

COLOR AND LUMINANCE SHARE A COMMON MOTION PATHWAY

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Abstract—Following exposure to a moving grating of bars differing only in luminance, a motion aftereffect (MAE) is observed on a stationary grating of bars differing only in chrominance. This suggests that the motion of equiluminous chromatic stimuli is sensed by a channel that responds to both luminance and chrominance and not by a separate channel specialized for the motion of colored stimuli. However, adding color to a low contrast luminance stimulus actually reduces its effectiveness at creating or nulling a MAE, indicating that the response of the motion pathway to color is qualitatively different from its response to luminance. In addition, a chromatic stimulus demonstrates a dissociation between perceived speed, MAE speed and speed required to null the MAE that is absent for a luminance stimulus.

Motion Motion aftereffects Color

INTRODUCTION

Zeki (1978) has reported that in the macaque monkey, whose visual system closely resembles that of humans, color and motion are analyzed in two separate areas of the prestriate cortex. If, as his evidence suggests, the movement area is not concerned with color and the color area is not concerned with movement, then the perception of the motion of stimuli defined solely by color should pose problems for the visual system.

In fact, motion can be seen with equiluminous, chromatic stimuli although the quality of the motion is degraded (Moreland, 1982; Cavanagh *et al.*, 1984; Ramachandran and Gregory, 1978; Cavanagh *et al.*, 1985). There may therefore be two independent motion channels, one that senses moving chromatic contours and the other moving luminance contours. We have previously reported a similar independence of chrominance and luminance pathways for the analysis of spatial frequency (Favreau and Cavanagh, 1981). Alternatively, there may be only a single motion channel that is sensitive primarily to luminance but that also has some response to equiluminous stimuli.

To examine these possibilities we studied the transfer of motion aftereffects between luminance and chrominance stimuli. After prolonged exposure to a stimulus drifting to the right, a subsequently viewed stationary display appears to move to the left (Sekuler and Pantle, 1978). This negative motion aftereffect has been attributed to the selective fatigue of motion detectors, in this case, those for rightward motion (Wohlgemuth, 1911; Sutherland, 1961; Mather, 1980). The resulting imbalance in the neural response to a stationary test stimulus then creates the impression that this stimulus is moving to the left. Transfer of a motion aftereffect induced by a stimulus

with luminance contrast to a colored test stimulus with no luminance contrast provides evidence that color and luminance share a common motion pathway.

EXPERIMENT 1

We used two techniques to measure the motion aftereffect: matching and nulling. In the first, the observer matched the apparent velocity of the MAE seen on a static colored test grating by adjusting the velocity of a comparison luminance grating; in the second, the observer nulled the MAE by adjusting the actual motion of the colored test grating until the test appeared stationary.

Method

In the matching procedure, observers adapted to a moving yellow/black sinewave grating in the lower half of the visual field while a uniform yellow field was presented in the top half. The test display consisted of a stationary red/green sinewave grating in the bottom (adapted) half of the field and a luminance comparison grating (a yellow/black sinewave) in the top (unadapted) half. The observers adjusted the velocity of the upper grating to match that of the MAE seen on the lower grating while fixating a central white cross.

The display subtended 10 by 10 deg of visual angle and the gratings had a spatial frequency of 1.6 c/deg. The adapting grating drifted at a velocity of 2.34 deg/sec, always from left to right. The luminance contrast of the adapting grating was 95%, and that of the comparison test grating 15%. The red/green test grating had 70% of the maximum chrominance modulation obtainable on the T.V. monitor. The CIE x and y coordinates of the monitor were 0.60, 0.35 for red and 0.29, 0.60 for green. The x and y coordinates

of the yellow mid-point used throughout were 0.48, 0.44. All displays had a mean luminance of 25 cd/m². The equiluminance setting of the colored test gratings was determined for each observer by minimum motion heterochromatic photometry (Anstis and Cavanagh, 1983). The setting of equiluminance also compensates for the effects of chromatic aberration.

Axial chromatic aberration of the eye makes it impossible for both red and green to be in focus simultaneously, and therefore the two colors must have different degrees of blurring on the retina. Since the sole effect of blurring on a sinewave is to reduce its contrast, the difference in focus between the red and green sinewaves creates only a shift in their relative contrasts. Once this artifactual shift is compensated by setting equiluminance, it remains compensated throughout the experiment as long as the observer does not change accommodation. Given the low spatial frequency of our stimuli, chromatic aberration effects were limited to a shift in the luminance ratio of the red and the green of less than 1% for the worst case change of accommodation during the experiment.

In order to eliminate this potential shift, a textured fixation field was used to ensure a constant state of accommodation. The fixation field separated the upper and lower gratings and spanned the entire display (10 deg by 1.88 deg). It was made up of 100% contrast black and white random dots, with dot size of 0.16 deg. Since chromatic stimuli have almost no influence on accommodation (Wolfe and Owens, 1981), the large, textured, black and white field provided a good stimulus to maintain a constant state of accommodation. A 0.31 deg white cross on a dark square was presented as a fixation target in the center of this field. To verify that this procedure was effective, we also made several observations using the PWC five-element achromatizing lens (Powell, 1981) and obtained readings consistent with those taken without correction. The adapting display was presented for 5 sec and the test display for 1 sec. The two displays alternated continuously and after waiting a short period for the MAE to build up, the observer adjusted the comparison velocity until an acceptable match was found. At least four trials were run in each condition. The luminance ratio of the red and green in the test grating was varied across conditions. Five values were used: -10, -5, 0, 5 and 10% luminance modulation between the red and green, with the preliminary estimate of the equiluminance point of each observer being arbitrarily equated to 0%. Therefore, for a photometric ratio, v , between green (G' , in cd/m²) and red (R' , in cd/m²) at equiluminance,

$$v = G' / R'$$

$$L_{\text{mod}} = (v \cdot R_{\text{amp}} - G_{\text{amp}}) / (v \cdot \bar{R} + \bar{G})$$

where L_{mod} is the amplitude of the luminance modulation of the red/green sinewave in percent, R_{amp} and

G_{amp} are the amplitudes of the red and green sinewaves in cd/m², respectively, and \bar{R} and \bar{G} are their mean luminances in cd/m².

The nulling procedure was identical to the matching procedure with the following exceptions. During the adapting phase, a high-contrast, yellow/black grating was presented in both the top and bottom halves of the display and the two halves moved in opposite directions (top to the left, bottom to the right). The test gratings were red/green sinewaves in both the top and bottom halves, and the two halves could be made to move in opposite directions by the subject in order to null the MAE.

The two authors served as observers.

Results

Figure 1 shows the matching velocity as a function of the luminance contrast of the red/green test grating. The equiluminance point of each subject is designated zero. Both observers showed a MAE at equiluminance. In general, the apparent MAE velocity appeared to be independent of the luminance contrast of the red/green test grating. The red/green tests with 10% luminance modulation were well above their luminance contrast threshold (De Valois and Switkes, 1983) so that if there were any difference between MAEs seen for chrominance and luminance stimuli it would have been readily demonstrated.

In contrast, the top two curves of Fig. 1 show that the nulling speed increased significantly around the equiluminance point. The nulling and the match procedures gave comparable estimates of the MAE speed when there was 10% luminance contrast in the

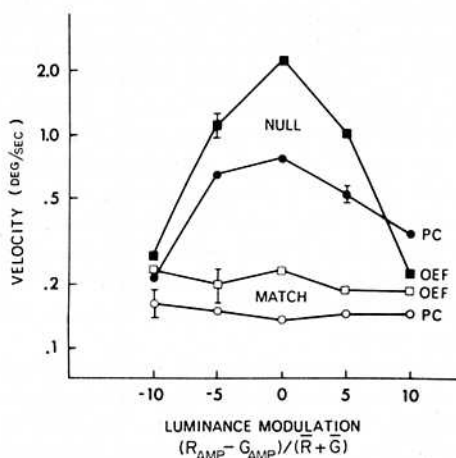


Fig. 1. Motion aftereffects measured by matching speed (open circles and squares) and nulling speed (solid circles and squares) as a function of the luminance modulation of the red/green sinewave test grating. Negative modulations indicate that green was more luminous than red, and positive modulation that red was more luminous than green. Spatial frequency of adapt and test stimuli was 1.6 c/deg, velocity of adapting grating was 2.34 deg/sec. Vertical bars represent typical standard errors. Observers P.C. and O.E.F.

colored test stimulus. The velocity required to match the apparent MAE speed was about 0.2 deg/sec while the velocity required to null the MAE was 0.2–0.3 deg/sec. The discrepancy between the two measures only becomes substantial around equiluminance. The required nulling for a test with 0% luminance contrast (equiluminance) was about five times that required when 10% luminance contrast was present in the test. This increase in nulling speed could indicate either that the MAE was stronger on an equiluminous test or that the nulling power of the moving equiluminous test grating was weaker. Since the matching task showed that there was no increase in the apparent MAE velocity at equiluminance, we conclude that the equiluminous test was, in fact, less efficient in nulling the MAE.

EXPERIMENT 2

Both techniques therefore show transfer of a MAE from an inducing luminance grating to an equiluminous test grating. However, after adapting to a moving stimulus, a MAE can be seen on a blank field and it could be argued that the MAE seen on the equiluminous test grating was a nonspecific MAE of this kind. To examine this possibility, we adapted the observers to a drifting luminance grating at one spatial frequency and measured the MAE for an equiluminous test grating at several different spatial frequencies. We tested three adapting spatial frequencies and five test spatial frequencies, using the nulling procedure.

Method

Equiluminance was preset individually for each spatial frequency of the chromatic test using the technique described by Anstis and Cavanagh (1983). At least four readings were taken at each of the 15 combinations of the three luminance adapting spatial frequencies (0.8, 1.6 or 3.2 c/deg) and the five chromatic test spatial frequencies (0.4, 0.8, 1.6, 3.2 and 6.4). The velocity of the adapting grating was always 2.34 deg/sec. The displays and nulling procedure were otherwise identical to those of Experiment 1. The two authors served as observers.

Results

The maximum MAE, measured by nulling, always occurred when the adapting and test gratings had the same spatial frequency [Fig. 2(a) and (b)], showing that the effect was stimulus specific. The transfer of the aftereffect to an equiluminous test grating cannot be due to a nonspecific MAE which could show no spatial frequency tuning.

The tuning of the curves in Fig. 2 shows that the motion channel is selective for the spatial frequency of a moving stimulus as Over, Broerse, Crassini and Lovegrove (1973) have shown. The curves show a marked asymmetry, however: the MAE nulling dropped off more rapidly above the spatial frequency

of the adapting stimulus than it did below. In several cases, the curves have almost a low-pass characteristic. The upper half-bandwidth at half-amplitude can be evaluated, however, and is about 0.6 octaves—similar to the value found by Over *et al.* (1973).

EXPERIMENT 3

Next we examined the four combinations of adaptation to drifting color or luminance gratings followed by color or luminance test, using the nulling

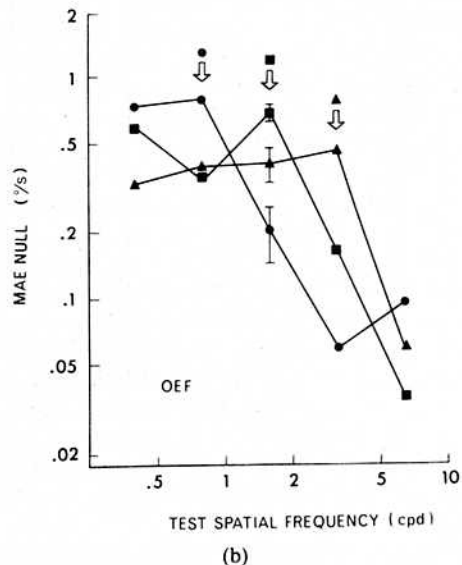
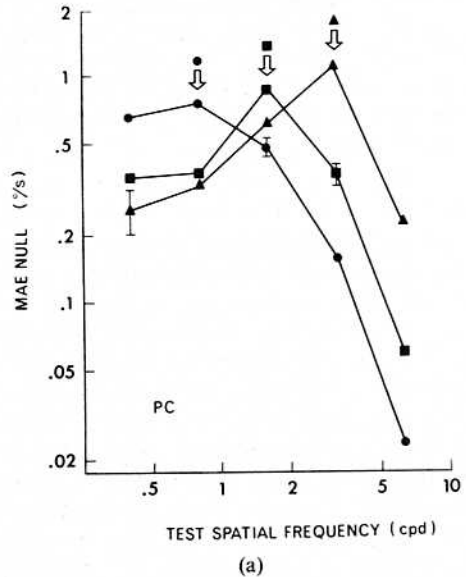


Fig. 2. MAE nulling speed as a function of the spatial frequency of the chromatic test for observers P.C. and O.E.F. The spatial frequency of the luminance adapting grating for each curve is indicated by the open arrows. The circles are the data points for the 0.8 c/deg adapting grating, the squares for the 1.6 c/deg adapting grating and the triangles for 3.2 c/deg adapting grating. The velocity of the adapting gratings was 2.34 deg/sec. Vertical bars represent typical standard errors.

procedure. The velocity of the adapting grating was varied to determine if there were any differences in velocity tuning of the MAE for chrominance and luminance stimuli.

Method

The spatial frequency of the adapting and test gratings was 1.6 c/deg. The nulling procedure was used as described for Experiment 1. Each observer made at least four settings at each of the 20 combinations of the five adapting speeds (0.59, 1.17, 2.34, 4.69 and 9.38 deg/sec), two adapting stimuli (95% luminance contrast, yellow/black or 70% chrominance modulation, red/green) and two test stimuli (15% luminance contrast, yellow/black or 70% chrominance modulation, red/green). The two authors served as observers.

Results

The amount of nulling required increased directly with the speed of the luminance adapting grating (Fig. 3) for both luminance and chrominance tests. As was seen in Experiment 1, about five times more nulling was required for the chromatic test than for the luminance test. When the adapting stimulus was a chromatic grating (Fig. 4), there was again approximately five times more nulling required for the chromatic test than for the luminance test. However, the required nulling reached a maximum at an intermediate speed of the chromatic adapting grating and dropped off with further increases. In addition the nulling required after adaptation to a chromatic grating was, in general, much reduced compared to that required after adaptation to a luminance grating (note the change in scale between Figs 3 and 4).

These data suggest that a drifting luminance grating generates a strong input to the motion system while a drifting color grating produces only a weak input. The fact that transfer was obtained in both directions again supports the idea that both signals are carried on a common pathway. In addition, the fact that the ratio between MAE nulling velocity for the chromatic test and that for the luminance test was similar whether the adapting stimulus was color or luminance suggests again one locus of adaptation. If there were separate color- and luminance-specific pathways, then we should have observed an interaction reflecting a stronger MAE when both adaptation and test were of similar type than when they were different.

The drop-off in nulling required at higher speeds of the adapting chromatic stimulus implies that the effectiveness of the adapting chromatic stimulus decreased at speeds above 2 or 3 deg/sec. Pantle (1974) reports that the effectiveness of an adapting luminance stimulus in creating a MAE also decreases above a certain speed but evidently we didn't reach the critical speed for the luminance stimuli in this experiment.

EXPERIMENT 4

We have previously observed (Cavanagh *et al.*, 1984) that drifting equiluminous gratings appear significantly slower than do gratings with luminance contrast moving at the same speed. It might be argued that the decrease in nulling effectiveness of chromatic gratings in our MAE task is directly related to their slower apparent speed. To examine this possibility, we measured the actual observed speed of the chromatic and luminance test gratings of Experiment 3 in the absence of adaptation.

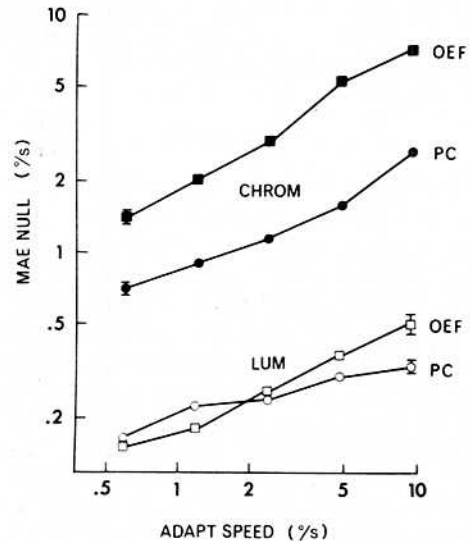


Fig. 3. MAE nulling speed as a function of the speed of the adapting luminance grating for observers P.C. and O.E.F. The data for the chromatic test gratings are given by the solid symbols and those for the luminance test gratings by the open symbols. Adapt and test spatial frequency was 1.6 c/deg. Vertical bars represent typical standard errors.

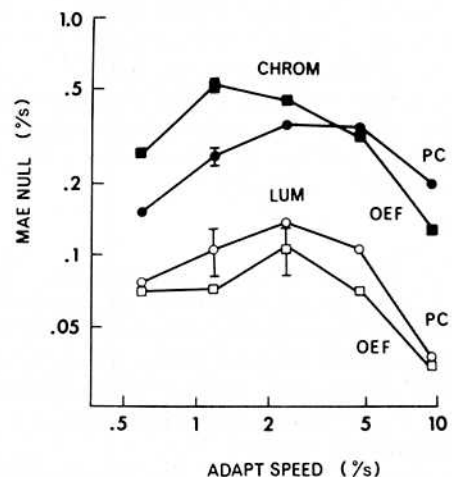


Fig. 4. MAE nulling speed as a function of the speed of the adapting chromatic grating for observers P.C. and O.E.F. The data for the chromatic test gratings are given by the solid symbols and those for the luminance test gratings by the open symbols. Adapt and test spatial frequency was 1.6 c/deg. Vertical bars represent typical standard errors.

Method

The procedure was identical to the matching procedure of Experiment 1 with the following exceptions. First, during the adapting intervals, the adapting field was blank. Velocity matches were therefore made during the 1 sec test intervals separated by 5 sec of a blank field. Second, during the test interval the lower grating was made to move at a predetermined speed and the observer adjusted the speed of the low contrast luminance comparison grating in the upper half to match the apparent velocity of the lower grating. Finally, both equiluminous red/green gratings and low contrast (15%) luminance test gratings were used as tests. For the chromatic tests, both authors served as observers and five different velocities were presented for the chromatic test (0.59, 1.17, 2.34, 4.69 and 9.38 deg/sec). For the luminance test only three velocities were used (0.59, 2.34 and 9.38) and readings were only taken by observer P.C.

Results

The matched speed was between 50 and 75% of the actual speed (Fig. 5) for the chromatic tests but was approximately 100% of the actual speed for the luminance tests. The luminance test at 15% contrast was considerably above the 3–5% contrast at which we previously reported a noticeable slowing of luminance gratings (Cavanagh *et al.*, 1984).

The test speed did not systematically affect the amount of slowing observed for the chromatic test. The apparent slowing alone does not seem to account for the reduction in nulling effectiveness at equiluminance (about 20% that of the luminance stimulus, Experiments 1 and 3) nor for the drop off in

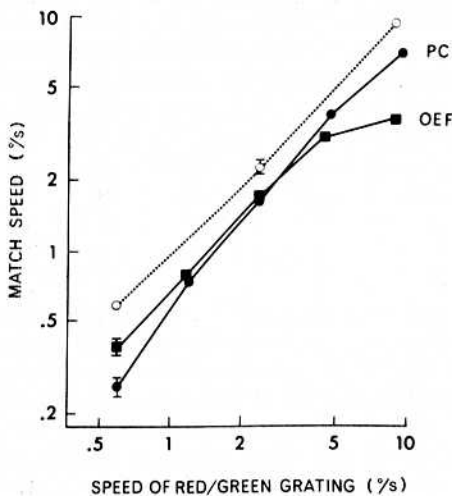


Fig. 5. Matched speed for a drifting grating with no adaptation as a function of actual speed. Solid symbols show the data for the equiluminous red/green stimulus for observers P.C. and O.E.F. The open circles show the matched speed for the control condition of a drifting luminance grating for observer P.C. The spatial frequency of the tests was 1.6 c/deg. Vertical bars represent typical standard errors.

adaptation effectiveness seen in experiment 3 for adapting speeds in excess of 2 or 3 deg/sec.

EXPERIMENT 5

Studies of cells in the lateral geniculate have shown a wide variation in the neutral point of their response to colored stimuli—the wavelength at which the cell crosses over from an excitatory to an inhibitory response (Zrenner, 1983; Schiller and Colby, 1983). If the equiluminance points of individual detectors in a luminance-specific motion pathway were equally variable, then no one luminance ratio would be able to silence all the detectors simultaneously. The transfer we observe from chrominance adaptation to luminance test, and vice versa, might then be mediated by a purely luminance-sensitive pathway for which there is no effective null point. If this were the case, the response to an equiluminous stimulus would be similar to that for a low-contrast luminance stimulus.

In at least two respects, a moving, equiluminous stimulus behaves like a low-contrast luminance stimulus. Compared with high-contrast displays, both are less effective at creating a MAE (Keck *et al.*, 1976) and appear to move more slowly (Cavanagh *et al.*, 1984; Thompson, 1982). However, the results we report from this final experiment imply that equiluminous stimuli are not treated by a luminance-sensitive pathway as simply low-contrast stimuli. We found that if chrominance is added to a low-contrast luminance grating it becomes even less effective in generating and in nulling a MAE.

Method

In the first condition, two observers (one of the authors and a naive observer) adapted to a high-contrast, drifting luminance grating. The MAE was measured by nulling, as described in Experiment 1, but now the test grating always had 5% luminance contrast—just above contrast threshold when in alternation with the adapting grating which had 95% contrast. The chrominance modulation of the test grating was varied from -64% to +64%, that is, from red/green with green more luminous than red, through yellow/black, and back to red/green but now with red more luminous than green. The luminance modulation was always 5%.

In the second condition, the observers (an author and a second naive observer) were adapted to a drifting grating of 5% luminance contrast combined with various levels of chrominance modulation. The test was always a red/green grating with 0% luminance modulation and 64% chrominance modulation where 100% chrominance modulation is defined as the maximum modulation obtainable between the red and green phosphors of the monitor.

Results

When the adapting stimulus was a high contrast

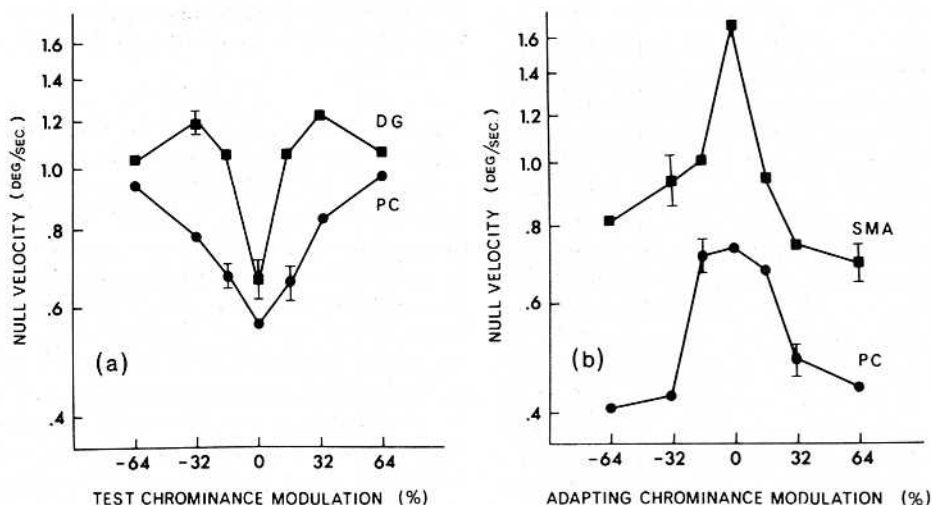


Fig. 6. (a) MAE nulling speed as a function of chrominance modulation of the test grating. Adapting grating was a high-contrast yellow/black sinewave. Test grating had 5% luminance modulation at all chrominance values. Green was more luminous than red at negative chrominance modulation and red was more luminous than green at positive values. Vertical bars indicate typical standard errors. Observers P.C. and S.M.A. (b) MAE nulling speed as a function of chrominance modulation of the adapting grating. The adapting grating had 5% luminance modulation at all chrominance values. The test grating was always an equiluminous red/green sinewave (70% chrominance modulation, 0% luminance modulation). Vertical bars indicate typical standard errors. Observers P.C. and D.G.

luminance grating and the test a low contrast luminance grating with varying amounts of chrominance modulation, the velocity required to null the MAE was lowest at 0% chrominance modulation [Fig. 6(a)]. As chrominance was added, the required nulling velocity increased, implying a less effective nulling stimulus even though the luminance contrast remained constant.

When the adapting stimulus was a low contrast luminance grating with varying amounts of chrominance modulation and the test was an equiluminous red/green grating, the maximum nulling velocity was required when the adapting grating had only luminance contrast—adding chrominance reduced the required nulling velocity [Fig. 6(b)]. Since the test grating was always the same, this indicated a decrease in the effectiveness of the adapting stimulus as chrominance was added. Again effectiveness decreased even though the luminance contrast had remained fixed.

Since the effects of luminance and chrominance did not add linearly, we conclude that color does not act on the motion channel simply as a low-contrast luminance input. Color and luminance information must somehow interact before converging on the motion channel. De Valois and Switkes (1983) have reported a similar interaction in terms of contrast sensitivity: the contrast threshold for a luminance grating increases in the presence of a chromatic grating. (The 5% luminance contrast that we used in this experiment is well above this raised threshold.) Whether or not the mechanisms of the interaction

between color and luminance are the same in both cases—contrast sensitivity and MAE—is not clear.

An interaction might arise if the overall motion signal were the average of the signals from separate luminance and chrominance inputs, each weighted according to its contrast (luminance and chrominance contrasts, respectively). A weighted average decreases as the weight of the lower-valued component increases. If the motion signal from the color input underestimates the actual motion (Cavanagh *et al.*, 1984), then as the chrominance in the stimulus is increased, the lower estimate from the color input would be given more weight and the stimulus as a whole would become less effective and appear to move more slowly.

CONCLUSIONS

Our data suggest that color and luminance share a common motion pathway to which color has only a weak input. This common pathway contrasts with the independent analysis of spatial frequency for chrominance and luminance inputs which we have reported previously (Favreau and Cavanagh, 1981). The existence of color-contingent motion aftereffects (Favreau *et al.*, 1972; Mayhew and Anstis, 1972) implies that some color-specific motion detectors exist. Color-contingent MAEs are much weaker than simple MAEs, however, suggesting that the proportion of color-specific motion detectors in the visual system is small. If there were a separate channel for detecting the motion of chromatic stimuli, MAEs

seen on a colored test should be greatest when the stimulus is also colored. Our own data in Fig. 6(b) show that when the adapting stimulus becomes more modulated in color there is actually a decrease in the MAE seen on a colored test grating.

Our evidence for the convergence of inputs onto a common motion pathway is consistent with Zeki's (1978) conjecture that there is only one cortical area for motion analysis. However, our data throw new light on the color sensitivity that we would expect for cells in such an area: they must respond to equiluminous colored stimuli, albeit weakly, as well as to luminance stimuli. De Valois and De Valois (1975) have reported "multicolor" cells in the striate cortex that respond to an edge whether defined by color or luminance contrast (see also Thorell *et al.*, 1984). These cells discriminate between colors but are indifferent to the colors involved. Our data suggest that it is cells of this type in the motion pathway that respond to moving equiluminous stimuli.

Finally, although these "multicolor" cells should respond to both color and luminance contrast, their response to color stimuli should be qualitatively different from that to luminance stimuli. In particular their response to color and luminance combined should be less than that to luminance alone, as we showed in Experiment 5. In addition, a luminance stimulus shows internal consistency in its perceived speed and nulling effectiveness. The luminance stimulus was perceived to move at its actual speed (Fig. 5) and the required nulling speed of an MAE observed on a luminance test was equal to the apparent speed of the MAE: the MAE matched speed was about 0.2 deg/sec in Fig. 1 for a stimulus with 10% luminance contrast; the required nulling was also about 0.2 deg/sec for this same stimulus in Fig. 1 as well as for the luminance tests in Fig. 3 for the same 2.34 deg/sec adaptation. However, none of this consistency was observed for color stimuli. The apparent speed of an equiluminous grating was about 50% of its actual speed (Fig. 5). The speed of an MAE on an equiluminous grating, about 0.2 deg/sec, was similar to that for a grating with luminance contrast when judged by matching (Fig. 1). However, the equiluminous grating had to move about five times faster than a luminance test to null the MAE (Figs 1 and 3). For the nulling velocity to be consistent with the decrease in the perceived speed, it should only have to be twice as fast for equiluminous tests as for luminance tests. These results imply that the effect of color stimuli on the "multicolor" motion cells is qualitatively different from the effect of luminance stimuli. They also imply that motion must be coded by several attributes as a single attribute code could not show the degrees of freedom involved in the dissociations we observed between perceived speed, MAE speed and required null speed.

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