
Effects of directional expectations on motion perception and pursuit eye movements

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Abstract

Expectations about future motions can influence both perceptual judgements and pursuit eye movements. However, it is not known whether these two effects are due to shared processing, or to separate mechanisms with similar properties. We have addressed this question by providing subjects with prior information about the likely direction of motion in an upcoming random-dot motion display and measuring both the perceptual judgements and pursuit eye movements elicited by the stimulus. We quantified the subjects' responses by computing oculometric curves from their pursuit eye movements and psychometric curves from their perceptual decisions. Our results show that directional cues caused similar shifts in both the oculometric and psychometric curves toward the expected motion direction, with little change in the shapes of the curves. Prior information therefore biased the outcome of both eye movement and perceptual decisions without systematically changing their thresholds. We also found that eye movement and perceptual decisions tended to be the same on a trial-by-trial basis, at a higher frequency than would be expected by chance. Furthermore, the effects of prior information were evident during pursuit initiation, as well as during pursuit maintenance, indicating that prior information likely influenced the early processing of visual motion. We conclude that, in our experiments, expectations caused similar effects on both pursuit and perception by altering the activity of visual motion detectors that are read out by both the oculomotor and perceptual systems. Applying cognitive factors such as expectations at relatively early stages of visual processing could act to coordinate the metrics of eye movements with perceptual judgements.

Keywords: Expectation, Pursuit, Perception, Visual motion

Introduction

In everyday situations, expectations about future events allow us to react more quickly and accurately than might otherwise be possible. For example, anticipating how a ball will travel permits us to closely track and perhaps catch the ball, even when a bounce abruptly changes the ball's trajectory or when it is occluded by other objects and disappears from view. In experimental settings, expectations are typically manipulated with visual cues that influence subsequent sensory processing and motor preparation (Posner, 1980). Expectations can increase the perceptual sensitivity to stimulus features including luminance, orientation, form, and motion (Downing, 1988; Kurylo et al., 1996). Expectations can also influence the programming of tracking eye movements, producing smooth pursuit and saccadic eye movements that anticipate the future motion and location of visual targets (Kowler & Steinman, 1979*a,b*; Posner, 1980; Findlay, 1981; Bronstein & Kennard, 1987; Kowler, 1989; Barnes & Asselman, 1991). Presumably, these effects are mediated by sets of neurons whose activity has been selectively altered, producing response biases that are appropriate for the behavioral context. Using the same sets of neurons to

bias both perception and eye movements would help guarantee that the oculomotor system aimed the line of sight in a manner that was consistent with perception. However, it is not yet known whether the same or different sets of neurons mediate the effects of expectations on perception and eye movements.

For visual motion, there are several lines of evidence indicating that a shared processing stage underlies perception and the generation of pursuit eye movements. The presence of a shared motion processing stage was initially suggested by the fact that pursuit can be guided or influenced by perceived motion (Yasui & Young, 1975; Steinbach, 1976; Wyatt & Pola, 1979). By directly comparing the quality of perception to the metrics of pursuit, it was subsequently shown that the thresholds for discriminating the speed (Kowler & McKee, 1987) and direction (Watamaniuk & Heinen, 1999) of moving stimuli were nearly identical for perception and pursuit. Using similar analysis techniques, but stimuli that produce systematic errors in the estimation of motion, Beutter and Stone (1998) showed that the directional errors associated with perception and pursuit were nearly identical. These findings support the idea of a shared motion processing stage, although it is possible they could have also resulted from separate, albeit very similar, motion mechanisms for perception and pursuit. Indeed, it has been proposed that there are separate cortical pathways for perception and action (Goodale & Milner, 1992), extending the distinction between the ventral "what" and dorsal "where" cortical

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streams of visual processing (Ungerleider & Mishkin, 1982). In contrast, recent preliminary results have shown that perception and pursuit produce the same answer on a trial-by-trial basis—even when there is no correct answer and the output is presumably determined by processing noise (Stone & Krauzlis, 2000). These results provide suggestive evidence that, at least for motion processing, the same set of neurons might constrain both perception and pursuit.

Physiological experiments have identified several brain areas that might contain the neurons responsible for such shared processing. The most likely candidates are those areas of extrastriate cortex that provide motion inputs for both pursuit and perception. Lesions of the middle temporal (MT) and medial superior temporal (MST) areas of extrastriate visual cortex produce deficits in both perception (Newsome & Pare, 1988; Rudolph & Pasternak, 1999) and pursuit (Dürsteler & Wurtz, 1988), and microstimulation of MT and MST introduces biases in perception (Salzman et al., 1992; Celebrini & Newsome, 1995; Britten & van Wezel, 1998) and alters the metrics of pursuit (Komatsu & Wurtz, 1989). These cortical areas provide the primary sensory inputs for pursuit, and can access the final motor pathways for pursuit *via* direct projections to the brain stem and cerebellum, as well as along less direct pathways through other cortical and subcortical areas (for reviews, see Lisberger et al., 1987; Krauzlis & Stone, 1999). Cortical areas MT and MST also project to several regions implicated in the formation of directional judgments based upon visual motion, including the superior colliculus, prefrontal cortex, the frontal eye fields, and the lateral intraparietal area (Horwitz & Newsome, 1999; Kim & Shadlen, 1999; Shulman et al., 1999). Neurons in several of these regions also exhibit pursuit-related activity (Gottlieb et al., 1994; Bremmer et al., 1997; Krauzlis et al., 2000), suggesting that they might represent additional sites beyond MT and MST that also make some contribution to both pursuit and perception.

Although expectations about motion can influence both perceptual judgments and pursuit eye movements, it is not known whether these effects are due to shared processing or to separate mechanisms with similar properties. For example, it is possible that the effects of expectations on judgments of motion are due to changes in the criteria that subjects apply while evaluating the stimulus, whereas the effects of expectations on pursuit are due to predictive mechanisms that contribute specifically to the motor system. In the current experiments, we have addressed this question by providing subjects with prior information about the likely direction of an upcoming random-dot motion display and measuring both the perceptual judgments and pursuit eye movements elicited by the stimulus. By computing oculometric functions for each subject's pursuit, as well as psychometric functions for their perception, we are able to directly compare the changes in performance caused by the subjects' expectation of motion direction. We find a close correspondence between perception and pursuit across our conditions, and even on individual trials, suggesting that the effects of expectations are also mediated, at least in part, by mechanisms that are common to both.

Methods

Subjects

Data were collected from three adult subjects—two of the subjects were the authors (R and S) and the third subject was naïve (N). All

experimental protocols were approved by the Institutional Review Board and each subject gave informed consent. Data were collected in individual sessions lasting approximately 45 min, and a total of 90 sessions were run on the three subjects.

Stimuli and paradigms

Stimuli were presented on a video monitor (Eizo FX-E7) at a viewing distance of 41 cm and were generated using VisionWorks software (Swift et al., 1997). The sequence of stimuli presented during a single experimental trial of experiments 1 and 2 is illustrated in Fig. 1. Subjects initially viewed a strip (45 deg horizontal by 0.5 deg vertical) of stationary random dots (density: 3.1 dots/deg²). A fixation ring (diameter 1.1 deg), partially occluded by the strip of random dots, was located at the center of the display and acted as a reference to help subjects maintain fixation. On some trials, after 900 ms, an additional larger dot was presented for 100 ms, offset by 0.3 deg either to the left or right. This dot acted as a cue to the subject: the direction of the offset (left or right) indicated the likely direction of motion (left or right, respectively) in the upcoming stimulus. The cue was valid on 80% of the trials and subjects were instructed that “the cue was usually, but not always correct”. On trials without a cue, subjects continued viewing the stationary dots and fixation ring for this 100-ms interval. Subjects next viewed the stationary dots for an additional randomized interval (1000–1500 ms) before viewing the random dot motion. At the onset of motion, the starting locations of the dots were randomly reassigned. Every dot moved at a constant speed of 5 deg/s and the lifetime of each dot was limited to 50 ms to prevent subjects from following individual dots. On each trial, a single random-dot motion was selected from among a set of 13 possible motion stimuli, ranging from all rightward moving dots (+100%) to all leftward moving dots (−100%), and 11 intermediate motion signal strengths (80, 60, 40, 20, 10, 0, −10, −20, −40, −60, and −80). The remaining dots (i.e. those not assigned either rightward or leftward motions) were randomly assigned other directions of motion. The different stimulus conditions (i.e. combinations of cues and motion stimuli) were presented in a pseudorandom sequence. In separate experiments, subjects were presented with either (1) moving random dots for either a fixed duration of 1500 ms followed by a blank display, or (2) moving random dots for one of several randomized durations (25, 50, 75, 100, 125, 150, 175, 200, 250, or 500 ms) followed by a masking stimulus (a static random checkerboard pattern that filled the display for 150 ms) and then a blank display. On each trial, the blank display persisted until the subject pressed a button indicating their perceptual judgment concerning the direction of motion, which ended the trial and triggered the next stimulus sequence.

We recorded the subjects' eye movements and psychophysical responses as subjects viewed the stimulus sequence described above in three experimental conditions. In experiment 1, the “follow” condition, subjects were instructed to let their eyes follow the motion stimulus, which was presented for 1500 ms. In experiment 2, the “fixation” condition, the stimuli were identical to experiment 1, but the subjects were instructed to not move their eyes and to stay within the fixation ring. We confirmed that subjects maintained fixation and did not generate smooth following movements by *post-hoc* analysis of the eye movement data from each trial. In experiment 3, the “brief fixation” condition, the subjects were again instructed to not move their eyes and to stay within the fixation ring, but the stimuli were presented for brief durations (75, 100, 125, 150, 175, 200, 250, or 500 ms), followed

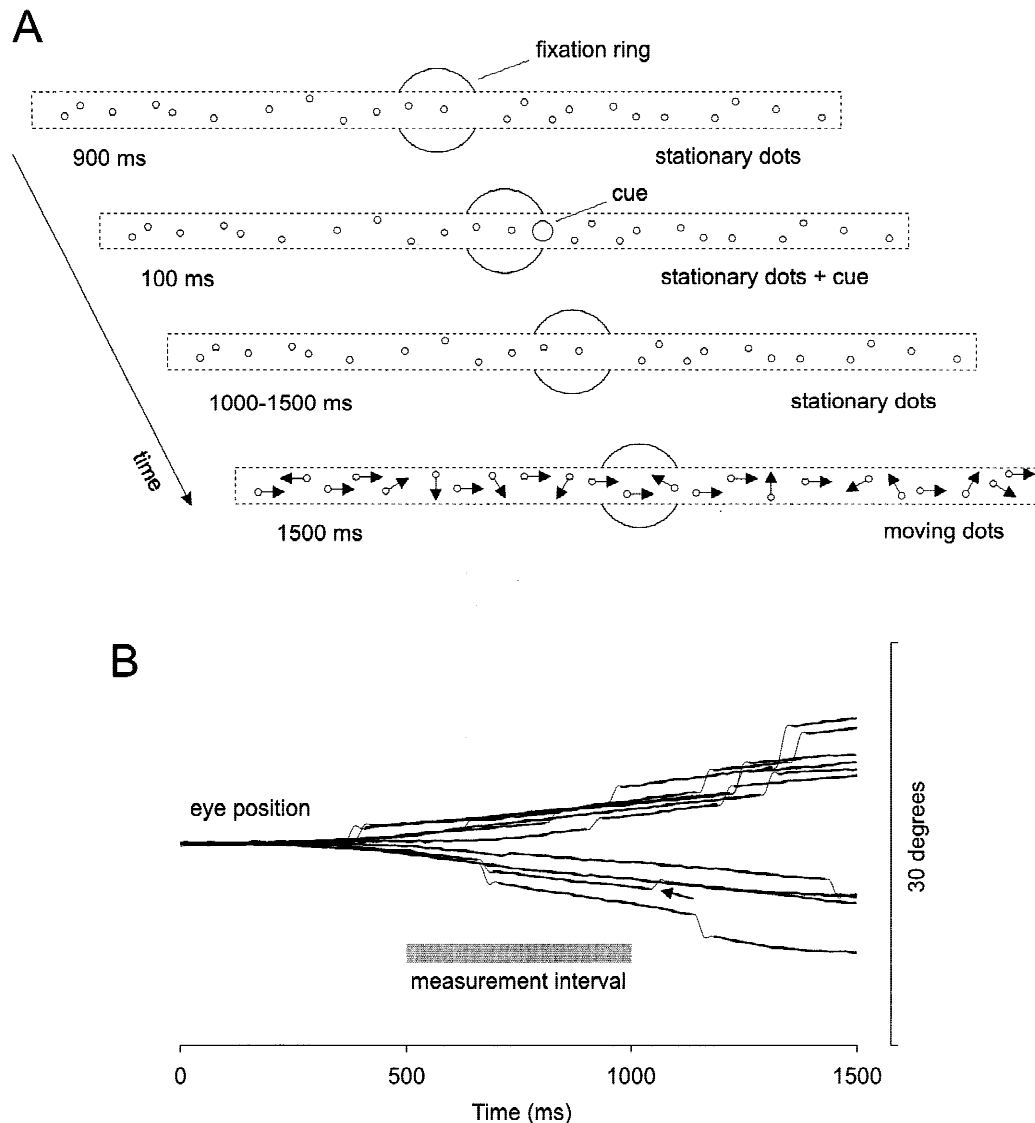


Fig. 1. Schematic diagram of the experimental conditions and sample eye position traces. A: The sequence of four images depict snapshots of the video display at successive moments during a single trial of experiments 1 and 2. In the actual experiment, the fixation ring, cue, and dots were white (87 cd/m^2) and were presented against a uniform gray background (33 cd/m^2). The dashed lines indicate the rectangular region in which the stationary and moving dots were presented and were not actually visible in the display. In experiment 3, the moving dots were followed by a masking stimulus (not shown). B: Sample eye position traces from individual trials from a single session (subject R). The motion stimulus was 10% rightward moving dots and no prior information was provided. Motion onset is defined as 0 ms. Gray segments of the eye position traces identify those intervals identified as saccades. The gray rectangle below the traces identifies the 500-ms interval used to calculate the oculometric functions.

by a masking stimulus. Data for the different experiments were collected in separate blocks of sessions.

Data collection and analysis

The presentation of stimuli, and the acquisition, display, and storage of data were controlled by a personal computer using the Tempo software package (Reflective Computing). A second personal computer, equipped with a high-speed graphics card (Cambridge Research Systems VSG2/3, Kent, England) and VisionWorks software (Swift et al., 1997), acted as a server device for presenting the visual stimuli, and received instructions from the Tempo computer via its serial and parallel ports. This visual display computer

returned trigger signals to the Tempo computer at the onset of each new stimulus, allowing us to synchronize data collection to stimulus presentation with 1-ms resolution.

Eye movements were measured with an infrared video-based eye tracker system (ISCAN Inc., RK-726, Burlington, MA). Subjects used a bite bar to minimize measurement errors due to head movements. The eye tracker reported the horizontal and vertical positions of the pupil with 12-bit resolution using a proprietary algorithm that computes the centroid of the pupil at 240 Hz. We calibrated the output from the eye tracker by recording the raw digital values as subjects fixated a set of known locations three times in a pseudorandom sequence. In the current experiments, we focused our analysis on the horizontal component of eye move-

ments, because the stimuli restricted movements to the horizontal meridian. We used the mean values during 500-ms fixation intervals at each location to generate a smooth function (using cubic spline interpolation) for converting the raw tracker values to horizontal and vertical eye position. Based upon the average standard deviation of these measurements, we estimate the measurement noise caused by the eye tracker to be approximately 0.05 deg.

All eye movement data, and events related to the onset of stimuli and to subjects' button presses, were stored on disk during the experiment, and later transferred to a freeBSD Linux-based system for subsequent off-line analysis. An interactive analysis program was used to filter, display, and make measurements from the data. Signals encoding horizontal eye velocity were obtained by applying a finite impulse response (FIR) filter (-3 dB at 54 Hz) to the calibrated horizontal eye position signals. Signals encoding eye acceleration were then obtained by applying the same FIR filter to the signals encoding velocity. For detecting saccades, the computer applied a set of amplitude criteria to the eye velocity and eye acceleration signals, as described previously (Krauzlis & Miles, 1996). With the eye tracker data, this algorithm permitted us to detect saccades with amplitudes as small as 0.3–0.4 deg. In addition, to be sure that our measurements of smooth eye movements were not contaminated by saccades, we excluded from analysis an additional 5 ms before and 10 ms after each detected saccade. To generate traces of smooth eye movements that did not contain high-frequency noise, we applied an additional low-pass FIR filter (-3 dB at 25 Hz) to the eye movement signals. For the oculometric analysis, we scored each eye movement response as either "rightward" or "leftward" based upon the average eye velocity in the interval 500–1000 ms after the onset of stimulus motion. For the analysis of pursuit initiation, we first estimated the average time of pursuit onset by determining when the average smooth eye velocities evoked by the -100% (all leftward moving dots) and 100% (all rightward moving dots) motion stimuli became significantly different from each other ($P < 0.05$, t test). We then measured the average eye velocity at the end of pursuit initiation, which we defined as the interval 90–100 ms after pursuit onset. Because our estimates of latency were based upon the average eye velocity with the strongest motion stimuli, the values we obtained are likely slightly shorter than the true average pursuit latency. However, these conservative estimates ensure that our measurements were confined to the initial open-loop interval of pursuit.

Psychometric and oculometric curves were obtained by fitting cumulative Gaussian functions to the tabulated perceptual judgements and pursuit responses. Because the number of samples was not uniform across stimulus conditions (in particular, there were four times as many valid as invalid trials), we weighted each point by its expected uncertainty (assuming a binomial distribution) and computed the minimum chi-square fits to the data. The bias and threshold were defined to be the offset and standard deviation of the best-fitting cumulative Gaussian, respectively. Curve fitting and statistical tests were performed with commercially available software (SigmaStat and Excel).

Results

Effects of motion strength and prior information on eye movements and perception

The eye movement responses recorded during a single session for one condition (10% rightward motion), comprising a total of ten

trials, is shown in Fig. 1B. The subject began to move their eyes smoothly approximately 200 ms after the onset of stimulus motion, which is defined as 0 ms in the plot. The gray rectangle indicates the 500-ms interval from which we made our measurements of smooth eye velocity for the oculometric analysis (Kowler & McKee, 1987; Beutter & Stone, 1998). We measured the percentage of trials in which average eye velocity during this interval exceeded 0 deg/s to determine the frequency of rightward eye movement decisions. For this subset of the data, the subject smoothly tracked to the right on six trials and to the left on four trials, producing a decision rate of 60% rightward. Saccades detected during smooth tracking, indicated by the thinner segments of the eye position traces, were usually but not always in the same direction as smooth tracking (the arrow indicates an exception), and were excluded from the analysis.

As expected, the frequency of rightward eye movement decisions was strongly affected by the strength of the motion signal. In the absence of prior information (circles in Figs. 2A–2C), changing the percentage of rightward moving dots from -100% (all dots move leftward) to 100% (all dots move rightward) changed the frequency of rightward eye movement decisions from 0% to 100%. The thresholds for the three subjects (i.e. the standard deviations of the fitted Gaussian curves) varied between 10–25% motion (26.2, 10.5, and 16.5% for subjects N, R, and S, respectively). Two of the three subjects showed small leftward biases in their eye movement decisions (bias: 7.5 and 8.1% for subject R and S); the third subject (N) exhibited a larger bias (21.4%).

Prior information had a large effect on eye movement decisions. When subjects were shown rightward cues (upright triangles in Figs. 2A–2C), their eye movement performance shifted in favor of rightward decisions (bias: -18.3 , -18.1 , and -8.4% , for subjects N, R, and S, respectively), as indicated by the leftward displacement of the oculometric curves, although the thresholds showed no systematic change (thresholds: 26.4, 10.8, and 19.1%). Conversely, with leftward cues (inverted triangles), eye movement performance shifted in favor of leftward decisions (biases: 41.3, 28.8, and 20.7%), again with little change in thresholds (23.9, 13.2, and 19.5%). For weaker motion stimuli (e.g. $\pm 10\%$), prior information often had the effect of largely reversing the direction of eye movement decisions. For example, with subject N, 10% rightward motion produced 92% rightward eye movement decisions when presented after rightward cues, but only 6% rightward eye movement decisions when presented after leftward cues.

Perceptual judgements were similarly affected by motion strength and prior information (Figs. 2D–2F). In the absence of prior information, the perceptual thresholds for the three subjects also varied between 10–25% (23.4, 10.1, and 11.4% for subjects N, R, and S, respectively) and the subjects showed small biases in their perceptual decisions (bias: 17.3, 7.7, and 5.4%). As we observed for the eye movement decisions, rightward cues (upright triangles in Figs. 2D–2F) shifted perceptual judgements in favor of rightward decisions (biases: -19.7 , -19.1 , and -13.1) and leftward cues (inverted triangles) shifted perceptual judgements in favor of leftward decisions (biases: 42.6, 28.1, and 22.7%), and neither cue had much effect on thresholds (rightward cues: 19.1, 10.2, and 17.8%; leftward cues: 28.3, 13.3, and 19.1%).

Comparison of oculomotor and perceptual judgements

To directly compare eye movement and perceptual performance, we first evaluated the similarity between the oculometric and psychometric functions. The graphs in Fig. 3 show the bias (Fig. 3A)

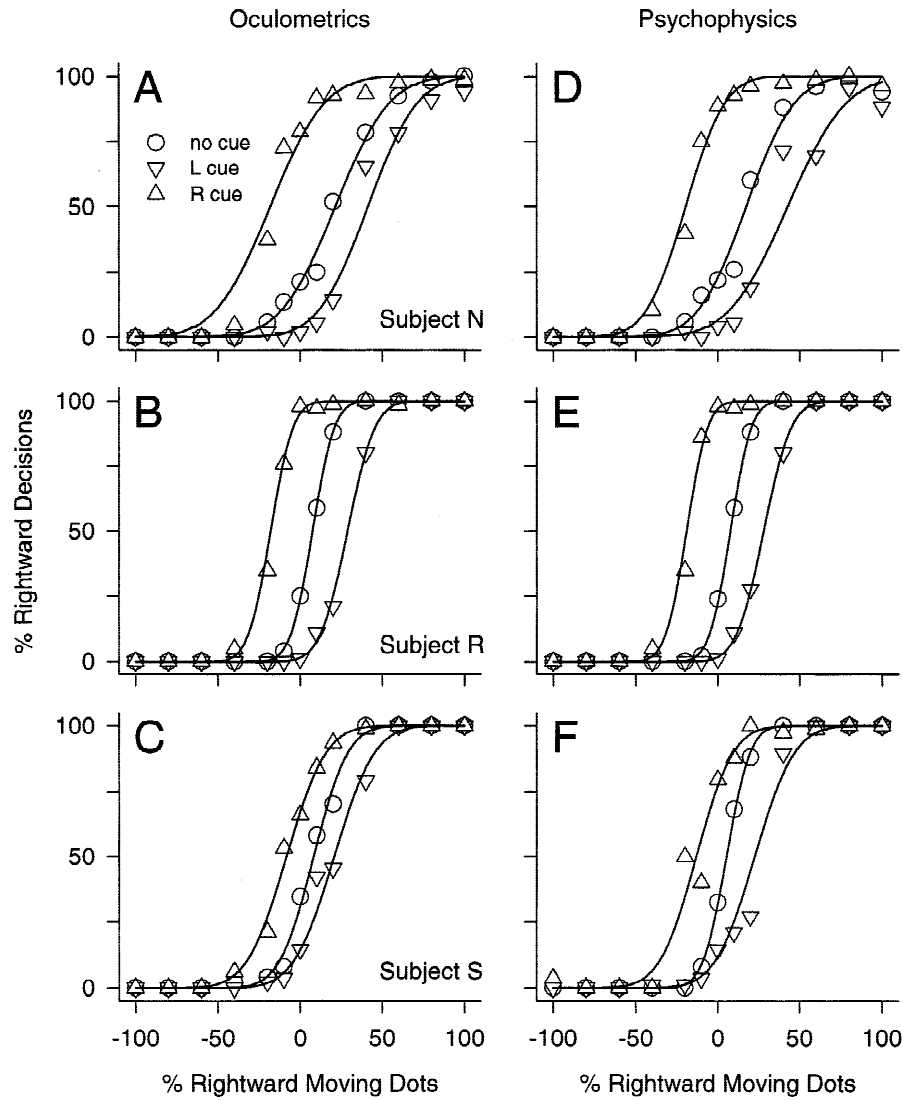


Fig. 2. Oculometric and psychometric functions. A–C: Oculometric functions obtained with no prior information (circles), rightward cue (upright triangles), and leftward cue (inverted triangles), for each of the three subjects. Each data point represents the fraction of trials in which eye velocity during the 500-ms measurement interval exceeded 0°/s. D–F: Psychometric functions obtained for each of the three subjects. Invalidly cued conditions correspond to the upright triangles (rightward cues) in the left half of each graph and to the inverted triangles (leftward cues) in the right half of each graph. Data points in A–F are each based upon approximately 50 individual trials.

and threshold (Fig. 3B) parameters for the oculometric functions (Figs. 2A–2C) plotted as a function of the bias and threshold parameters for the corresponding psychometric functions (Figs. 2D–2F). The data points in both plots lie near the line of unity slope (dashed lines), and linear regression confirms that a linear model with a slope near 1 provides a good fit to the data (solid lines). These results indicate that, on average, eye movement and perceptual judgements were similarly affected by both motion strength and prior information.

We next measured the trial-by-trial correlation between eye movement and perceptual judgements. For each subject and stimulus condition, we determined the fraction of trials on which the eye movement and perceptual decisions were the same (i.e. both were either “leftward” or “rightward”). The observed probability that the eye movement and perceptual decisions were the same is

plotted separately for each subject and cue condition in Fig. 4 (symbols connected by solid lines). In addition, we calculated the expected probabilities based upon chance, if the two decisions occurred independently (dashed lines). The expected probabilities were calculated according to the equation:

$$P(\text{same}) = [P_{\text{oculo}}(R) * P_{\text{psycho}}(R)] + \{[1 - P_{\text{oculo}}(R)] * [1 - P_{\text{psycho}}(R)]\},$$

in which $P_{\text{oculo}}(R)$ and $P_{\text{psycho}}(R)$ were the frequencies of rightward eye movement and perceptual decisions, respectively. For example, in stimulus conditions with 100% rightward motion, the frequency of rightward eye movement and perceptual decisions was 100%, thus the probability of them being the same through

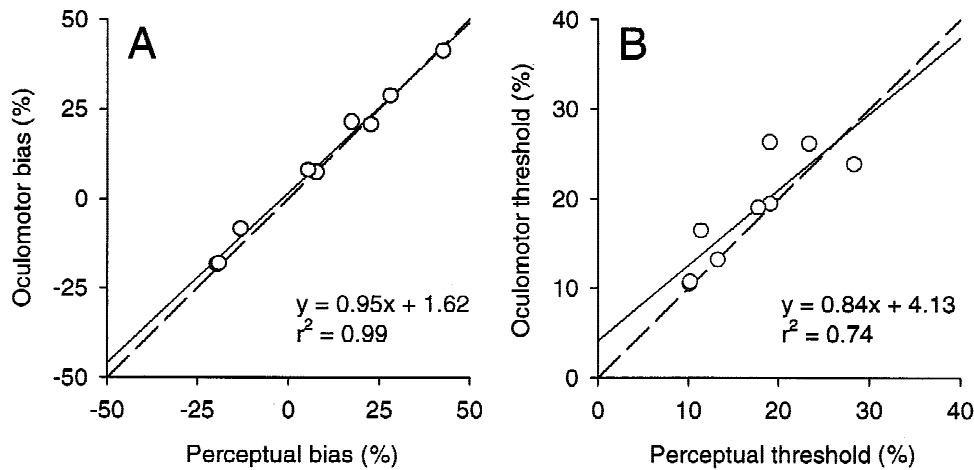


Fig. 3. Comparison of oculometric and psychometric performance. A: Oculomotor bias plotted as a function of psychometric bias, for each of the three subjects. B: Oculomotor threshold plotted as a function of psychometric threshold. Dashed lines indicate a slope of one.

chance alone was 1.0 [i.e. $P(\text{same}) = 1 \cdot 1 + 0 \cdot 0$]. In contrast, with 0% rightward motion, the frequency of rightward eye movement and perceptual decisions was close to 50%, thus the probability of them being the same through chance alone was approximately 0.5 [i.e. $P(\text{same}) = 0.5 \cdot 0.5 + 0.5 \cdot 0.5$]. As indicated by the separation between the solid and dashed lines in Fig. 4, the observed probabilities were consistently higher than the probabilities expected through chance alone, except for those cases in which both probabilities approached a value of 1. The filled symbols identify the stimulus conditions in which the observed probability was significantly higher than that expected through chance ($P < 0.05$, t test). These results indicate that, on a trial-by-trial basis, motion strength and prior information tended to have the same effects on eye movement and perceptual judgements. However, the absence of an exact correspondence also indicates that the outcomes for pursuit and perception were not mutually determined.

Perceptual judgements in the absence of tracking eye movements

To further examine whether the effects of motion strength and prior information depended upon the occurrence of smooth eye movements, we repeated the experiments with the same stimuli, but instructed subjects to maintain fixation during the entire trial. As shown by the psychometric curves in Figs. 5A–5C, perceptual judgements made during fixation were very similar to those made during active tracking of the motion stimulus (Figs. 2D–2F). In the absence of prior information, the perceptual thresholds for the three subjects again ranged from 10% to 25% (22.7, 11.7, and 13.9% for subjects N, R, and S, respectively) and all three subjects showed slightly smaller biases (bias: -1.9 , 3.3 , and 1.7%) than when instructed to track the motion stimulus. Nonetheless, rightward cues (upright triangles) shifted perceptual judgements in favor of rightward decisions (biases: -22.1 , -15.9 , and -10.7%) and leftward cues (inverted triangles) shifted perceptual judgements in favor of leftward decisions (biases: 20.4 , 24.1 , and 18.1%). Neither cue had much effect on thresholds (rightward cues: 16.7 , 10.3 , 14.8% ; leftward cues: 15.2 , 12.5 , 18.4%). Thus, although the perceptual judgments during fixation showed smaller biases than those during tracking, rightward and leftward cues

biased perceptual judgments during fixation by an amount similar to that observed during tracking. These results indicate that eye movements were not necessary to obtain the effects of prior information on perceptual judgements.

Effects of motion strength and prior information on initial pursuit eye velocity

Motion signal strength and prior information also affected the smooth eye velocity during the initiation of pursuit, similar to the effects observed during the 500-ms interval of maintained pursuit used for the oculometric analysis. The graphs in Figs. 6A–6C show the average eye velocity at the end of pursuit initiation for each subject, measured from each trial in the interval 90–100 ms after the average onset of pursuit. For comparison, the graphs in Figs. 6D–6F show the average eye velocity during the 500-ms interval of maintained pursuit used to generate the oculometric curves in Fig. 2. Within each graph, the three superimposed plots show data from trials with rightward cues (upright triangles), leftward cues (inverted triangles), or no cues (circles). Not surprisingly, varying the strength of the motion stimulus had a graded effect on eye velocity, especially during the initiation of pursuit. In addition, prior information had a significant effect on eye velocity during the initiation of pursuit, as well as during maintained pursuit. The filled symbols identify conditions in which the average eye velocities obtained after rightward and leftward cues were significantly different from each other ($P < 0.05$, one-way ANOVA with pairwise comparisons using the Tukey test). These results indicate that the shifts in the oculometric curves caused by prior information (Figs. 2A–2C) reflected changes in eye movement performance that were evident in the earliest intervals of smooth tracking.

Time course of oculomotor and perceptual judgements

The observation that prior information affected the initiation of pursuit, as well as steady-state pursuit, prompted us to measure the time course of the oculomotor and perceptual judgements. To assess the time course of the oculomotor judgements, we reanalyzed the eye movement data, but rather than using a single 500-ms

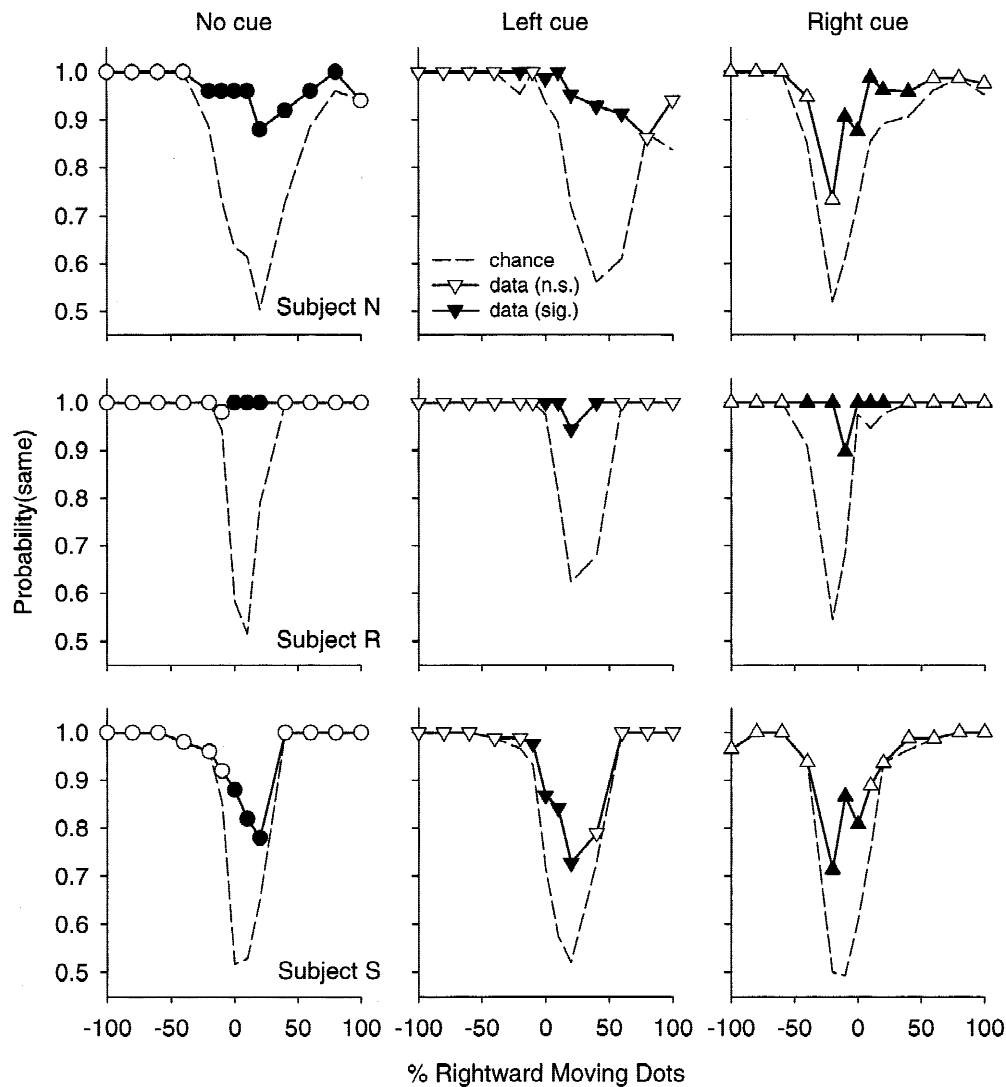


Fig. 4. Comparison of eye movement and perceptual judgements on a trial-by-trial basis. The symbols and solid lines in each graph show the fraction of trials in which the eye movement and perceptual decisions agreed, plotted as a function of motion stimulus condition. The dashed lines show the fraction of trials in which the two decisions would be expected to be the same due to chance, based upon the frequencies of rightward and leftward decisions for each condition. Filled symbols indicate those cases in which the observed fraction of same decisions is significantly greater than that expected by chance.

interval starting at 1000 ms after stimulus onset, we used a sequence of nonoverlapping 25-ms intervals starting at the onset of stimulus motion. For each of these intervals, we performed the same oculometric analysis that we did previously for the fixed 500-ms interval (Figs. 2A–2C). To permit a direct comparison with perceptual judgements, we performed an additional set of psychophysical experiments in which subjects again judged the direction of motion while maintaining fixation (as in Fig. 5), but the motion stimulus was presented for only brief intervals (75, 100, 125, 150, 175, 200, 250, or 500 ms) and followed by a full-field random checkerboard masking stimulus. We then computed separate psychometric curves for each of these presentation intervals.

The graphs in Fig. 7 show a sample set of the oculometric and psychometric data from one subject (R). To temporally align the two types of data, we assumed that (1) the processing of visual inputs for pursuit is continuous and involves a fixed transmission delay, and (2) that the latency of pursuit provides a reasonable

estimate of this delay. Consequently, the output of the pursuit system at any point in time may be viewed as the result of the visual inputs presented up until one latent period ago. In comparing the eye movement and perceptual results for each subject, we therefore took into account the estimated pursuit latency (latencies: 135, 135, and 166 ms for subjects N, R, and S, respectively). The graphs under the heading “75 ms” compare psychometric data (open diamonds) obtained with a stimulus presentation duration of 75 ms and oculometric data (filled circles) obtained in the temporal interval 200–225 ms after the onset of the motion stimulus (i.e. 75 ms plus 135 ms, rounded to the nearest 25-ms bin). In the absence of prior information (Fig. 7, row of graphs labeled “no cue”), the oculometric and psychometric data exhibited a similar progression over the first 75–200 ms of stimulus presentation. The bias for both remained near zero and the thresholds for both steadily decreased, although the psychometric thresholds tended to decrease more rapidly (24.4, 15.5, and 13.9% for 75, 100, and

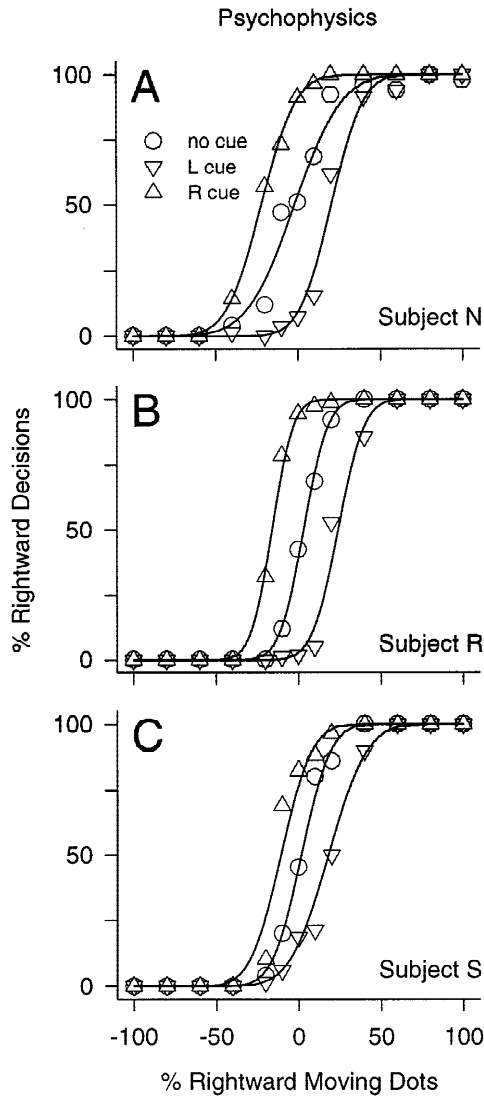


Fig. 5. Oculometric and psychometric functions during fixation. Oculometric functions obtained with no prior information (circles), rightward cue (upright triangles), and leftward cue (inverted triangles), for each of the three subjects while maintaining fixation during stimulus presentation. Data points are each based upon approximately 50 individual trials.

200 ms) than the oculometric thresholds (45.1, 34.9, and 15.4%). In the presence of prior information (Fig. 7, rows of graphs labeled “left cue” and “right cue”), the oculometric and psychometric data were dissimilar during the earliest time intervals, with the psychometric data exhibiting larger biases and lower thresholds than oculometric data. These differences were mostly eliminated at 200 ms after stimulus motion onset.

To summarize the results of this analysis from all of the subjects, we plotted the threshold (Figs. 8A–8C) and bias (Figs. 8D–8F) parameters from each subject as a function of time. Although there is considerable intersubject variation in these results, a couple of trends are evident in each subject. First, the oculometric thresholds (filled symbols and black lines in Figs. 8A–8C) are consistently higher than the psychometric thresholds (open symbols and gray lines) during the first several hundred milliseconds of stimulus motion, but this difference largely disappears by

300–500 ms, by which time both sets of thresholds have dropped to near their asymptotic values. Second, the psychophysical biases (open symbols and gray lines in Figs. 8D–8F) tend to be larger than the oculometric biases (filled symbols and black lines) during the first several hundred milliseconds of stimulus motion, and this difference also largely disappears by 300–500 ms. Thus, the oculometric data tend to differ from the psychometric data during the first 300 ms of stimulus motion, corresponding to the period of pursuit initiation. However, the oculometric and psychometric data changed over the same time course toward similar values after 300 ms, corresponding to the period of maintained pursuit.

Discussion

Our results show that providing subjects with prior information about the likely direction of an upcoming random-dot motion display has similar effects on both perceptual judgements and pursuit eye movements. Directional cues shifted the oculometric and psychometric curves toward the expected motion direction, with little change in the shapes of the curves. These results indicate that prior information altered the biases, but not the thresholds, applied in forming both types of judgements.

Several features of our data lead us to conclude that the similar effects on perception and pursuit reflects a common stage of processing, rather than similar but independent mechanisms. First, prior information caused subjects to commit the same pattern of errors for both perceptual judgements and pursuit. For some stimulus conditions (e.g. those with less than 20% coherent motion), subjects often perceptually reported and smoothly followed the weaker motion signal matching the cue, rather than the much stronger motion signal present in the stimulus. The occurrence of such shared biases indicates either that there is a common processing stage, or that there are two mechanisms that can exhibit the same selectivity for a much weaker motion signal. A similar line of argument in favor of shared processing has been made previously in interpreting the errors made by pursuit and perception during a direction discrimination task (Beutter & Stone, 1998). Second, in addition to reaching similar decisions on average (as indicated by the oculometric and psychometric curves), pursuit and perception also tended to reach the same decisions on a trial-by-trial basis. The observed correlations exceeded those expected based upon chance, including those conditions that elicited random performance. Because the decisions reached in those cases were presumably determined by random factors, the frequency of such common outcomes directly supports the idea that pursuit and perception were constrained by a shared processing step.

Other aspects of our data argue against the notion that the shared effects on pursuit and perception are due to some trivial interaction. For example, it might be argued that subjects decided on their eye movement direction only after their perceptual judgement had been made—that is, perception might have guided pursuit through an indirect route as part of a deliberate strategy on the part of the subjects. However, the effects of prior information were evident even in the earliest interval of the pursuit eye movement (Fig. 6), which is assumed to reflect the initial evaluation of stimulus motion (Lisberger et al., 1987). Thus, pursuit was influenced by prior information at least as early as the perceptual judgement. Alternatively, subjects might have formed their perceptual decisions based upon their perceived direction of eye movement. The fact that prior information had similar effects on perceptual judgements during fixation (Fig. 5) as during tracking (Fig. 2) argues that the effect of directional cues did not depend

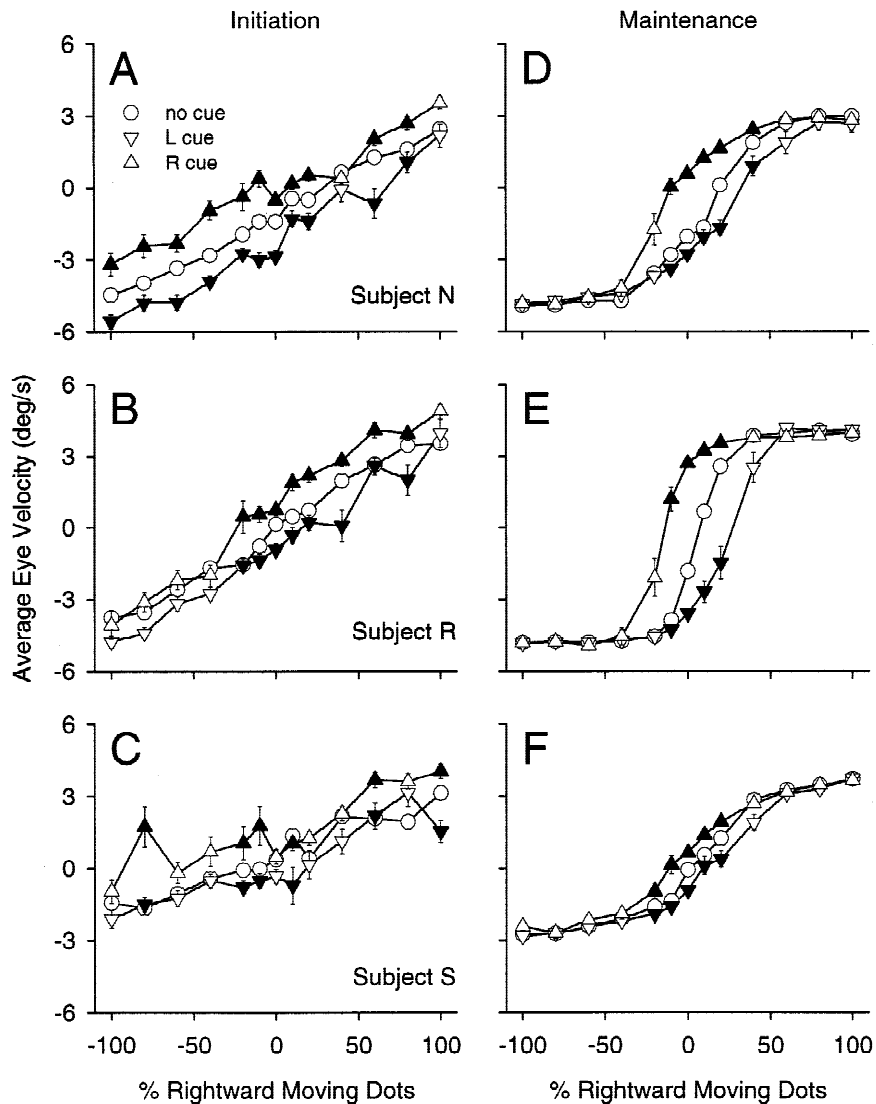


Fig. 6. Effects of motion strength and prior information on pursuit eye velocity. A–C: Average eye velocity measured at the end of pursuit initiation, defined as the time interval 90–100 ms after the average pursuit latency for each subject. D–F: Average eye velocity measured during maintained pursuit, defined as 500–1000 after the onset of stimulus motion. Functions in each graph show eye velocity with no prior information (circles), rightward cue (upright triangles), and leftward cue (inverted triangles). Filled symbols indicate conditions for which rightward and leftward cues produced significantly different eye velocities.

upon eye movements. It might be argued that in cases where subjects maintained fixation, they nonetheless prepared an eye movement, and this motor preparation might have formed the basis of the perceptual decision. However, this interpretation does not question whether there is shared processing, but only the location of the shared processing, because it suggests that motor preparation might be a step that influences both pursuit and perception. Finally, the observation that the perceptual and eye movement decisions progressed over the same time course and that perceptual thresholds tended to be lower than oculomotor thresholds during these early time periods (Fig. 8) indicates that perceptual judgments were not constrained by eye movement performance. Together, these results are most consistent with the idea that the effects of directional expectations on pursuit and perception involved a common stage of processing.

Even if pursuit and perception share a common stage of processing, as appears to be the case, it does not necessarily follow that the two will always produce the same answer. As might be inferred from first principles, and as has been shown directly in previous experiments (Beutter & Stone, 2000), there are additional sources of noise in the processing for eye movements that are not

shared with perception. The contribution of these additional sources will tend to eliminate the concordance between pursuit and perceptual decisions. In our own data, there is evidence of this in the initial responses to the motion stimulus (Figs. 7–8), which corresponds to the initiation interval of pursuit. The thresholds during this early time period are higher for pursuit than for perception, probably because this interval of pursuit includes additional motor noise associated with accelerating the eye. Also, the biasing effects of prior information appear more rapidly for the perceptual judgments than for pursuit. This difference may be due to acceleration nonlinearities that constrain changes in pursuit eye speed (Robinson et al., 1986), but do not apply to perception. Another possibility is that the initial smooth eye movement in our experiments (Figs. 6A–6C) was dominated by lower order visual processes that quickly encode the average motion (Lisberger & Ferrera, 1997), whereas later phases of pursuit (Figs. 6D–6F) incorporated higher order visual processes that more selectively encode the attended direction of motion (Treue & Martinez Trujillo, 1999). Perceptual judgments, by contrast, might have been largely unaffected by lower order visual processing, because they were reported at the end of each trial regardless of the stimulus duration. These obser-

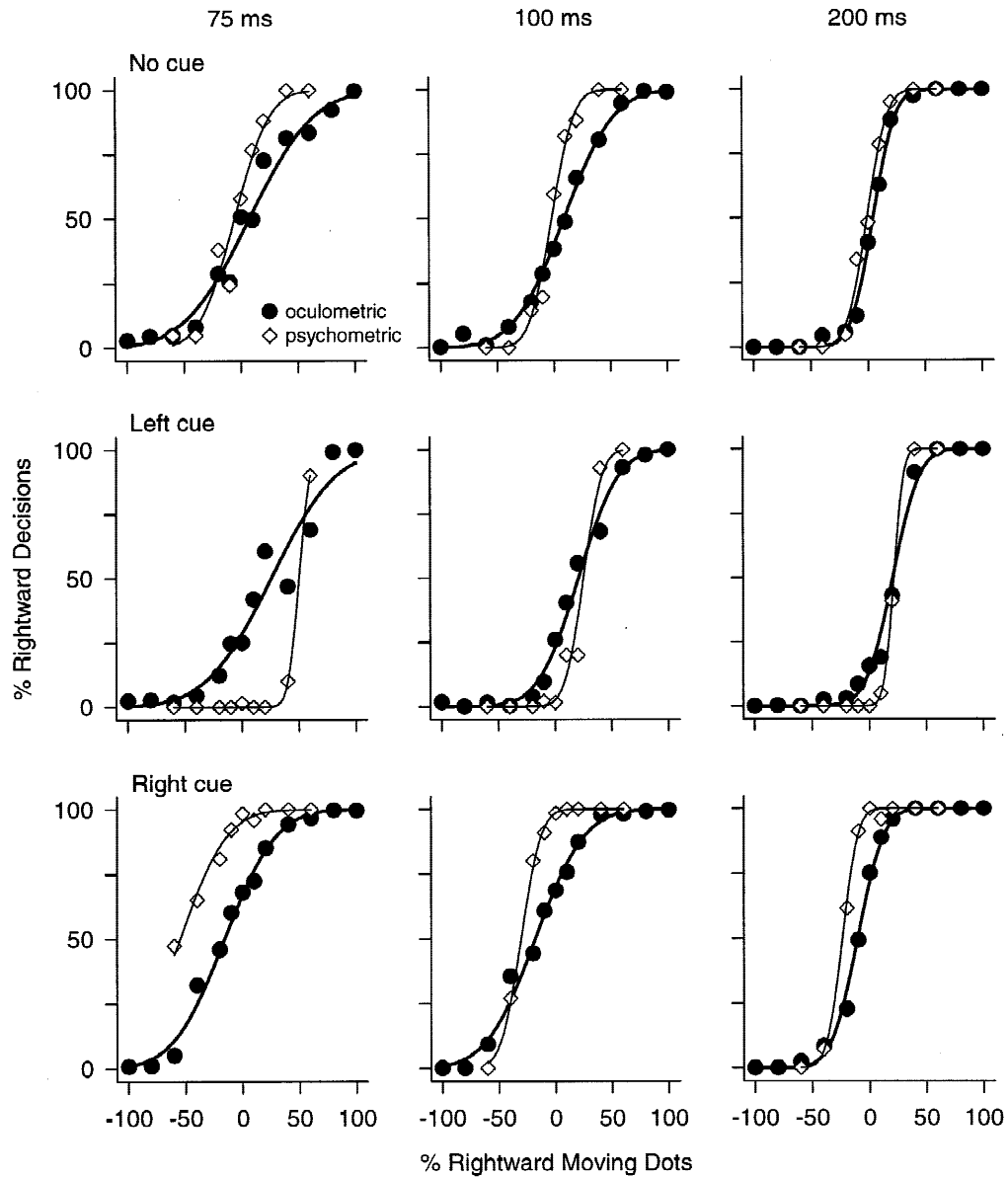


Fig. 7. Time course of oculometric and psychometric functions. Each column of graphs shows the oculometric (filled circles) and psychometric (open diamonds) functions obtained with a different stimulus duration (75, 100, or 200 ms) with one subject (R). Each row of graphs shows the functions obtained with either no prior information (top), leftward cue (middle), or rightward cue (bottom).

variations suggest that pursuit can provide a reliable measure of perception when motor noise is low and after lower order visual effects have subsided—for example, during maintained pursuit—but that otherwise pursuit may appear to be unrelated to perception. It is unclear whether similar considerations about the time course of sensory and motor processing might account for other cases in which motor outputs have been dissociated from perceptual judgements (Goodale & Milner, 1992).

Finally, our pattern of results allows us to assess the likely neural mechanisms underlying the effects of prior information on pursuit and perception. One possible site for these effects is the frontal eye fields (FEF), which contains a pursuit subregion that is especially important for predictive and anticipatory movements (Keating, 1991; MacAvoy et al., 1991). The activity of saccade-related neurons in the FEF appears to be related to the categorical

decisions of when to initiate or cancel a saccade (Hanes et al., 1998), and may also be related to differences in perceptual reaction time (Thompson et al., 1998), although the pursuit-related neurons in the adjoining eye field have not been studied with these same types of tasks. If pursuit-related FEF neurons had similar properties, modulating their activity might alter the strength of motion required to trigger a pursuit eye movement, consistent with our results. However, two observations suggest that the critical changes in our task actually occurred at the level of motion processing, rather than at a subsequent stage of evaluating the motion signal. First, prior information biased performance toward the cued direction without changing the threshold, as would be expected if a consistent criterion were applied to an altered motion signal. Second, prior information altered the eye velocity during the initiation of pursuit, a phase of the movement that reflects the

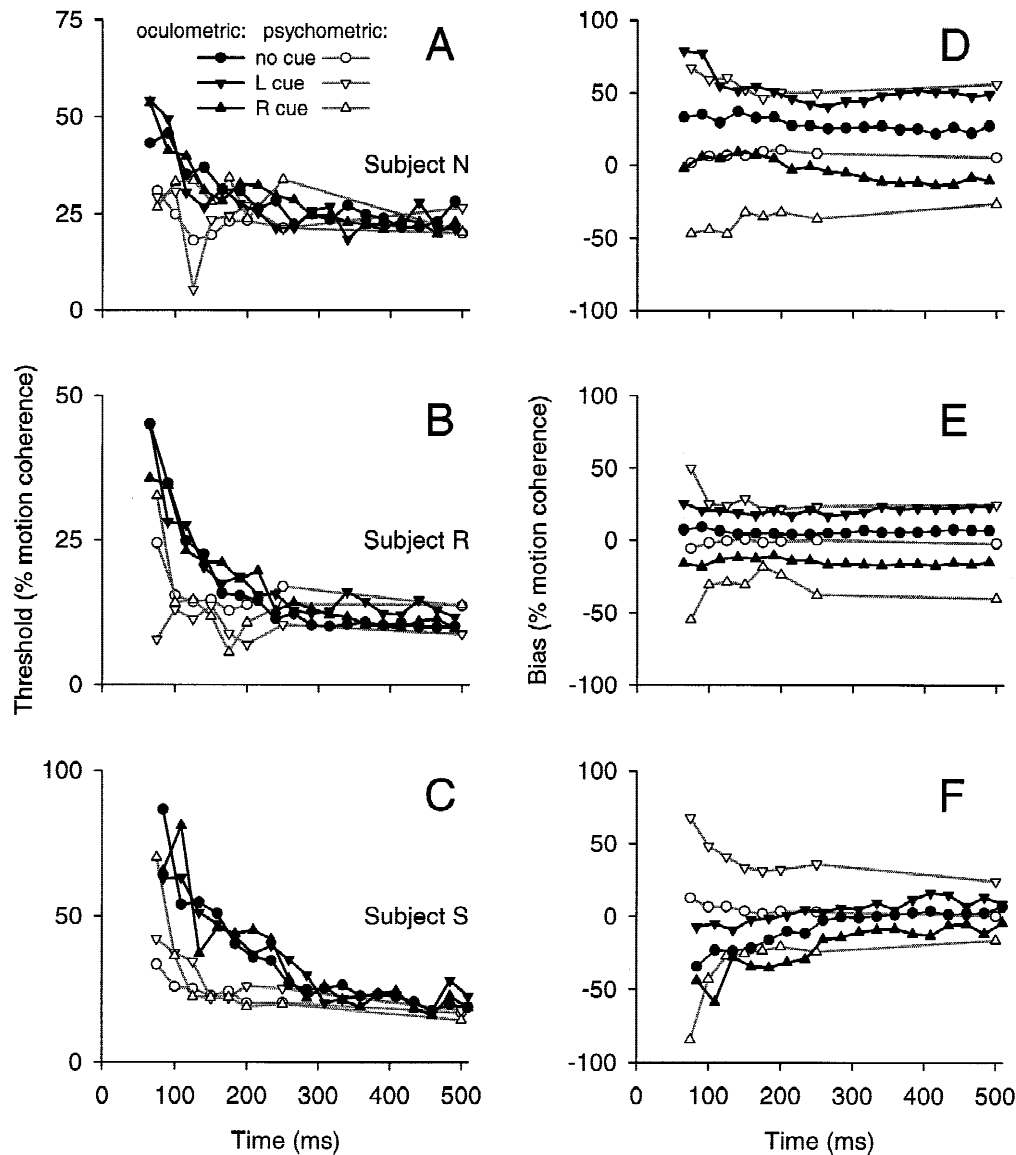


Fig. 8. Summary of the time course of oculometric and psychometric performance. A–C: The bias terms for oculometric (filled triangles and black lines) and psychometric (open triangles and gray lines) functions are plotted as a function of stimulus duration. D–F: The thresholds for oculometric and psychometric functions are plotted as a function of stimulus duration. Different symbols identify different conditions with no cues (circles), rightward cues (upright triangles), and leftward cues (inverted triangles).

initial estimate of motion processing. This type of altered motion processing is consistent with recent findings that neurons in MT can exhibit feature-based attentional modulation (Treue et al., 1999). In addition, competitive interactions between oppositely tuned motion sensors have been proposed as a plausible mechanism for selecting the direction of motion for pursuit eye movements (Ferrera & Lisberger, 1995, 1997). The effects we observed could be explained with such a model if we assume that prior information biased the distribution of activity toward those neurons that encoded the cued direction of motion. Applying such biases at relatively early stages of visuomotor processing, rather than only at later decision stages, could act to ensure that the metrics of the movement, as well as the decision to initiate the movement, was consistent with perception (Krauzlis & Stone, 1999).

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