical. At least qualitatively, adding luminance contrast to one component of a chromatic plaid has the expected effect of moving the plaid's perceived direction toward the direction of the apparently faster luminance-plus-color grating.

Data for the two conditions are consistent with the expectations generated by Experiment 1: Adding luminance to one component of a chromatic plaid has a major effect on perceived direction, while adding color to one component of a luminance plaid produces no effect. Yet in both cases the addition changes the perceived speed of the component when it is viewed as an isolated 1-D pattern.

4. Experiment 3: motion nulling

Whether assessed by judgments of speed (Experiment 1) or direction (Experiment 2), the motion of 2-D patterns defined by both luminance and color is largely immune to the slowing that color imposes on the perceived motion of 1-D patterns. Another technique for assessing the contribution of color is motion nulling. Cavanagh and Anstis (1991) superimposed two gratings that drifted in opposite directions. One was a luminance grating and the other was a compound grating containing both luminance and chromatic contrast. Observers adjusted the luminance contrast of the compound grating in order to cancel the motion of the luminance-only grating. The motion null, undisturbed by either a net rightward or leftward drift, typically occurred when the luminance contrast of the compound grating was less than that of the simple grating drifting in the opposite direction; this contrast difference is a measure of the color's equivalent luminance contrast for motion nulling. The nulling method is applied to plaids here, to examine color's contribution to 2-D motion.

4.1. Methods

Motion nulls were measured between oppositely drifting gratings, as in Cavanagh and Anstis's (1991) study, and between oppositely drifting plaids. In one condition observers adjusted the luminance contrast of a luminance-plus-color grating to null the motion of a superimposed luminance grating drifting in the opposite direction. The drift directions of the two gratings were reversed from trial to trial with a probability of 0.5. In the other condition the procedure was the same except that plaids were used instead of gratings, as shown in Fig. 4a. The luminance-only plaid had fixed contrast; the luminance-plus-color plaid had adjustable luminance contrast. In both conditions all the gratings presented within a run had the same spatial frequency (0.5, 1.0, or 2.0 c deg^{-1}) and speed (2 deg s^{-1}). Orientations of 45 or 135° were used in the grating nulling condition and gratings of these two orientations were combined in the plaid nulling condition. The plaid drift direction was leftward or rightward. A range of contrasts was used for the simple luminance grating (20 ×, 40 ×, or 80 × detection threshold) and chromatic component of the compound grating (10 ×, 20 ×, or 40 × detection threshold). All combinations of these luminance and color contrasts, of which only one appeared within a run, were used at each spatial frequency. The opposed-motion patterns, either gratings or plaids, were combined optically.

Trials were untimed and observers could take as long as needed to achieve a motion null. A nulling contrast was found by sliding the mouse to the left or right, to lower or raise contrast. When satisfied with the setting, the observer terminated the trial with a click of the mouse; the following trial started with the next click, but only after the previous setting had been erased by moving the mouse leftward or rightward beyond a critical distance. It typically took less than 10–15 s to find a null after the initial practice period.

4.2. Results

The ratio of the fixed luminance contrast and the variable luminance contrast at the null setting is an index of color's contribution to motion nulling. Fig. 4b shows that this contrast ratio for observer LR averaged over the various fixed levels of both luminance and color contrast. This contrast ratio—color's relative equivalent luminance contrast—is non-zero and increases with spatial frequency. Our main interest is in comparing values for 1-D motion (gratings) and 2-D motion (plaids) and these values (closed and open symbols, respectively) are approximately the same at all spatial frequencies tested. Therefore, it seems that color's contribution to 2-D motion, measured by its power to null the motion of luminance stimuli, does not differ from its contribution to 1-D motion. These data are not in agreement with the speed and direction data of Experiments 1 and 2, which show color making little or no contribution to the 2-D motion of luminance-bearing patterns. By the criterion of motion nulling, the motion signals derived from luminance and color appear to be qualitatively equivalent and interchangeable, and quantitatively the same for 1- and 2-D patterns.

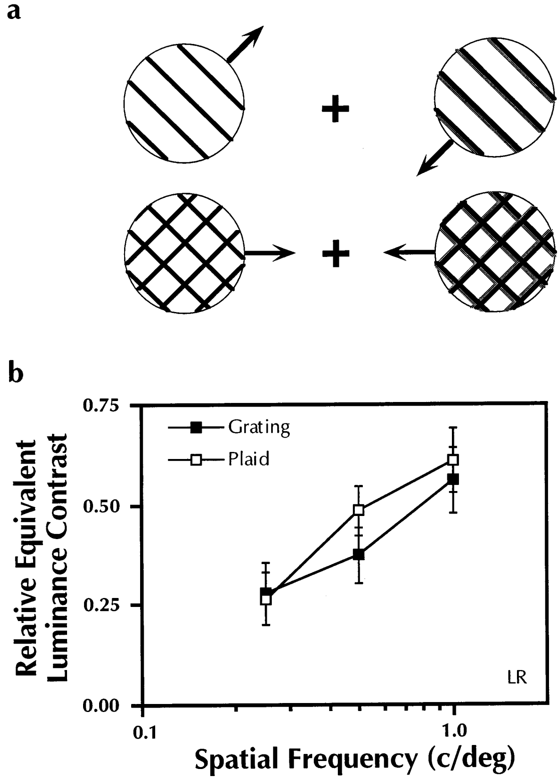

Fig. 4. (a) Stimulus configurations in motion nulling. Luminance (left) and luminance-plus-color (right) gratings or plaids with opposite directions of motion were optically superimposed. The luminance contrast of the luminance-plus-color combination was adjusted to achieve a cancellation of directional motion. (b) Equivalent luminance contrast of color for gratings (closed symbols) and plaids (open symbols) as a function of spatial frequency. Equivalent luminance contrast was measured as the ratio of the luminance contrasts at the motion null of the oppositely moving components. A value of 1 indicates that the motion of luminance was canceled by the opposed motion of color alone, without added luminance contrast; a value of 0 indicates that color did not contribute to the cancellation. Equivalent luminance contrast varies with spatial frequency but does not statistically differ between 1- and 2-D motion. Error bars are ±1 S.E. Luminance and chromatic contrast (variations of which have been averaged in the figure) traded off approximately linearly; i.e. raising the contrast of the simple luminance grating decreased, close to proportionately, the relative contribution of a given chromatic contrast to the motion null. Conversely, raising the chromatic contrast decreased the variable luminance contrast that had to be added to cancel motion in the opposite direction.

One idea for reconciling this lack of agreement over color's contribution to 1-D versus 2-D motion is that nulling results from a cancellation of 1-D motion signals irrespective of whether the stimulus is a grating or a plaid. In this case, motion nulling between plaids would occur before 1-D motion signals are combined to yield 2-D motion. Suppose, to the contrary, that the derivation of 2-D motion precedes nulling, so that motion signals from both 1- and 2-D patterns might coexist at the site of cancellation. Then it should be possible to null the motion of a plaid with the motion of a grating drifting in the opposite direction. An experiment was run in which two observers attempted to null the coherent motion of a plaid with a variable-contrast grating having the opposite drift direction. The grating was oriented perpendicular to the plaid's drift direction, its spatial period was the same as the plaid's in this direction, and the temporal frequencies of the plaid and the grating differed only in sign; i.e. same speed, opposite directions. Both patterns were modulated in luminance only. If nulling occurs only between 1-D motion signals, no nulling should occur between these patterns at any contrast ratio, because there are no 1-D motion signals with opposite drift directions, and no nulling, or trend toward nulling, was observed. There was only transparent motion at all contrast settings for both observers.

In sum, this experiment was intended to compare color's equivalent luminance contrast for 1- and 2-D motion. The relative luminance and color contrasts required for nulling grating motion were expected to differ from those required for nulling plaid motion, yet no difference was found. One possibility is that nulling depends on motion mechanisms that are separate from those underlying perceived speed and direction. Another possibility, supported by attempts to null the motion of a plaid with the motion of a grating, is that the experiment did not measure what it was intended to measure; instead, the nulling procedure measured color's equivalent luminance contrast for 1-D motion whether the stimuli were 1- or 2-D.

5. Discussion

The experiments show two main things. The first, that the perceived speed of drifting gratings varies with the ratio of luminance and color contrast, has been known from previous research (Cavanagh & Favreau, 1985; Mullen & Boulton, 1992). Isoluminant gratings appear to move slowly compared to pure luminance gratings, and gratings modulated in both luminance and color lie somewhere in between. The second finding, that these results for drifting gratings do not generalize to drifting plaids, is surprising in its own right and in what it implies. A plaid modulated in luminance or in color is seen to move with a speed and direction that are commensurate with the perceived speeds of its 1-D components. Yet the perceived speed or direction of a plaid modulated in both luminance and color is not limited by the perceived speed of the 1-D components. For non-isoluminant stimuli, the visual system appears to derive 2-D speed (Experiment 1) and direction (Experiment 2) from luminance. Color makes no contribution to the perception of 2-D motion of patterns defined by both color and luminance. Whether color affects the nulling of 2-D motion signals is unclear, but the evidence that it does is not convincing (Experiment 3). Note that the perceived speed of color gratings and plaids will depend on how close these nominally isoluminant patterns are to a true isoluminant red/green balance, but a red/green imbalance would not affect the critical finding that perceived 1- and 2-D motion differ qualitatively in their sensitivities to the chromatic content of the stimulus.

The differing effects of luminance/color ratio on perception of 1- and 2-D motion were shown not to result from physical speed or contrast differences between gratings and plaids. Attentional tracking can influence perceived speed (Cavanagh, 1992) and is another possible source of the results. It is possible that attention is especially attracted to, or especially adept at tracking, 2-D luminance patterns. This could weaken the influence of color on 2-D motion. However, color gratings were the stimuli used to demonstrate attentional tracking and its ability to make apparent speed more veridical (Cavanagh, 1992). So, the more likely effect of tracking is to decrease the difference in the perceived speeds of color and luminance stimuli and, if it is not engaged consistently, to increase the variability of the data for color stimuli, either within or between observers. In any case, there seems to be no basis for differential tracking of 1- and 2-D motion.

There is another route by which color might affect perceived speed when it is combined with luminance, via contrast masking. Near threshold contrast, luminance gratings are masked by chromatic gratings (e.g. De Valois & Switkes, 1983; Switkes, Bradley & De Valois, 1988). If suprathreshold luminance contrast is similarly affected by color, we might expect that adding color contrast to a luminance pattern would result in apparent slowing for two reasons. Not only would the apparently slow-moving color component contribute directly to the slowing of the composite pattern, but it might also reduce the contributing speed of the luminance component by lowering its apparent contrast (Thompson, 1982; Stone et al., 1990; Kooi et al., 1992a; Stone & Thompson, 1992). Yet, while this might have occurred with gratings, there is no evidence that it occurred with plaids, where color did not affect perceived speed. Hence, there is no evidence that it occurred at all. The masking effect might simply have been too small to be noticed. A more likely explanation is that masking of luminance by color does not occur in motion pathways. This is suggested by the data of Experiment 2, where luminance contrast in $C/L+C$ plaids was low and scarcely visible when combined with color, yet strongly affected perceived plaid speed and direction.

5.1. Relation between coherent motion and motion nulling

As noted in Section 1, the evidence has not been consistent in showing how color and luminance combine in motion pathways. Some studies support the independence of color- and luminance-based motion and some support interaction. What is especially puzzling is that the few studies that show independence are methodologically almost identical to some of the studies that show strong interactions. The results obtained here clarify why this is so.

If we superimpose an isoluminant opponent-color grating and a luminance grating with differing orientations and drift directions, we see independent moving transparent surfaces (Krauskopf & Farell, 1990; Cropper et al., 1996; Krauskopf et al., 1996). Yet, if we superimpose a leftward-drifting color grating and a rightward-drifting luminance grating, we usually do not see transparent motion. Instead, we see that color and luminance interact, resulting in motion cancellation (Chichilniski et al., 1993). Despite the opposing results, the only major stimulus differences are the relative grating orientations, and hence the drift directions: Motion nulling is obtained using gratings that are parallel, with collinear but opposite drift directions; motion coherence is obtained using gratings that are not parallel and whose drift directions are not collinear.

The importance of this seemingly minor difference is that the nulling paradigm assesses the processing of 1-D motion while the coherence paradigm assesses the processing of 2-D motion. The experiments reported here show that color contributes to motion perception when it is added to a drifting 1-D luminance pattern (just as color contributes to the nulling of a drifting luminance grating), and that color does not contribute to motion perception when it is added to a drifting 2-D luminance pattern (just as color does not contribute to the coherent motion of a plaid created by superimposing color and luminance gratings). Thus, the motion nulling and motion coherence paradigms do not yield incompatible results after all—motion is 1-D in the former and 2-D in the latter—and both are compatible with the present results. Color's contribution to motion appears to be contingent on both luminance and stimulus spatial structure: In the absence of 2-D luminance contrast, color is as effective a stimulus for 2-D motion as it is for 1-D motion; in the presence of 2-D luminance contrast, color is discounted by the motion system. This appears to hold across various motion paradigms: nulling, coherence, perceived speed, and perceived direction.

5.2. Relation to motion coherence

The contingency of color- and luminance-based motion interactions on spatial structure—1-D versus 2-D pattern—also converges unexpectedly with the results of Krauskopf et al. (1996). Krauskopf et al. (1996) examined the relative coherence of plaids as a function of the angular separation of the color-space modulations of the component gratings. They found that within the isoluminant plane coherence was minimal for grating whose color-space modulations were separated by 90°. Within a plane containing the luminance axis and a cardinal opponent-color axis, however, they found that coherence was minimal for gratings whose modulations were along different cardinal axes (see also Dobkins, Stoner & Albright, 1998). These data suggest that the isoluminant plane is populated by multiple motion-sensitive mechanisms (or contains interacting cardinal-axis mechanisms) and that outside this plane there is a single independent motion mechanism that is selective to luminance. As a result, any grating not confined to the isoluminant plane will be seen by the luminance mechanism. This is why pairs of these gratings, even with color-space separations of 90°, are seen to move coherently (Krauskopf & Farell, 1990). But another way of saying this is that luminance alone contributes to the coherent motion of non-isoluminant stimuli. And this is none other than the conclusion drawn from the perceived speed and direction data presented here—that color makes no contribution to the 2-D motion (e.g. coherent motion) of luminance-bearing patterns.

5.3. Relation to physiology

Single-unit recording suggests that primary visual cortex contains neurons responsive to 1-D component motion, but not to 2-D pattern motion, and that the middle temporal cortical area MT contains neurons responsive to 1-D component motion and less-numerous neurons that respond to 2-D pattern motion (Movshon, Adelson, Gizzi & Newsome, 1985; Rodman & Albright, 1989). MT neurons show a reduced sensitivity near photometric isoluminance and little selectivity to color (Saito, Tanaka, Isono, Yasuda & Mikami, 1989; Dobkins & Albright, 1994; Gegenfurtner, Kiper, Beusmans, Carandini, Zaidi & Movshon, 1994; Tootell, Reppas, Kwong, Malach, Born, Brady et al., 1995). It is tempting to draw a link between the weakness of color's contribution to perceived 2-D motion and MT's preference for luminance. However, 2-D motion perception is neither color blind nor less effectively driven than 1-D motion perception by pure chromatic modulations. Not only are isoluminant color plaids seen to move coherently as 2-D patterns (Krauskopf & Farell, 1990; Kooi et al., 1992b; Krauskopf et al., 1996), but they also have a perceived speed commensurate with the perceived speeds of their 1-D components (Figs. 1 and 2), just as luminance plaids do (Stone et al., 1990; Kooi et al., 1992a). One can deduce from this that coherent motion of chromatic stimuli is not mediated primarily by area MT.

5.4. Relation to two-stage models

The data of this study support separate processing of 1- and 2-D motion in the following two senses. First, the data show that 1- and 2-D motion signals do not derive exclusively from successive processing stages (cf. Adelson & Movshon, 1982), for the perceived motion of 1-D luminance-plus-color components does not predict the perceived motion of composite 2-D patterns. Second, and for the same reason, the data are not consistent with the idea that the perception of 1-D motion and the perception of 2-D motion depend on the same two-stage analysis (cf. Wright & Gurney, 1992). With differing susceptibility to the influence of color, 1- and 2-D motion perception must derive, in part, from separate processes—though not from distinct processing *stages*. Consider first an unadorned two-stage model of object motion (Adelson & Movshon, 1982) that integrates across directions of color space before integrating across directions of motion. Motion signals from luminance and color gratings would be combined in a first stage, giving rise to apparently slow luminance-plus-color 1-D motion signals, in agreement with the data. But then these 1-D signals would be combined at the second stage, yielding correspondingly slow 2-D motion of luminance-plus-color plaids, which, as Experiments 1 and 2 show, is wrong.

Next consider the alternative, in which stages 1 and 2 run in parallel for luminance and color. In the case of plaid stimuli, this gives rise to separate 2-D motion signals, one for luminance and one for color, which are then combined to give a final luminance-dominated velocity signal. But this implies that motion signals from luminance and color are combined at one site for 1-D motion and a different site for 2-D motion. This is problematic. The decision to combine the luminance and color motion signals for, say, a 45° grating at stage 1 would be contingent on the presence of another luminance-plus-color grating at, say, 135°. A model with a Fourier energy first stage would have difficulty implementing such a contingency. The upshot is that a two-stage analysis works for the motion of luminance-defined and color-defined stimuli, but breaks down when the motion is defined by luminance-plus-color. Thus, the implication is that 1- and 2-D motions are computed separately (or with feedback, which undermines with the very notion of stages).

It might seem that the data support the notion of three separate motion pathways, one for luminance, one for isoluminant color, and another for luminance-color combinations (Gorea & Papathomas, 1989; Webster et al., 1992). While there are three apparent-speed regimes evident in the data, the luminance-plus-color regime is distinct only in 1-D motion. Thus we can more parsimoniously conclude that motion analysis has access to parallel color and luminance pathways, which are combined differently for 1- and 2-D patterns.

5.5. Relation to motion perception in the real world

Compared to their performance with luminance stimuli, humans tend to see isoluminant stimuli as moving more slowly (Moreland, 1982; Cavanagh et al., 1984), to judge the direction of 2-D isoluminant patterns less accurately (Gegenfurtner, 1998), and to be more contrast-dependent in their motion perception at isoluminance (Hawken et al., 1994; Krauskopf & Li, 1996; Burr et al., 1998b). This suggests that color-based motion perception is less veridical than luminance-based motion perception (Gegenfurtner & Hawken, 1996). It would seem, then, that there is adaptive value in discounting color's motion signal.

The data of Experiments 1 and 2 suggest the visual system does something more subtle, that it discounts color's motion signal contingently, varying color's contribution with the spatial structure of the stimulus. This contingency offers an added adaptive advantage. By discounting color, we are able to see 2-D luminance-plus-color patterns as moving nearer their true speeds and directions. By discounting color contingently, we can also see 2-D isoluminant patterns (which, being rare and fortuitous in natural scenes, provide little selective pressure toward veridical perception) as moving at all.

By comparison, the visual system's lack of compensation for color's slowing of 1-D patterns seems curiously remiss. But the oversight is more apparent than real, for 1-D motion is ambiguous, having an underdetermined 2-D velocity whether it is signaled by luminance or color; there is no veridical 2-D signal that can be recovered from 1-D motion by ignoring color.

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