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Eye movements affect the perceived speed of visual motion

Kathleen A. Turano [a,*], Susan M. Heidenreich [b]

[a] *The Johns Hopkins University School of Medicine, Wilmer Eye Institute, Baltimore, MD, USA*
[b] *University of San Francisco, San Francisco, CA, USA*

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Abstract

Eye movements add a constant displacement to the visual scene, altering the retinal-image velocity. Therefore, in order to recover the real world motion, eye-movement effects must be compensated. If full compensation occurs, the perceived speed of a moving object should be the same regardless of whether the eye is stationary or moving. Using a pursue-fixate procedure in a perceptual matching paradigm, we found that eye movements systematically bias the perceived speed of the distal stimulus, indicating a lack of compensation. Speed judgments depended on the interaction between the distal stimulus size and the eye velocity relative to the distal stimulus motion. When the eyes and distal stimulus moved in the same direction, speed judgments of the distal stimulus approximately matched its retinal-image motion. When the eyes and distal stimulus moved in the opposite direction, speed judgments depended on the stimulus size. For small sizes, perceived speed was typically overestimated. For large sizes, perceived speed was underestimated. Results are explained in terms of retinal-extraretinal interactions and correlate with recent neurophysiological findings.

Keywords: Speed perception; Eye movements; Retinal-image motion; Smooth pursuit eye movements; Motion perception

1. Introduction

Within our field of view, objects move in various directions at various speeds. Depending upon the saliency of the visual information and the task at hand, our eyes pursue or track one of the many moving objects. In doing so, the motion of that object, as well as the motion of the other moving objects, and the visual scene in general, are altered in the image on our retinas. Smooth pursuit eye movements add a velocity field to the visual scene that determines the velocity of the retinal motion. That is, the motion vectors for the distal stimulus and the eye-movement are added [illustrated in Fig. 1 of Turano & Heidenreich (1996)].

One important question is whether smooth pursuit eye movements affect speed perception in a manner consistent with the transformed retinal speed. We have previously shown that speed discrimination performance varies with the eye motion relative to the distal motion. Although discrimination measures indicate the precision of performance, they do not reveal whether the percept of the moving distal stimulus is systematically biased in a particular fashion. In the present study, we determined how the perceived speed of a distal stimulus changes as a function of the speed and direction of the eye movement relative to the motion of the distal stimulus.

Several studies have investigated the effects of eye movements on object motion perception (Wertheim, 1981; Pola & Wyatt, 1989; Brenner & van den Berg, 1994; Wertheim, 1994) and self-motion perception (Warren & Hannon, 1990; Royden, Banks & Crowell, 1992; Royden, Crowell & Banks, 1994; Freeman, Crowell & Banks, 1996) and have reached various conclusions. Some studies have concluded that eye movements do not affect the perception of distal motion (Warren & Hannon, 1990; Royden, Banks & Crowell, 1992; Royden, Crowell & Banks, 1994), whereas other studies have demonstrated that, at least in some situations, eye movements do affect distal motion perception (Wertheim, 1981; Pola & Wyatt, 1989; Brenner & van den Berg, 1994; Wertheim, 1994; Freeman, Crowell & Banks, 1996; Turano & Heidenreich, 1996).

* Corresponding author. Present address: Lions Vision Center, 550 North Broadway, 6th floor, Baltimore, MD 21205, USA. Tel.: +1 410 5026434; fax: +1 410 9551829; e-mail: kathy@lions.med.jhu.edu

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One prevailing view is that the perception of distal motion is based on an internal representation that consists of retinal and extraretinal signals (Wertheim, 1981; Pola & Wyatt, 1989; Brenner & van den Berg, 1994; Wertheim, 1994; Turano & Heidenreich, 1996). However, other findings suggest that under certain conditions, the only information used to judge distal motion is the retinal-image motion (Brenner & van den Berg, 1994; Turano & Heidenreich, 1996). We (Turano & Heidenreich, 1996) found that changes in retinal-image motion due to eye movements can account for the elevated speed-discrimination thresholds, except when the eyes move faster than the distal stimulus. In that case, speed-discrimination thresholds are higher than predicted on retinal-image motion alone indicating that some factor other than retinal-image motion is involved.

In this study we test the distal-motion model and the retinal-motion model in a speed-matching experiment to determine how the perceived speed of a distal stimulus changes as a function of the speed and direction of eye movements. The distal-motion model assumes that the effects of eye movements can be fully compensated, and therefore the perceived motion of a stimulus should be the same whether the eye is stationary or moving. According to this model, perceived speed, P, obeys a vector summation rule of the retinal, S_R, and extraretinal, S_{eye}, signals (Eq. (1)).

$$P = \sqrt{S_R^2 + S_{eye}^2 + 2\cos\theta\, S_R S_{eye}} \quad (1)$$

When the angle, θ, between the retinal and the extraretinal signals is 0, Eq. (1) reduces to

$$P = S_R + S_{eye} \quad (2)$$

and when the angle is 180°, Eq. (1) reduces to

$$P = |S_R - S_{eye}|. \quad (3)$$

In contrast, the retinal-motion model assumes that there is no compensation for the retinal effects of the eye movements, and therefore observers should make perceptual judgments of the real-world motion only on the basis of the retinal-image motion.

We investigated whether the perceived speed of a moving stimulus viewed with a moving eye is the same as the perceived speed of the same stimulus viewed with a stationary eye. We used a perceptual-matching task to estimate a threshold point on the psychometric function that anchors the function (i.e. the point of subjective equality); this differs from discrimination measures that reflect the slope of the psychometric function and only provide an estimate of the precision of the judgments. In effect, the perceptual-matching threshold indicates the speed of a test stimulus viewed while making pursuit eye movements that appears to be equal to the speed of a reference stimulus viewed while fixating a stationary point.

2. General method

2.1. Pursue-fixate procedure

Perceptual matches were determined using a pursue-fixate procedure in a perceptual matching paradigm, illustrated in Fig. 1. On each trial, the subject was presented with two motion sequences of a translating distal stimulus. In the first motion sequence, the stimulus moved at a test speed (reference speed $\pm\Delta$ speed). In the second motion sequence, the stimulus always moved at the reference speed. The subject's task was to indicate in which of the two motion sequences the stimulus moved faster. No feedback was given.

To test the interaction of eye and distal stimulus motion, the subject was instructed to pursue (or track) a translating pursuit target during the presentation of the first sequence until the distal stimulus disappeared and then to fixate the centrally-located stationary point during the presentation of the second sequence. By keeping the eye relatively still during the presentation of the distal stimulus moving at the reference speed, the end result is an estimate of the perceived motion of the stimulus during eye movements relative to the same stimulus viewed with a stationary eye. A brief interval (2 s) between the two motion sequences allowed the subject to switch from pursue to fixate. A tone indicated the start of each trial. The time between trials was approximately 3.5 s.

2.2. Staircase procedure

Two independent interleaved staircases were used; one was initiated from the negative side ($-\Delta$ speed) and the other was initiated from the positive side ($+\Delta$ speed). On each trial, one of the two staircases was randomly chosen, designating the Δ speed based on the subject's previous response for that staircase. After a single correct judgment, the Δ was decreased by half and after one incorrect response, the Δ was increased in a similar manner, with a minimum delta set at 0.05 °/s. The procedure was such that the two interleaved staircases could potentially cross and recross (Cornsweet, 1962). The test session ended after ten reversals per staircase, requiring approximately 50 trials per session. Speed match error was computed as the mean of all the Δ speed (for both staircases) presented after the data collection began (Fendick, 1985). Response variability was calculated as half the difference between the independently calculated signed means of the two staircase Δ speeds (Fendick, 1985).

2.3. Eye-movement recording

We followed the same procedure used previously to record eye movements (Turano & Heidenreich, 1996).

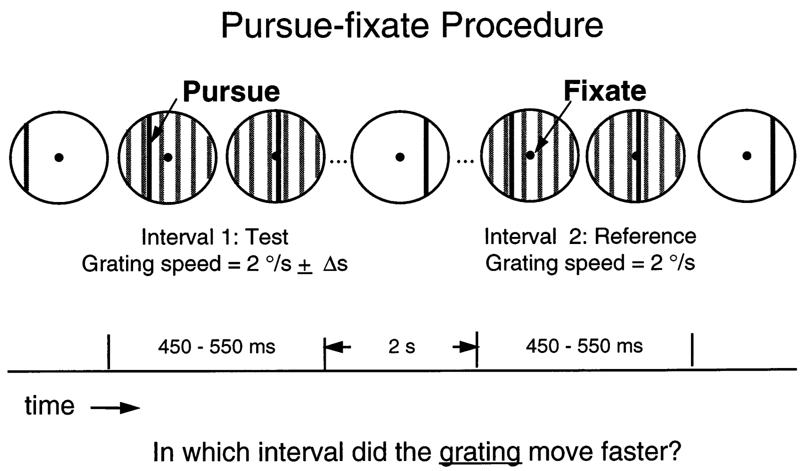

Fig. 1. Illustration of the time course for the pursue-fixate procedure. The dark bar represents the pursuit target and the grating represents the distal stimulus. The grating was presented twice in succession. Subjects were instructed to pursue the bar until the grating disappeared and then to fixate a centrally-positioned stationary point during the second interval. The bar and fixation point were visible throughout the experimental session. The subjects' task was to indicate in which interval the grating moved faster.

Because accurate eye-movement records are critical to our evaluation of the models, the procedure is described again here. Eye velocity was measured throughout each trial using an SRI Generation-V dual Purkinje-image eyetracker (Crane & Steele, 1985). The subject viewed the display with the right eye and wore an opaque patch over the left eye. The head was stabilized with a bite bar and headrest. Eye velocity for the right eye was determined from the voltage analogs of horizontal eye position. The voltages were fed into an analog-to-digital converter every 10 ms and stored on a computer for off-line analysis. Voltage was converted to degrees of visual angle, on the basis of each subject's calibration results. The calibration procedure was as follows: 25 equally spaced points, extending 6° horizontally and vertically, were displayed in sequence on a CRT display screen positioned 2 m in front of the subject. To calibrate each position, a dot appeared at the center of the monitor and the subject pushed a button when she or he was fixating the dot. The central dot then disappeared, and a calibration dot appeared. The subject fixated that dot, and the voltage and screen position were recorded. To convert voltage to degrees of visual angle, a regression line was fit to the dots' horizontal positions, expressed in terms of visual angle, plotted against the horizontal positions of the eye, expressed in terms of voltage.

2.4. Eye-movement analysis

Average horizontal eye velocity was computed as the slope of horizontal eye position over time and was determined separately for the pursuit and fixation intervals of each trial. Prior to calculating pursuit eye velocity, saccadic eye movements were identified and eliminated in the following manner: A threshold velocity was set at 14 °/s. If the eye velocity between any two successive samples exceeded the threshold, those two and the next four samples were excluded from the analysis. For motion sequences in which samples were removed, eye velocity was defined as the average, weighted by the number of samples, of the separately-computed slopes for the individual segments.

3. Experiment 1: speed matching of optimal distal speed

3.1. Methods

The stimuli were generated by a graphics display board (Cambridge Research Systems), controlled by an IBM-compatible AT computer, and displayed on a Joyce DM2 monitor with a refresh rate of 100 Hz. The display screen was masked with a circular aperture that was 8° in diameter. Viewing distance was 2 m. The parameters of the distal stimulus were chosen to stimulate the most efficient motion sensor (Watson & Turano, 1995). The stimulus was a vertically-oriented, 3-c/° sine-wave grating, moving at a reference speed of 2.0 °/s. The contrast of the grating was 20%.

A vertical bar (0.06° wide, 10% positive contrast) that served as the pursuit target moved across the display screen at a specified velocity and was continuously present throughout the experimental session. The bar's speed (0–4 °/s) and direction (same or opposite to the grating) were the same within a block of trials and randomly manipulated across blocks. The pursuit target moved across the display screen at a constant velocity and wrapped around when it reached the edge. The pursuit target and stimulus velocities were independent of each other. The fixation point was a black

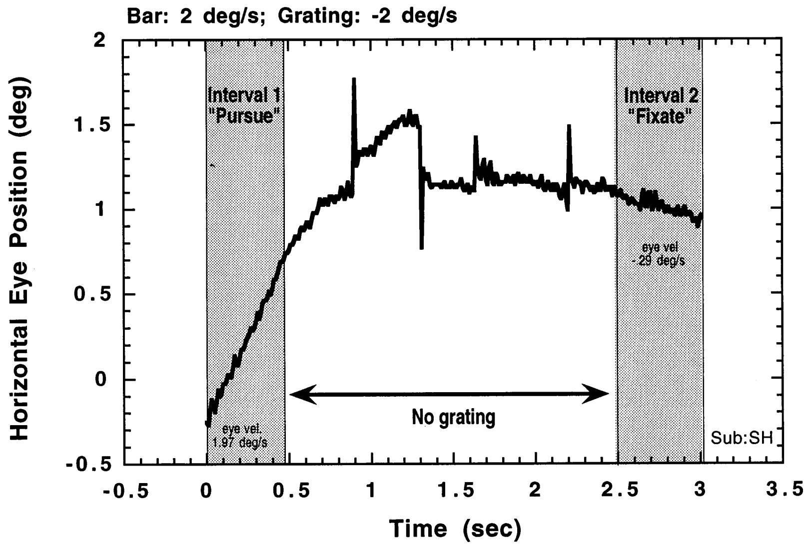

Fig. 2. Horizontal eye position plotted against time. Average eye velocity, computed as the slope of eye position over time, was determined separately for the "pursue" and the "fixate" intervals. Data from one trial in Experiment 1; distal grating velocity = −2°/s; pursuit target velocity = 2°/s, "pursue" interval eye velocity = 1.97°/s; "fixate" interval eye velocity = −0. 29°/s.

opaque circle (0.2° diameter) which remained taped on the display screen at its central position.

The duration of each of the two motion sequences within a trial was randomly chosen from a Gaussian distribution centered at 500 ms (S.D. = 50 ms). The stimuli in the two motion sequences always moved in the same direction, right or left, and the direction of motion remained fixed throughout each experimental session. The direction of grating motion was systematically alternated across sessions.

Three observers (including the two authors) with normal or corrected-to-normal acuities, well trained in the pursue-fixate procedure, served as subjects.

3.2. Results

Fig. 2 is the eye-movement record of one trial. Horizontal eye position is plotted against time. The two shaded areas represent the intervals in which the two motion sequences were presented. During the first motion sequence the subject was instructed to pursue the bar until the grating disappeared and then to fixate the stationary mark throughout the period of the second motion sequence. In the time period between the two intervals there was no grating pattern on the screen. The eye positions presented in Fig. 2 are from a trial in which the pursuit target moved rightward at a speed of 2 °/s and the reference stimulus moved leftward at a speed of 2 °/s. During the first interval the eye moved rightward at a speed of 1.97 °/s and during the second interval the eye moved leftward at 0.29 °/s.

Subjects were able not only to switch from pursuit to fixation during the 2-s time interval, but they were also able to keep their eyes fairly stable during the second interval. The average eye velocities measured during interval 2 ("fixate") are 0.21 °/s (S.D. = 0.14) for subject FT, 0.41 °/s (S.D. = 0.22) for subject SH, and 0.16 °/s (S.D. = 0.07) for subject KT.

In Fig. 3, we plot the speed of the test grating that appears equal to the speed of the reference speed (i.e. speed match) as a function of the eye velocity. According to the retinal-motion model (prediction shown as solid line in Fig. 3), speed match should vary in proportion to eye velocity because, to equate the perceived speeds of the reference and test gratings, the speed of the test grating needs to be adjusted by an amount equivalent to the eye velocity. According to the distal-motion model (prediction shown as dashed line in Fig. 3), speed match should equal the reference speed regardless of the eye velocity.

The symbols in Fig. 3 represent the three subjects' speed match data. The eye velocity is the mean eye velocity calculated during the first interval, averaged over all the trials in a session. The horizontal error bars on each data point indicate the standard deviation of the eye velocities for that test session. The mean gains (i.e. eye speed divided by pursuit target speed) were 0.67 (S.D. = 0.21), 0.88 (S.D. = 0.15), and 0.74 (S.D. = 0.28) for subjects FT, KT, and SH, respectively.

The speed match data cannot be fully explained by either of the two models. For eye movements in the same direction as the distal stimulus (unshaded area in Fig. 3), the speed matches fall between the predictions of the retinal-image and distal motion models. For eye movements in the opposite direction to the distal stimulus, the data of two subjects approximate the prediction of a distal motion model and the data of the third subject fall between the predictions of the distal-motion and retinal-motion models.

3.3. Discussion

The results of Experiment 1 demonstrate that eye movements can affect the perceived speed of distal-stimuli. An eye movement of only 1°/s in the same direction as a 2°/s distal stimulus can decrease its perceived speed by as much as 25% of its speed (0.5°/s), when compared to its perceived speed when viewed with a stationary eye. However, the effects of eye movements on the perceived speed of distal-stimuli are not determined by eye speed alone. The results show an asymmetry in the speed match errors with respect to the relative direction of eye and distal motion. An eye movement of 1.5°/s in the opposite direction of the distal motion produces a speed match error less than 0.3°/s, whereas a 1.5°/s eye movement in the same direction produces an error greater than 1°/s.

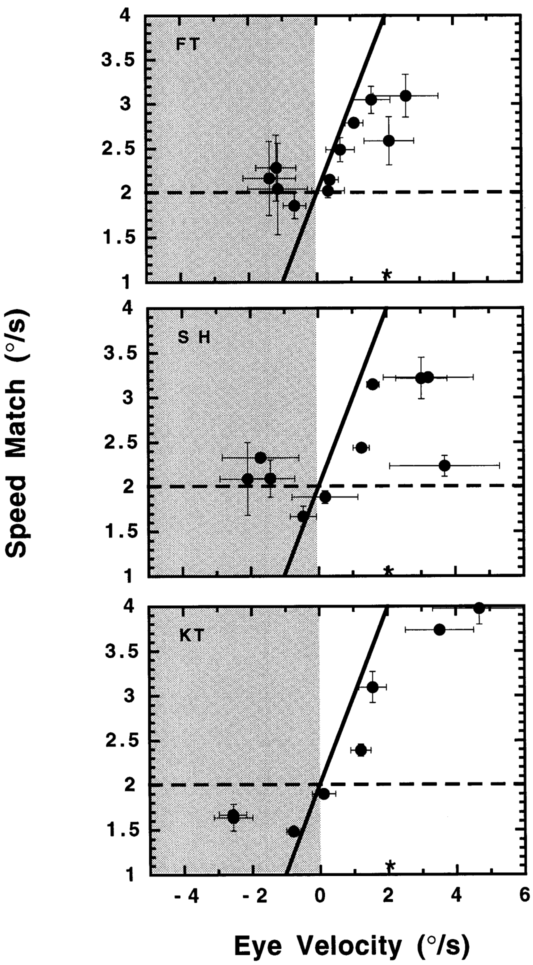

Fig. 3. Speed match plotted as a function of actual eye velocity. Positive and negative values of eye velocity indicate movement in the same and opposite direction as the grating, respectively. The predicted match for the retinal-motion model is shown as a solid diagonal line. The predicted match for the distal-motion model is shown as a broken horizontal line at 2.0°/s. Shaded area, eye movement in the opposite direction to the distal stimulus motion; unshaded area, eye movement in the same direction as the distal stimulus motion. Error bars represent ±1 S.D. Stars indicate the velocity of the reference distal stimulus (2°/s). Data are for subjects FT (a), SH (b), and KT (c).

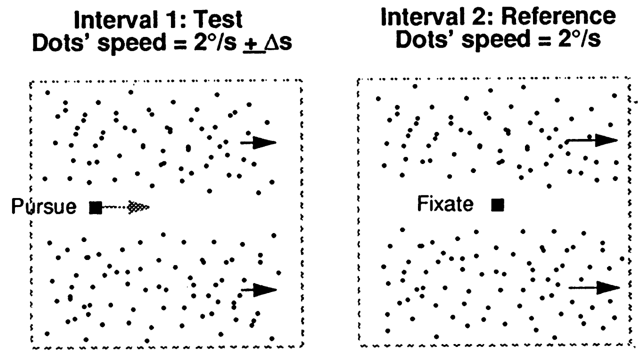

Fig. 4. Illustration of the display in the pursue and fixates phases in Experiment 2. The distal stimulus was an array of randomly positioned dots that moved horizontally within a stationary window. A single square, positioned within a horizontal gap that divided the window, served as both the pursuit target (in the pursue phase) and the stationary fixation point (in the fixate phase). The dashed box outlining the window is for illustration purpose only; it was not present in the display.

It is possible that the spatial superposition of the pursuit target (as well as fixation point) and the grating would excite local relative motion detectors; this in turn may have affected the perceived speed of the grating. In the next experiment, we modified the display to eliminate the spatial superposition and re-examined the subjects' judgments using the same pursue-fixate task.

4. Experiment 2: effect of non-overlapping pursuit target and grating

4.1. Methods

The stimuli were generated by a Silicon Graphics OCTANE workstation and displayed on a Silicon Graphics Color Graphics Display (Model GDM 20E21) with a refresh rate of 72 Hz. Viewing distance was 0.57 m. The distal stimulus was an array of randomly positioned dots (density of 1 dot/deg^2) that moved horizontally within a stationary $8 \times 8°$ window. Each dot was composed of a 3×3 pixel array ($0.09 \times 0.09°$) and had a luminance of 28.5 cd/m^2. A single square (5×5 pixel array—$0.15 \times 0.15°$, 28.5 cd/m^2), positioned within a horizontal gap (2.5°) that divided the window, served as both the pursuit target (in the pursue phase) and the stationary fixation point (in the fixate phase). Fig. 4 illustrates the display in the pursue and fixate phases.

A trial proceeded as follows: The display screen was uniformly illuminated at 5.3 cd/m^2 for the first 0.1 s. Next, the pursuit target appeared and traversed horizontally within the gap at a specified velocity for a total of 1.5 s. When the pursuit target had been presented for 1 s, the dots appeared and moved within the window for 0.5 s. The dots and pursuit target disappeared, and the screen was again uniformly illuminated for 1 s. The fixation point then appeared centered within the gap and remained stationary for 1.5 s. During the last 0.5 s of fixation the dots appeared and moved within the window at the reference velocity of 2.0°/s. The two authors served as subjects.

4.2. Results

In Fig. 5, we plot speed matches as a function of eye velocity, using the same plotting conventions as in Fig. 3. Solid symbols represent the data of Experiment 1, replotted for comparison purposes. The open symbols represent the data obtained with the display using the non-overlapping pursuit target and distal stimulus.

For eye movement in the same direction as the distal stimulus, the general trend in speed match as a function of eye velocity was the same regardless of the display type; performance was the same when the pursuit target (and fixation point) were superimposed on the distal stimulus and whether the distal stimulus was a grating or an array of randomly positioned points.

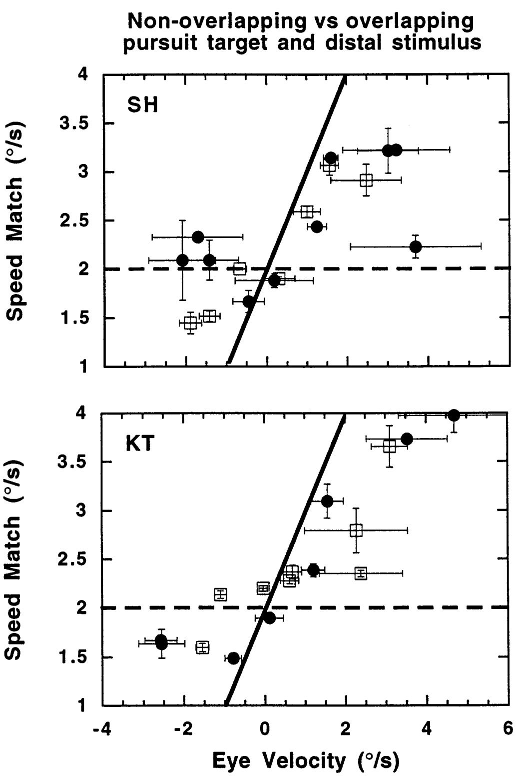

Fig. 5. Speed match plotted as a function of eye velocity, using the same plotting conventions as in Fig. 3. Solid symbols represent the data of Experiment 1, replotted from Fig. 3 for comparison purposes. The open symbols represent data obtained with the display using the non-overlapping pursuit target and distal stimulus.

The distal stimulus was perceived to move more slowly when the eye moved in the same direction than when the eye was stationary. However, with the modified display, when the eye moved in a direction opposite the distal stimulus it was perceived more often to move slightly faster than when the eye was stationary.

In our pursue-fixate procedure, not only did the retinal motion of the distal stimulus differ between the pursue and fixate intervals, but so did the retinal motion of the stimulus aperture. The relative motion of the grating and aperture may have affected the perceived speed of the distal stimulus. In the first two experiments, the display window subtended a relatively small visual angle (8 × 8°) which may have increased the salience of the relative motion of the grating and aperture. To test whether stimulus size had an impact on the estimated distal stimulus speed, we repeated the procedure with a larger display. In addition, we tested the generalizability of the effect using additional reference speeds.

5. Experiment 3: effects of display size and reference speed

5.1. Methods

The methods were the same as described in Experiment 2 with the exception that speed matches were determined for three reference speeds (2.0, 4.0, and 6.0°/s) for each of two window sizes (38 × 28° and 8 × 8°).

5.2. Results

Fig. 6 plots the speed matches obtained with the large (38 × 28°, solid symbols) and small displays (8 × 8°, open symbols) for the three different reference speeds for subjects SH and KT. Plotting conventions are the same as described for Fig. 3. Table 1 lists the mean pursuit gains of the two subjects for the various conditions. Note that there is little difference between the mean gains for the large and small stimulus sizes and for the stimulus speeds.

The most striking difference between the datasets for the large and small stimulus displays is the difference in the perceived speed of the distal stimulus when the eye moves in the opposite direction (indicated on the x-axis by the negative eye velocities). With the larger stimulus, when moving their eyes subjects chose a faster distal stimulus as a perceptual match, indicating that they perceived the distal stimulus to be moving slower during pursuit eye movements than when the eye was stationary. With the

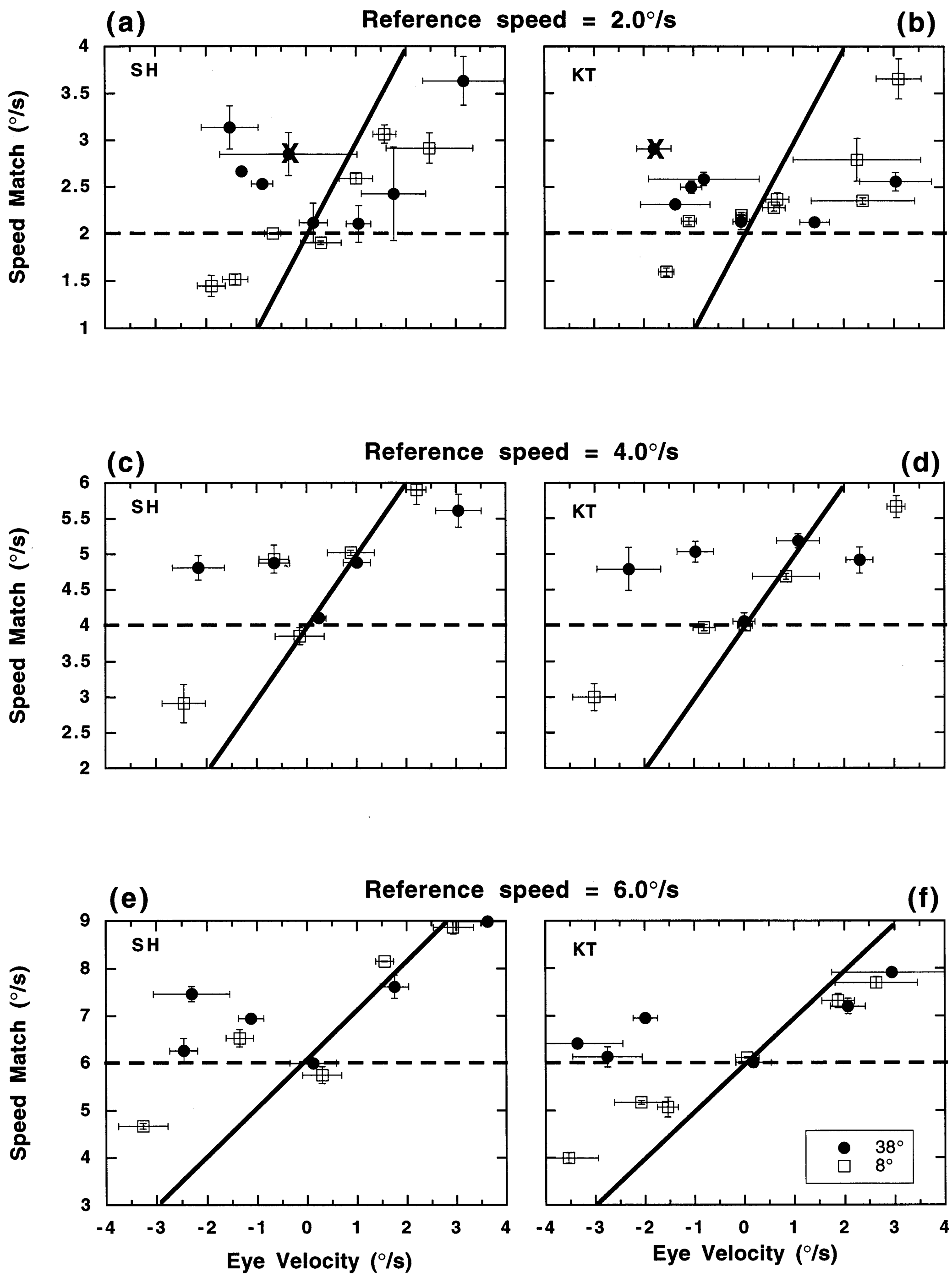

Fig. 6. Speed match plotted as a function of eye velocity obtained with the large (38 × 28°, solid symbols) and small displays (8 × 8°, open symbols). Data for the three different reference speeds are shown in separate graphs: 2.0°/s (a, b), 4.0°/s (c, d), and 6.0°/s (e, f), for subjects SH and KT, respectively. The symbols denoted by an X in a and b represent data obtained with a 38 × 28° display with an opaque border outlining a square (8 × 8°) superimposed. The reference speed was 2.0°/s and eye velocity was −2.0°/s. Plotting conventions are the same as described for Fig. 3.

small stimulus, however, the subjects generally perceived the distal stimulus to be moving faster than when the eye was stationary; this effect occurred with all three reference speeds. Thus, the size of the distal stimulus had a significant effect on the perceived speed of the distal-stimuli when the eye moved in the opposite direction to the distal stimulus.

The pattern of results was different, however, when the eye moved in the same direction as the distal stimulus. There was little difference in the

Table 1
Mean values and S.D. of eye velocity-to-pursuit target gain

Stimulus speed (°/s)	Stimulus size (°)	Subject			
		KT		SH	
		Mean	S.D.	Mean	S.D.
2.0	8	0.69	0.24	0.79	0.15
2.0	38	0.72	0.23	0.83	0.14
4.0	8	0.92	0.11	0.77	0.10
4.0	38	0.90	0.16	0.85	0.19
6.0	8	0.86	0.15	0.75	0.06
6.0	38	0.86	0.15	0.71	0.17

speed matches obtained with the large and small windows. The distal stimulus was perceived to be moving more slowly than when the eye was stationary. Again, the effect was replicated across all three reference speeds.

5.3. Discussion

The results of Experiment 3 suggest that when the eye moves in the opposite direction to the distal stimulus the display size plays a role in determining perceived speed. To ascertain whether the size of the display, per se, was a critical factor or whether the critical factor was the location of motion signals generated at the window boundaries, subjects repeated a session (pursuit target velocity $-2°/s$, window size $38 \times 28°$) with a superimposed opaque border (1° wide black masking tape) outlining a square ($8 \times 8°$) positioned at the center of the display. These black edges would have generated motion signals at the same spatial location as the motion signals at the boundaries in the small display condition. The results for this manipulation are indicated by an X in Fig. 6a,b. The data show that the perceived speed of the distal stimulus is not affected by the absence or presence of boundaries in the near periphery.

To more fully map the function of perceived speed versus stimulus size at a particular pursuit velocity ($-2°/s$), subjects participated in two ancillary sessions. The experimental methods of the ancillary sessions were the same as described in Experiment 2 with the exception that the window sizes were 12° in one session and 18° in the other. Fig. 7 plots speed match as a function of window size. The horizontal line at 2°/s indicates an equivalent match in perceived speed between the moving-eye and stationary eye viewing conditions. The graph shows that the perceived speed of a distal stimulus varies in a systematic manner with stimulus size. For a small stimulus (8°), eye movements in the opposite direction to the stimulus serve to increase the perceived speed of the stimulus. For stimulus sizes of 18° and greater, eye movements in the opposite direction to the stimulus serve to decrease the perceived speed of the stimulus.

6. General discussion

The results of this study demonstrate that, in general, eye movements affect the perceived speed of a distal stimulus. We find no evidence to support the distal-motion model. We have identified an interaction between two factors that influence the eye-movement effect on perceived speed. One factor is the direction of the eye-movement relative to the distal stimulus motion, and the other factor is the size of the distal stimulus.

When a person's eyes move in the same direction as a distal stimulus, it appears slower than when the person's eyes are still. Under these conditions, speed judgments are relatively close to the predictions generated by the retinal-motion model particularly for the faster reference speeds; the effects of eye movements on the retinal-image motion are not compensated. For the stimulus parameters that we tested, an extra-retinal

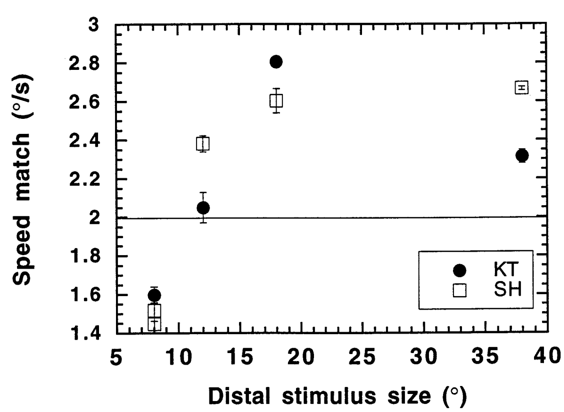

Fig. 7. Speed match plotted as a function of stimulus display width at a pursuit velocity of $-2.0°/s$ for subjects KT (solid symbols) and SH (open symbols). The horizontal line at 2°/s indicates an equivalent match between the moving-eye and stationary-eye viewing conditions. Data for the 8 and 38° sizes were obtained in Experiment 3 (reference speed, 2.0°/s; pursuit velocity, $-2.0°/s$), replotted from Fig. 6.

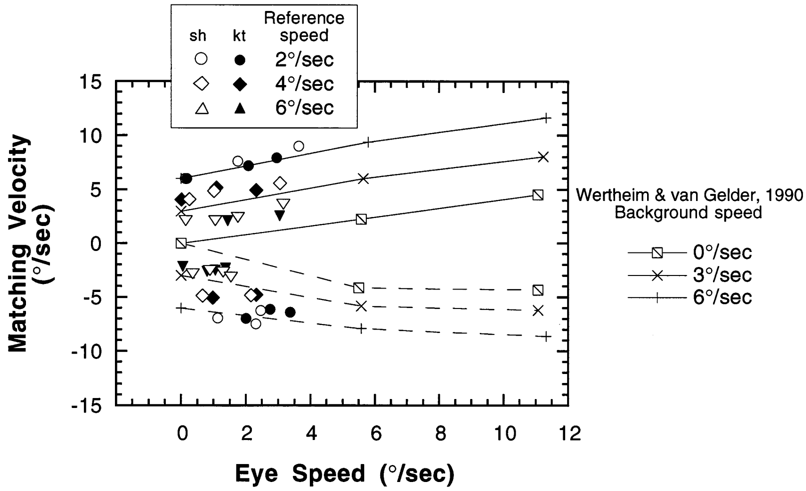

Fig. 8. Speed match data plotted as a function of eye speed. The speed match data (for the 38° display size) from Fig. 6 of the present paper are plotted together with a subset of the data from Wertheim & van Gelder (1990). The solid and dashed lines connect symbols for the same and opposite directions of eye and background motion, respectively, of the Wertheim and van Gelder study. Different symbols represent different background speeds.

signal does not appear to contribute significantly to the distal stimulus speed judgments.

When a person's eyes move in the opposite direction to a distal stimulus, its perceived speed depends on its size. When the stimulus is small ($< \sim 12°$) most judgments fall between a retinal-image match and a distal stimulus match. Data falling between the two could be accounted for by the contribution of an extra-retinal signal that under-represents eye velocity. The idea that the extra-retinal signal could under-represent eye velocity has been purported by several researchers (Gibson, Smith, Steinschneider & Johnson, 1957; Mack & Herman, 1973; Wertheim, 1987) and demonstrated by the Aubert-Fleischl phenomenon (i.e. a pursued stimulus appears slower than the same stimulus viewed with a stationary eye). When the stimulus is large, however, the judgments indicate that the perceived speed is underestimated. This could be explained by the contribution of an extra-retinal signal that over-represents eye velocity (i.e. the extra-retinal signal amplifies or over-estimates the speed of the eye).

6.1. Possible neurophysiological correlates

The idea that the extra-retinal signal could over-represent the eye velocity has some support from recent neurophysiological studies by Komatsu & Wurtz (1988). Recordings were made of cells located in the medial superior temporal (MST) area of the monkey cortex that have both an extra-retinal input and a visual response input. Some of these "pursuit" cells responded preferentially to small stimulus displays and others to large stimulus displays. The firing rate of many of the cells that responded preferentially to the large stimulus displays was greater when there was retinal motion of the background in the opposite direction to the pursuit than when pursuit was in the dark. The retinal motion served to increase the output of the pursuit cells. This was not the case when the preferred direction of stimulus motion and pursuit was the same. In this situation, interaction between the pursuit-related response and the visual stimulation was highly variable.

In the same study, Komatsu and Wurtz demonstrated that the pursuit cells that responded preferentially to the large stimulus displays showed a reversal in preferred direction as the stimulus size increased. This response change indicates that for some MST cells display size plays a role in modulating the retinal-extraretinal interaction (Komatsu & Wurtz, 1988).

6.2. Relation to other psychophysical studies

Using a speed magnitude estimation procedure and a $60 \times 20°$ display, Wertheim & van Gelder (1990) showed that the speed of the background pattern was underestimated when the eyes moved in the same direction as the background and, for background speeds slower than 9°/s, when the eyes moved in the opposite direction to the background. At a faster background speed, it was no longer underestimated. In our study we only investigated stimulus speeds of up to 6°/s. At these speeds, our results with the large stimulus display are comparable to theirs; background (stimulus) speed is underestimated during pursuit eye movements. In order to more directly compare the results of the two studies, we have replotted a subset of the data from the two studies together in Fig. 8. The data from the present study are shown as unconnected symbols, and the data from the Wertheim and van Gelder study are shown as symbols connected by lines. The solid and dashed lines connect symbols for the same and opposite direction of eye and background motion, respectively. As shown, the pattern of results for the two studies is similar across the range of common background velocities.

Brenner & van den Berg (1994) also found an asymmetry in perceived speed that depended on the relative direction of eye and background motion. Unlike the task in the Wertheim-van Gelder and present studies, the subjects in the Brenner and van den Berg study judged the perceived speed of the pursuit target, not the background motion (display size of $35 \times 22°$). Subjects pursued a target that moved across a textured background. At some point in the presentation, the background velocity could be manipulated and at the same time the target's speed would either increase, decrease, or remain the same. Subjects had to indicate whether the target's speed had changed. The results showed that when the eyes moved in a direction opposite the background motion, pursuit target velocity was perceived to be constant regardless of changes in the velocity of the pursuit target or background, provided the relative motion between the two remained the same. When the eyes moved in the same direction as the background, the pursuit target was perceived to remain the same at a velocity between the constant relative-motion velocity and the initial target velocity. They proposed that when the eyes moved in the same direction as the background motion, perceived speed was influenced by an extraretinal signal that underrepresented eye motion. However, when the eyes and background motion were in opposite directions, the perceived speed of the pursuit target was based on the retinal slip of the background motion. Their results and interpretation are opposite to ours. In our study, with the large display, perceived speed appears little influenced by an extraretinal signal when the eyes move in the same direction as the background. But when the eyes move in the opposite direction to the background, perceived speed appears to be influenced by an extraretinal signal that over-represents eye motion. The difference in results and interpretation between the two studies may be due to the fact that the subjects in our study judged the speed of the background motion and the subjects in the Brenner and van den Berg study judged the speed of the pursuit target. Further studies are needed to determine the reason for the discrepancy.

The results of our study appear to contradict the claim made in other studies that eye movements have little to no effect on the perception of distal stimulus motion (Warren & Hannon, 1990; Royden, Banks & Crowell, 1992; Royden, Crowell & Banks, 1994). These experiments investigated the role of eye movements on the accuracy of heading judgments. The size of the displays used in the these experiments is comparable to our large stimulus display where the subjects underestimated the speed of the distal stimulus during eye movements. The fact that the experimental designs of the heading studies are different from the experimental design of our study may account for the discrepancy. For example, the optic flow patterns used in the heading experiments were composed of motion vectors of various directions and speeds whereas in our experiments the motion vectors were of a uniform speed and direction. The heading experiments also differed from ours in that they examined heading perception which is a direction task unlike the speed-perception task in the present study. Whether or not either of these two methodological differences can account for the differences in results between the studies remains to be seen.

It is interesting to note that the results of another recent study demonstrate that heading perception during eye movements is not always accurate (Freeman, Crowell & Banks, 1996). Subjects perceived an oscillation in the heading direction as they pursued an oscillating target. Using a procedure where subjects canceled the perceived heading oscillation by varying the amplitude and phase of a simulated eye rotation, Freeman, Crowell & Banks determined that the gain of the cancellation signal was from 0.5 to 0.8.

6.3. Functional roles

From an ecological perspective, one may ask why the visual system would respond differently depending on the size of the stimulus and the relative direction of eye movements. Komatsu & Wurtz (1988) have provided a logical neurophysiological argument based on cells in MST. Cells in MST that show a synergistic effect between retinal-image motion and eye movements in the opposite direction could distinguish figure from ground or object motion from self motion. Whereas cells that do not show an effect with a large stimulus display could provide information such as retinal slip that drives the pursuit system.

6.4. Summary

Our results demonstrate that eye movements affect the perceived speed of distal-stimuli. Perceived speed depends on the interaction between the distal stimulus size and the eye velocity relative to the distal stimulus motion. When a person's eyes move in the same direction as a distal stimulus, it appears slower than when the person's eyes are still. When a person's eyes move in the opposite direction to a distal stimulus, its perceived speed depends on its size. For small distal stimuli, eye movements in the opposite direction to the stimulus serve to increase the perceived speed of the stimulus. For large distal stimuli, eye movements in the opposite direction to the stimulus serve to decrease the perceived speed of the stimulus.

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