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Absence of Smooth Motion Perception in Color Vision

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We have tested the behavioral evidence for a separation of the processing of color contrast from motion in the human visual system. Two different aspects of motion perception are examined; the identification of the direction of movement of a chromatic grating and the perception of smooth motion. The results show that color vision is at no great disadvantage in the identification of direction of movement, since this can be done at color contrasts quite close to detection threshold over a wide range of spatial and temporal frequencies. However, we find that subjects can identify direction without having the genuine perception of smooth motion. Smooth motion perception is revealed to be highly impaired since it is detected only at very high color contrasts and over a narrow range of spatial and temporal conditions.

Color Motion Isoluminance Direction discrimination Velocity perception

INTRODUCTION

Anatomical and physiological data suggest that separate color selective and motion selective "streams" can be identified in the primate visual cortex from amongst a complex set of parallel and interconnecting pathways (Zeki, 1978; Ungerleider & Mishkin, 1982; Van Essen & Maunsell, 1983; Hubel & Livingstone, 1987; DeYeo & Van Essen, 1988). The functional, physiological extent and the behavioral significance of this division, however, remain controversial (Lee, Martin & Valberg, 1988; Saito, Tanaka, Isomo, Yasuda & Mikami, 1989; Lennie, Krauskopf & Sclar, 1990; Shiller, Logothetis & Charles, 1990; Logothetis, Shiller, Charles & Hurlbert, 1990; Bullier, 1990).

A true functional parallel processing of color and motion would suggest that color contrast cannot be used to see motion in the image, in other words that color vision is motion blind. There is evidence to suggest that color contrast is deficient in supporting the perception of motion. It has been found (Ramachandran & Gregory, 1978) that isoluminant chromatic stimuli fail to produce the perception of movement from an apparent motion stimulus, although it remains unclear whether the failure is dependent on the choice of spatial and temporal parameters. It is also known that color-only (isoluminant) stimuli are perceived to move more slowly than stimuli with luminance contrast, or may even appear stationary (Moreland, 1982; Cavanagh *et al.*, 1984; Livingstone & Hubel, 1987). While these results point to significant differences in the processing of motion from color and luminance contrast, the nature of the chromatic deficit and its spatial and temporal extent remain ill-defined.

We have measured two different aspects of the performance of color vision on motion tasks; direction discrimination and the perception of smooth motion. The two measures were adopted since we found that the perception of smooth motion can fail even though the direction of movement can be correctly perceived. For example, direction information may be derived from the sequence of spatial positions of the stimulus without requiring a motion percept *per se*. Performance was measured for a wide range of spatial and temporal conditions in an attempt to reveal any conditions which may be favorable to chromatic motion processing for central vision.

METHODS

We used isoluminant chromatic test gratings to reveal the response of the chromatic mechanisms by depressing or eliminating the responses of achromatic mechanisms. Vertical red-green gratings were produced from two luminance modulated gratings displayed on Joyce DM2 monitors, viewed monocularly through narrow band interference filters, and combined in antiphase. The longitudinal and transverse chromatic aberrations of the human eye were corrected (Boulton & Mullen, 1990; Mullen, 1985). The contrast of the chromatic grating was defined as the Michelson contrast of its component luminance gratings. Stimuli were presented in a hard edged circular patch with at least four spatial cycles displayed, and with a mean luminance of 42 cd m^{-2}. A small fixation spot (4 min in dia) was provided (except for the lowest temporal frequency at the two smallest field sizes). Results were obtained on two subjects (KTM and JCB),

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and the key parts of the results were obtained on a third subject (GJ).

The isoluminant point was determined using a minimum motion method (Moreland, 1982; Cavanagh *et al.*, 1984; Boulton & Mullen, 1990) for each different temporal and spatial condition that was used. The perceived drift rate of a grating of a fixed high contrast was measured as a function of the ratio of red to green mean luminance in the stimulus using the velocity matching paradigm described below. This reveals a sharply defined minimum in perceived drift rate which was taken to indicate the isoluminant point (see Fig. 1, upper panels). We ascertained that the isoluminant point measured in this way is no different from one which would be obtained from a minimum in contrast sensitivity, although under these conditions the minima obtained in contrast sensitivity are broad and so provide a less accurate means of defining the isoluminant point (Fig. 1, lower panels). No variation in the isoluminant point was found with either spatial or temporal frequency.

In the first set of experiments contrast thresholds for the detection of an isoluminant chromatic grating and the threshold for discriminating its direction of drift were measured simultaneously using a forced choice technique. There were two intervals in time and in one the grating stimulus appears, drifting either to the left or the right. Stimuli onset and offset were in the form of a raised temporal cosine waveform, and the given duration refers to the display time at maximum contrast. Control experiments were done to ensure that the duration of the stimuli was sufficiently long so as not to limit performance on the discrimination task. It was found that at the lowest temporal frequencies of drift (0.4 Hz), thresholds for direction discrimination are dependent on duration, whereas there was no change in the contrast detection thresholds over the range of durations measured (see Fig. 2). For a temporal frequency of drift of 0.4 Hz thresholds for direction discrimination (and hence the ratio of detection to discrimination thresholds) reach an asymptotic level at around 600 msec. A dependence on duration was not apparent at higher temporal frequencies of drift (see results for 3.2 Hz). For the temporal frequency of 0.4 Hz a presentation duration of 600 msec was used whereas for all other frequencies it was 365 msec. An effect of stimulus duration on the discrimination of the direction of motion for chromatic stimuli has also recently been reported by Cropper and Derrington (1991).

The chromatic contrast, the interval of presentation and the direction of drift were randomly selected. The subject indicated in which interval the stimulus occurred and the direction of its drift. A pair of psychometric functions was obtained from each 2 AFC experiment and a Weibul function was fitted to obtain threshold (at

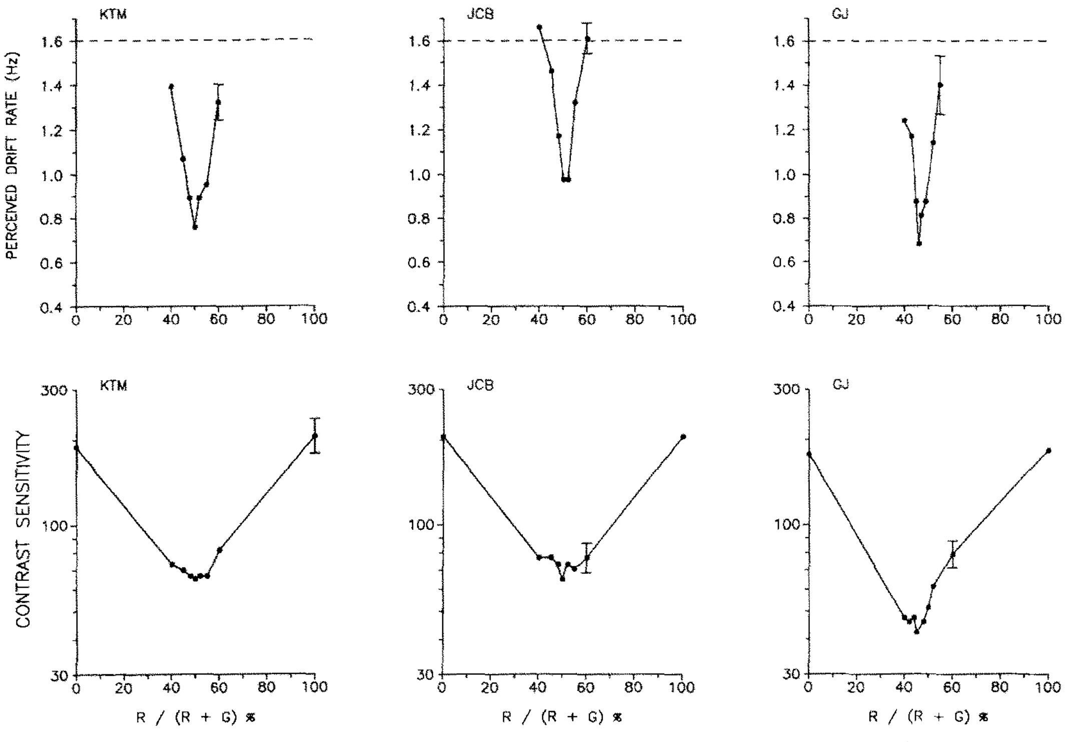

FIGURE 1. Upper panels. The perceived drift rate (matched temporal frequency) is plotted as a function of the ratio of red to green mean luminances of the test stimulus. The spatial frequency of the stimulus is 1.05 cpd and the temporal frequency of drift is 1.6 Hz (given by the dashed line). The contrast of the grating is 48.7% for KTM and JCB, and 23.7% for GJ. The match is made to a luminance grating of variable drift rate and with the same spatial parameters as the chromatic grating (see text). Each data point represents the mean of at least 3 to 5 methods of adjustment settings made non-sequentially. Error bars give ±1 SD. Results are for three subjects. Lower panels. Contrast sensitivity is plotted as a function of the red to green mean luminance ratio in the stimulus using the same spatial and temporal conditions as for the results shown in the panel above. Error bars give ±1 SD. The two vertical axes have been scaled so that the size of the standard deviations are similar and allow a comparison between the shapes of the functions.

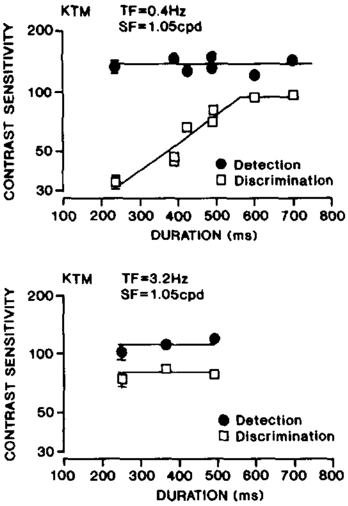

FIGURE 2. Color contrast sensitivities are plotted as a function of the duration of the maximum contrast of the stimulus (msec) for detection thresholds (solid circles) and for direction discrimination (open squares). The rising part of the function for direction discrimination shown in the top panel has been fitted by a linear regression. Subject: KTM.

81.3% correct). Each psychometric function is based on 4–6 contrast levels with at least 50 trials per point.

In the second set of experiments a velocity matching technique was used to investigate the perceived drift rate and appearance of the motion at color contrasts above the threshold for direction discrimination. The variable (standard) stimulus was a black and white luminance grating (17.8% contrast) of variable drift rate and the same spatial frequency, field size, and mean luminance as the chromatic test grating. Its direction reversed regularly to avoid direction specific adaptation. The test and standard gratings were simultaneously displayed but arranged so that both were not simultaneously visible. The subject was instructed to carefully fixate the test and standard stimulus in turn and to adjust the drift rate of the standard to match the perceived drift rate of the chromatic grating. Results are for at least three to five threshold settings made non-sequentially.

RESULTS

Chromatic detection and direction discrimination

Thresholds for detection and direction discrimination were measured over a range of drift rates and spatial frequencies of the stimulus and the results are shown for two subjects in Figs 3 and 4 with the different panels showing the results for different spatial frequencies. In each panel, contrast sensitivity for the detection of the stimulus (circles) and contrast sensitivity for determining its direction (squares) is plotted as a function of the temporal frequency of drift rate. There is a small separation between these two thresholds over the temporal range. At contrasts in between, the stimulus appears to be contrast reversing and its direction cannot be identified. This separation occurs for the four spatial frequencies of the stimulus examined (0.3–2.1 cpd).

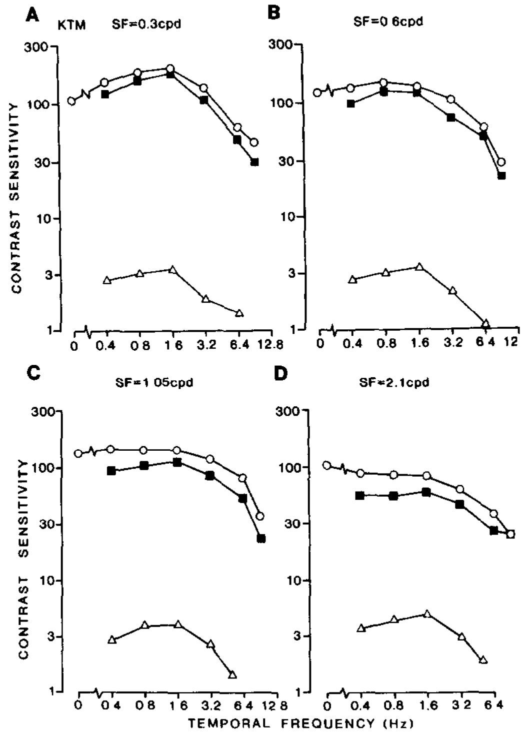

FIGURE 3. Color contrast sensitivities are plotted as a function of the drift rate (Hz) of an isoluminant chromatic grating for three different types of threshold. Circles and squares indicate the thresholds for detection and discrimination of the direction of drift respectively. The standard deviations (± 1) are similar to the symbol size. Triangles show thresholds for the detection of smooth motion. These thresholds are determined from the end points of the velocity matching functions measured in Fig. 5 (see text). Results are for 4 spatial frequencies. Subject: KTM.

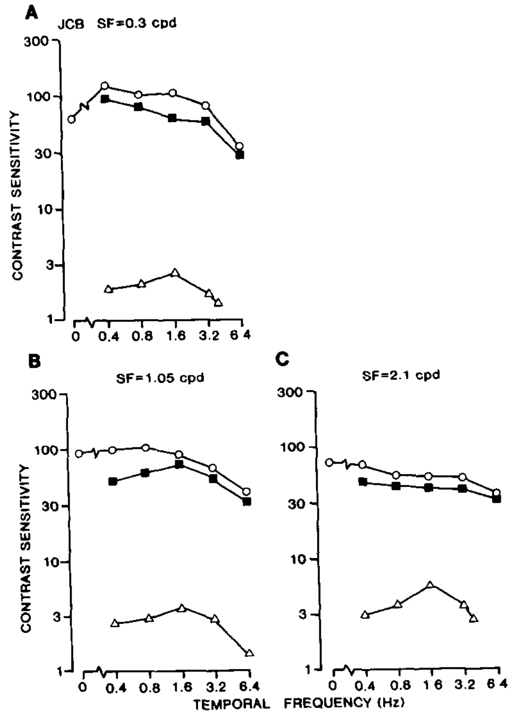

FIGURE 4. See legend of Fig. 3. Subject: JCB. The thresholds for smooth motion (triangles) are determined from the end points of the velocity matching functions measured in Fig. 6 (see text).

Many of these results were also obtained on the third subject and were very similar.

Our results show that direction sensitivity is good over most of the contrast range, only breaking down just before detection threshold. As a control experiment we repeated our measurements on luminance gratings under the same spatial and temporal conditions. Our results showed that detection and direction discrimination thresholds for luminance contrast are the same over the spatial and temporal ranges we have investigated in the chromatic experiments, confirming previous results (Watson, Thompson, Murphy & Nachmias, 1980; Kelly, 1979). Hence, the performance on direction discrimination relative to detection threshold we obtain for chromatic gratings is somewhat worse than that found for luminance only gratings.

All subjects observed that even when the direction can reliably be discriminated the motion of the chromatic stimuli does not appear to be smooth. The experiments in the following section were designed to test whether a smooth motion percept can be obtained from a chromatic stimulus.

Velocity perception and thresholds for smooth motion

In this experiment we measured the perceived drift rate of isoluminant gratings at different chromatic contrasts. The different chromatic contrasts were presented in a random order, unknown to the subject. We found that for many of the presented stimuli a velocity match could not be made by the subject since the motion of the chromatic stimulus did not appear to be smooth, at a uniform velocity. Subjects reported that the stimulus appeared "jumpy" or "jerky". We continued to present such stimuli but introduced an option to the subject of rejecting a presented stimulus without making a velocity match and recorded the rejection rate of each of the stimuli. Subjects were instructed to pay particular attention to the fixation of the stimuli, to avoid any disruptive effects of eye movements on the velocity match.

The perceived drift rate of the chromatic grating is plotted as a function of its chromatic contrast in Figs 5, 6 and 7, which show the results we obtained for three subjects. Our paradigm ensures that for all plotted points the stimuli are seen to move smoothly. The small vertical arrows indicate the contrast at which the stimuli were rejected at a rate of 50% of their presentations. Hence, we have taken this point to determine a contrast threshold for the perception of smooth motion.

These results show that, firstly, the perception of smooth motion is restricted to very high color contrasts. Secondly, the perceived drift rate of the smooth motion depends on the color contrast and slows down linearly on the logarithmic contrast axis. This resembles the dependence of perceived drift rate on luminance contrast found close to detection thresholds (Thompson, 1982). The threshold for smooth motion as a function of the drift rate is plotted on Figs 3 and 4 (triangles) for subjects KTM and JCB. It is confined to a narrow

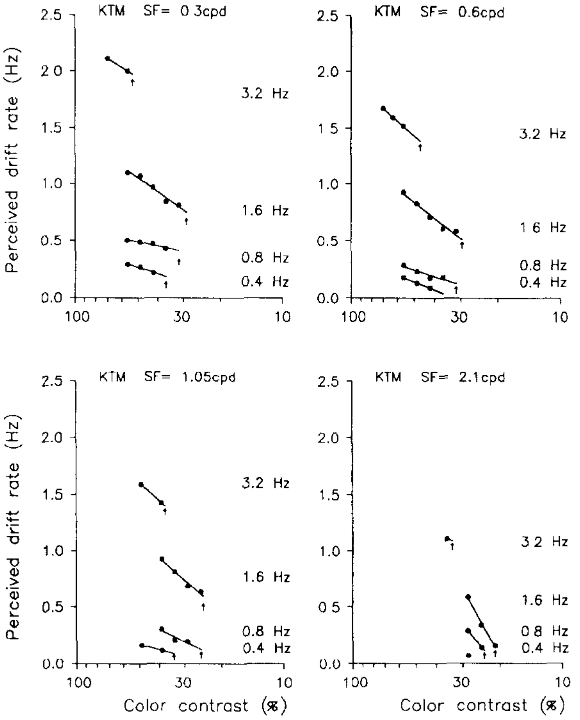

FIGURE 5. The matched temporal frequency (perceived drift rate) is plotted as a function of the color contrast of the isoluminant chromatic stimulus. The true drift rate of the chromatic test grating is given beside each function. Each data point represents the mean of at least 3 to 5 methods of adjustment settings made non-consecutively. The average standard deviation is 0.08 Hz. The arrows mark the threshold for smooth motion which is the contrast at which the perception of smooth motion fails (see text), and these are plotted in Fig. 3 (triangles). Subject: KTM.

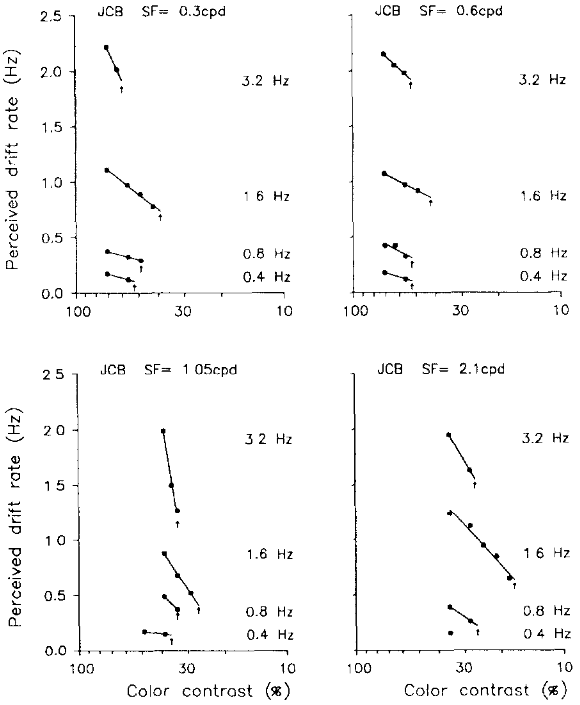

FIGURE 6. See legend of Fig. 5. The average standard deviation is 0.07 Hz. The arrows mark the thresholds for smooth motion and these are shown in Fig. 4 (triangles). Subject: JCB.

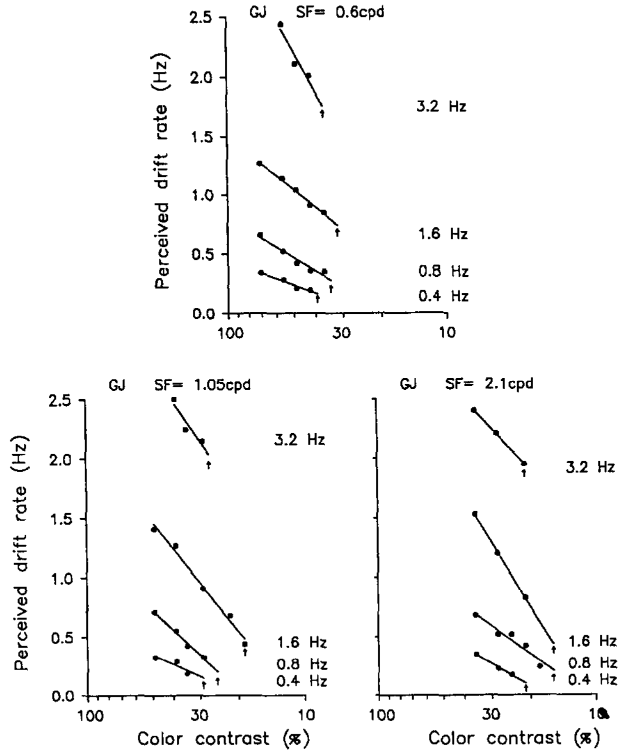

FIGURE 7. See legend of Fig. 5. The average standard deviation is 0.09 Hz. The arrows mark the threshold for smooth motion. Subject: GJ.

temporal range broadly peaking at around 1 Hz at each spatial frequency. Our informal observations suggest that this residual perception of smooth motion disappears with parafoveal viewing.

DISCUSSION

Other recent studies have also observed some separation between thresholds for detection and direction discrimination for stimuli isolating both the L/M and S/(L + M) cone chromatic mechanisms (Lindsey & Teller, 1990; Cavanagh & Anstis, 1991) and for isolated S cone mechanisms (Lee & Stromeyer, 1989). However, with the exception of some of Lindsey and Teller's results, in all of these studies a substantial contrast range remains over which direction can be determined. In our study we have chosen the stimulus and viewing conditions to provide optimum performance for color vision on the direction discrimination task. Our control studies suggest that other conditions, notably a smaller field size with a lower number of spatial cycles, parafoveal viewing, and the duration of the stimulus presentation (Fig. 2), will potentially reduce performance on the direction discrimination task relative to detection threshold. Differences in the stimulus arrangements, such as foveal vs parafoveal viewing, may account for why Lindsey and Teller (1990) find a rather greater separation between detection and discrimination thresholds than we and Cavanagh and Anstis (1991) report. We repeated some of our measurements of direction discrimination and detection thresholds for a stimulus centered at 2 deg in the temporal field, hence using the parafoveal viewing conditions of Lindsey and Teller (1990) (our stimulus was at 1.05 cpd, drifting at 0.4–6.4 Hz, on KTM; see Fig. 3 for the foveal results). We found a greater threshold separation under parafoveal conditions than for foveal viewing, in the region of 2:1. This goes some way towards accounting for the gap between our results and those of Lindsey and Teller who find a threshold separation of around 3:1 to 4:1 for red/green stimuli.

The temporal tuning of the residual smooth motion suggests that it does not arise from any artifactual luminance contrast which might remain in the high contrast chromatic stimulus. For the 1 and 2 cpd stimuli, for example, the chromatic smooth motion sensitivity peaks at around 1 Hz whereas luminance contrast sensitivity at this spatial frequency has a broad maximum at temporal frequencies over three octaves higher (8–10 Hz) (Robson, 1966) which we confirmed for our viewing conditions. Hence the dissociation between the behavior for luminance contrast and color contrast suggests that the possibility of artifactual luminance contrast at first or second harmonics of the test grating frequency cannot account for the chromatic effects.

The presence of some residual chromatic sensitivity to smooth motion implies that in human vision the pathways responsible for motion perception may have some reduced color sensitivity or, alternatively, that the chromatic pathways may have a low sensitivity to motion. The former finds some support from recent physiological findings in primates (Lee *et al.*, 1988; Saito *et al.*, 1989; Shiller *et al.*, 1990; Logothetis *et al.*, 1990).

Overall, the key feature of our results is that they suggest that performance on direction discrimination alone is not a sufficient measure of the chromatic encoding of motion, as direction can be determined without the perception of smooth motion. It is interesting to note that, under quite different conditions and with achromatic stimuli, the presence of a "motion sensation" without the perception of direction has been reported (Foster, 1968). We find that a smooth motion percept is absent over most of the detectable color contrast range. Adopting this criterion, we find that there is evidence for a very substantial physiological separation between the visual mechanisms subserving the detection of color contrast and those subserving the perception of motion. The loss of smooth motion perception, rather than the loss of direction discrimination, may be the human behavioral correlate of the anatomically and physiologically defined streams in the primate cortex.

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