Target Selection for Pursuit and Saccadic Eye Movements in Humans

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Abstract

■ Eye movements were recorded from three subjects as they initiated tracking of a small circle ("target") moving leftward or rightward, above or below the horizontal meridian, either alone or in the presence of a small square ("distractor") moving leftward or rightward on the other side of the horizontal meridian. At the start of each trial, subjects were provided with either a "form" cue (always centrally positioned and having the circular shape and color of the upcoming moving target) or a "location" cue (a small white square positioned where the upcoming target would appear). The latency of pursuit increased in the presence of an oppositely moving distractor when subjects were provided the form cues but not when they were provided the location cues. The latency of saccades showed similar, but smaller, increases when subjects were given the form cues. On many trials with the form cues, pursuit started in the direction of the distractor and then reversed to follow the target. On these trials, the initial saccade often, but not always, also followed the distractor. These results indicate that the mechanisms of target selection for pursuit and saccades are tightly coordinated but not strictly yoked. The shared effects of the distractor on the latencies of pursuit and saccades probably reflect the common role of visual attention in filtering the inputs that guide these two types of eye movements. The differences in the details of the effects on pursuit and saccades suggest that the neural mechanisms that trigger these two movements can be independently regulated. ■

INTRODUCTION

Primates have the ability to track small moving objects with their eyes even when those objects must be discriminated against a background of irrelevant stimuli. These tracking eye movements have two components: Pursuit moves the eyes slowly and smoothly to keep retinal images relatively stationary, whereas saccades move the eyes rapidly to foveate eccentric retinal images. Much is known about the sensory regions of the brain that provide inputs for these movements and the motor pathways that execute them (Lisberger, Morris, & Tychsen, 1987; Sparks & Mays, 1990). However, much less is known about the mechanisms responsible for selecting which sensory inputs will be used to guide the movements.

The selection of targets for pursuit and saccades is of interest beyond the control of eye movements because it addresses the more general problem of how sensory inputs are filtered and combined to produce discrete appropriate actions. Numerous previous studies in humans have examined the relationship between the programming of saccadic eye movements and the directing of spatial attention. Although shifts in spatial attention can be made in the absence of eye movements (Klein & Farrell, 1989; Posner, 1980), it is more common for such shifts to accompany or precede saccades (Posner, 1980; Shepard, Findlay, & Hockey, 1986). In addition, identification of a visual stimulus is best when the location of the stimulus coincides with the saccade endpoint (Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995), providing evidence in favor of overlap between the mechanisms for spatial attention and saccade generation. Related studies have also shown that there is a relationship between saccades and the process of visual search. When subjects are instructed to make a saccade to one of several simultaneously presented stimuli, the latency and accuracy of saccades can be altered by the presence of other distracting stimuli (Ottes, Van Gisbergen, & Eggermont, 1985; Williams, 1967; Zelinsky, 1996). When the target is readily distinguished from the surrounding distractors, saccades are typically made directly to the target. However, when identification of the target is less obvious, saccades are often made to distractors or to the empty spaces between stimuli. These patterns of eye movements suggest that saccade endpoints are determined by the location or spatial distribution of attention rather than by the location of visual stimuli per se.

Considerably less is known about the selection of

targets for pursuit. The selectivity of pursuit is evident in the ability to smoothly follow a small target moving against a textured background, although the presence of the background does produce a reduction in pursuit eye velocity (Collewijn & Tamminga, 1984; Keller & Khan, 1986; Kimmig, Miles, & Schwarz, 1992). Perceptual judgments are also better for tracked targets than for untracked backgrounds, indicating that the same attentional filter is used for both pursuit and perception (Khurana & Kowler, 1987). A few recent studies have examined the effects of presenting multiple stimuli for pursuit. These studies in the monkey have shown that the presence of distractor stimuli increases the latency of pursuit eye movements made to a previously cued target stimulus (Ferrera & Lisberger, 1995; Ferrera & Lisberger, 1997). The existing data are therefore consistent with the idea that the inputs for pursuit, like saccades, are influenced by attention.

In the current study, we have examined the selection of targets for pursuit and saccades in humans by presenting target stimuli that differed from a distractor stimulus in either shape or both color and shape. Parafoveal stimuli were presented in single trials (Figure 1A) during which subjects were first provided with either a form or a location cue. Form cues indicated the color and shape of the upcoming target, and location cues indicated the position of the upcoming target. The moving target stimulus (10°/sec) appeared either alone or accompanied by a distractor stimulus whose shape was always different, but whose color and motion could be either the same or different (Figure 1B). Thus, in contrast to previous studies in monkeys, our human subjects were sometimes required to identify the target based on a salient combination of features (color and shape) or a less-salient single feature (shape). In addition, we have also documented the latencies of the vertical saccades required to foveate the target.

RESULTS

We measured the latency of pursuit and saccades made to the target stimulus by three subjects (rk, fm, jm) on a total of 9025 trials (2881, 3297, and 2847, respectively). The histograms in Figure 2 show the frequency distribution of pursuit latencies for subject rk for each of the 10 stimulus conditions. The average latency of pursuit with the target alone (Condition 1) was 161 and 153 msec on trials with form (Figure 2A) and location (Figure 2B) cues, respectively. When the target was accompanied by a distractor moving in the same direction (Conditions 2 and 3), the latency of pursuit was little different from that observed with the target alone. However, when the distractor moved in the direction opposite to the target, the latency of pursuit increased and became more variable after form cues (Figure 2A, Conditions 4 and 5). In contrast, when the distractor moved in the direction opposite to the target after location cues (Figure 2B, Conditions 4 and 5), the latency of pursuit was relatively unaffected.

The increased variability in pursuit latency when the distractor moved in the direction opposite to the target was caused by the fact that subjects sometimes started by briefly following the distractor. On these trials, an example of which is shown in Figure 3A, horizontal eye velocity initially increased in the direction of the distractor's motion and was typically, although not always, ac-

Figure 1. Schematic diagrams of the experimental conditions. Each rectangle depicts a snapshot of the video display at a particular moment during the trial. (A) The sequence of snapshots illustrates the structure of each trial. (B) The individual snapshots indicate the five stimulus conditions that were randomly interleaved on separate trials during the experiment. The moving stimuli appeared at an eccentricity of 1.5° horizontal and 2° vertical.
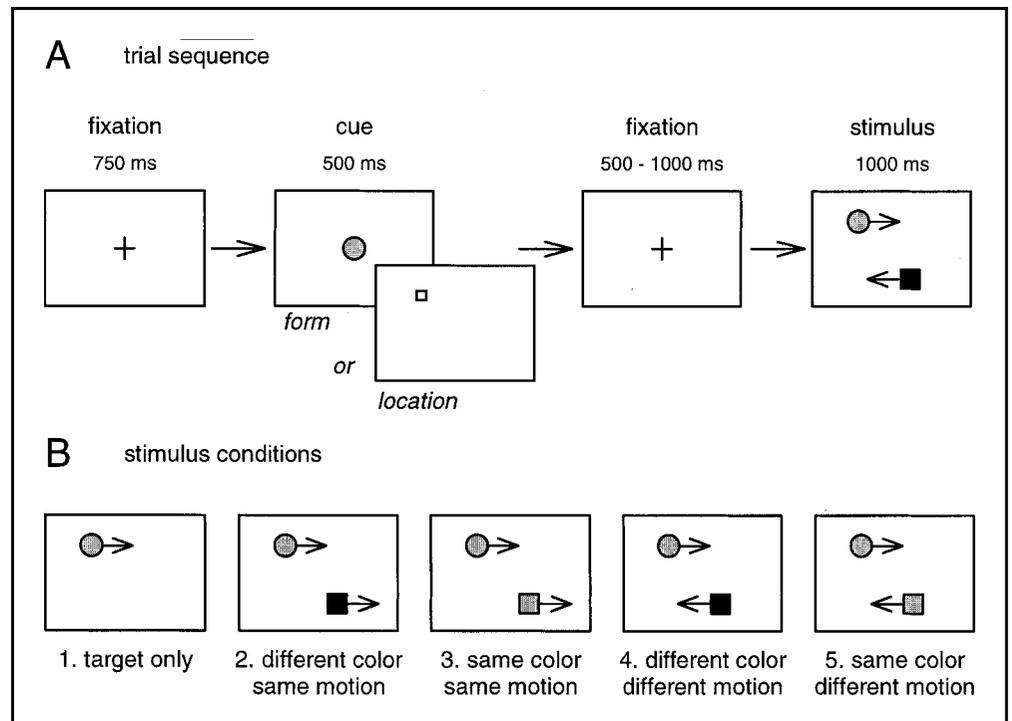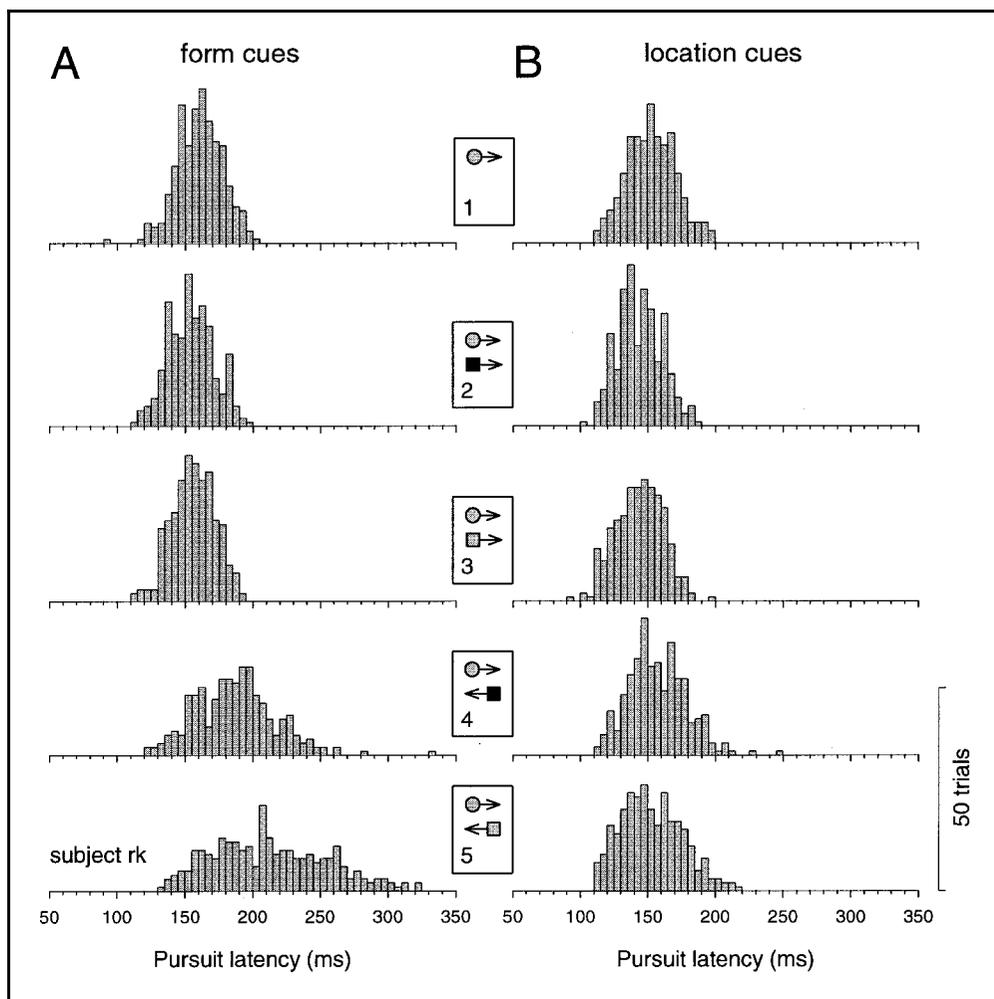
Figure 2. Distribution of pursuit latencies in the five experimental conditions, with either form (A) or location (B) cues. Each histogram shows data for each experimental condition from subject rk, pooling data from different directions of target motion and different color stimuli.


companied by a vertical saccade toward the location of the distractor. Horizontal eye velocity then reversed and subsequently increased in the direction of the target's motion, again accompanied by a saccade. Such reversals in pursuit eye velocity were observed exclusively with form cues in Conditions 4 and 5. The latency of pursuit on these trials, as on all of the other trials, was identified by the deflection of horizontal eye velocity in the direction of the target motion. To distinguish these measurements, we referred to these delayed movements in the direction of the target as "corrective" pursuit, whereas we referred to movements that followed the target from the outset as "regular" pursuit. On trials with corrective pursuit, we also measured the latency of the initial "wrong" pursuit in the direction of the distractor. For example, in Figure 3, the upward-pointing arrow indicates the latency of wrong pursuit and the downward-pointing arrow indicates the latency of corrective pursuit.

Pursuit latency was significantly affected by the presence of a distractor in all three subjects. In particular, consistent increases in latency were observed with form cues when the target moved in the direction opposite to that of the target (Figure 4A, C, and E). Compared to

the latency with the target alone (161, 141, and 175 msec for subjects rk, fm, and jm, respectively in Condition 1), the latency of regular pursuit (circles) in these two conditions increased an average of 24 msec when the distractor differed in both shape and color (20, 20, and 33 msec in Condition 4) and increased an average of 30 msec when the distractor differed only in shape (35, 18, and 38 msec in Condition 5). Not surprisingly, the latency of corrective pursuit (diamonds) was even longer, on average by 81 msec in Condition 4 (53, 96, and 94 msec) and 123 msec in Condition 5 (93, 130, and 146 msec). As indicated by the percentages above each black diamond in Figure 4, trials with wrong and subsequent corrective pursuit were most common in Condition 5 (33 to 43% of the trials), in which the only cue available for identification of the target was shape.

As a control, we presented the same stimulus conditions but explicitly indicated the location of the impending target stimulus (Figure 1A). With these location cues (Figure 4B, D, and F), the changes in pursuit latency were modest, and subjects never tracked the distractor stimulus. When the target moved in the direction opposite to that of the target, significant increases in pursuit latency were observed in two subjects (fm and jm) but not in

Figure 3. Sample trial illustrating wrong pursuit and a wrong saccade. Pursuit initially moves the eye leftward, as shown by the initial downward deflection in horizontal eye velocity (lower solid trace). This changes eye velocity in the direction of distractor motion (−10°/sec). At about 200 msec, pursuit velocity changes in the direction of target motion (+10°/sec). The trace of vertical eye position (upper solid trace) shows that pursuit is initially accompanied by a vertical saccade towards the location of the distractor (−2°), followed by a saccade toward the location of the target (+2°). The horizontal components of these saccades are responsible for the rapid deflections seen in the trace of horizontal eye velocity. Arrows indicate the estimated latency of wrong (upward arrow) and corrective (downward arrow) pursuit.
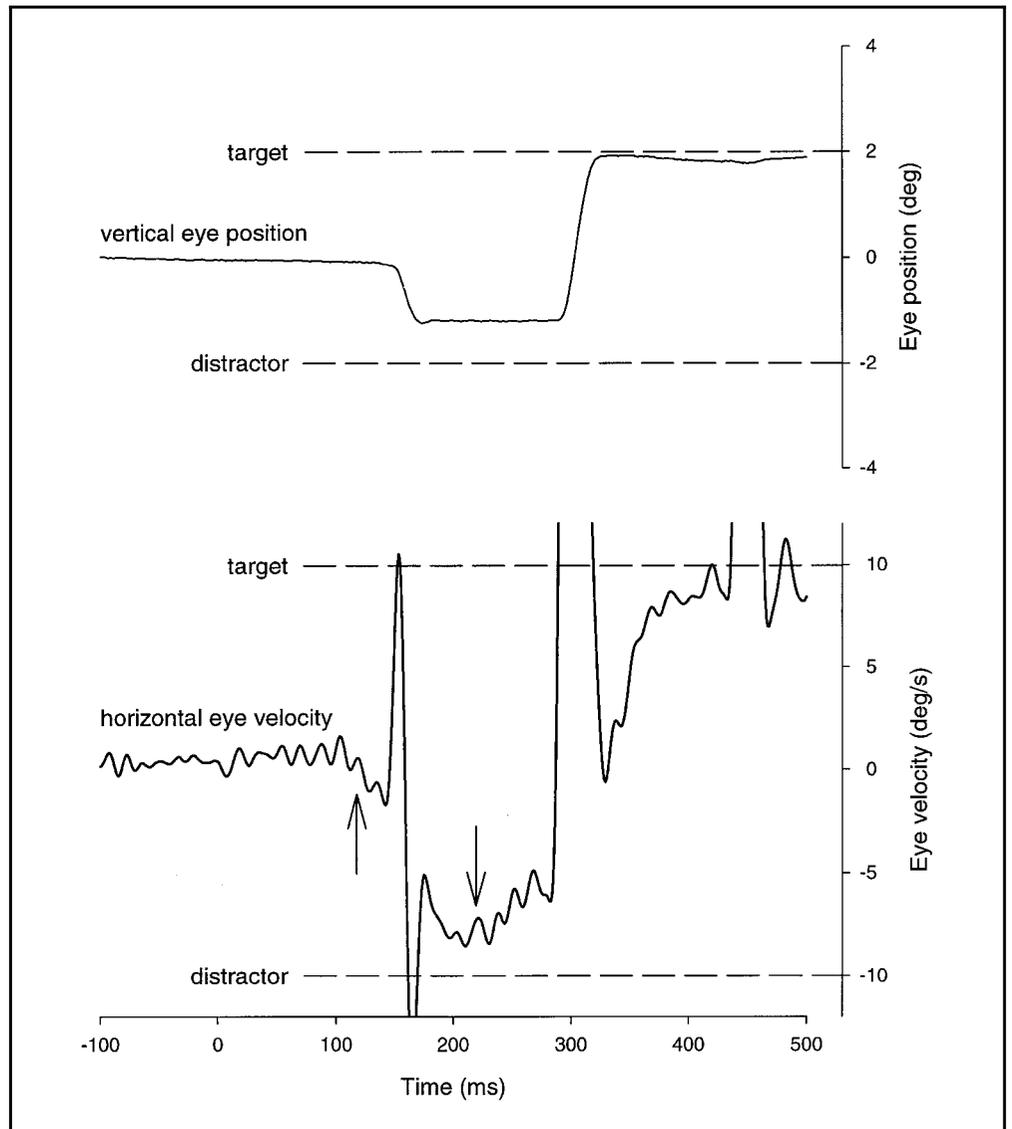

the third (rk). The average increases in pursuit latency for these two cases (Conditions 4 and 5) were 12 msec (5, 14, and 18 msec) and 9 msec (0.4, 10, and 17 msec). When the distractor moved in the same direction as that of the target (Conditions 2 and 3), there were small but significant *decreases* in latency for two of the subjects (−9 and −12 msec for rk and jm, respectively) but not for the third (fm).

The latencies of regular (vertical) saccades that accompanied pursuit were typically much longer than the latencies of pursuit and were only slightly affected by the presence of a distractor. With form cues, the latencies of regular saccades were only slightly longer in the presence of a distractor (circles in Figure 5A, C, and E): Significant (small) increases were observed in subjects rk and fm but not in subject jm. With location cues, the latencies of saccades were virtually unchanged by the presence of a distractor (Figure 5B, D, and F). All three subjects sometimes made wrong saccades to the distractor and subsequent corrective saccades to the target on

trials with form cues (as in Figure 3). The latencies of wrong saccades were slightly shorter than the latencies of regular saccades recorded in each condition and about the same as the latencies of the saccades made to the target in the absence of the distractor (indicated by the horizontal dashed lines).

In contrast to pursuit (Figure 4), saccades sometimes occurred in the wrong direction in Conditions 2 and 3, as well as in Conditions 4 and 5 (Figure 5A, C, and E). This might be expected, because these Conditions required the subjects to choose between two locations but not between two motions. Despite the occurrence of wrong saccades in additional stimulus conditions, the frequency of wrong saccades was lower (3 to 31%) than that of wrong pursuit in conditions 4 and 5 for each of the subjects. In 15% of trials, subjects initiated wrong pursuit and started corrective pursuit before making a regular saccade. However, on the majority of trials (72%) subjects generated both regular pursuit and a regular saccade, and on a minority of trials (13%) they generated

Figure 4. Changes in pursuit latency observed in the five stimulus conditions. Each graph summarizes the data from a single subject with either form cues (A, C, and E) or location cues (B, D, and F). Within each graph, different symbols are used to represent the mean latency of regular (circles or squares), wrong (triangles), and corrective (diamonds) pursuit. The dashed horizontal lines in each graph indicate the mean latency measured for the first stimulus condition, in which there was no distractor. Filled symbols indicate measurements that were significantly different ($p < 0.05$, Kruskal-Wallis) from the mean latency in this condition. For stimulus conditions that produced eye movements in the wrong direction, percentages are provided (graphs A, C, and E) to indicate the proportion of trials that contained wrong pursuit.
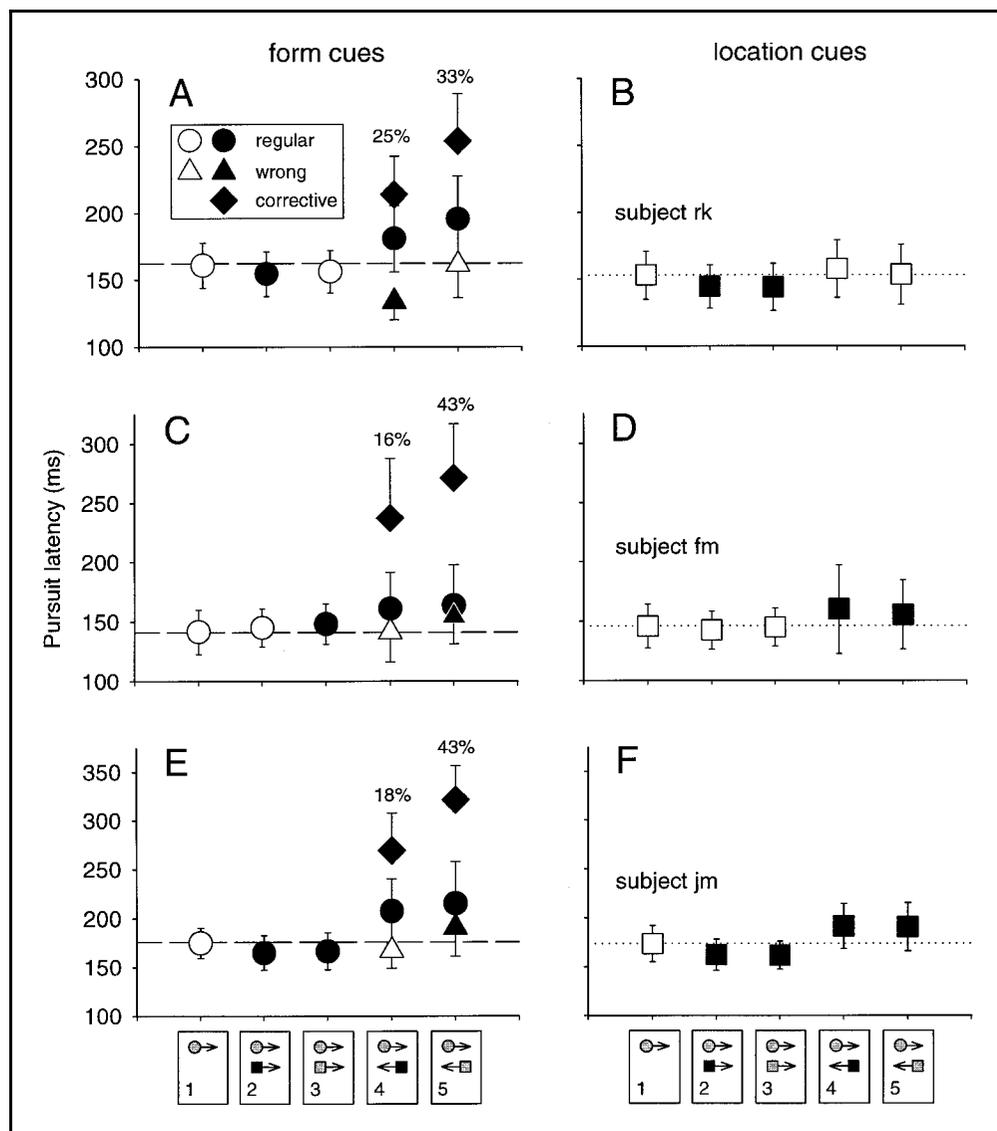
both wrong pursuit and a wrong saccade. On only one trial did a subject generate regular pursuit followed by a wrong saccade.

DISCUSSION

We have found that the initiation of pursuit in humans is altered by the presence of a distractor stimulus. In contrast to most previous studies of pursuit, which have used single target stimuli, subjects in our experiments were required to identify and track a previously cued target among two possible stimuli. The additional requirement of selecting the target extended the processing time preceding the initiation of pursuit. When subjects were given the form but not the location of an upcoming moving target, the presence of an oppositely moving distractor increased the latency of pursuit by an amount that depended on whether the target differed from the distractor in both color and shape (24 msec) or just in shape (30 msec). These values are similar to

the estimate of approximately 25 msec for the visual search process obtained in the monkey (Ferrera & Lisberger, 1995), although the exact values obtained are likely influenced by the salience of the target and distractor stimuli. The shorter processing time observed when the target differed in color as well as in shape is also consistent with previous observations for saccades that color is an especially effective cue in guiding visual search (Williams, 1967). When subjects were informed of the location of the upcoming target stimulus, the presence of an oppositely moving distractor still increased the latency of pursuit slightly in two of the three subjects. Even though the aim of providing a location cue was to dispense with the need to identify the upcoming target, these results suggest that subjects may have executed at least a partial visual search before initiating pursuit in these conditions.

In a minority of cases, we also observed that subjects initially generated a pursuit eye movement in the direction of the distractor, followed by pursuit in the direction

Figure 5. Changes in saccade latency observed in the five stimulus conditions. Conventions are the same as in Figure 4.
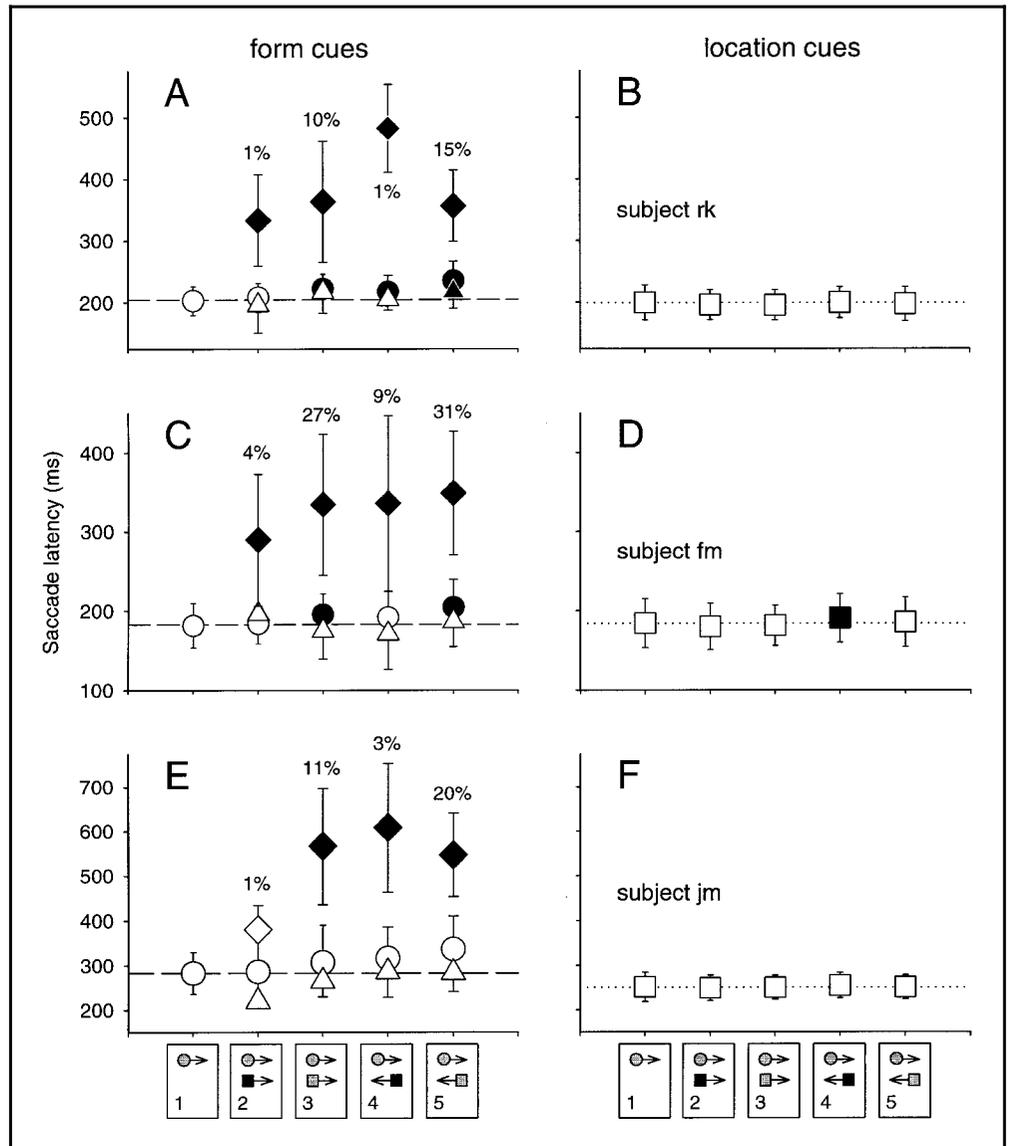
of the target. As with the increases in the latency of regular pursuit, the occurrence of this wrong pursuit was most pronounced when the target and distractor differed only in shape. One possibility is that subjects simply guessed on these trials. However, the frequency of wrong pursuit was always less than 50%, indicating that subjects were capable of correctly identifying the target stimulus, even when it differed only in shape. Notably, the latency of wrong pursuit was not much different from the latency of pursuit in the absence of distractors, indicating that wrong pursuit was initiated before the estimated 24–30 msec required for stimulus selection had elapsed. On these wrong trials, pursuit appears to have been triggered before the alternative stimuli were fully evaluated, producing eye movements that initially followed the distractor rather than the target. This interpretation implies that the responses on some regular trials were also triggered early but resulted in the subjects following the target rather than the dis-

tractor. Therefore, our estimate of 24 to 30 msec as the time required for visual search in these conditions might be an underestimate. This explanation for the occurrence of wrong pursuit is also consistent with a growing body of evidence supporting a distinction between those processes responsible for triggering—and hence for the latency of—pursuit and those that provide the drive signals—and hence the direction of—pursuit (Grasse & Lisberger, 1992; Krauzlis & Miles, 1996).

The observation that subjects generated regular pursuit on some trials and wrong pursuit on others provides some insight into the process of target selection. Because these two types of responses were observed for the same stimulus conditions, on each trial that resulted in wrong pursuit, the subjects might have forestalled their responses and initiated regular pursuit at slightly longer latencies. Subjects therefore apparently confronted a trade-off between speed and accuracy, and the presence of variability in how they resolved this trade-off on

individual trials could account for their pattern of behavior. Presumably, if subjects are given explicit instructions, the relative fractions of wrong and regular pursuit could be actively manipulated. The rapid change from wrong to corrective pursuit suggests that the two stimuli were selected in rapid succession, perhaps as part of a strategy of serial search, similar to the pattern of saccade endpoints sometimes observed during visual search (Zelinsky & Sheinberg, 1997). Alternatively, visual attention might not act directly to determine when pursuit is initiated or changes direction but instead might act indirectly by influencing the trigger mechanism for pursuit. This interpretation would be consistent with the suggestion incorporated into a model of target selection for pursuit (Ferrera & Lisberger, 1995), namely, that attention acts to bias the outcome of a competitive network, but the timing of the outcome is determined by network dynamics.

In addition to the effects on the latency of pursuit, we also observed similar, albeit smaller, effects on the latency of saccades. These results are consistent with evidence from previous studies indicating that the same attentional mechanism that underlies perception is used by pursuit (Khurana & Kowler, 1987) and saccades (Hoffman & Subramaniam, 1995; Kowler et al., 1995). Although our study did not include a perceptual task, our data suggest there is coordination between the mechanism that selects targets for pursuit and that which selects targets for saccades. Almost without exception, wrong saccades were accompanied by wrong pursuit. However, wrong pursuit was often not accompanied by wrong saccades because saccades were delayed until after the start of corrective pursuit, at which point subjects made a regular saccade to the target. This asymmetry suggests that subjects may have employed different trade-offs between speed and accuracy for pursuit versus saccades, preferring to initiate pursuit more quickly but to make saccades more accurately.

In previous work using the gap paradigm (Krauzlis & Miles, 1996), we found a much tighter correlation between decreases in the latency of pursuit and saccades and concluded that the initiation of pursuit and saccades had inputs in common. However, because pursuit and saccades exhibited different dependencies on the eccentricity of the tracked stimulus, we also concluded that these shared inputs acted through different mechanisms. We think our current results are consistent with and extend these previous conclusions. The correspondence between the occurrence of wrong pursuit and saccades indicates that there are shared inputs to the mechanisms that select stimuli for pursuit and saccades. However, the lack of a tight correlation between the latencies of pursuit and saccades indicates that these mechanisms can operate independently.

METHODS

Data were collected from three human subjects (34, 57, and 57 years of age), each with extensive experience as subjects in eye movement studies. Two of the subjects (rk and fm) were also authors of the current study, whereas the third subject (jm) was unaware of the experimental design and served as our naïve control. All procedures were approved by the Institutional Review Committee for the use of human subjects, and each subject gave informed consent.

Subjects were seated in a cushioned chair with their heads restrained gently by means of foam-padded chin and forehead rests. The position of the head was adjusted so that the eyes were located near the center of a magnetic field generated by a pair of 24-in. field coils. The horizontal and vertical positions of one eye were monitored with the electromagnetic induction technique (Fuchs & Robinson, 1966), using scleral search coils embedded in silastin rings (Collewijn, Van Der Mark, & Jansen, 1975). Coils were placed on the eye after application of one or two drops of anesthetic (proparacaine HCl). Each subject participated in five or six sessions, each lasting 36 to 60 min. The alternating current (AC) induced in the eye coil was processed with a phase detector circuit that provided separate direct current (DC) outputs proportional to horizontal and vertical eye position, with a corner frequency (−3 dB) at 1 kHz (CNC Engineering). The eye position signals were calibrated at the beginning of each recording session by having the subject fixate small target lights located at known eccentricities along the horizontal and vertical meridia.

Stimulus Presentation

Subjects viewed stimuli presented on the screen of a monitor located at a distance of 42 cm. Two of the subjects (fm and jm) wore their normal spectacle corrections during experimental sessions. The second subject (rk), a myope, preferred to view the stimuli without corrective lenses. Subjects were instructed to look at the fixation stimulus (cross-hairs) during presentation of the cue and subsequently to follow the cued moving stimulus promptly when it appeared. The form cue was a replica of the upcoming target stimulus (blue or yellow circle); the location cue was a 0.1° white square presented at the upcoming target location. During the initial fixation and cue period of each trial, which had a duration of 1750 to 2250 msec, subjects were required to remain within 2° of the fixation stimulus. This requirement aborted any trials that may have contained anticipatory saccades or slow drifts. If this requirement was not met, a new trial was selected and the paradigm reverted to the start of the fixation period. If this requirement was met, the fixation stimulus was extinguished and was immediately replaced with the target stimulus,

either alone or accompanied by a distractor stimulus. On individual trials, the initial location of the target could be either above or below the horizontal meridian (±2°) and its motion could be either rightward or leftward toward the vertical meridian. Rightward- and leftward-moving stimuli appeared 1.5° to the left or right of the vertical meridian, respectively. The target was always a circle (0.8° diameter) and the distractor was always a square (0.7° on a side); each could be either blue or yellow (luminance, 24 cd/m^2) and appeared against a uniform gray background (luminance, 9 cd/m^2). These stimulus variables produced a total of 80 trial types. Because there were no consistent differences based upon color or direction of motion, these trial types were collapsed into the 10 stimulus conditions described in Figure 1.

Data Collection and Analysis

The stimulus presentation and the acquisition and storage of data were controlled by a personal computer with the use of a real-time experimentation (REX) software package (Hays, Richmond, & Optican, 1982). Voltage signals encoding the horizontal and vertical components of eye position were low-pass filtered (6-pole Bessel, −3 dB at 180 Hz) and then digitized to a resolution of 12 bits, sampling at 1 kHz (analog-to-digital converter: National Instruments).

Eye movement data were analyzed off-line using an interactive program run under Linux on a Pentium PC (Dell Computer Corporation). Signals encoding horizontal and vertical eye velocity were obtained by applying a 29-point finite impulse response (FIR) filter (−3dB at 54 Hz) to the recorded horizontal and vertical eye position signals. Signals encoding eye acceleration were then obtained by applying the same FIR filter to the signals encoding eye 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). The computer recorded the onset time of each saccade, and these values were stored in a file that was later accessed to calculate means and other statistics. For smooth pursuit, the latency was determined by visual inspection of the eye velocity records from each trial. The marking of latency by hand was required because the vertical offset of the stimuli produced small vertical corrective saccades on every trial. We initially attempted to measure pursuit latency with an automated procedure (e.g., Krauzlis & Miles, 1996) but obtained unreliable results. Although we would have preferred an automated procedure, we think that our method of visual inspection nonetheless produced objective estimates of pursuit latency. Most importantly, all of the latencies reported in this paper were marked by a trained naïve observer. This observer was not one of the authors and was not involved in either the design or the interpretation of the experiments. In addition, to confirm the reliability and reproducibility of these measurements, the observer reanalyzed randomly selected data from each of the three subjects, unaware of the conditions from which they came. None of the measurements made in this blind fashion were significantly different from the original measurements. For measurements of both saccade and pursuit latencies obtained from single trials, statistical significance of differences across stimulus conditions was assessed with the Kruskal-Wallis test for multiple comparisons, using commercially available software (Jandel Scientific).

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