

Primacy of spatial information in guiding target selection for pursuit and saccades

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Previous studies have examined the facilitative effects of prior spatial information on target selection for saccadic eye movements. More recently, studies have shown that prior spatial information also influences target selection for smooth pursuit. However, direct comparisons of the effects of prior information on target selection for pursuit and saccades have not been made. To this end, we provided different classes of prior information and measured their effects on target selection for pursuit and saccades. In Experiment 1, we assessed the relative effects of spatial cues (indicating the target stimulus' initial location) and color cues (indicating the target stimulus' color) on eye movement latencies. In Experiment 2, we assessed the effects of motion cues (indicating the target stimulus' direction of motion) in addition to spatial cues. For both pursuit and saccades, we found that spatial cues reduced eye movement latencies more than color cues (Experiment 1). Spatial cues also reduced eye movement latencies more than motion cues (Experiment 2), even for pursuit, despite the fact that stimulus motion is essential for the generation of pursuit eye movements. These results indicate that both pursuit and saccades are affected to a greater degree by spatial information than motion or color information. We suggest that the primacy of spatial information for both pursuit and saccades reflects the importance of spatial attention in selecting the stimulus target for both eye movements.

Keywords: eye movements, information cues, attention, spatial, motion, saccades, pursuit

Introduction

Our visual world is populated with many simultaneously available objects that are possible inputs for visual processing and for guiding behavior, yet we are constrained by a limited amount of processing resources. As a result, particular items in space must be selected as targets in order for visual processing and behavior to proceed efficiently. The problem of target selection has been a particularly enduring focus in the study of the allocation of processing resources, leading to discussions of whether selection occurs “early” or “late” during information processing (Broadbent, 1982; Deutsch & Deutsch, 1963; Fox, 1995; Treisman, 1964; Yantis & Johnston, 1990) and whether it occurs via a “parallel” or “serial” mechanism (Kinchla, 1977; Sagi & Julesz, 1985; Treisman & Gelade, 1980).

An important stimulus parameter upon which attentional selection is based is the spatial location of visual information (Van der Heijden, 1992; Yantis, 1996). Numerous models of attention, including the “spotlight” hypothesis (Posner, Snyder, & Davidson, 1980; Tsal & Lavie, 1988), have proposed that processing resources are restricted to particular areas of visual space and are moved around to highlight locations where items of interest exist, yielding enhanced processing of stimuli at the

highlighted regions (Hawkins et al., 1990; Hoffman & Nelson, 1981; Posner, 1980; Remington & Pierce, 1984; Tsal, 1983). Evidence for selection due to the spatial placement of attention has been provided by studies that use a spatial cueing paradigm, in which a cue is briefly presented at the location where the target will subsequently appear. Findings from these spatial cueing studies have demonstrated that attending to the particular location indicated by the preceding cue results in faster and more accurate detection and discrimination of briefly presented items at that location compared to items at unattended locations (Cheal & Gregory, 1997; Jonides, 1981; Kröse & Julesz, 1989; Posner, Nissen, & Ogden, 1978; Robertson & Kim, 1999; Yantis & Johnston, 1990). Thus, selection of the spatial location of visual information is a crucial component in the allocation of attentional resources.

Studies have indicated that the effect of the spatial allocation of attentional resources is not limited to perceptual processing but is also intimately linked with the programming of voluntary eye movements (Crawford & Müller, 1992; Deubel & Schneider, 1996; Hoffman & Subramanian, 1995; Klein, 1980; Kowler, Anderson, Doshier, & Blaser, 1995; Posner, 1980). Voluntary eye movements come in two classes: pursuit is a slow, continuous movement that stabilizes the images of

moving visual targets on the retina, whereas saccades are rapid, discrete movements that bring the images of peripheral visual targets to the fovea. For saccades, investigations have examined the association between spatial selective attention and the programming of the eye movements and have revealed effects similar to those found for perceptual processing. Hoffman and Subramanian (1995), for example, determined that target detection prior to eye movement initiation is superior when target location and the location of a saccade coincide than when they do not, suggesting that the allocation of spatial attention is an important element of generating a saccadic eye movement. Similarly, Kowler et al. (1995) found that subjects could not allocate attention to one location while at the same time preparing to make a voluntary saccadic eye movement to a different location. Further, saccade latencies increase as a function of the distance between the saccade target and the attended location (Rizzolatti, Riggio, Dascola, & Umiltà, 1987), and the latency and accuracy of the initial saccade in a visual search paradigm are a function of the spatial certainty of the target (Bravo & Nakayama, 1992; Findlay, 1997). These findings demonstrate an intimate link between saccades and spatial attention in the selection of targets, leading some to theorize that the selective allocation of spatial attention is a prerequisite for the programming of saccades (e.g., Rizzolatti et al., 1987).

For the other type of voluntary eye movement, smooth pursuit, the influence of spatial attention on target selection is an open question. Smooth pursuit eye movements, in contrast to saccades, are guided by visual motion. The importance of motion information for pursuit eye movements is supported by the fact that retinal velocity errors rather than retinal position errors elicit pursuit initiation (Morris & Lisberger, 1987; Rashbass, 1961). Neurophysiological studies have further demonstrated that the extrastriate areas specified for processing this visual motion, such as the medial temporal (MT) and the medial superior temporal (MST) areas (Albright, 1984; Zeki, 1978), are critical for pursuit (Komatsu & Wurtz, 1988; Newsome, Wurtz, & Komatsu, 1988). Chemical lesions of areas MT (Newsome, Wurtz, Dürsteler, & Mikami, 1985) and MST (Dürsteler & Wurtz, 1988) cause impairments in a monkey's ability to match the velocity of a pursuit eye movement to the velocity of a moving target. Stimulation of these areas during tracking of a moving target, but not during fixation of a stationary target, produced an eye acceleration toward the side of the visual field that corresponded to the area that was stimulated (Komatsu & Wurtz, 1989). Pursuit initiation is additionally affected by the directional specificity of the motion information, as evidenced by pursuit latency increasing when two stimuli move in opposite directions but not when they move in the same direction (Ferrera & Lisberger, 1997; Krauzlis, Zivotovsky, & Miles, 1999). This dependence on movement direction might reflect the need to select the

target and allocate attentional resources for pursuit on the basis of motion information, rather than on the basis of spatial information, as is the case with saccades.

A few studies exist, however, that have hinted at the importance of spatial information for target selection, not only for saccades, but even for smooth pursuit eye movements. Khurana and Kowler (1987) showed that subjects could not attend to one stimulus and track another, suggesting that target selection for pursuit and the allocation of spatial attention cannot be easily dissociated. In studies with monkeys, Ferrera and Lisberger (1995, 1997) found that a second, oppositely moving distractor stimulus increased the latency to initiate smooth pursuit eye movements to a target stimulus that has been previously cued. Krauzlis et al. (1999) further found that the increase in pursuit latency due to the addition of an oppositely moving distractor stimulus was attenuated when the target stimulus was preceded by a peripheral cue indicating the target's starting location, but not when it was preceded by a central cue indicating the target's shape. This finding is similar to the facilitating effects of spatial cueing on saccades, suggesting that a common attentional mechanism might mediate the target selection process for both types of voluntary eye movements. To test this possibility, we compared the effect of spatial and motion cues on pursuit and saccade latencies. We predicted that target selection and the initiation of pursuit would be facilitated to a greater degree by motion cues than spatial cues, whereas saccades would show the opposite pattern.

The relationship between the allocation of attentional resources and the selection of an eye movement target, however, has not been established. Most studies of the influence of attentional allocation on the initiation of voluntary eye movements have typically presented only a single stimulus as the goal of the eye movement (e.g., Posner, 1980). For example, Posner (1980), in his classic experiment, demonstrated that presentation of a cue facilitated saccadic eye movements to a single target that appeared in the same spatial location than when they appeared in different locations. In contrast, investigations of the role of target selection in the initiation of eye movements have used an array containing two stimuli (e.g., Ferrera & Lisberger 1997; Krauzlis et al., 1999). In the present study, we compared the effects of spatial and motion cueing when target selection was required (i.e., two stimuli) and when it was not (i.e., one stimulus). If there exists an interaction between attentional allocation and target selection, then the facilitative effects of attentional cueing on eye movement latency should be enhanced when two stimuli are presented, compared to when only one is presented. Alternatively, if attentional allocation and target selection are unrelated, then the effects of attentional cueing should be equivalent whether two stimuli or a single stimulus are presented.

In studies that have used peripheral spatial cues, the cues are typically presented at the same location as the

forthcoming eye movement target. As a result, it is possible that the peripheral cues prime a bottom-up exogenous component of attentional processing rather than a top-down endogenous attentional biasing of target selection (see Ferrera & Lisberger, 1997). Therefore, to ensure that the effect of prior spatial cues on target selection for both pursuit and saccades was related to top-down endogenous attentional biasing, the present study also assessed the influence of a central, symbolic spatial cue (i.e., an arrow pointing to the target location). Previous studies of spatial selective attention have indicated that central, symbolic cueing is associated with the endogenous control of selection in a top-down, expectancy-driven, and voluntary manner, whereas peripheral spatial cueing is associated with the exogenous control of attention in a bottom-up, stimulus-driven, and automatic manner (Jonides, 1981; Klein, Kingstone, & Pontefract, 1992; Posner, 1980; Van der Heijden, 1992; Yantis & Jonides, 1984). If pursuit and saccades share an attentional mechanism for target selection, then peripheral and central spatial cues should have a similar pattern of effects on both types of eye movements.

To examine the effect of attentional modulation and the efficacy of different types of prior information in guiding target selection for the different eye movements, in the current study, we directly compared the effect of prior spatial and motion information on target selection for both smooth pursuit and saccadic eye movements. In Experiment 1, we compared the effect of cues indicating the target's spatial location to cues indicating the target's color. In Experiment 2, we compared the effect of cues indicating the target's direction of motion to cues indicating the target's spatial location. The subject was required to make the appropriate eye movement to the stimulus indicated by prior information provided by the cue, either a saccade to a stationary target or pursuit to a moving target, and the latency of these eye movements were measured. In overview, our results indicated that the latency of pursuit and saccades are facilitated to a greater extent by prior spatial information than either prior motion or color information.

Methods

Four human subjects (aged 16, 23, 33, and 37 years) participated in the two experiments, three of whom had previous experience as subjects in eye-movement studies. Two of the subjects (S.A. and R.K.) were authors of this study, whereas the other two subjects (N.D. and H.C.) were naïve as to the experimental conditions and hypotheses. All experimental procedures for use with human subjects were reviewed and approved by the Institutional Review Board, and all subjects gave their informed consent. Because the 16-year-old was underage, her parents also provided informed consent. Data were collected in individual sessions lasting approximately 45

min, and the four subjects were tested in a total of 24 sessions in Experiment 1 and 56 sessions in Experiment 2. The latencies of smooth pursuit and saccades were measured for the four subjects (S.A., R.K., N.D., and H.C.) on a total of 10,236 trials (2,563, 2,631, 2,516, and 2,526, respectively) in Experiment 1 and 8,290 trials (2,136, 2,068, 2,053, and 2,033, respectively) in Experiment 2.

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, Panish, & Hippensteel, 1997). The sequence of stimuli presented during a single experimental trial is illustrated in Figure 1. To view the stimuli, two of the subjects (S.A. and R.K.) wore their normal spectacle corrections during each experimental session. Subjects were instructed to look at the initial central fixation stimulus (0.7° cross hair) and then to continue fixating during the subsequent presentation of the cues. After cue presentation, in half of the trials in both experiments, a distractor stimulus was presented simultaneously with the target stimulus (distractor trials), and in the other half of the trials only a single target stimulus was presented (no-distractor trials). In both experiments, a block design was used in which subjects alternately completed separate blocks of pursuit trials and blocks of saccade trials. Whether each session began with a pursuit block or a saccade block was randomly determined, but across all sessions, the first block was pursuit or saccades an equal number of times. Prior to the commencement of both experiments, subjects were informed that the cues were 100% valid in indicating the subsequent stimulus target for their eye movement. In both experiments, the background on which the cues and stimuli appeared was a uniform gray with a luminance of 33 cd/m².

Experiment 1

At the beginning of each trial, the initial fixation cross was presented for 750 ms, after which either one of three possible cues or no cue was presented for 250 ms (Figure 1A). All cues and stimuli in this experiment had a luminance of 57 cd/m². The three possible cues were as follows (Figure 1B): (1) A peripheral spatial cue, which was white so that it did not provide information about the target's color, was identical in size, shape (0.7° square), and spatial location as the upcoming target; (2) a central spatial cue, which was a 0.7° elongated triangle (white in color), was presented centrally and pointed to the upcoming target's spatial location; or (3) a color cue, presented centrally so that it did not provide any spatial information, was the same size and shape as the target stimulus and indicated the upcoming target's color (blue

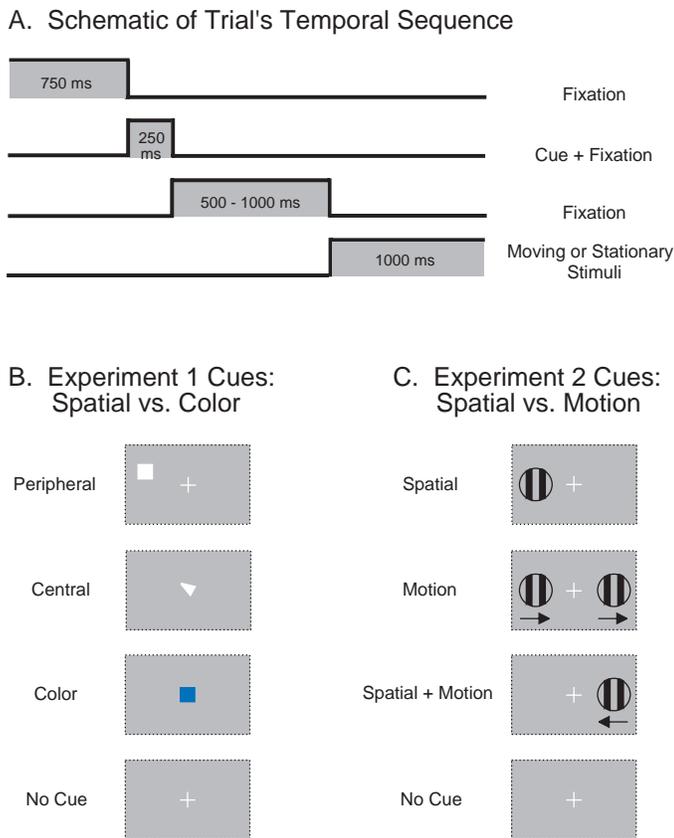


Figure 1. Schematic diagram of the temporal sequence of an individual trial and the types of cues used in the two experiments. A. The temporal sequence of steps through which a single trial progressed in both experiments. In both experiments, the fixation cross, cues, and stimuli were presented against a uniform gray background (33cd/m^2). The cues and stimuli in Experiment 1 were 0.7° squares that were white, blue, or yellow (57cd/m^2). The cues and stimuli in Experiment 2 were Gabor patches that were constructed by applying a 2.1° Gaussian filter to a 2-cycles/deg horizontal grating that had a contrast level of 60% and was isoluminant with the background. To decrease the likelihood that subjects would anticipate the presentation of the target stimulus, the interval between presentation of the cue and stimuli randomly varied from 500 to 1000 ms. B. Schematic of the cues used in Experiment 1 that indicated the location of the target stimulus or its color. Peripheral and color cues were 0.7° squares that were white (peripheral) and blue or yellow (color). The central cue was a 0.7° elongated triangle that pointed to the location of the target stimulus. C. Schematic of the Gabor cues used in Experiment 2 to indicate the initial location, motion, or motion and location of the target stimulus. The motion cue consisted of two simultaneously presented stationary Gabor patches in which the gratings both moved either rightward or leftward at a speed of $12.0^\circ/\text{s}$ and were presented at both possible target locations to ensure that the motion cue provided no information about the target's spatial location.

or yellow). For the no-cue condition with a target and distractor, subjects were instructed that they were free to select either of the stimuli and make an eye movement to that stimulus. During the presentation of the peripheral cue, the fixation cross remained on so that the subjects would not initiate an eye movement to the cue, whereas presentation of the color cue and the central cue replaced the fixation cross. After presentation of the cue, the fixation cross was presented for a variable duration between 500 and 1000 ms. This was done to minimize the possibility that subjects would anticipate the onset of the target due to predictable timing. If subjects did anticipate on any given trial, it was excluded from the analyses; this accounted for less than 1% of all trials.

The target stimuli appeared at 3.0° left or right of the vertical meridian and 0.7° above or below the horizontal meridian, and were presented for 1000 ms. When two stimuli were presented, they appeared on opposite sides of each meridian; for example, if one stimulus was 3.0° to the left and 0.7° up, then the other stimulus was 3.0° to the right and 0.7° down. Target stimuli were either blue or yellow (57cd/m^2), and when two stimuli were presented, there was one of each color. On pursuit trials, the stimuli moved horizontally and toward the fovea at a speed of $16.0^\circ/\text{s}$ in a step-ramp paradigm (Rashbass, 1961). We adjusted the position offset of the stimuli in order to minimize the occurrence of catch-up saccades during the initiation of pursuit. Within each session, the spatial location and color of the target stimulus were randomly determined but appeared at all four possible locations and in each color equally often. Because there were no significant differences based on target color or location, data were collapsed together across these trial types.

Experiment 2

The timing parameters for fixation, cue, and stimuli duration were identical to those used in Experiment 1 (Figure 1A). The cues and stimuli in this experiment, instead of being 0.7° squares, were Gabor patches that were constructed by applying a 2.1° Gaussian filter to a 2 cycles/deg horizontal grating that had a contrast level of 60% and had the same luminance as the background. As in Experiment 1, a 0.7° fixation cross was presented in the center of the screen, and the cues and stimuli were presented either 3.0° to the left or right of the vertical meridian. However, in contrast to Experiment 1, there was no vertical offset for the cues and stimuli, so they appeared on the horizontal meridian. Again, one of three possible cues or no cue could be presented on a given trial (Figure 1C). The location cue consisted of a replica of the upcoming target (2.1° Gabor patch), and was presented at the forthcoming target's spatial location. The motion cue consisted of two simultaneously presented, stationary Gabor patches in which both gratings moved either rightward or leftward at a speed of $12.0^\circ/\text{s}$ and was presented at the two possible target locations. By indicating the motion of the target with two

simultaneously presented Gabor patches at both possible target locations, the motion cues provided no information about the target's spatial location. As a result, the only information in the motion cues that is available to guide subjects' target selections and eye movements is the direction of the velocity signal. For pursuit trials, the motion cue indicated to the subject to follow the moving target that translated in the same direction, whereas for saccade trials, the motion cue indicated to the subject to make an eye movement to the stationary target in which the grating motion matched the motion in the cue. A spatial + motion cue consisted of a single Gabor patch presented at the forthcoming target's spatial location and with grating motion that indicated the target's motion direction. For each type of cue, the fixation cross remained on during cue presentation.

On pursuit trials, the Gabor patches translated horizontally across the screen at a speed of 12.0°/s in a step-ramp paradigm. Because in Experiment 1 the target always moved toward the fovea from its initial location, it is possible that subjects could form an expectation for the direction of motion of the target when presented with either the peripheral or central spatial cue. To remove this possibility, in Experiment 2, both stimuli were equally likely to move either toward the fovea or away from it. As a result, subjects could not predict the direction of the target motion. However, because pursuit of a target that moves away from the fovea did not include a measurable pre-saccadic pursuit phase, latency of pursuit was impossible to determine. Consequently, we did not include these trials in our calculation of pursuit latency. On saccade trials, the Gabor patches remained stationary but the grating within the Gabor patches moved at a speed of 12.0°/sec. To be analogous to the pursuit trials, the grating motion could either be toward or away from the fovea. Further, to be consistent with the measurement of pursuit latencies, we did not include trials in which the grating motion in the stationary Gabor patches was away from the fovea in our measurement of saccade latencies.

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) 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). 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 pseudo-random sequence. In the current experiments, we focused our analysis on the horizontal component of eye movements. 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 eye position. The average deviation of these measurements was approximately 0.05 deg, which provides an estimate of the noise in our measurement of eye position.

All eye movement data and events related to the onset of stimuli were stored on disk during the experiment, and later transferred to a free BSD 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 (-3dB at 54 Hz) to the calibrated horizontal eye position signals. The average standard deviation of eye velocity during the same 500-ms fixation intervals mentioned above was approximately 5 deg/s, which provides an estimate of the noise in our measurement of eye velocity. 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°. In addition, to be sure that our measurements of smooth eye movements were not contaminated by saccades, we excluded from analysis each detected saccade and 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 (-3dB at 25 Hz) to the eye movement signals. For the analysis of pursuit latency, we applied a refinement of the linear regression technique described previously (Krauzlis & Miles, 1996). In the previous technique, the variance associated with a "baseline" interval is used to detect the beginning of a "response" interval. A linear regression of the response interval as a function of time is used to determine when the response intersects the baseline - this was defined as the latency of pursuit. Unfortunately, the extrapolation used in this method renders the latency estimates sensitive to noise in the response interval and this problem is made worse with the higher noise associated

with video-based methods of eye movement recording. To address this problem, we constrained the response interval to immediately follow, and be continuous with, the baseline interval, forming a “hinge” (Figure 2). The baseline interval had a duration of 100 ms and the response interval had a duration of 80 ms, and we tested possible hinge placements ranging from ± 30 ms from an initial subjective estimate of pursuit latency. For each of these hinge placements, the slope of the response interval was determined by linear regression, and we measured the mean squared error between the data and the model (baseline plus response intervals). The hinge placement that provided the best fit was defined as the latency of pursuit.

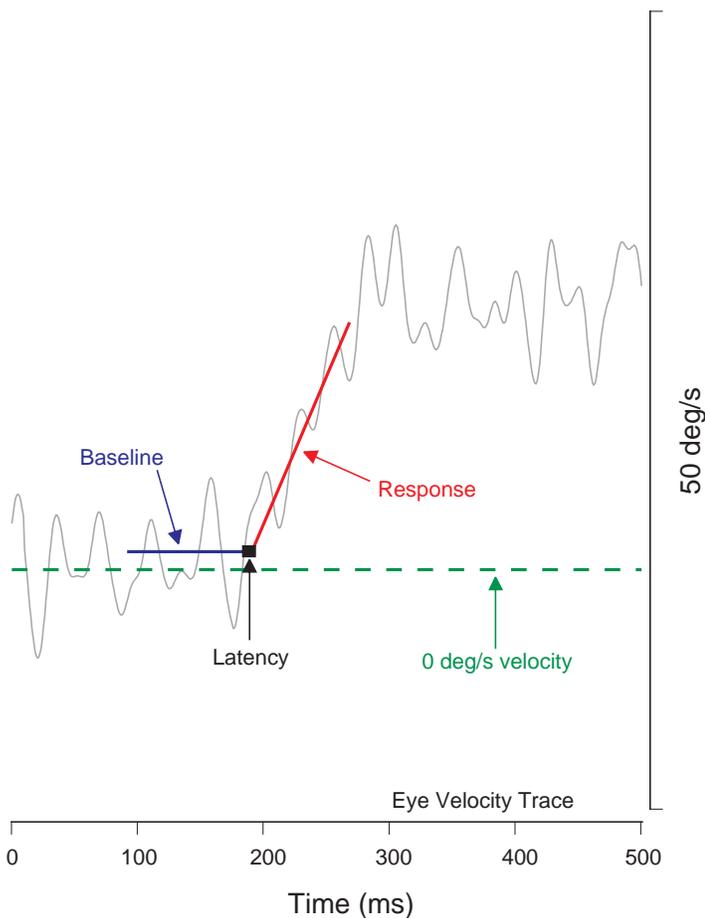


Figure 2. Sample eye velocity trace from one pursuit trial in the peripheral cue condition in Experiment 1 (subject N.D.). The stimulus appeared 3.0° to the right or left of the vertical meridian and 0.7° above or below the horizontal meridian, and then moved horizontally and foveally at a speed of $16.0^\circ/\text{s}$ for a duration of 1000 ms. The green dashed line indicates the location of $0^\circ/\text{s}$ eye velocity. Also represented is the hinge model used to calculate the latency of pursuit onset. The baseline (blue line) and response (red line) intervals used by the hinge model are indicated, as well as the calculated pursuit latency. The latency for this trial was 188 ms.

Statistical analyses of latencies in the different cue conditions for both pursuit and saccadic eye movements were conducted on the mean latency of all trials, pooled across the four subjects, in a given condition. The statistical significance of differences across the conditions was assessed with the Kruskal-Wallis analyses of variance, using commercially available software (SigmaStat; SPSS Science, Chicago, IL). Overall, these analyses indicated a significant effect, $p < .01$, of the different cue conditions for both pursuit and saccades in Experiments 1 and 2. In order to isolate specific differences between experimental conditions, post hoc analyses were conducted using multiple Mann-Whitney pairwise comparisons ($p = .05$), with a Bonferroni correction.

Results

Experiment 1: Spatial Versus Identity Information

Pursuit

The presence of a target and a distractor in the visual array (distractor trials) produced significantly longer pursuit latencies in all cue conditions (Figure 3A) compared to no-distractor trials when only a single target was presented (Figure 3B). When prior spatial information was given, pursuit latency on distractor trials was 153 ms with peripheral cues and 154 ms with central cues. Pursuit latency did not differ, however, between the two types of spatial cues. Two subjects showed this same pattern of effects when comparing performance after the two spatial cues, but the other two subjects exhibited conflicting effects: one subject had a shorter latency after a peripheral cue than a central cue (H.C.) and the other subject had a shorter latency after a central cue than a peripheral cue (S.A.). The mean pursuit latency in the peripheral spatial cue condition was significantly shorter than in the color cue condition (177 ms; $p < .0001$, Mann-Whitney rank sum test) (Figure 3A, dashed line), and all of the subjects exhibited this same effect (Table 1). Further, all of these cue conditions had significantly shorter pursuit latencies than when no cue was provided on distractor trials (185 ms). All subjects showed this same pattern except that R.K. had similar latencies in the color cue and no-cue conditions.

The mean latency of pursuit on no-distractor trials was 137 and 136 ms with prior peripheral and central spatial cues. As on distractor trials, the two types of spatial cues again produced similar mean pursuit latencies. This same pattern of latency effects with spatial cues was exhibited by three of the subjects with the exception that H.C. had a shorter latency after a peripheral cue than a central cue (Table 1). Pursuit latency was significantly shorter in the peripheral cue condition than after presentation of a color

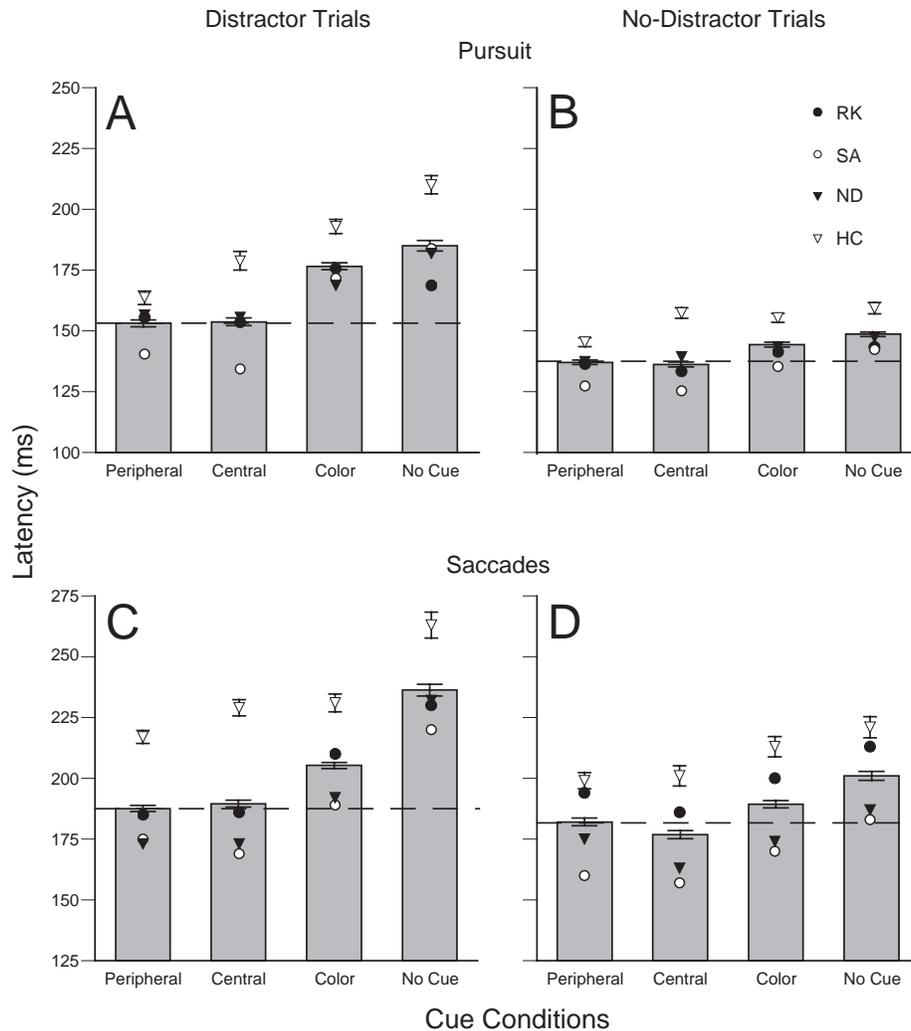


Figure 3. Pursuit and saccade latencies in no-cue, peripheral, central, and color cue conditions in Experiment 1. In all graphs, bars represent the mean latency of all trials, pooled across all four subjects, in the different cue conditions. The dashed horizontal lines in each graph indicate the mean latency in the peripheral spatial cue conditions, to which the mean latencies in the other cue conditions were compared (Mann-Whitney pairwise comparisons, $p = .05$). The different symbols correspond to mean latencies for each individual subject in each cue condition. SEs are shown for one subject (H.C.) to indicate the typical error of eye movement latencies in this experiment. A and B. Pursuit latencies on distractor and no-distractor trials. C and D. Saccade latencies on distractor and no-distractor trials.

cue (144 ms; $p < .0001$, Mann-Whitney rank sum test) (Figure 3B, dashed line). This facilitative effect of the spatial cue compared to the color cue was exhibited by all of the subjects (Table 1), though the latency difference did not reach significance for any of them. Again, mean pursuit latency was shorter in all of the cue conditions than when no prior cue was given (149 ms).

Saccades

Overall, the different cue conditions produced the same pattern of latency changes for saccades as for pursuit. Mean saccade latency when spatial cues were presented prior to presentation of the stimuli on distractor trials was 188 ms with peripheral cues and 190 ms with central cues ($p < .0001$, Mann-Whitney rank sum

test). As with pursuit, presentation of peripheral and central spatial cues had similar effects on saccade latencies. Confirming the lack of any systematic differential effect of the two spatial cues was the lack of a consistent pattern of differences in individual subjects' saccade latencies due to peripheral and central cues (Table 1). As with pursuit, a peripheral cue produced a shorter mean saccade latency than a cue to the target's color (205 ms; $p < .0001$, Mann-Whitney rank sum test) (Figure 3C, dashed line), an effect that was also exhibited by all four subjects. Further, all cues generated mean saccade latencies that were significantly shorter than in the no-cue condition (236 ms) on distractor trials. This difference between the cue conditions and the no-cue condition was obtained with all of the subjects.

Table 1. Individual Subject's Pursuit and Saccade Latencies (and SEs) for each Cue Condition on Distractor and No-Distractor Trials in Experiment 1.

Conditions	Pursuit Latencies (ms)				Saccade Latencies (ms)				
	RK	SA	ND	HC	RK	SA	ND	HC	
Distractor Trials	Peripheral Cue	155 (3.2)	140 (2.0)	156 (2.7)	163 (2.7)	185 (1.7)	175 (2.5)	173 (2.0)	217 (2.7)
	Central Cue	153 (2.9)	134* (2.1)	155 (3.0)	178* (3.8)	186 (1.8)	169* (2.5)	173 (11.2)	229* (3.3)
	Color Cue	175* (3.1)	171* (2.6)	168* (2.8)	192* (2.9)	210* (1.5)	189* (1.8)	192* (3.6)	231* (3.6)
	No Cue	168* (3.5)	183* (4.1)	181* (4.7)	209* (3.7)	230* (3.8)	220* (3.9)	233* (5.4)	263* (5.3)
No-Distractor Trials	Peripheral Cue	137 (1.5)	128 (1.7)	138 (2.1)	146 (1.9)	194 (2.3)	160 (2.8)	175 (2.2)	199 (3.4)
	Central Cue	134 (1.6)	126 (1.6)	140 (2.1)	158* (2.2)	186 (2.4)	157 (3.1)	163* (4.0)	201 (4.1)
	Color Cue	142* (1.6)	136* (1.8)	144* (2.0)	156* (1.9)	200* (2.0)	170* (2.3)	174 (2.5)	213* (4.2)
	No Cue	144* (1.7)	143* (1.5)	148* (1.8)	160* (2.3)	213* (2.5)	183* (4.2)	187* (4.6)	221* (4.4)

* Significantly different ($p < .005$) than the peripheral cue condition.

On no-distractor trials, mean saccade latency after providing prior spatial cues, peripherally and centrally, was 182 ms and 177 ms ($p < .0001$, Mann-Whitney rank sum test), respectively. The effect of the different spatial cues on saccade latency was exhibited by each of the subjects (Table 1). In contrast with distractor trials and pursuit, the central spatial cue produced a significantly shorter mean saccade latency on no-distractor trials than a peripheral cue. However, only one subject (N.D.) showed evidence of a latency difference between the peripheral and central spatial cues. The peripheral spatial cue again produced a significantly shorter mean saccade latency than the color cue (189 ms; Figure 3D, dashed line); three subjects (R.K., S.A., and H.C.) showed this same effect, though the latency difference reached significance for only one (H.C.). As before, saccade latencies were significantly shorter after all cues than when no cue was provided (201 ms) – an effect that was exhibited by all subjects.

Comparison of distractor and no-distractor trials

For both pursuit and saccades, spatial cues produced shorter latencies than in the color cue or the no-cue conditions on distractor and no-distractor trials. Because the cues decreased latencies whether or not selection was required, it is possible that the facilitative effect on attentional allocation by spatial cueing was independent

of the process of target selection. Alternatively, the facilitative effect on attentional allocation by spatial cueing might interact with target selection mechanisms by biasing the process of selecting between competing stimuli (e.g., Ferrera & Lisberger, 1995).

To determine which alternative best accounts for the patterns of latency decreases exhibited on distractor and no-distractor trials, we performed separate weighted regression analyses for pursuit and saccades comparing latencies on distractor versus no-distractor trials. If the first alternative is correct and attentional effects are independent from the process of target selection, then the regression line should have a slope near 1.00, indicating equivalent latency decreases due to attentional cueing whether selection was required or not. If the second alternative is correct and attention biases the selection process, then the regression line should have a slope greater than 1.00, indicating that latency decreases were greater when selection was required.

The dependent variable in these analyses was the mean latency for each subject in the different cue conditions on distractor trials, and the independent variable was the mean latency for each subject on no-distractor trials. For pursuit (Figure 4A), this analysis revealed a significant regression, $r^2 = 0.84$, $p < .05$, indicating that the pattern of decreases due to the different cues was similar on distractor and no-distractor trials. The slope of the regression line ($m = 1.76$),

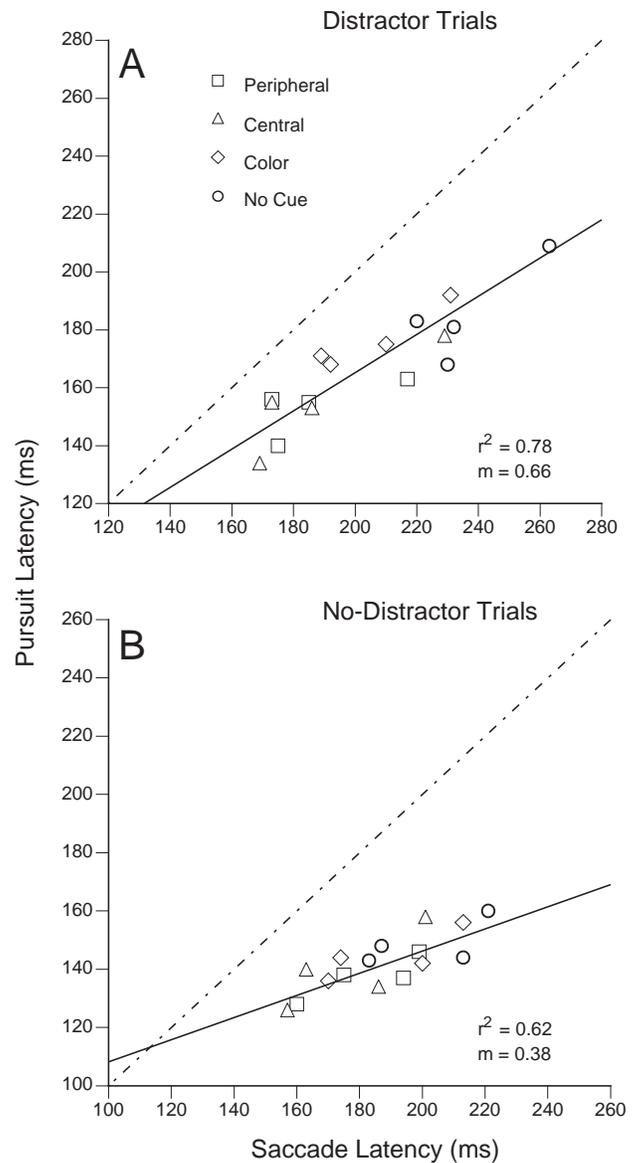
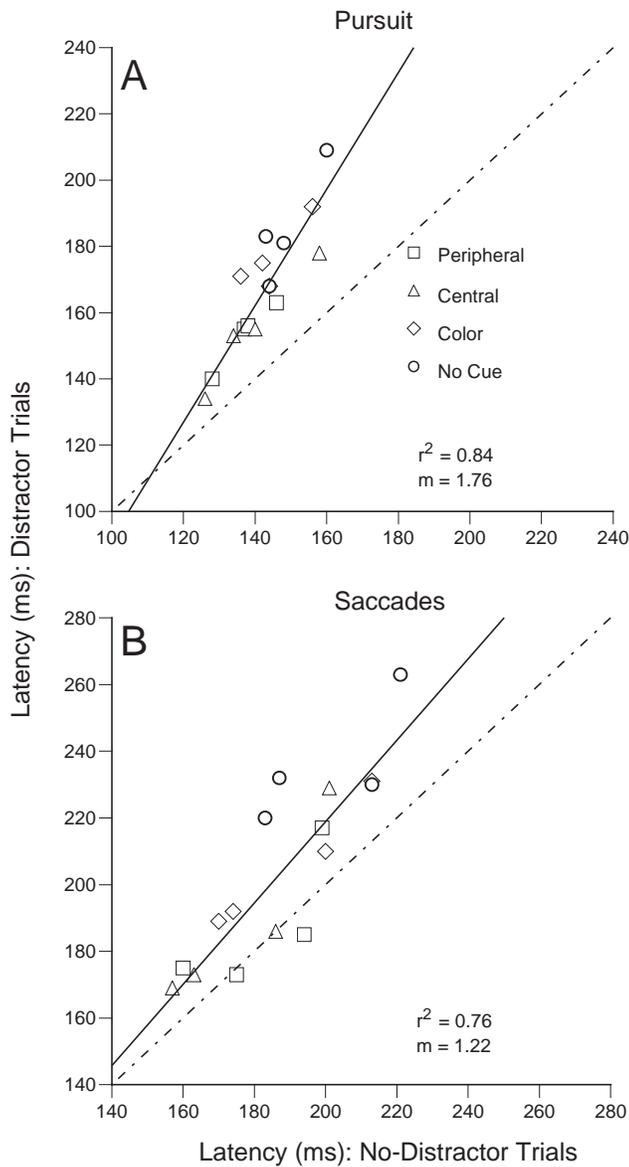


Figure 4. Comparison of latencies on distractor and no-distractor trials for pursuit and saccades in Experiment 1. Each data point represents an individual subject's mean latency in a particular cue condition, with the different symbols representing peripheral (square), central (triangle), color (diamond) cue, and no-cue (circle) conditions. In the bottom right corner of each graph is the value of weighted regression score (r^2) and the slope of the regression line (m). The dotted lines represent slopes of 1.00. A. Pursuit latencies on distractor trials plotted as a function of latencies on no-distractor trials. B. Saccade latencies on distractor trials plotted as a function of latencies on no-distractor trials.

Figure 5. Comparison of pursuit and saccade latencies on distractor and no-distractor trials in Experiment 1. A. Pursuit latencies on distractor trials plotted as a function of saccade latencies on distractor trials. B. Pursuit latencies on no-distractor trials plotted as a function of saccade latencies on no-distractor trials. Other conventions same as in Figure 4.

however, indicates that the cues produced an approximately 76% greater decrease in latency when selection was required (i.e., distractor trials) than when it was not (i.e., no-distractor trials).

For saccade latencies, this analysis also revealed a significant relationship between distractor and no-distractor trials, $r^2 = 0.76$, $p < .05$. The slope of the regression line was not as high as for pursuit but was still greater than 1.00, $m = 1.22$ (Figure 4B). These findings indicate that, like pursuit, saccade latencies exhibited similar patterns of decreases due to the different cues on distractor and no-distractor trials. Furthermore, this analysis revealed that saccade latencies were also facilitated to a greater degree by prior information when selection was required (i.e., distractor trials) than when it was not (i.e., no-distractor trials).

Comparison of pursuit and saccades

A central issue in the present study was whether a common attentional mechanism might mediate target selection for both pursuit and saccades. To address this issue, we examined whether or not the different cues produced similar effects on both eye movements by conducting weighted regression analyses comparing pursuit latencies (dependent variable) to saccade latencies (independent variable) on distractor and no-distractor trials. On distractor trials (Figure 5A), the analysis revealed a significant regression between pursuit latencies and saccade latencies, $r^2 = 0.76$, $p < .05$. The slope of the

regression line was less than 1.00, $m = 0.66$, indicating that the prior information facilitated the latency to initiate a saccade by approximately 34% more than the latency to initiate pursuit. On no-distractor trials (Figure 5B), this analysis again revealed a significant relationship between pursuit and saccade latencies across the cue conditions, $r^2 = 0.62$, $p < .05$. The slope of the regression line was again less than 1.00, $m = 0.38$, indicating that presentation of prior information decreased saccade latencies by approximately 62% more than pursuit latencies.

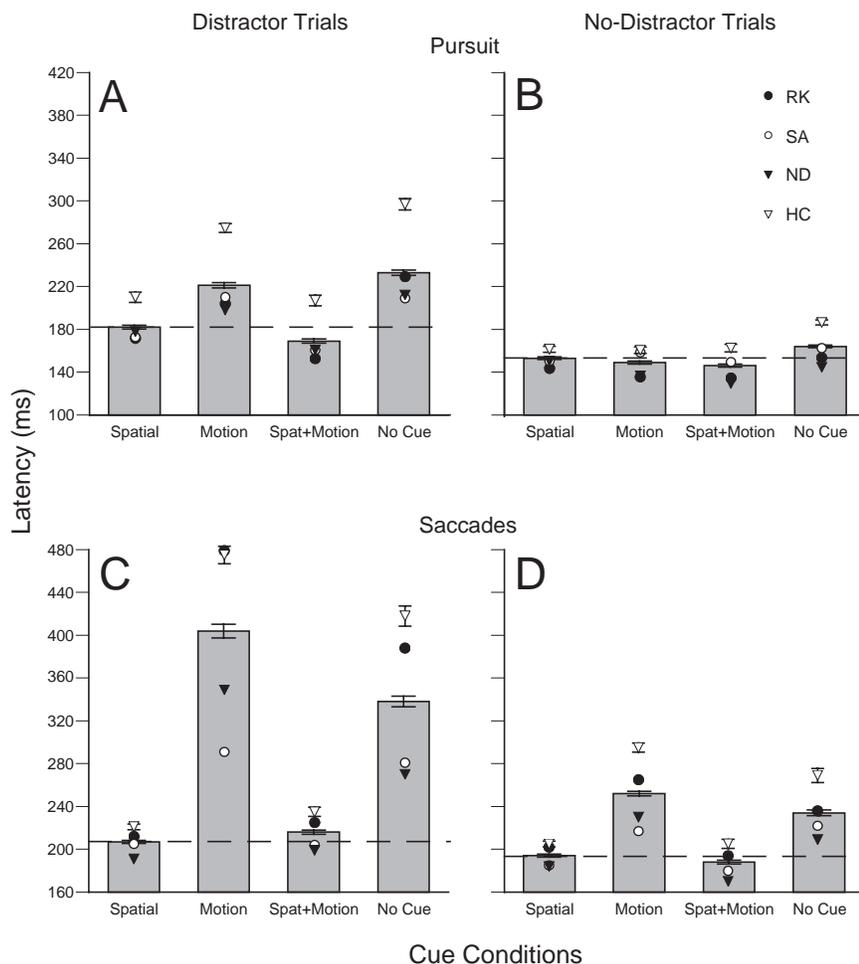


Figure 6. Pursuit and saccade latencies in the spatial, motion, spatial + motion cue conditions and the no-cue condition in Experiment 2. In all graphs, bars represent the mean latency of all trials, pooled across all four subjects, in the different cue conditions. The dashed horizontal lines in each graph indicate the mean latency in the spatial cue conditions, to which the mean latencies in the other cue conditions were compared (Mann-Whitney pairwise comparisons, $p = .05$). The different symbols correspond to mean latencies for each individual subject in each cue condition. SEs are shown for one subject (H.C.) to indicate the typical error of eye movement latencies in this experiment. A and B. Pursuit latencies on distractor and no-distractor trials. C and D. Saccade latencies on distractor and no-distractor trials. (independent variable) on distractor and no-distractor trials. On distractor trials (Figure 5A), the analysis revealed a significant regression between pursuit latencies and saccade latencies, $r^2 = 0.76$, $p < .05$. The slope of the regression line was less than 1.00, $m = 0.66$, indicating that the prior information facilitated the latency to initiate a saccade by approximately 34% more than the latency to initiate pursuit. On no-distractor trials (Figure 5B), this analysis again revealed a significant relationship between pursuit and saccade latencies across the cue conditions, $r^2 = 0.62$, $p < .05$. The slope of the regression line was again less than 1.00, $m = 0.38$, indicating that presentation of prior information decreased saccade latencies by approximately 62% more than pursuit latencies.

Table 2. Individual subject's pursuit and saccade latencies (and SEs) for each cue condition on distractor and no-distractor trials in Experiment 2.

Conditions	Pursuit Latencies (ms)				Saccade Latencies (ms)				
	RK	SA	ND	HC	RK	SA	ND	HC	
Distractor Trials	Spatial Cue	171 (3.0)	172 (2.7)	177 (3.1)	209 (4.8)	212 (2.9)	205 (2.7)	191 (2.0)	221 (2.7)
	Motion Cue	203* (5.0)	209* (3.4)	197* (4.1)	273* (4.1)	479* (13.2)	291* (5.5)	349* (11.2)	475* (8.1)
	Spatial + Motion Cue	152* (3.1)	160* (2.2)	160* (3.1)	206 (5.0)	225 (5.3)	204 (2.4)	199 (3.6)	235* (4.2)
	No Cue	228* (4.1)	208* (4.0)	211* (3.4)	295* (5.3)	388* (10.2)	281* (7.8)	270* (5.4)	418* (9.4)
No-Distractor Trials	Spatial Cue	145 (1.9)	152 (1.9)	152 (2.6)	163 (2.8)	202 (3.0)	185 (2.2)	184 (2.2)	205 (2.7)
	Motion Cue	137* (1.9)	160* (1.9)	138* (2.6)	162 (2.9)	265* (2.9)	217* (2.8)	230* (4.0)	295* (4.2)
	Spatial + Motion Cue	136* (1.9)	151 (1.8)	131* (2.3)	164 (3.5)	194* (2.6)	180* (3.7)	170* (2.5)	205 (4.3)
	No Cue	155* (1.7)	164* (1.5)	146* (1.8)	188* (2.4)	236* (3.4)	222* (5.3)	209* (4.6)	269* (6.7)

* Significantly different ($p < .005$) than the spatial cue condition.

Experiment 2: Spatial Versus Motion Information

The previous experiment demonstrated that prior information, particularly cues to the target's spatial location, decreased the latencies of both pursuit and saccade eye movements, although this effect was larger for saccades than for pursuit. The larger effect of spatial cueing on saccades may be due to the fact that saccades are driven by spatial information, whereas pursuit is driven by motion information. If this is the case, then motion cues, which provide the sensory input necessary for generating pursuit, should show the opposite pattern of latency effects as spatial cues and facilitate pursuit to a greater degree than saccades.

Pursuit

As in Experiment 1, pursuit latency significantly increased in all cue conditions when a distractor was present in the visual array (Figure 6A) compared to when there was not (Figure 6B). With a prior spatial cue, mean pursuit latency on distractor trials was 182 ms. Mean pursuit latency after a motion cue was 221 ms, a significant increase ($p < .0001$, Mann-Whitney rank sum test) from the latency in the spatial cue condition (Figure 6A, dashed line), which was substantiated by the same effect of the motion cue on pursuit latencies of all of the subjects. Pursuit latency obtained with a motion + spatial

cue, which indicates both the motion and the spatial location of the forthcoming target, decreased further to 169 ms, which represented 13 ms and 52 ms decreases compared to that obtained with either spatial or motion cues. Mean pursuit latency on distractor trials in all of the cue conditions were significantly shorter than in the no-cue condition (233 ms), an effect that was exhibited by each of the subjects except for one subject (S.A.) who had equivalent latencies in the motion cue and no-cue conditions (Table 2).

On no-distractor trials, the mean latency of pursuit was 153 ms in the spatial cue condition and 149 ms in the motion cue condition, but there was no significant difference between these two cue types. Furthermore, individual subjects did not show any consistent pattern when comparing performance in the spatial cue condition to the motion cue condition (Table 2). The mean latency obtained with a spatial + motion (146 ms) cue was significantly shorter ($p < .0001$, Mann-Whitney rank sum test) than with either a spatial cue or a motion cue. Two of the subjects (R.K. and N.D.) exhibited the same significant difference between the spatial and spatial + motion cue conditions, and only one subject (S.A.) exhibited a significant difference between the motion and spatial + motion cue conditions. Finally, the mean pursuit latency on no-distractor trials in each of the cue conditions was significantly shorter than in the no-cue condition (164 ms), an effect exhibited by each subject

except for one (S.A.) who had equivalent latencies in the motion cue and no-cue conditions.

Saccades

The mean saccade latency in the no-cue condition on distractor trials was 338 ms (Figure 6C), 104 ms longer than on no-distractor trials (Figure 6D). With a spatial cue, mean saccade latency was 207 ms. Presentation of a motion cue produced a significant increase in the mean saccade latency (404 ms) on distractor trials ($p < .0001$, Mann-Whitney rank sum test), 197 ms longer than that obtained with a spatial cue (Figure 6C, dashed line). This significant difference between the spatial and motion cues was exhibited by each of the subjects (Table 2). Further, the mean saccade latency after presentation of a spatial + motion cue (216 ms) was not different than the latency obtained with a spatial cue but was significantly shorter than with a motion cue. Three of the four subjects failed to show a significant difference between saccade latencies after spatial + motion and spatial cues, whereas all subjects showed a significant difference between saccadic latencies after spatial + motion and motion cues. The mean saccade latency in each of the cue conditions was significantly different than in the no-cue condition (338 ms); latency in the spatial and spatial + motion cue conditions was shorter and latency in the motion cue condition was longer than in the no-cue condition. All of these latency differences due to the presentation of a spatial, motion, or spatial + motion cue compared to no cue were also exhibited by each of the subjects (Table 2).

On no-distractor trials, presentation of a prior spatial cue produced a saccade latency of 194 ms. However, in contrast to pursuit, a motion cue significantly increased saccade latency on no-distractor trials to 252 ms ($p < .0001$, Mann-Whitney rank sum test). This effect of the motion cue was consistent across the subjects, with all of the subjects also exhibiting an increase in their pursuit latency after a motion cue relative to a spatial cue (Table 2). Presenting a spatial + motion cue, mean saccade latency was 188 ms, not significantly different, unlike pursuit, than in the spatial cue condition but significantly shorter than in the motion cue condition. However, saccade latency after a spatial + motion cue was significantly less than the latency after a spatial cue for three of the subjects (Table 2). As on distractor trials, mean saccade latency in each of the cue conditions on no-distractor trials was significantly different than in the no-cue condition (234 ms), and these differences were also exhibited by each of the subjects.

Comparison of distractor and no-distractor trials

To again examine whether attentional allocation is independent from or biases the process of target selection for the initiation of eye movements, we performed separate weighted regression analyses for

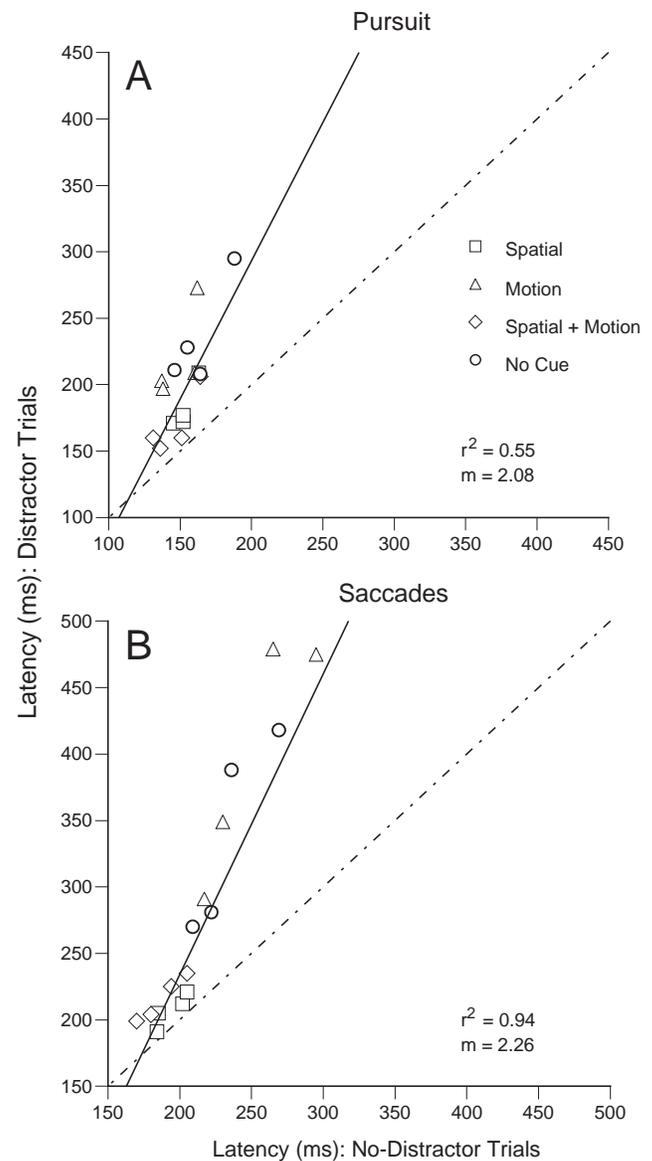


Figure 7. Comparison of pursuit and saccade latencies on distractor and no-distractor trials in Experiment 2. Each data point represents an individual subject's mean latency in a particular cue condition, with the different symbols representing no-cue (circle), spatial (square), motion (triangle), and spatial + motion (diamond) cue conditions. In the bottom right corner of each graph is the value of weighted regression score (r^2) and the slope of the regression line (m). The dotted lines represent slopes of 1.00. A. Pursuit latencies on distractor trials plotted as a function of latencies on no-distractor trials. B. Saccade latencies on distractor trials plotted as a function of latencies on no-distractor trials.

pursuit and saccades on distractor and no-distractor trials. For pursuit, the weighted regression analysis revealed a significant relationship ($r^2 = 0.55$, $p < .05$) indicating that the effects of the different cues on latency were similar for distractor and no-distractor trials (Figure 7A). The slope of the regression line ($m = 2.08$)

indicated that when selection was required (i.e., distractor trials), the cues produced an approximately 108% greater decrease in latency than when selection was not necessary (i.e., no-distractor trials).

For saccade latencies, the weighted regression analysis also revealed a significant relationship ($r^2 = 0.94$, $p < .05$) between data from distractor and no-distractor trials. The slope of this regression line was also greater than 1.00, $m = 2.26$ (Figure 7B). Once again, these findings indicate that the pattern of effects on saccade latencies obtained in the different cue conditions were similar for distractor and no-distractor trials. Moreover, as before, this analysis revealed that when selection was required, the different sensory cues subsequently produced much greater changes in the latencies to initiate a saccade to a target stimulus than when selection was not required.

Comparison of pursuit and saccades.

As in Experiment 1, to address whether target selection is mediated by a common attentional mechanism for pursuit and saccades, we compared the two eye movements for similar effects of the different cue conditions. We again used weighted regression to compare pursuit latencies (dependent variable) to saccade latencies (independent variable) on distractor and no-distractor trials. For distractor trials (Figure 8A), the weighted regression analysis revealed a significant relationship between pursuit latencies and saccade latencies ($r^2 = 0.71$, $p < .05$) indicating that the two eye movements had similar latency patterns across the cue conditions. The slope of the regression line was less than 1.00, $m = 0.33$, indicating that the latency to initiate a saccade was affected by prior information to a larger extent than the latency to initiate pursuit. However, this result may have been influenced by the fact that the motion cue produced different directions of latency changes for pursuit and saccades, and we, therefore, repeated this analysis without the motion cue condition. A significant relationship was still exhibited ($r^2 = 0.71$, $p < .05$) and the slope of the regression line was still less than 1.00, $m = 0.47$, indicating that spatial cues generated similar effects on pursuit and saccade initiation, but the latency decrease was approximately 53% greater for saccades than for pursuit.

For no-distractor trials, the weighted regression analysis failed to reveal a significant relationship across the cue conditions ($r^2 = 0.16$, n.s.; Figure 8B), suggesting that the pattern of effects on latencies produced by the different sources of prior information was not similar for the two types of eye movements. The difference resulted from the motion cue, which again produced different effects on latency for the two eye movements: a latency decrease for pursuit but a latency increase for saccades. Eliminating the motion cue condition from the analysis produced a significant regression of pursuit on saccade latencies ($r^2 = 0.63$, $p < .05$), indicating that prior spatial

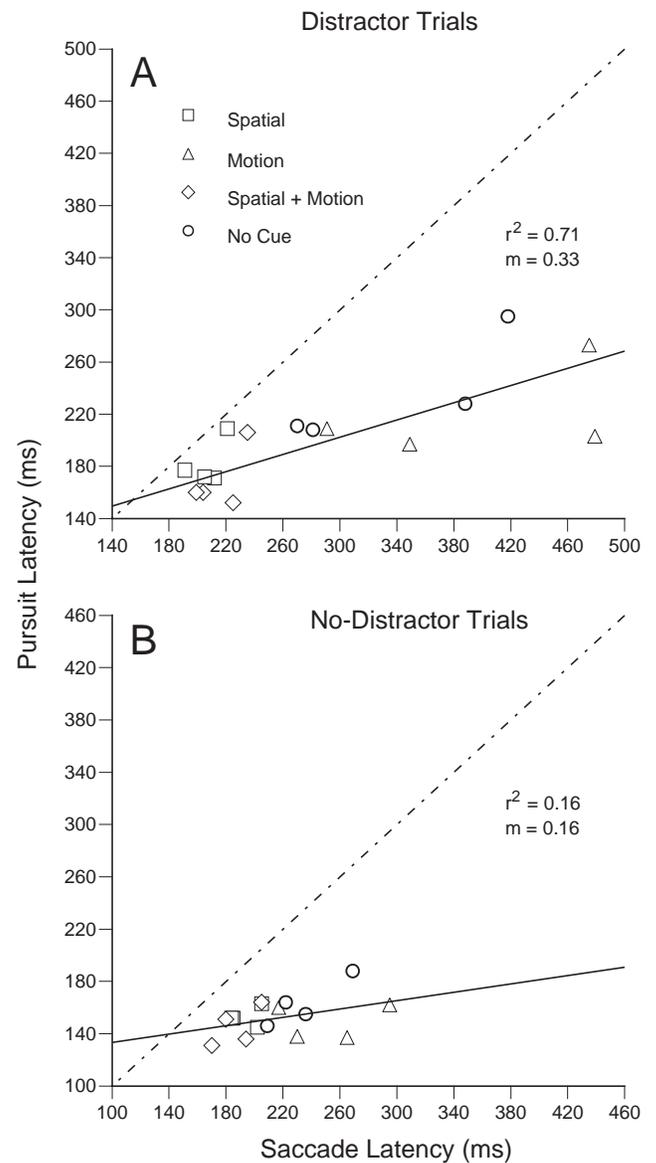


Figure 8. Comparison of pursuit and saccade latencies on distractor and no-distractor trials in Experiment 2. A. Pursuit latencies on distractor trials plotted as a function of saccade latencies on distractor trials. B. Pursuit latencies on no-distractor trials plotted as a function of saccade latencies on no-distractor trials. Other conventions as in Figure 7.

information produced similar facilitation of pursuit and saccade latencies. The slope of this regression line ($m = 0.43$) indicated that prior spatial information decreased saccade latencies 57% more than pursuit latencies.

Discussion

The focus of the current study was to examine the effect of attentional modulation on target selection for the initiation of both smooth pursuit and saccadic eye movements. We found that the pattern of effects on

target selection by different types of prior information was similar for both pursuit and saccades. However, different types of prior information facilitated target selection to differing degrees. In particular, the biasing of target selection was facilitated for both eye movements more by prior spatial information than by feature information (color cue) or motion information. That spatial information had a greater facilitative influence on target selection and eye movement latency than did motion information was true even for smooth pursuit, even though this type of eye movement has been shown to be largely dependent on motion input for its generation.

Warning Signal Effect

Numerous studies have indicated that in reaction time experiments, cues, whether visual or auditory, can serve as warning signals to the temporal onset of a target stimulus (Abrams, Oonk, & Pratt, 1998; Letourneau, Denis, & Londorf, 1986; Reuter-Lorenz, Oonk, Barnes, & Hughes, 1995; Walker, Kentridge, & Findlay, 1995; Wright, Richard, & McDonald, 1995). As a result, reaction time may be facilitated just on the basis of the cue serving as a warning signal, distinct from the effect of the stimulus-specific prior information the cue is intended to impart to the subject. The facilitative effects on eye movement latency of spatial and motion cues found in the present experiments, however, could not be due solely to such warning signal effects but must be due to the benefit (or cost) of the stimulus-specific prior information the cues provided to the attentional and eye movement systems. In Experiment 1, the peripheral and central spatial cues and the color cue all provide the same warning signal to the temporal onset of the target stimulus, yet the spatial cues produced significantly shorter eye movement latencies than the color. In Experiment 2, the spatial and motion cues also provided equivalent warning signals to target onset, yet latencies after spatial cues were significantly shorter than after motion cues. These findings indicate that the spatial and motion cues were having specific effects on the attentional and eye movement systems that were above and beyond a warning signal effect.

Primacy of Spatial Information for Target Selection

That saccadic eye movements were preferentially facilitated by prior spatial information is not particularly surprising when one considers that saccades are generated to specific locations in visual space. In fact, the spatial precision of saccades has been shown to be nearly equivalent to perceptual judgments of target location (Kowler & Blaser, 1995), and the landing location of saccades in an extended random dot stimulus is narrowly focused with high precision to the center-of-gravity of the object (McGowan, Kowler, Sharma, & Chubb, 1998).

When there are stimuli at multiple locations, the generation of saccades has been shown to be related to the mechanism of spatial attention, which selects a target stimulus from among the competing stimuli (Kowler et al., 1995; Sheliga, Craighero, Riggio, & Rizzolatti, 1997). In the present study, consistent with this role of spatial attention in selecting targets for saccades, spatial cues produced the greatest decreases in saccade latencies.

At the outset, an analogous argument concerning motion cueing was expected to hold true for pursuit. Studies had shown that smooth pursuit eye movements require motion information for their generation (for review, see Lisberger, Morris, & Tychsen, 1987). That motion information is crucial for the generation of pursuit eye movements has been demonstrated by the fact that pursuit initiation is elicited by retinal velocity errors rather than retinal position errors (Morris & Lisberger, 1987; Rashbass, 1961). The importance of motion for pursuit eye movements is also provided by neurophysiological evidence that the MT and the MST areas in the extrastriate cortex, which process visual motion (Albright, 1984; Zeki, 1978), play a key role in the generation of pursuit eye movements (Komatsu & Wurtz, 1988; Newsome, Wurtz, & Komatsu, 1988). Furthermore, chemical lesions of direction-selective areas MT (Newsome et al., 1985) and MST (Dürsteler & Wurtz, 1988) have been found to impair the matching of eye velocity to target velocity during smooth pursuit, whereas stimulation of these areas has been found to facilitate eye acceleration during tracking of a moving target but not during fixation of a stationary target (Komatsu & Wurtz, 1989).

With this dependence of pursuit eye movements on motion input as a foundation, Ferrera and Lisberger (1995) proposed a computational model in which target selection for smooth pursuit is based on a competitive network of direction-selective units whose outcome can be biased by attention to a specific motion direction. Consistent with this model, behavioral studies have found that pursuit latency is longer when two stimuli move in opposite directions, thereby requiring selection of a target on the basis of a particular motion direction, than when they move in the same direction or when there is only a single stimulus (e.g., Ferrera & Lisberger, 1997; Krauzlis et al., 1999). Consequently, we expected that attentional modulation of motion processing by cueing a particular direction of motion would facilitate target selection for the initiation of pursuit to a much greater degree than cueing a particular spatial location.

A number of our findings are congruent with the prediction that motion information serves as the input for target selection for pursuit, whereas spatial information would be the input for saccades. First, prior motion information produced a facilitative effect on pursuit latency but not on saccade latency. In fact, motion cues not only failed to produce a facilitation but actually produced a significant increase in saccade latency, a result

that is consistent with the finding that direct stimulation of the motion areas MT-MST, in addition to facilitating pursuit, produced increases in saccade latencies (Komatsu & Wurtz, 1989). Second, the regression analyses in both experiments showed that spatial cues decreased latencies to a greater degree for saccades than for pursuit.

However, contrary to the prediction that motion cues would be best for facilitating target selection for pursuit, whereas spatial cues would be best for facilitating saccades, we found that spatial cues facilitated target selection for pursuit much more than motion cues. Spatial cues also facilitated target selection for pursuit (and saccades) more than color cues. Thus, for both pursuit and saccades, spatial cues decreased the time to generate the eye movement to a much larger extent than cues to the target's color or motion. Further, spatial cues (presented centrally) that guided target selection in a voluntary top-down manner (Jonides, 1981; Posner, 1980; Van der Heijden, 1992; Yantis & Jonides, 1984) produced eye movement latencies equivalent to those obtained with bottom-up (peripheral) spatial cues, and this was true for both pursuit and saccades. Together, this suggests that the competitive selection of a target for both pursuit and saccades is biased by a common top-down attentional mechanism that is largely mediated by targets' locations in space rather than their motion direction or an object feature such as color. That the attentional biasing of target selection is mediated by spatial information, even for pursuit, is contrary to the Ferrera and Lisberger (1995) proposal that the attentional biasing of target selection for pursuit is mediated by motion direction. As a result of a shared attentional mechanism in which spatial information mediates the biasing of target selection, spatial cues were superior to either color or motion cues for facilitating the selection of the appropriate target regardless of eye movement.

The Relation Between Attention and Target Selection for Guiding Eye Movements

Previous studies have typically used only a single stimulus when investigating the role of attentional allocation on the initiation of voluntary eye movements (e.g., Posner, 1980) but have used two stimuli when investigating the role of target selection in the initiation of eye movements (e.g., Krauzlis et al., 1999). As a result, how the processes of attentional allocation and the selection of an eye movement target are related has not been delineated. In the present study, in addition to the effect of spatial attention on eye movement latencies when selection between two competing stimuli was required (i.e., distractor trials), we found that both pursuit and saccade latencies also decreased when selection of a target was not required (i.e., no-distractor

trials). What does this finding tell us about the relation between attentional allocation and target selection?

It is possible that the facilitative effect on attentional allocation by cueing is independent of the process of target selection for guiding eye movements. As a result, cueing would produce equivalent effects on attentional processing when selection was and was not required, in which case eye movement latencies would be equivalently affected regardless of whether there was competition for selection or there was not. Although the pattern of latency effects across the cue conditions in both experiments was indeed correlated for when selection was and was not required, the slopes of the regression lines when comparing distractor (i.e., selection) and no-distractor (i.e., no selection) trials indicated that the effects on eye movement latencies were larger when selection was required. This finding suggests that, rather than being independent, the effects on attentional allocation by the administration of information cues, particularly spatial cues, interact with target selection mechanisms by biasing the process of selecting between competing stimuli.

Researchers have theorized that additive and superadditive effects of experimental factors on reaction time measures (e.g., latency) indicate more than just the unrelatedness or relatedness of the underlying processes (Colonius, 1990; Schweickert, 1978; Sternberg, 1998; Townsend, 1984, 1990; Townsend & Ashby, 1983). Instead, additive effects on reaction time measures imply that distinct stages of processing occur in a serial order rather than in parallel. In this work, superadditive effects were found indicating that attentional allocation and target selection are related. Additionally, this finding implies that these processes overlap and interact in a parallel manner. Sternberg (2001) suggests that to evaluate the relation between processing nodules, determining whether processes are separate and serial or interact and parallel is not sufficient – it is also necessary to determine the rule by which these processes combine to affect reaction times. The present study, however, was not designed to test beyond whether attentional allocation and target selection were related or unrelated in affecting the latency of eye movement initiation.

Neural Correlate of the Shared Attentional Mechanism

Is there a candidate neural correlate that could be the mediator of this spatially dependent target selection mechanism that is shared by both pursuit and saccades? Research has shown that neural responses in the superior colliculus are modulated by shifts in attention (Robinson & Kertzman, 1995) and have been related to the generation of eye movements (Dorris, Paré, & Munoz, 1997; Kustov & Robinson, 1996; Robinson, 1972; Wurtz & Goldberg, 1972). Kustov and Robinson (1996), for example, found that attentional modulation by spatial cues (peripheral and central) yielded faster saccade

latencies when the cue was valid than when it was invalid. Further, they found that stimulation of the superior colliculus after cue presentation produced evoked saccades in the direction of the cue. This result suggests a tight coupling of the focus of spatial attention with preparation of a saccadic eye movement and suggests that this coupling occurs in the superior colliculus.

Extending this idea to pursuit, the findings from a number of more recent studies support the contention that the superior colliculus serves as the neural locus for the shared spatially dependent target selection mechanism for both eye movement types (Basso, Krauzlis, & Wurtz, 2000; Krauzlis, Basso, & Wurtz, 1997, 2000). For example, Krauzlis et al. (1997) found that mismatches between the position of the eye relative to the position of the target produced increases in neural discharges in the superior colliculus, regardless of whether the subject generated pursuit or saccadic eye movements. More recently, Krauzlis and Dill (2002) have shown that activity in the superior colliculus can predict target choices made by both pursuit and saccades. The present finding that spatial cues were best at facilitating target selection and eye movement initiation irrespective of eye movement type is consistent with the idea that a spatially dependent target selection mechanism is shared by both the pursuit and saccade systems.

Conclusions

In sum, the principal finding from this set of experiments is that prior spatial information facilitated target selection and eye movement initiation significantly more than either prior color information or prior motion information for both smooth pursuit and saccades. Surprising, and somewhat counterintuitive, was the finding that prior spatial information was better than prior motion information, even for pursuit eye movements. We have suggested that this is due to the workings of a spatial attention mechanism for target selection that provides an input for both the pursuit and saccadic eye movement systems.

Acknowledgments

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