



Position-based motion perception for color and texture stimuli: effects of contrast and speed

Adriane E. Seiffert *, Patrick Cavanagh

Department of Psychology, Harvard University, 33 Kirkland Street, Cambridge, MA 02138, USA

Received 18 August 1998; received in revised form 1 June 1999

Abstract

Motion can be perceived either through low-level, motion-energy detection or through tracking the change in position of features. Previously we have shown that, while luminance-based motion likely is detected with velocity-sensitive motion-energy units, patterns defined by texture or binocular disparity ('second-order' stimuli) were tracked by a position-sensitive mechanism (Seiffert & Cavanagh (1998) *Vision Research*, 38, 3569–3582). Here, we use the same technique, measuring motion amplitude thresholds of oscillating gratings over a range of temporal frequencies and find that the motion of low-contrast equiluminant red/green gratings is also detected with position tracking. In addition, we find that as contrast or speed increases these results change: high-contrast or high-speed equiluminant color or texture-based motion is detected by velocity-sensitive mechanisms. These results help resolve the dispute over the processes which detect the motion of non-luminance based stimuli. Both systems are available, but their relative efficiency changes as a function of contrast and speed. A position-tracking process is more sensitive at low contrasts and low speeds whereas a motion-energy system is more sensitive at high contrasts and high speeds. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Motion; Position tracking; Color; Texture

1. Introduction

Max Wertheimer (1912) described two possible ways that motion perception could be accomplished in the brain. The first was an elementary process, like a 'sensation of change', and the second was derived by a 'higher psychic process' (p. 1034, Wertheimer, 1912). Since that time the field of motion perception has seen many proposals that two independent motion detection systems exist (Braddick, 1974; Ullman, 1979; Anstis, 1980; Sperling, 1989). In each case, one system is analogous to the elementary process, usually described with an array of motion detectors based on correlational mechanisms. This type of low-level, 'motion-energy' analysis has had great success at modeling our perception of luminance contours in motion (Reichardt, 1961; Adelson & Bergen, 1985; van Santen & Sperling, 1985). The other system is a more 'cognitive' motion system that codes motion after the extraction of ele-

ments or forms, thereby solving the motion correspondence problem by tracking the position of these over time (Ullman, 1979). Notice that the motion is only signaled after the position of elements has been secured. To emphasize this, we will refer to this type of process as a 'position-sensitive' or 'position-tracking' mechanism. Although few researchers still argue over the existence of these two mechanisms, many debate when and how they are engaged.

Recently, debates have centered around two stimulus classes: moving equiluminant color stimuli and moving equiluminant 'second-order' stimuli, where motion is defined by contrast, texture or binocular disparity. In both cases, some studies have shown that the motion is detected by a low-level, motion-energy process similar to, but not identical to, that used for detecting the motion of luminance contours, whereas others support the idea that some type of tracking process is being used. The following paragraphs briefly review some of this literature and describe how the present work helps categorize these findings.

* Corresponding author. Fax: +1-617-495-3764.
E-mail address: aeseiffe@wjh.harvard.edu (A.E. Seiffert)

1.1. *Equiluminant color stimuli in motion*

Several studies have shown that the motion of color contours is perceived differently from that of luminance contours. Equiluminant color motion is often perceived to be moving more slowly than luminance motion presented at the same rate and with the same effective contrast (Cavanagh, Tyler & Favreau, 1984; Hawken, Gegenfurtner & Tang, 1994). Also, unlike luminance stimuli, pattern detection thresholds are much lower than motion detection thresholds for equiluminant-color stimuli presented in the periphery (Lindsey & Teller, 1990; Derrington & Henning, 1993), although this difference was small for central presentations (Cavanagh & Anstis, 1991; Mullen & Boulton, 1992; Derrington & Henning, 1993). In other words, observers can detect the contours of low-contrast color stimuli, but not see their motion (originally reported by Ramachandran & Gregory, 1978). In absence of a low-level, spatio-temporal correlation, subjects may still be able to detect the motion of the stimulus by tracking the location of stimulus features over time. In support of this notion, studies have shown that observers viewing low contrast, equiluminant-color gratings report that the motion appears jerky, not smooth and difficult to differentiate from of apparent motion (Mullen & Boulton, 1992; Cropper & Badcock, 1994).

However, evidence has also accumulated showing that there is strong low-level motion energy processing of color input. For example, Cavanagh et al. (1984) showed that adding chromatic contrast to a luminance grating decreases its perceived speed, suggesting that motion perception is a combination of analysis from separate luminance and color motion systems. In addition, equiluminant color stimuli have been shown to elicit a motion-specific after-effect with a static test, which is often attributed to the adaptation of low-level receptors (Cavanagh & Favreau 1985; Derrington & Badcock, 1985b; Mullen & Baker, 1985). Color provides observers with more sensitivity to visual motion than luminance, at slow rates (Stromeyer, Kronauer, Ryu, Chaparro & Eskew, 1995). Finally, motion was detected in a color stimulus presented for a duration too short to support tracking, when the color contrast was high enough, even with a luminance mask present (Cropper & Derrington, 1996). These and other studies of color motion show that color has a significant, independent input to our motion perception that is not carried by a slow, position-tracking system. So it seems that under some conditions, equiluminant color motion is detected via position tracking, where in other conditions it elicits low-level motion-energy analysis.

1.2. *Second-order stimuli in motion*

A parallel debate focused on the process underlying motion detection of patterns defined by contrast, differ-

ences in texture or binocular disparity. These stimuli have been called 'second-order' stimuli because motion is produced by two areas with the same mean luminance, but with different spatial, temporal or ocular distributions of luminance (Cavanagh & Mather, 1989). The name 'second-order' refers to the fact that to define the stimulus one must, first, take two samples of the stimulus to ascertain its local value. For example, one would need the luminance of two nearby points of a textured pattern to determine its contrast, or two ocular images to determine its disparity. Then, the distribution of these can to be processed over space and time to detect motion. Correspondingly, for 'first-order' stimuli, only one sample (e.g. luminance) needs to be taken to identify the local value (Cavanagh & Mather, 1989). After these two classes were described, much research was directed towards comparing the two across well-known visual motion effects. Most of this research has concentrated on second-order stimuli defined by differences in texture contrast, and here we only address this category.

Some early research suggested that second-order motion did not elicit the same type of motion-energy analysis as luminance-based motion. Motion after-effects with static test patterns were virtually non-existent for contrast modulated stimuli (Derrington & Badcock, 1985a; McCarthy, 1993; Ledgeway, 1994), under the same conditions that they are strong for luminance-based stimuli. Similarly to chromatic motion, presentation of second-order motion in the periphery gave rise to little or no motion perception, even though observers still readily perceived the pattern (Pantle, 1992; Smith, Hess & Baker, 1994; Zanker, 1997). In addition, observers could only discern the direction of motion of a contrast-modulated pattern if the duration was at least 200 ms, indicating that a slow, cumulative process was used (Derrington, Badcock & Henning, 1993).

Concurrent research, however, showed that second-order motion perception can be mediated by a process very similar to the motion-energy analysis used for luminance stimuli. Comparisons between motion perception of luminance-based and second-order stimuli show that the two have similar profiles along many dimensions, such as velocity difference thresholds (Turano & Pantle, 1989), threshold aperture width (Cavanagh & Mather, 1989), the effects of eccentricity (Solomon & Sperling, 1995; Smith & Ledgeway, 1998) and adding a stationary pedestal (Lu & Sperling, 1995; although see contrasting results in Zeman, Stromeyer, Chaparro & Kronauer, 1998). In fact, most mathematical models posit that second-order motion is perceived with a system very similar to the low-level motion system (Chubb & Sperling, 1988; Johnston, McOwen & Buxton, 1992; Zanker, 1996). In light of these differing results, much of the literature has concluded that two

low-level motion systems exist: one for detecting luminance-based motion, and another for detecting second-order motion (for a demonstration of the two processes at work, see Smith, 1994).

1.3. Current directions

For both types of motion stimuli, researchers have suggested that under some conditions a low-level motion energy system is used while for others a position-tracking system is used. However, none of these studies has tested the core difference between the two strategies. Namely, low-level motion analysis implies that it is the velocity or temporal frequency of motion that is coded, whereas position tracking implies what is coded is the change in position. Velocity or temporal frequency sensitivity comes about from the fact that the proposed motion-energy detectors are tuned to a specific spatio-temporal pattern¹. Position sensitivity is inherent to tracking because the position of stimulus features are detected first, then followed over time. Nakayama and Tyler (1981) used motion in oscillation to dissociate these two possible motion detection mechanisms. By measuring amplitude thresholds over a range of temporal frequencies, we replicated their pro-

cedure and their result that luminance-based motion is detected with a velocity-sensitive mechanism, and not through position-tracking (Seiffert & Cavanagh, 1998). More interestingly, however, we showed that second-order motion perception was based on detecting the change in position (Seiffert & Cavanagh, 1998). In the present work (experiment 1), we used the same procedure to find that equiluminant color stimuli was also detected with a position-based mechanism. Experiments 2 and 3 demonstrate that increasing the contrast of the stimulus for both equiluminant color and texture-based stimuli yields different results in this test. Experiment 4 show the same over changes in speed. These results lead to the conclusion that both a position-tracking and motion-energy mechanism are available to detect equiluminant color and texture stimuli, but the use of each mechanism depends on the stimulus characteristics, such as the contrast and speed.

2. Experiment 1: position tracking of equiluminant color gratings

Experiment 1 tested whether equiluminant red/green gratings were detected by a mechanism sensitive to velocity or position. We used the same paradigm as in our previous work (Seiffert & Cavanagh, 1998) in which a sine-wave grating oscillated sinusoidally. With oscillation, one can determine if observers are sensitive to a specific velocity or to a change in position by measuring amplitude thresholds over a range of oscillation frequencies. Figure 1 shows examples of the paths taken over time of a point on an oscillating grating. If motion is detected with a position-based system, only the amplitude of the motion, the amount of spatial change, will determine thresholds. As oscillation frequency increases, the threshold amplitude remains the same (Fig. 1A). In other words, no matter how fast the stimulus is moving, it must go a certain distance before motion can be detected. However, if motion is detected with a velocity-based system, both amplitude and oscillation frequency will determine thresholds. As oscillation frequency increases, to maintain the same threshold velocity, the amplitude decreases proportionally (Fig. 1B). Because the spatial frequency of the stimulus was fixed in these experiments, velocity sensitivity corresponds directly to temporal-frequency sensitivity, so we will use the term ‘velocity-sensitivity’ to avoid confusion. With this paradigm, measuring the slope of the amplitude thresholds as a function of oscillation frequency reveals the mechanism used. If the slope is close to zero, amplitude thresholds remain the same over oscillation frequency, so a position-sensitive mechanism is implicated. If the slope is close to -1 , a trade-off between oscillation frequency and amplitude has occurred, reflecting a velocity-sensitive mechanism.

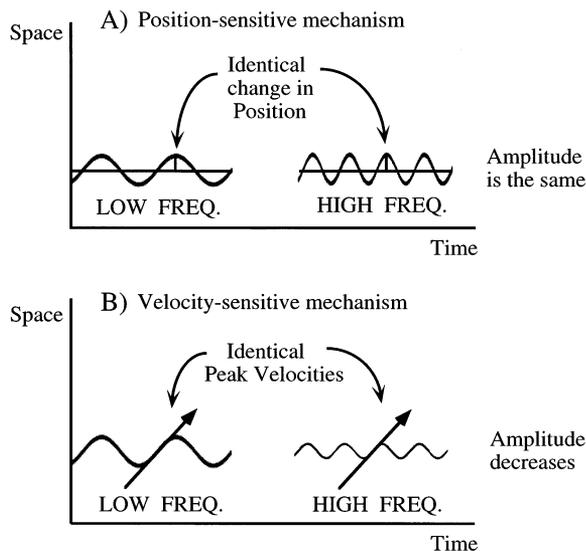


Fig. 1. (A) Space-time plot showing the path taken by a point on a grating in oscillation. Left line and right line show low and high oscillation frequency, respectively. Oscillation frequency does not affect the amount of change in position, so at threshold, as oscillation frequency increases, amplitude remains the same. (B) The peak velocity that the grating attains is shown by the slope of the oblique arrow. As oscillation frequency increases, the same peak velocity is maintained only if the amplitude decreases proportionally.

¹ Note that, for the present case we will not differentiate between velocity and temporal frequency sensitivity, as in our paradigm, both types of motion detection will differ from position tracking in the same way.

Oscillation can be detected on the basis of stimulus motion or local flicker. To eliminate the flicker cue, an additional paradigm was used in which the oscillating grating was split into two parts. Observers discriminated trials in which the two halves of the display oscillated together as if rigidly connected, from those trials in which they did not. Because the spatial phase of the gratings were randomized on every trial, a local flicker cue alone cannot mediate performance in this task.

3. Method

3.1. Subjects

Four subjects participated in this experiment. All observers were naive to the purposes of the study, except the first author (AES). Two observers (FT and AES) participated in the detection task, and three (PM, AD and AES) participated in the discrimination task. All had normal or corrected to normal acuity and were experienced psychophysical observers. A subset of these observers participated in all of the following experiments.

3.2. Stimuli

For the detection task, stimuli were radial gratings displayed in an annulus (3.6–8.1° of eccentricity) centred about a fixation bull's-eye (0.5° diameter) on a black (0.51 cd/m²) background. Gratings were either luminance-defined or equiluminant color-defined, as described below. Mean luminance of both displays was 26.6 cd/m², and the viewing distance was 57 cm, set by a headrest. Eight cycles of the grating appeared around the annulus, so the spatial frequency varied from 0.37 cycles/deg at the inner edge to 0.164 cycles/deg at the outer edge. The grating oscillated by rotating about its center point with a sinusoidal temporal course.

For the discrimination task, the display annulus was drawn as above with a 1.8° wide strip taken out of the top and bottom, so that each side of the display contained a semi-annulus section. Each of the two sections contained gratings with randomly selected spatial phase. On half the trials, the two gratings rotated such that they oscillated in phase, making the whole display look like a rotating wheel with parts occluded. On the other half of the trials, the gratings moved in anti-phase with respect to their rotation, to loosely resemble the motion of flapping wings. Subjects were asked to discriminate between the 'wheel' motion and the 'wings' motion on each trial.

Luminance gratings were sine wave gradations from light to dark, specified by their Michelson contrast. Equiluminant color gratings were sine wave gradations

from red to green. The color contrast was arbitrarily defined on the scale from 0% at white (CIE $x = 0.333$, $y = 0.334$) to 100% at the maximum chromaticity available from the red (CIE $x = 0.614$, $y = 0.351$) and green (CIE $x = 0.285$, $y = 0.598$) phosphors of the monitor while keeping the luminance over the grating constant.

3.3. Apparatus

Stimuli were generated on a Power Macintosh 7500/100 and displayed on an Apple High-Resolution Color monitor. The 640 × 480 pixel video signal, with a refresh rate of 67 Hz, used a Radius video board for 10 bits of intensity resolution for each of the three (R, G, B) guns and was calibrated for linearity.

3.4. Procedure

The experiment consisted of three data-collecting procedures, each performed independently for each subject in separate block of trials. In the first block, contrast thresholds for pattern detection were estimated with the yes–no method of constant stimuli. Each trial began with the presentation of the fixation point on a black background and the display annulus with uniform luminance equal to the test display mean luminance. After a 1.5 s interval, the sinusoidal pattern appeared and immediately began to oscillate at 2 Hz with an amplitude of 100% of the cycle. The spatial phase of the pattern at onset was chosen randomly to decrease inter-trial effects of contrast adaptation. Subjects reported whether or not they perceived the grating, and the threshold was taken as the contrast at which each observer detected the stimulus half the time (50% threshold). The contrast of the stimulus was then fixed at ten times this threshold level for next experimental sessions. Contrast thresholds for all observers and all stimuli used in this study are given in Table 1.

In the second block of trials, the contrast equiluminance point was found for each observer with the minimum motion technique of Cavanagh, MacLeod and Anstis (1987). A red/green grating was displayed at ten times the observers detection contrast level, and flickered in counter-phase at 2 Hz. A luminance grating, also counter-phasing at 2 Hz, was superimposed on the color grating such that the two gratings were 90° out of phase both spatially and temporally. This arrangement produces unidirectional motion perception in the combined stimulus whenever the color grating deviates from equiluminance (for more information see Cavanagh et al., 1987). The method of constant stimuli was used to determine the relative luminance of the red and green segments of the color grating that produced

Table 1
Contrast threshold for each observer and stimulus type

Observer	Contrast threshold
<i>Luminance</i>	
FT	0.400
PM	0.758
AES	0.392
AD	0.663
<i>Equiluminant color</i>	
FT	1.200
PM	1.190
AES	0.952
AD	1.100
<i>Contrast-modulated texture</i>	
AES	0.739
AD	0.871

the minimum perceived motion. This ratio defined each observers equiluminant point, and was used in the next phase of the study.

In the third session, observers either performed the motion detection task, or the motion discrimination task. In both cases, amplitude thresholds were estimated with the method of constant stimuli over a range of oscillation temporal frequencies. Each trial began with the presentation of the blank display annulus (of mean luminance) and the fixation point. After a 1.5 s interval, the sinusoidal pattern appeared and immediately began to oscillate. The spatial phase of the pattern at onset was chosen randomly to decrease inter-trial

effects of contrast adaptation. For the yes–no detection task, observers were instructed to judge whether or not the display was moving, and were asked to keep a high criterion for the procedure. The experimenter told subjects to say ‘yes’ only if they were sure that the stimulus was moving. Because this method of establishing threshold is not criterion-free, we also employed a motion discrimination procedure. For the motion discrimination task, observers were instructed to judge whether the two halves of the display were moving together like a wheel, or opposing like flapping wings. This is equivalent to asking subjects to detect if the two halves of the display were rotating in the same direction at the same time. Observers were asked to maintain fixation on the central bull’s eye throughout a trial, and all reported doing so without difficulty for all conditions. Each observer completed two blocks of trials, each consisting of 64 random presentations of eight different amplitudes of the same display pattern at the same oscillation frequency.

3.5. Data analysis

For each observer, each pattern and each oscillation frequency, the number of positive responses for the motion detection task, and the number of correct responses for the motion discrimination task were plotted as a function of amplitude. Cumulative normal functions were fit to these data, and the amplitude thresholds were defined as the amplitude corresponding to the point on the curve at 50% detections, or 75% correct on the discrimination task. Because spatial frequency of the pattern changed with eccentricity, amplitude thresholds were reported in terms of the percentage of the spatial cycle of the grating rather than in terms of absolute distance. An amplitude of 100% represents exactly one spatial cycle. Error bars shown in the amplitude threshold graphs are 95% confidence intervals based on these curve fits.

3.6. Results and discussion

Amplitude thresholds as a function of oscillation frequency are shown in Fig. 2 for the motion detection task and Fig. 3 for the motion discrimination task. Solid circles denote the luminance condition, and the open squares denote the color (equiluminant red/green) condition. Dashed lines show the slope of -1.00 which mark the points of constant peak velocity. Thresholds for the luminance condition fell with increasing oscillation frequency. The mean peak velocity corresponding to these thresholds are reported in Table 2, for each observer. This finding replicates earlier results showing that luminance gratings are detected with a velocity-sensitive mechanism (Nakayama & Tyler, 1981; Seiffert

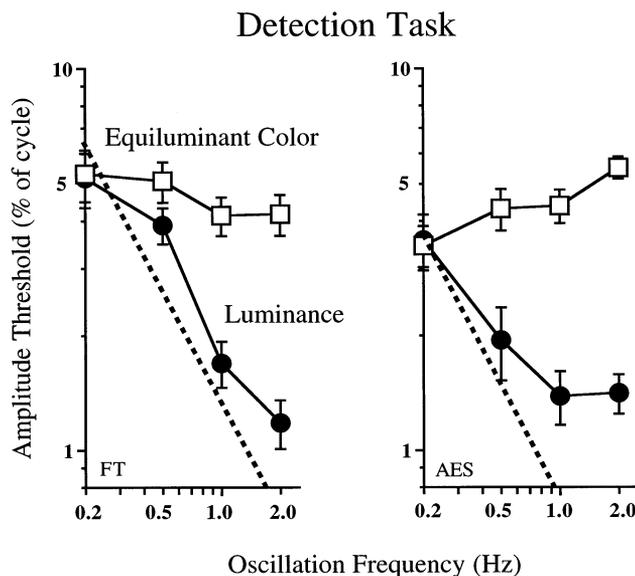


Fig. 2. Experiment 1: amplitude thresholds for oscillation detection of equiluminant red/green color gratings (open symbols) and luminance gratings (filled symbols) for two observers. Error bars show the 95% confidence intervals. Dashed lines are iso-velocity lines (slope of -1), plotted at an arbitrary height for easy slope comparison.

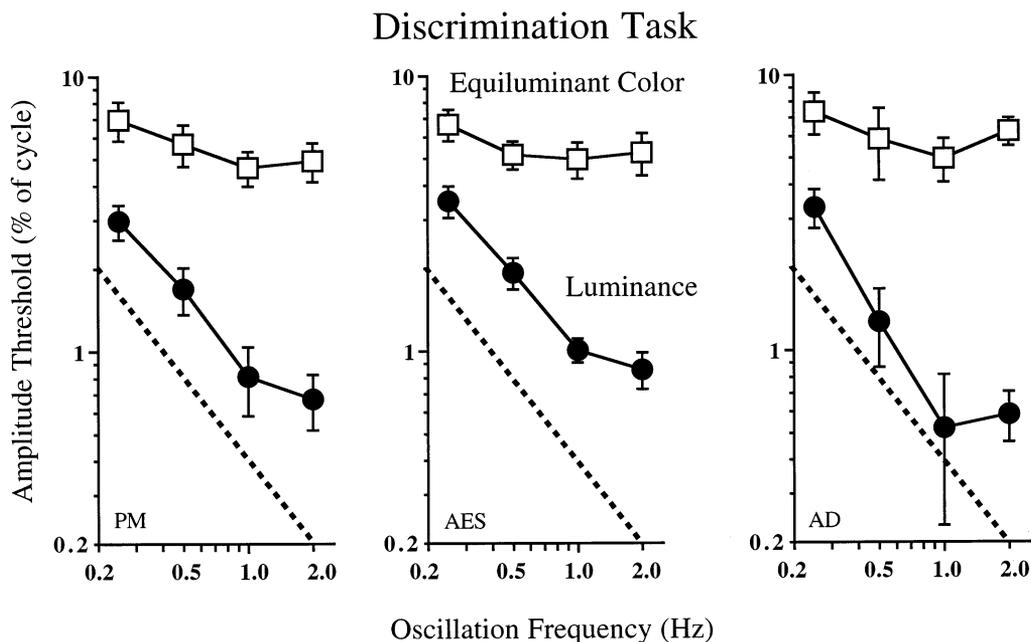


Fig. 3. Experiment 1: amplitude thresholds for oscillation discrimination for equiluminant red/green color gratings (open symbols) and luminance gratings (filled symbols) for three observers. Error bars show 95% confidence intervals. Dashed lines are iso-velocity lines (slope of -1) plotted at arbitrary height for slope comparison.

& Cavanagh, 1998). In contrast, thresholds for the equiluminant condition remained roughly constant across oscillation frequency, indicating subjects required a minimum change in position to detect motion, regardless of the speed of oscillation. All observers reported seeing motion, and not flicker, in these threshold displays.

Tyler and Cavanagh (1991) found very similar results in an experiment designed to investigate the perception of equiluminant color stimuli moving in depth. Their stimuli differed from ours in three ways. They used linear vertical gratings with a higher spatial frequency (2 cycles/deg) than the current work (maximum was 0.37 cyc/deg), and their stimuli were presented foveally (subtending $2^\circ \times 1^\circ$ of visual angle), and oscillated horizontally. The fact that similar results were found in our experiment and in theirs suggests that this is a robust result, not highly dependent on grating orientation or eccentricity.

To show that results for the color gratings were not highly dependent on equiluminance settings, two observers were tested with red/green gratings that were off their estimated equiluminance point. For one observer (PM) amplitude thresholds for off-equiluminance color patterns (by adding about 20% luminance contrast to either red or green) followed a negative slope across oscillation frequency, so they were more similar to the luminance thresholds than the equiluminant red/green thresholds. The other observer (AES), showed much less of an effect; threshold functions had little to no slope even for moderate additions (40%) of luminance.

As well as demonstrating interesting individual differences, these data indicate that the estimated equiluminance point for these subjects was accurate enough to illustrate that a different mechanism is used for stimuli with little or no luminance differences, than for luminance-based stimuli.

Notice that there was very little difference between the pattern of results for the motion detection and discrimination tasks; namely, thresholds for the luminance condition decreased while thresholds for the equiluminant condition did not. The advantages and disadvantages of the detection and discrimination techniques were discussed previously (Seiffert & Cavanagh, 1998). Because the results showed little difference between these two threshold measuring techniques over the range tested, the remainder of the experiments reported here use only the motion discrimination procedure.

Table 2
Peak-velocity of threshold stimulus by observer (exp. 1)

Observer	Mean peak velocity(cycles/s)	S.D.
<i>Detection</i>		
FT	3.522	1.114
AES	2.950	1.887
<i>Discrimination</i>		
PM	1.799	0.6316
AES	2.194	0.8649
AD	1.494	0.5769

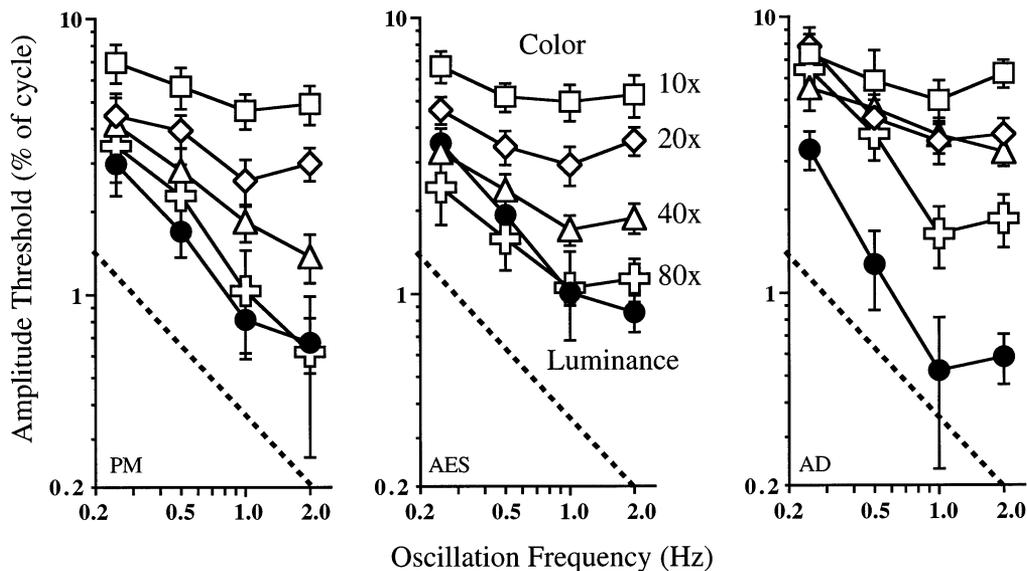


Fig. 4. Experiment 2: amplitude threshold functions as in Fig. 3. Equiluminant color conditions (open symbols) include contrasts at 10 times (squares), 20 times (diamonds), 40 times (triangles) and 80 times (crosses) detection threshold. Luminance condition shows thresholds with contrast at ten times detection threshold (closed circles).

4. Experiment 2: higher color contrasts

Previous reports indicate that the mechanism used to detect the motion of color contours may be different for high contrasts than for low contrasts. Cropper and Derrington (1994) showed that the minimum duration needed to detect the motion of high contrast color gratings was about equal to that required for luminance gratings (15 ms) whereas low contrast color gratings required much longer duration (120 ms). These authors concluded that high contrast color gratings are detected with a ‘fast-acting’ motion system, similar to the luminance-detecting system, where low contrast color motion was detected with a slow system, similar to the second-order motion system. In a recent study, Cavanagh, Hénaff, Michel, Landis, Troscianko and Intriligator (1998) showed that patients with cerebral achromatopsia perceive the motion of color-defined stimuli normally at high contrast, but perceived little or no motion (relative to control subjects) for low contrast stimuli. In experiment 2, we obtained oscillation motion thresholds for equiluminant color stimuli at various contrasts to determine the range of contrasts over which the position-sensitive mechanism is involved.

4.1. Method

The methods used for this experiment were identical to that of experiment 1, except that, in different experimental sessions, the contrast of the equiluminant color gratings were set at 10, 20, 40 and 80 times pattern detection threshold. Only the motion discrimination task was used.

4.2. Results and discussion

Seiffert and Cavanagh (1998, exp. 2) found that for luminance gratings, oscillation detection was mediated by a velocity-sensitive mechanism at all luminance contrasts. However, the results from the present study, plotted in Fig. 4, show that increasing color contrast does affect the results for the equiluminant red/green stimulus. As color contrast increases, the slope of the amplitude threshold function steepens, becoming closer to the luminance threshold function. This trend can be more readily observed in Fig. 5, which shows the slopes of the amplitude threshold functions plotted against contrast. Slopes were calculated for each observer in each condition, using least-squares best-fit model of the four thresholds across oscillation frequency. For equiluminant color, it appears that the slope decreases as contrast increases, indicating that as color contrast is raised a low-level, velocity-sensitive mechanism becomes available. At lower contrasts, only the position-tracking system is available for motion detection.

5. Experiment 3: higher contrasts of texture-defined stimuli

As in the previous experiment with color stimuli, this experiment determines, for second-order stimuli, whether the stimulus contrast affects the process underlying motion detection. Our previous results with second-order motion, using low contrasts, showed that a position-sensitive mechanism was used to detect motion

of contrast-modulated texture (Seiffert & Cavanagh, 1998). Experiment 3 investigated whether higher con-

trast textures give rise to velocity coding similarly to high contrast color stimuli.

5.1. Method

The stimuli were radial gratings of the same dimensions as in experiment 1, however gratings were defined by a sinusoidal contrast modulation of a pattern of 30 concentric circles which alternated light and dark. Each circle was approximately 0.15° of visual angle in width, thereby matching luminance changes in the direction of motion (circumferentially) in every 0.3° of visual angle. Note that the contrast between the light and dark circles of the pattern was modulated over the annulus between 0% contrast and some maximum value. This maximum contrast defined the contrast of the texture. Contrast thresholds for each subject are given in Table 1. The monitor used for these displays produced carefully linearized luminance output, thus ensuring that the 0% contrast (grey) parts of the grating could be accurately maintained at the mean level between the light and dark circles in the high contrast parts of the grating. However, because the visual system does not transduce linear increments of luminance into perfectly linear signals (Hood, Finkelstein & Buckingham, 1979), we also assessed the perceived equivalence of the grey parts of the display to the mean of the high-contrast parts. To find the equiluminance point the minimum motion method described in experiment 1 was used, substituting the contrast-modulated pattern for the red/green pattern. The method for this experiment was otherwise identical to that of experiment 2.

5.2. Results and discussion

Fig. 6 shows that amplitude thresholds for low contrast ($10\times$ threshold) texture-based stimuli remained roughly constant across oscillation frequency, indicating position tracking occurs. This replicates our previous results (Seiffert & Cavanagh, 1998). For the higher contrast stimuli, the results change qualitatively; amplitude threshold functions become more sloped, notably for one observer (AES) and less so for the second observer (AD). Fig. 7 shows how the slopes of the threshold functions decrease as contrast increases. The effect is smaller than that found with equiluminant color stimuli, but the tendency for the slopes to decrease with increasing contrast is consistent for both observers.

Smith and Ledgeway (1997) first suggested that the effect of carrier contrast on motion thresholds would be diagnostic of the underlying motion-detection mechanism. Their study gauged the extent to which global distortion products in texture-defined patterns contributed to the perception of motion. The idea was that small residual luminance differences between the textured and untextured parts of contrast-modulated pat-

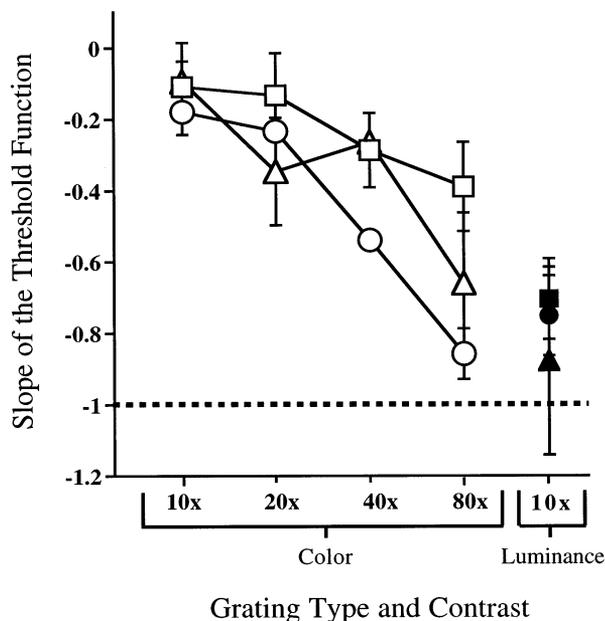


Fig. 5. Experiment 2: slopes of the amplitude threshold functions for the three observers, AES (squares), AD (triangles) and PM (circles), for each color and luminance contrast tested. Contrasts are reported in multiples of detection threshold. Error bars are the standard errors of the straight line fit of the slope, and are plotted only if larger than the point symbol. Dashed line marks the slope of -1 , corresponding to velocity sensitivity.

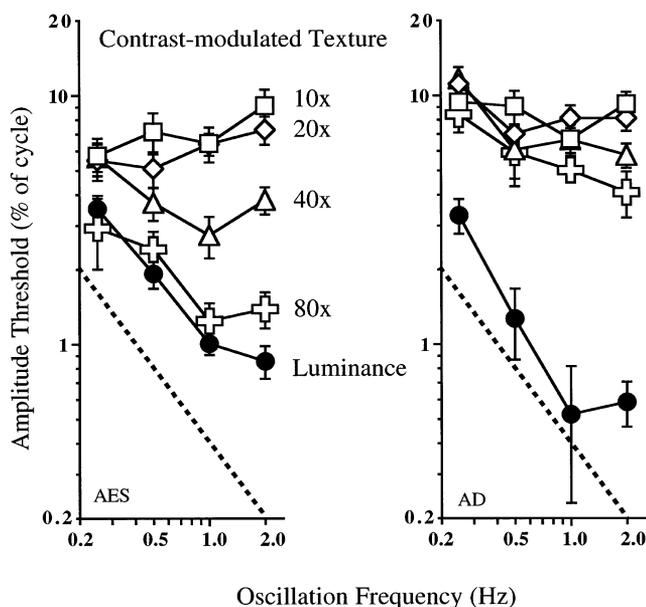


Fig. 6. Experiment 3: amplitude threshold functions as in Fig. 3. Contrast-modulated texture conditions (open symbols) include contrasts at 10 times (squares), 20 times (diamonds), 40 times (triangles) and 80 times (crosses) detection threshold. Luminance condition shows thresholds with contrast at ten times detection threshold (closed circles).

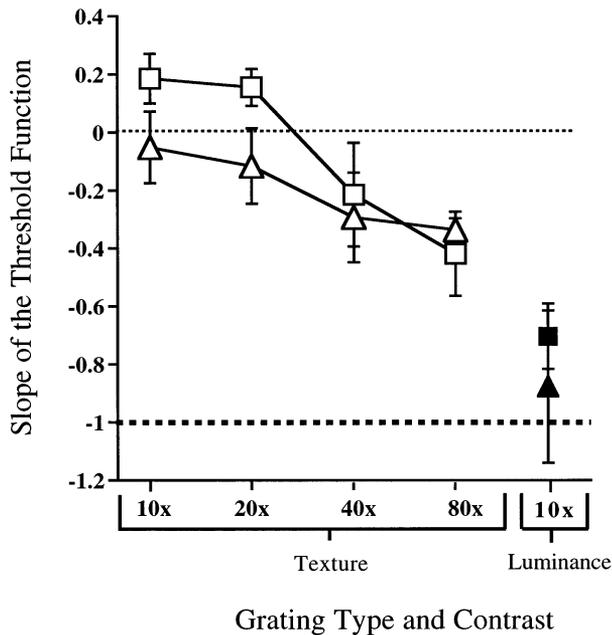


Fig. 7. Experiment 3: slopes of the amplitude threshold functions for the two observers, AES (squares) and AD (triangles), as in Fig. 5. Dotted line marks the slope of zero, corresponding to position sensitivity, and the dashed line marks the slope of -1 , corresponding to velocity sensitivity.

terns would increase in amplitude with increasing carrier contrast. So, while the lower contrast texture stimuli may be detected by a second-order motion system, the motion of higher contrast patterns may be detected by the luminance-based system. However, Smith and Ledgeway found that increasing the carrier contrast of contrast-modulated dynamic random-dot patterns had little effect on motion thresholds, indicating that their stimulus had few or no luminance artifacts.

The contrast-modulated static texture in the current study, put to the same test, yielded different results. Contrast of the pattern did affect the thresholds found from second-order stimuli, in that they approached those found from luminance-based stimuli. Following Smith and Ledgeway's argument, this finding may indicate that residual luminance differences are present in the contrast-modulated texture used in this study, and that these luminance signals only become strong enough to drive motion detection at high texture contrasts. Given the careful linearization process employed and the psychophysical luminance equalization procedure, it is unlikely that any obvious global luminance differences could have produced this effect. However, our equiluminance setting procedure only balances luminance differences at the fundamental or envelope frequency of the pattern, so residual luminance differences at other frequencies could have provided a luminance-based motion signal. If there are no residual

luminance signals, these data require a velocity-sensitive second-order motion system of the type proposed in previous research (Chubb & Sperling, 1988; Johnston et al., 1992; Lu & Sperling, 1995). In this case, our results suggest that such a system must be relatively less sensitive than a position-based system at low texture contrasts. In fact, regardless of the mechanism used at high contrasts, we have shown that at low contrasts the position-based mechanism generates the perception of second-order motion.

6. Experiment 4: suprathreshold velocities

The oscillation paradigm measures motion thresholds in terms of the minimum motion required for perception, either in terms of the slowest speed or the shortest distance. These tests, then, have only indicated the motion mechanism used by observers at motion detection threshold. However, in natural settings, motion is most often present at suprathreshold speeds. In experiment 4 we asked the following question: Which of the two mechanisms — position-based or velocity-based — is used to detect the motion of suprathreshold velocities for stimuli defined by luminance, equiluminant color and equiluminant texture?

To test for a difference in mechanism at higher speeds, a new version of the oscillation paradigm was used. Instead of oscillating about a fixed point in space, the pattern oscillated about an imaginary point that was circling the center of the screen; in other words, the radial grating rotated with an oscillation added to a continuous drift in the clockwise or counter-clockwise direction. To examine this stimulus more closely, consider the same type of motion, only of a linear grating moving in one dimension. A point on such a grating would follow the paths depicted in Fig. 8. The signal to be detected in this case is the deviation from the constant-velocity trajectory (thin, straight lines in Fig. 8).

Consider how a mechanism sensitive to velocity would detect such a signal. We assume that a velocity-based system would be sensitive to the change in velocity (depicted by the angle θ in Fig. 8A) from the expected value (the mean, depicted by the slope of the thin lines in Fig. 8A). To maintain the same change in velocity (θ), as oscillation frequency increases, the oscillation amplitude must decrease proportionally. As in the previous paradigm, a trade-off between amplitude and oscillation frequency maintains a fixed change in velocity, so a velocity-sensitive system would produce amplitude thresholds that would decrease as oscillation frequency increased.

In a similar manner, we assume that a position-based system can operate predictively, estimating the trajectory of a object moving with constant speed. Deviations

from constant speed would be detected as a difference between the expected position and the actual position

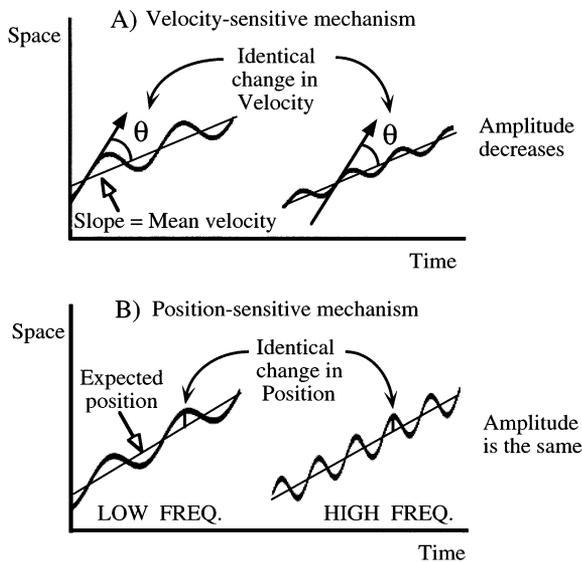


Fig. 8. (A) Space-time plot showing the path taken by a point on a grating moving with a constant mean speed plus an oscillation. As in Fig. 1, the left line and right line show low and high oscillation frequency, respectively. The velocity is the slope of these functions. The slope of the thin, straight line shows the mean velocity of the grating and the slope of the arrows show the peak velocity. Oscillation can be detected through the change in velocity, shown by the angle θ . As oscillation frequency increases, maintaining the same change in velocity requires decreasing the amplitude proportionally. (B) The change in position from an expected position (as shown) is constant as oscillation frequency increases, if the amplitude remains the same (see text).

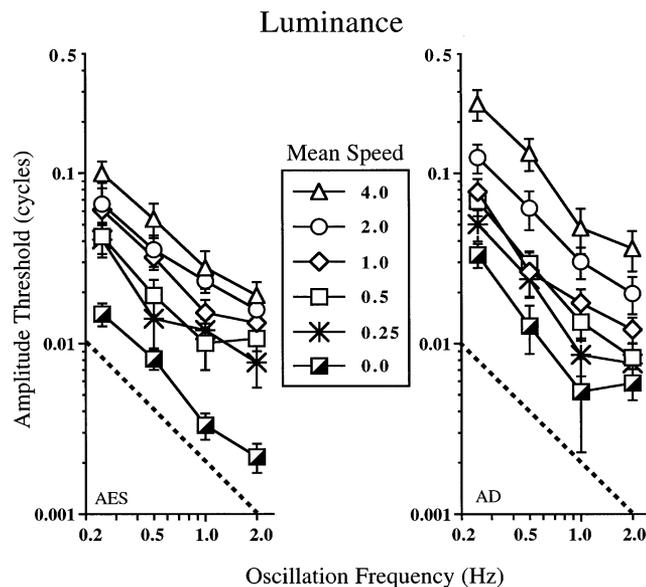


Fig. 9. Experiment 4: luminance condition — amplitude threshold functions for two observers shown as a function of mean speed of the grating. Dashed lines show the slope of -1 predicted by velocity sensitivity.

of the object at some point in time. In our paradigm, using this mechanism would require that oscillation amplitude would solely determine amplitude thresholds, because, as in the previous paradigm, position-change is independent of oscillation frequency (Fig. 8B). Therefore, the pattern that amplitude thresholds make over oscillation frequency can be interpreted the same way in this experiment as in the previous one: Amplitude threshold functions with zero slope indicate position sensitivity, while functions with a slope of -1 indicate velocity sensitivity.

6.1. Method

The stimuli were those used in the previous experiments set to a contrast of ten times pattern detection threshold for each observer for each mean speed. The mean speed of the gratings was set to either 0.25, 0.5, 1.0, 2.0 or 4.0 Hz, and each was tested in a separate session. The method used for this experiment was identical to the previous experiments, except for the addition of a drift to the oscillating grating. On each trial, the direction of this drift alternated from clockwise to counterclockwise to minimize adaptation effects. Because an overall mean rotation was added to the oscillating motion, the gratings appeared to rotate with a periodic ebb and sway. On half the trials, the gratings in the two sides of the display slowed and accelerated together; in the other half of the trials, one grating slowed while the other accelerated.

6.2. Results and discussion

Amplitude threshold functions for the two observers for each mean speed tested are shown in Figs. 9–11, for the luminance, equiluminant color and texture-defined stimuli, respectively. Luminance threshold functions (Fig. 9) are all roughly parallel to each other, with a steep negative slope, indicating that the velocity sensitivity of luminance motion detection does not change as mean speed increases. In contrast, for both equiluminant color stimuli (Fig. 10) and contrast-modulated texture (Fig. 11), threshold functions are roughly flat across oscillation frequency for low mean speeds, but for higher speeds the functions have a steep negative slope similar to the luminance curves. This is more easily seen in the graphs showing the slopes as a function of mean speed (Fig. 12). At low speeds, slopes are close to zero for color and texture conditions, and fall to the same value as the luminance condition at about 2 Hz. Because our display was a radial grating, 2 Hz corresponds to a range of absolute speed between 5.5 and 12 deg/sec. To summarize, the results indicate that a velocity-sensitive mechanism detected deviation from a mean speed of luminance contours, regardless of the value of the mean speed, and also detected the same

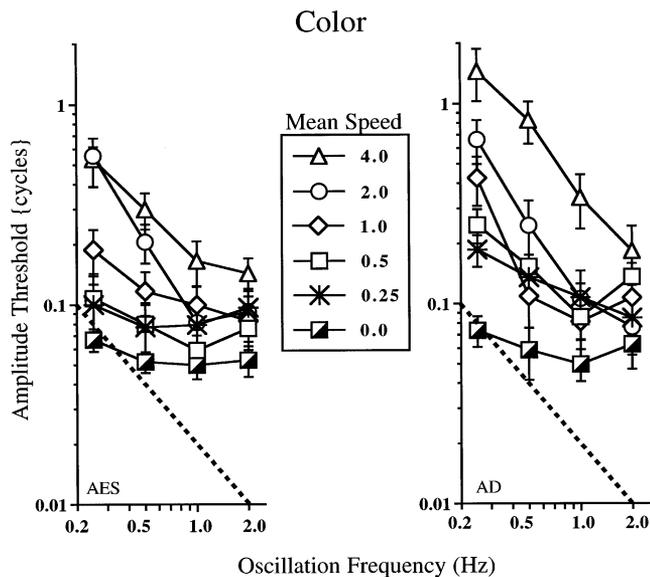


Fig. 10. Experiment 4: equiluminant color condition — amplitude threshold functions for two observers across mean speed. Dashed lines show the slope of -1 predicted by velocity sensitivity.

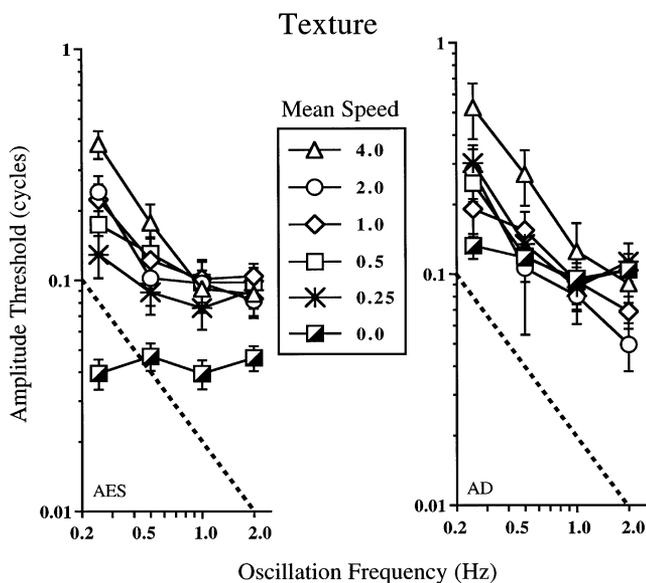


Fig. 11. Experiment 4: contrast-modulated texture condition — amplitude threshold functions for two observers shown as a function of mean speed of the grating. Dashed lines show the slope of -1 predicted by velocity sensitivity.

signal in quickly moving equiluminant color and texture stimuli. However, slowly moving equiluminant color and texture patterns required position tracking to detect speed deviation.

Previous studies using very different paradigms have also found critical process differences emerge as speed increases. Hawken et al. (1994) found that at high speeds, both luminance and equiluminant color showed little change in perceived speed with increasing contrast,

as would be expected from a system that calculates motion energy. Conversely, at low speeds, they found perceived speed of equiluminant color gratings became highly dependent on contrast, and concluded that a different mechanism was at work. Derrington et al. (1993) found that apparent motion correspondence of contrast-modulated (beat) patterns changed direction at 2 Hz or about 2.15 deg/s. Derrington et al. postulated that at the higher rates observers were responding to one of the luminance-based components of the beat instead of to the combined pattern. In effect, observers were able to pick out an unambiguous luminance motion when the speed was high enough, but were only sensitive to the combined stimulus, the contrast-modulated pattern, at slower speeds.

The present results are consistent with previous work. Both equiluminant color and texture stimuli produced thresholds that changed qualitatively as mean speed increased, such that they approached the pattern shown by the luminance thresholds. Furthermore, the threshold functions of color and texture changed at approximately the same rate, for both observers. This suggests that the transformation to a dependence on velocity information was independent of the stimulus type, and possibly reflects a limitation in a more general process. This process, the position tracking mechanism, was the most sensitive mechanism to motion of these patterns at slow speeds, but was not most sensitive at high speeds.

7. General discussion

Measurement of the spatial extent of oscillation required to detect motion has provided a diagnostic tool for distinguishing two motion mechanisms. The first, a position-sensitive mechanism, detects the motion of low

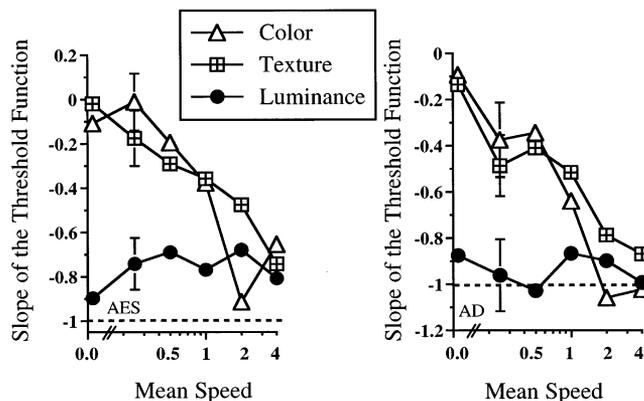


Fig. 12. Experiment 4: slopes of the amplitude threshold functions for each mean speed in each condition. Horizontal dashed line shows the -1.00 slope predicted by velocity sensitivity. Error bars reflect the average standard error within each condition plotted arbitrarily on the second data point.

contrast, slowly moving gratings with no net luminance differences, such as equiluminant color gratings and contrast-modulated texture gratings. The second, a velocity-sensitive mechanism, detects luminance-based patterns, and equiluminant color and contrast-modulated texture gratings that either have: (1) contrasts above about ten times detection threshold; or (2) speeds over approximately 2 Hz.

7.1. Characterizing previous research

Previous research on equiluminant color and second-order stimuli has provided conflicting conclusions. Evidence for a tracking mechanism and for a low-level, motion-energy mechanism exist for both the detection of equiluminant color and contrast-modulated texture motion. The evidence presented here suggest that these opposing results could be reconciled by taking stimulus contrast and velocity into account. A preliminary review of the literature is consistent with this notion. Studies that have shown that equiluminant color motion perception is unlike luminance motion most often used contrasts at or near threshold and slow speeds (such as Lindsey and Teller, 1990; Mullen and Boulton, 1992; Cropper and Badcock, 1994). Whereas studies that showed equiluminant color motion perception to be similar to luminance motion most often used higher contrasts, or speeds that were much higher than 2 Hz (such as Hawken et al., 1994; Cropper and Derrington, 1996). Similarly, previous results showing that motion perception of contrast-modulated textures differs from luminance used contrasts and speeds that were low (such as Derrington and Badcock, 1985a; Derrington et al., 1993), whereas studies showing that the two are similar used much higher contrasts or speeds (such as Smith et al., 1994; Solomon and Sperling, 1995; Smith and Ledgeway, 1998).

A more thorough review of the literature reveals several studies that do not fit into this framework. For example, Pantle (1992) showed that even at very high contrasts, the motion direction of texture-defined gratings was difficult to discriminate while the pattern was easy to detect. This particular demonstration of the difference between second-order and luminance-based stimuli may arise from the high eccentricity (8° of visual angle) and small window size ($0.6^\circ \times 6.4^\circ$) used. These factors, as well as others such as stimulus duration and spatial frequency, may also determine which mechanism is most sensitive for a particular stimulus.

7.2. Position tracking as a motion detection system

Although the idea that motion detection may be

governed by a higher process is an old one, few studies have systematically investigated the effective range of such a system. Here, we have reported the contrast and speed domains over which the higher order, position-tracking system is the more effective motion system. Observers seem to rely on the position-sensitive mechanism with equiluminant stimuli that are at low contrasts and moving a slow speeds. It is unlikely that these conditions make up the preferred stimuli for a position-tracking system because higher contrasts, at least, would be easier for any system that has to localize stimulus elements. However, our results indicate that the position-tracking system is relatively more sensitive to the movement of these stimuli than a spatio-temporal filtering mechanism.

Interestingly, our results show that the upper limit speed for which the position-tracking system is most effective is similar for both color or texture, indicating that the system is at least partially form-cue invariant. The notion that motion perception is independent of the attribute defining the cue was also supported by Cavanagh, Arguin and von Grünau (1989) who showed that apparent motion between elements defined by different attributes (e.g. color, texture or stereopsis) was quite strong. Form-cue invariance, as a property of a motion system, was also suggested by Albright (1992) with his neurophysiological work showing that some directionally selective neurons in the primate middle temporal area (MT) were insensitive to the motion-defining attribute (see also O'Keefe & Movshon, 1998). This property of the position tracking process is consistent with the our proposal that the system first identifies the position of the borders or forms to be tracked (however they may have been constructed), and then follows them across time. Position tracking is a slow, sensitive and independent motion detection system which is available as an alternative to the low-level system.

Acknowledgements

This work was supported by Grant EY09258 from the National Eye Institute to Patrick Cavanagh, and Graduate Fellowship from the National Science Foundation awarded to Adriane Seiffert.

References

- Adelson, E. H., & Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America, A*, 2(2), 284–299.

- Albright, T. D. (1992). Form-cue invariant motion processing in primate visual cortex. *Science*, 255, 1141–1143.
- Anstis, S. M. (1980). The perception of apparent movement. *Philosophical Transactions of the Royal Society of London, B*, 290, 153–168.
- Braddick, O. (1974). A short-range process in apparent motion. *Vision Research*, 14, 519–527.
- Cavanagh, P., Arguin, M., & von Grünau, M. (1989). Intertribute apparent motion. *Vision Research*, 29, 1197–1204.
- Cavanagh, P., & Anstis, S. (1991). The contribution of color to motion in normal and color-deficient observers. *Vision Research*, 31, 2109–2148.
- Cavanagh, P., & Favreau, O. E. (1985). Color and luminance share a common motion pathway. *Vision Research*, 25, 1595–1601.
- Cavanagh, P., Hénaff, M. A., Michel, F., Landis, T., Troscianko, T., & Intriligator, J. (1998). Complete sparing of high-contrast color input to motion perception in cortical color blindness. *Nature Neuroscience*, 1(3), 242–247.
- Cavanagh, P., & Mather, G. (1989). Motion: the long and short of it. *Spatial Vision*, 4(2/3), 103–129.
- Cavanagh, P., MacLeod, D. I. A., & Anstis, S. M. (1987). Equiluminance: spatial and temporal factors and the contribution of blue-sensitive cones. *Journal of the Optical Society of America A*, 4(8), 1428–1438.
- Cavanagh, P., Tyler, C. W., & Favreau, O. E. (1984). Perceived velocity of moving chromatic gratings. *Journal of the Optical Society of America A*, 1(8), 893–899.
- Chubb, C., & Sperling, G. (1988). Drift-balanced random stimuli: a general basis for studying non-Fourier motion perception. *Journal of the Optical Society of America A*, 5, 1986–2007.
- Cropper, S. J., & Badcock, D. R. (1994). Discriminating smooth from sampled motion: chromatic and luminance stimuli. *Journal of the Optical Society of America A*, 11(2), 515–530.
- Cropper, S. J., & Derrington, A. M. (1996). Rapid color-specific detection of motion in human vision. *Nature*, 379, 72–74.
- Cropper, S. J., & Derrington, A. M. (1994). Motion of chromatic stimuli: first-order or second-order? *Vision Research*, 34(1), 49–58.
- Derrington, A. M., & Badcock, D. R. (1985a). Separate detectors for simple and complex gratings patterns? *Vision Research*, 25, 1869–1878.
- Derrington, A. M., & Badcock, D. R. (1985b). The low level motion system has both chromatic and luminance inputs. *Vision Research*, 25, 1879–1884.
- Derrington, A. M., Badcock, D. R., & Henning, G. B. (1993). Discriminating the direction of second-order motion at short stimulus durations. *Vision Research*, 33(13), 1785–1794.
- Derrington, A. M., & Henning, G. B. (1993). Detecting and discriminating the direction of motion of luminance and color gratings. *Vision Research*, 33(5/6), 799–811.
- Hawken, M. J., Gegenfurtner, K. R., & Tang, C. (1994). Contrast dependence of color and luminance motion mechanisms in human vision. *Nature*, 367, 268–270.
- Hood, D. C., Finkelstein, M. A., & Buckingham, E. (1979). Psychophysical tests of models of the response function. *Vision Research*, 19, 401–406.
- Johnston, A., McOwen, P. W., & Buxton, H. (1992). A computational model of the analysis of some first-order and second-order motion patterns by simple and complex cells. *Proceedings of the Royal Society of London Series B*, 250, 297–306.
- Ledgeway, T. (1994). Adaptation to second-order motion results in a motion after effect for directionally-ambiguous test stimuli. *Vision Research*, 34(21), 2879–2889.
- Lindsey, D. T., & Teller, D. Y. (1990). Motion at isoluminance: discrimination/detection ratios for moving isoluminant stimuli. *Vision Research*, 30(11), 1751–1761.
- Lu, Z., & Sperling, G. (1995). The functional architecture of human visual motion perception. *Vision Research*, 35(19), 2697–2772.
- McCarthy, J. E. (1993). Directional adaptation effects with contrast modulated stimuli. *Vision Research*, 33(18), 2653–2662.
- Mullen, K. T., & Baker, C. L. Jr. (1985). A motion after-effect from an isoluminant stimulus. *Vision Research*, 25, 685–688.
- Mullen, K. T., & Boulton, J. C. (1992). Absence of smooth motion perception in color vision. *Vision Research*, 32, 483–488.
- Nakayama, K., & Tyler, C. W. (1981). Psychophysical isolation of movement sensitivity by removal of familiar position cues. *Vision Research*, 21, 427–433.
- O'Keefe, L. P., & Movshon, J. A. (1998). Processing of first- and second-order motion signals by neurons in area MT of the macaque monkey. *Visual Neuroscience*, 15, 305–317.
- Pantle, A. (1992). Immobility of some second-order stimuli in human peripheral vision. *Journal of the Optical Society of America A*, 9(6), 863–867.
- Ramachandran, V. S., & Gregory, R. L. (1978). Does color provide and input to human motion perception? *Nature*, 275, 55–56.
- Reichardt, W. (1961). Autocorrelation, a principle for the evaluation of sensory information by the central nervous system. In W. A. Rosenblith Jr., *Sensory Communication*. New York: Wiley.
- Seiffert, A. E., & Cavanagh, P. (1998). Position, not velocity, is the cue to motion detection of second-order stimuli. *Vision Research*, 38, 3569–3582.
- Smith, A. T. (1994). Correspondence-based and energy-based detection of second-order motion in human vision. *Journal of Optical Society of America A*, 11(7), 1940–1948.
- Smith, A. T., Hess, R. F., & Baker, C. L. Jr. (1994). Direction identification thresholds for second-order motion in central and peripheral vision. *Journal of the Optical Society of America A*, 11(2), 506–514.
- Smith, A. T., & Ledgeway, T. (1998). Sensitivity to second-order motion as a function of temporal frequency and eccentricity. *Vision Research*, 38(3), 403–410.
- Smith, A. T., & Ledgeway, T. (1997). Separate detection of moving luminance and contrast modulations: fact or artifact? *Vision Research*, 37(1), 45–62.
- Solomon, J. A., & Sperling, G. (1995). 1st- and 2nd-order motion and texture resolution in central and peripheral vision. *Vision Research*, 35(1), 59–64.
- Sperling, G. (1989). Three stages and two systems of visual processing. *Spatial Vision*, 4(2/3), 183–207.
- Stromeyer, C. F. III, Kronauer, R. E., Ryu, A., Chaparro, A., & Eskew, R. T. Jr. (1995). Contributions of human long-wave and middle-wave cones to motion detection. *Journal of Physiology, London*, 485, 221–243.
- Turano, K., & Pantle, A. (1989). On the mechanism that encodes the movement of contrast variations: velocity discrimination. *Vision Research*, 29(2), 207–221.
- Tyler, C. W., & Cavanagh, P. (1991). Purely chromatic perception of motion in depth: two eyes as sensitive as one. *Perception and Psychophysics*, 49(1), 53–61.
- Ullman, S. (1979). *The interpretation of visual motion*. Cambridge, MA: MIT Press.
- van Santen, J. P. H., & Sperling, G. (1985). Elaborated Reichardt detectors. *Journal of the Optical Society of America A*, 22, 300–321.
- Wertheimer, M. (1912). Experimentelle Studien über das Sehen von Bewegung. (Experimental studies on the seeing of motion) *Zeitschrift für Psychologie* 61, 161–265. Partial English translation.

- tion. In T. Shipley, *Classics in psychology* (pp. 1032–1089). New York: Philosophical Library.
- Zanker, J. M. (1996). On the elementary mechanism underlying secondary motion processing. *Philosophical Transactions of the Royal Society London B Biological Science*, 351, 1725–1736.
- Zanker, J. M. (1997). Second-order motion perception in the peripheral visual field. *Journal of the Optical Society of America A*, 14(7), 1385–1392.
- Zemany, L., Stromeyer, C. F. III, Chaparro, A., & Kronauer, R. E. (1998). Motion detection on flashed, stationary pedestal gratings: evidence for an opponent-motion mechanism. *Vision Research*, 38(6), 795–812.