

Initiation of Saccades During Fixation or Pursuit: Evidence in Humans for a Single Mechanism

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SUMMARY AND CONCLUSIONS

1. In four human subjects, we measured the latency of saccadic eye movements made to a second, eccentric target after an initial, foveated target was extinguished. In separate interleaved trials, the targets were either both stationary ("fixation") or both moving with the same velocity ("pursuit"). For both fixation and pursuit trials, we extinguished the first target at randomized times during maintained fixation or pursuit and varied the time interval ("gap duration") before the appearance of the second target.

2. During both fixation and pursuit, the presence of a 200-ms gap reduced the latencies of saccades, compared with those obtained with no gap. For two subjects, we imposed additional, intermediate gap durations and found that saccade latencies varied as a function of gap duration. Furthermore, the latencies of saccades elicited during pursuit displayed the same dependence on gap duration as those elicited during fixation.

3. Our results demonstrate that the "gap effect" observed for saccades made during fixation also occurs for saccades made during pursuit. To the extent that the gap effect on saccade latency reflects a mechanism underlying the release of fixation, our results suggest that the same mechanism is invoked for saccades made during pursuit. From the viewpoint of initiating saccades, the existence of separate fixation and pursuit systems may be irrelevant.

INTRODUCTION

The processes underlying the initiation of saccades have been studied by manipulating the temporal sequence in which the visual targets are presented. If a second target is presented at an eccentric position immediately after an initial, stationary and foveated target has been extinguished, saccades to the second target occur at latencies of 150–200 ms. However, if the first target is turned off a few hundred milliseconds before the new one appears (the so-called "gap paradigm"), saccadic latency is reduced (Becker 1972; Fischer and Boch 1983; Saslow 1967). The amplitude of the reduction in latency depends on the exact duration of the gap interval, with maximal reductions occurring for gap durations of ~200 ms in both humans (Fischer and Ramspurger 1984) and monkeys (Fischer and Boch 1983; Fischer et al. 1984). The observation of activity related to visual fixation in several regions of the brain (e.g., Matsumura et al. 1992; Munoz and Wurtz 1993; Noda and Suzuki 1979; Sakata et al. 1980; Schlag and Schlag-Rey 1984; Schlag et al. 1992; Segraves and Goldberg 1987) suggests that there may exist a "fixation system," acting as the functional complement to the saccadic system. The changes in latency in the gap paradigm are believed to occur because extinction of the foveated stimulus results in an early release from this

fixation mechanism, permitting saccades to be initiated more quickly when the eccentric target appears.

The suggestion of a fixation system is also relevant to smooth pursuit eye movements, because it has been recognized for some time (Robinson 1965) that fixation is not simply pursuit at zero velocity. This distinction has been amplified by more recent demonstrations that some visual stimuli can modify eye speed during ongoing pursuit, although they cannot initiate pursuit during fixation of a stationary target (Goldreich et al. 1992; Morris and Lisberger 1987; Schwartz and Lisberger 1994). These results indicate that the initiation of pursuit involves elevating the status of at least some visual inputs from the fettered state accorded them during fixation. However, this distinction between pursuit and fixation is not directly concordant with the idea that the initiation of saccades likewise involves a release from fixation. Because saccades not only transfer fixation between stationary targets, but also punctuate the pursuit of moving ones, the initiation of saccades must either employ different mechanisms during fixation and pursuit, or not recognize the distinction between fixation and pursuit. In the current study, we addressed this issue by testing whether the "gap effect" observed for saccades made during fixation also occurs for saccades made during pursuit. Our results demonstrate that such a gap effect does exist, suggesting that, from the viewpoint of saccade initiation, pursuit is equivalent to fixation.

METHODS

Data were collected from four human subjects. All procedures were approved by the Institutional Review Committee concerned with the use of human subjects, and all subjects gave informed consent. For two subjects (*FM* and *RK*), the horizontal and vertical positions of one eye were recorded with the electromagnetic induction technique (Robinson 1963), using scleral search coils embedded in silastin rings (Collewyn et al. 1975). Coils were placed on the eye after application of one or two drops of anesthetic (proparacaine HCl). For both subjects, coils were worn in individual sessions lasting 60–70 min for a total of five or six sessions. In each session, subjects completed 1,440–1,620 trials, divided equally among 36 conditions. For the other subjects (*MB* and *KP*), the horizontal positions of both eyes were recorded with an infrared limbus tracker (Applied Science Laboratory, model 210) in three or four sessions, each lasting 30–45 min (720 trials, divided equally among 12 conditions). Subjects were each provided with one practice session before acquisition of the data reported here. 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 meridians. During the experiments, the subjects binocularly viewed

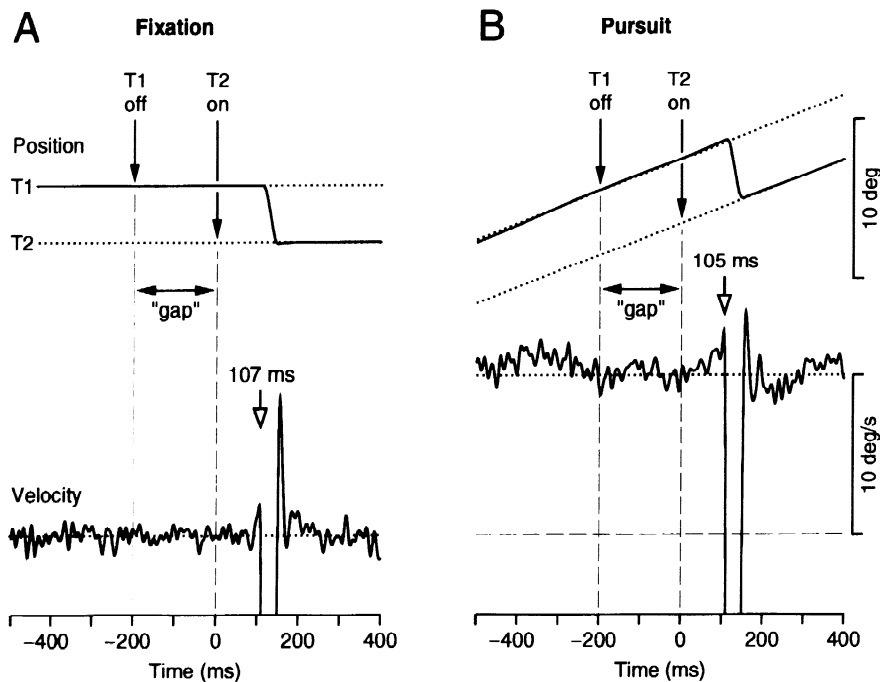


FIG. 1. Examples of "fixation" and "pursuit" trials with a gap duration of 200 ms. *A, top traces:* during a fixation trial, the subject's eye position (solid line) initially matches the position of the 1st target (top dotted line), which is extinguished at a randomized time (T1 off). The subject then makes a leftward saccade (downward deflection of eye position trace) shortly after the appearance of the 2nd target (T2 on, bottom dotted line). *A, bottom traces:* subject's eye velocity (solid line) remains near $0^\circ/\text{s}$ (dotted horizontal line), except when saccade occurs at 107 ms (time zero is the appearance of the 2nd target). Velocity trace is clipped at $-5^\circ/\text{s}$. *B, top traces:* during a pursuit trial, the subject's eye position (solid line) initially tracks the 1st target (top dotted line) but then makes a leftward saccade to track the 2nd target (bottom dotted line), which moves at the same speed and in the same direction. *B, bottom traces:* subject's eye velocity (solid line) remains near $10^\circ/\text{s}$ (dotted horizontal line), except when saccade occurs at 105 ms (downward-pointing arrow). Thin dashed horizontal line indicates $0^\circ/\text{s}$. Target motion began at -900 ms. Data are from subject FM.

light-emitting diode stimuli that were projected as 0.25° spots onto a translucent tangent screen located at a distance of 33.3 cm.

Individual trials began with the appearance of a target that either remained stationary ("fixation trial") or moved at a constant speed of $10^\circ/\text{s}$ to either the left or the right ("pursuit trial") after a delay of 500 ms. On fixation trials, after a randomized period of 1,000–1,450 ms, the first target was extinguished and a second target appeared 4° to either the left or the right of the first target (Fig. 1A). On pursuit trials, the first target appeared at an eccentric location on the horizontal meridian and moved toward the center of gaze for a randomized duration of 500–950 ms, after which it was extinguished and a second target appeared 4° to either the left or the right of this first target, moving at the same speed and in the same direction (Fig. 1B). We randomly interleaved fixation and pursuit trials, and the duration of the interval ("gap") between the disappearance of the first target and the appearance of the second target. For two subjects (FM and RK) we used gap durations of 0, 30, 50, 100, 150, and 200 ms; for the other subjects, we used gap durations of 0 and 200 ms. On pursuit trials with nonzero gap durations (e.g., Fig. 1B), the second target appeared 4° to either the left or the right of where the first target would have been had it not been extinguished. The position of the first target on fixation trials was randomly varied among a set of locations contrived to match those reached by the moving target on pursuit trials at the time the target was extinguished. Controlled movements of the target spot were achieved by interrupting the projector beam with a mirror galvanometer system under negative feedback control (General Scanning, CCX101). The luminances of the targets and the background were 22.7 and $0.08 \text{ cd}/\text{m}^2$, respectively.

The presentation of stimuli and the acquisition, display, and storage of data were controlled by a personal computer using a Real-time EXperimentation software package (REX) developed by Hays et al. (1982). Voltage signals encoding the horizontal component of eye position, and the horizontal mirror position provided by transducers in the galvanometer system, were low-pass filtered (6-pole Bessel, -3 dB at 180 Hz) and then digitized to a resolution of 16 bits, sampling at 1 kHz (analog-to-digital converter: National Instruments). All data were stored on disk (Wren Runner II SCSI disk) during the experiment and later transferred

to a Unix-based system for subsequent analysis using an interactive analysis program run on a Silicon Graphics workstation. Signals encoding horizontal eye velocity were obtained by applying a 29-point finite impulse response (FIR) filter (-3 dB at 54 Hz) to the signals encoding horizontal eye position. 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 and Miles 1996). The computer recorded the onset time of each saccade, and these values were stored in a file that was later accessed for the purposes of generating histograms and calculating mean values and other statistics.

RESULTS

In all four subjects, the presence of a 200-ms gap reduced the latencies of saccades during both fixation and pursuit. This point is illustrated by the bar graphs in Fig. 2, which show the mean saccade latencies obtained from each of the four subjects (rows) for both directions of saccades (columns). In each case, the latencies obtained with a 200-ms gap (cross-hatched bars) were significantly lower ($P < 0.05$, Kruskal-Wallis) than those obtained with no gap (gray bars). These decrements (mean changes in ms are indicated by the numbers in the cross-hatched bars) were observed regardless of whether the target was stationary ("fixation"), moving at $10^\circ/\text{s}$ to the left ("leftward pursuit"), or moving at $10^\circ/\text{s}$ to the right ("rightward pursuit").

Two additional points should be made about these results. First, for both the gap and no-gap conditions, saccade latencies were not consistently altered by pursuit: for 27 of the 32 pursuit cases illustrated in Fig. 2, there was no significant difference between the latency of saccades elicited during pursuit and those elicited during fixation ($P > 0.05$, Kruskal-Wallis, asterisks indicate the 5 exceptions). Second, in the gap condition, subjects were able to sustain pursuit in the

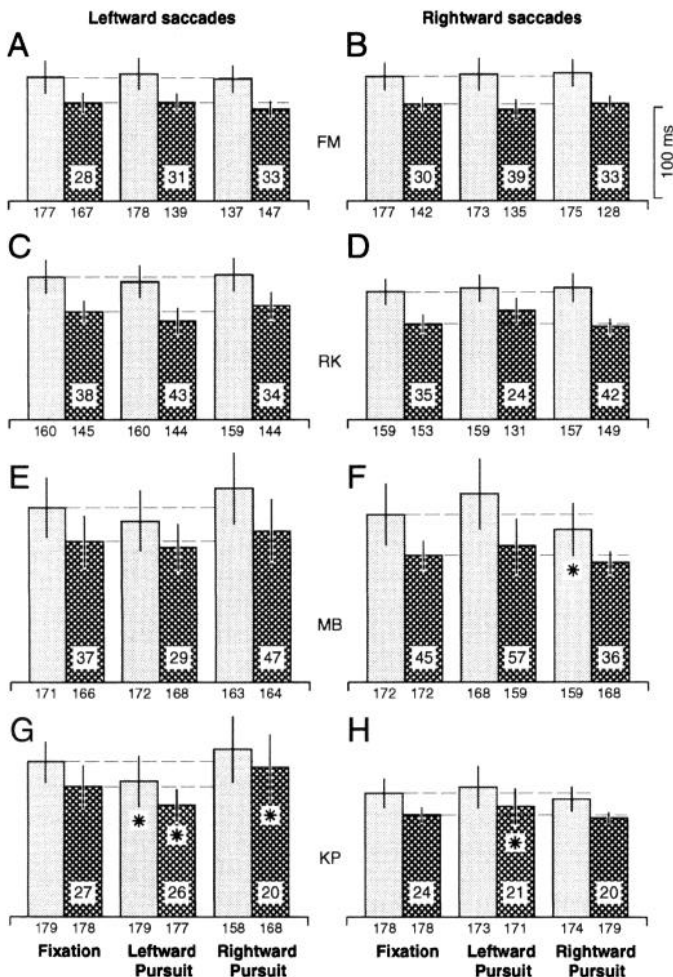


FIG. 2. Mean saccade latencies during fixation and pursuit: comparison of no-gap and 200-ms gap conditions. *A* and *B*: data from *subject FM*. *C* and *D*: data from *subject RK*. *E* and *F*: data from *subject MB*. *G* and *H*: data from *subject KP*. Each pair of bars compares the mean saccade latency obtained with a gap duration of 0 ms (gray bars) and 200 ms (cross-hatched bars) for one experimental condition: fixation, leftward pursuit, or rightward pursuit (see below). Numbers within the cross-hatched bars indicate the decrement in latency obtained with a 200-ms gap; numbers below each bar indicate the number of saccades used to compute the mean. Data from leftward and rightward saccades were analyzed separately and are shown *left* and *right*, respectively. Error bars: ± 1 SD.

absence of the visual target. Consistent with previous studies (Becker and Fuchs 1985; Mitrani and Dimitrov 1978), eye velocity decreased when a 200-ms gap was imposed, but retained average values of $8.0^\circ/s$ (*FM*), $8.0^\circ/s$ (*RK*), $7.6^\circ/s$ (*MB*), and $7.2^\circ/s$ (*KP*) at the time of saccade onset. In the no-gap condition, the corresponding average values were 9.5 , 8.6 , 8.2 , and $7.9^\circ/s$.

To compare the effects obtained during pursuit and fixation in more detail, we used additional gaps with intermediate durations in experiments with two of the subjects. The data from one of these subjects are shown in Fig. 3; virtually identical data were obtained from the other subject. Each histogram in Fig. 3 shows the number of saccades with latencies ranging from 50 to 200 ms. The histograms are organized into three groups, each showing six rows of data obtained during either fixation (Fig. 3, *A* and *B*), leftward pursuit (Fig. 3, *C* and *D*), or rightward pursuit (Fig. 3, *E* and *F*). The individual histograms

within each group display the distribution obtained with a single gap duration (0, 30, 50, 100, 150, or 200 ms). To facilitate comparisons, the mean latency obtained with a 0-ms gap duration is shown by the vertical dashed lines.

The distributions shown in Fig. 3 illustrate that saccade latency varied systematically as a function of gap duration. During both fixation and pursuit, significant decreases in saccade latency were observed even with the shorter gaps tested (30 and 50 ms), as indicated by the presence of square symbols (cross-hatched), each signifying that a distribution is significantly different from the distribution obtained with a 0-ms gap duration ($P < 0.05$, Kruskal-Wallis). Progressively longer gaps generally produced additional decrements in latency, but these were not always significant; this aspect of the data is indicated by the inverted triangle symbols, each signifying a distribution that is significantly lower than the one immediately above ($P < 0.05$, Kruskal-Wallis).

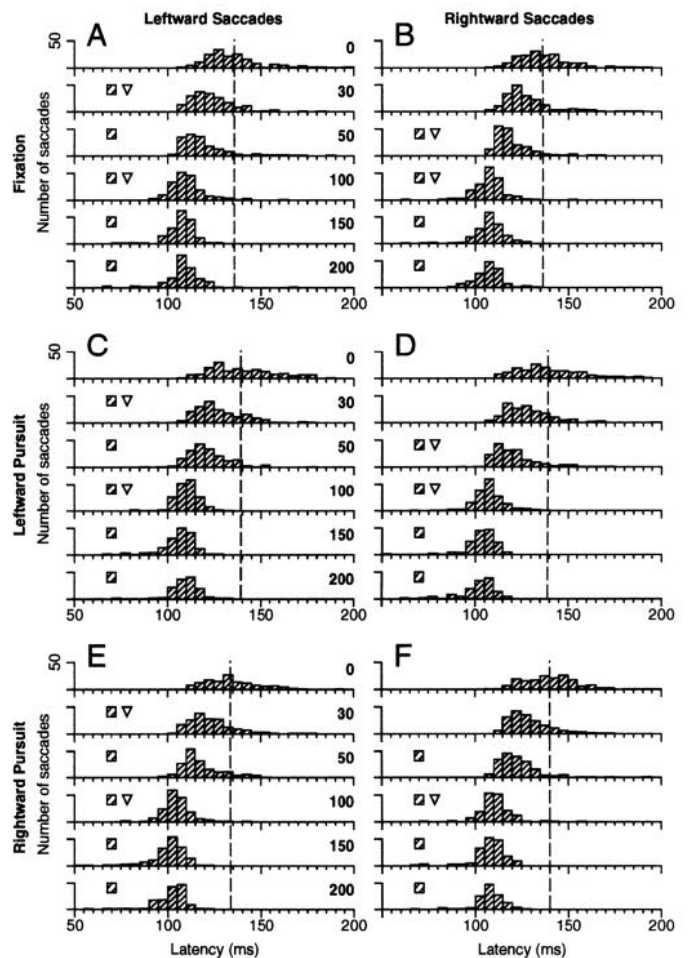


FIG. 3. Distribution of saccade latencies during fixation and pursuit: dependence on gap duration. Three groupings of histograms show data obtained from fixation (*A* and *B*), leftward pursuit (*C* and *D*), and rightward pursuit (*E* and *F*) trials. Individual histograms show data obtained for a single gap duration, as indicated by the numbers at the right edge in *A*, *C*, and *E*, either for leftward (*A*, *C*, and *E*) or for rightward saccades (*B*, *D*, and *F*). Dashed vertical lines indicate the mean pursuit latencies obtained for a 0-ms gap duration. Cross-hatched square symbols indicate that the distribution differed significantly ($P < 0.05$, Kruskal-Wallis) from that for the 0-ms gap condition. Inverted triangle symbols indicate that the distribution was significantly lower than the distribution in the histogram immediately above. Data are from *subject FM*.

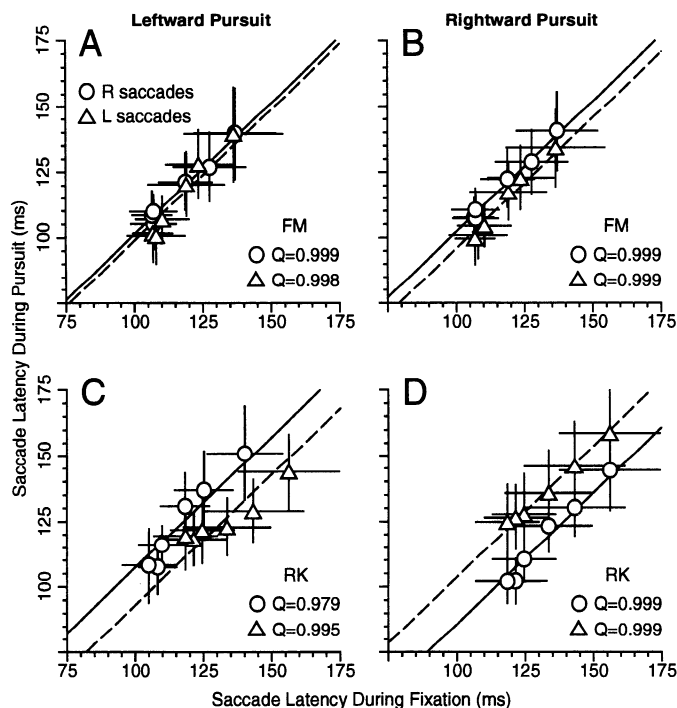


FIG. 4. Dependence of saccade latency on gap duration: comparison of saccades during fixation and pursuit. *A* and *B*: data from *subject FM*. *C* and *D*: data from *subject RK*. In each graph, mean saccade latency during either leftward (*A* and *C*) or rightward (*B* and *D*) pursuit is plotted as a function of mean saccade latency during fixation. Individual symbols represent the mean latency of leftward (triangles) or rightward (circles) saccades for a given gap duration. Dashed lines indicate slopes of unity, with the intercept adjusted to minimize mean squared error. Numbers in each graph report the Q value from a χ^2 test of the linear fit. Error bars indicate ± 1 SD.

The similarity of the decreases in saccade latency across the conditions described above suggested that the latencies of saccades during fixation and pursuit may have the same dependence on gap duration. To test this idea, we plotted the mean latency of saccades elicited during pursuit trials as a function of the mean latency of saccades elicited during fixation trials. In Fig. 4, each of the two rows shows data from one subject, and the *left* and *right* columns compare the data obtained during leftward and rightward pursuit, respectively, with the data obtained during fixation. Each data point represents a single gap duration for either leftward (triangles) or rightward (circles) saccades. The dashed oblique lines represent lines of unity slope, and the y -intercept has been adjusted to minimize the mean squared error between the data points and the straight line. The data points in each plot lie near the line of unity slope, and a χ^2 test confirms that a linear model provides a good fit to the data in each case, as indicated by the Q value reported in each plot. These results demonstrate that not only do saccades elicited during pursuit display a gap effect, but they exhibit the same dependence on gap duration as saccades elicited during fixation.

DISCUSSION

Previous studies have shown that the latency of saccades to stationary targets can be decreased by the presence of a temporal gap between the extinction of a foveated target and

the appearance of an eccentric target (Becker 1972; Fischer and Boch 1983; Fischer et al. 1984; Saslow 1967). Our current results demonstrate that this gap effect is not limited to saccades made to stationary targets, but can also be observed for saccades made between moving targets during maintained pursuit. For the four subjects in our study, introducing a 200-ms gap reduced the latency of saccades between stationary targets by an average of 33.0 ms (range 24–45 ms) and reduced the latency of saccades between moving targets by an average of 33.4 ms (range 20–57 ms). In addition, the amplitude of the decrease in saccadic latency in both conditions depended on the exact duration of the gap interval. By directly comparing the saccade latencies obtained with different gap durations during fixation and pursuit in two subjects, we were able to demonstrate that saccades in both cases exhibited the same dependence on gap duration.

Our data therefore indicate that the same mechanism may underlie the initiation of saccades during both fixation and maintained pursuit. This suggestion agrees with that of a recent study (Boman et al. 1996), which found that the latency of saccades made from moving targets to stationary ones is shortened by the presence of temporal gaps. Although superficially similar, there are major differences between the two studies. First, whereas the saccades in our present study were directed toward a moving target during maintained pursuit, the saccades studied by Boman et al. (1996) were directed toward a stationary target as pursuit was ending; it is therefore ambiguous whether those saccades reflect the properties of pursuit or fixation. Second, whereas the saccades in our study had closely similar directions during fixation and pursuit, those in the study of Boman et al. (1996) could differ: during fixation, saccades were always vertical, whereas during pursuit they were often oblique. These methodological differences may have contributed to an important difference in our results: we found almost identical latencies for saccades made during fixation and pursuit, whereas Boman et al. (1996) reported that saccade latencies during pursuit were consistently longer.

Our current results do not discriminate between the several proposed mechanisms underlying the gap effect for saccades, an issue that remains controversial (for review, see Fischer and Weber 1993). However, regardless of the exact mechanism, our data are consistent with the notion that the trigger for saccadic eye movements does not recognize the distinction between pursuit and fixation. Such empirical grouping of fixation and pursuit is consistent with the functional role of the two behaviors, because both serve to maintain foveation of a visual object. Conversely, the interruption of fixation or pursuit by a saccadic eye movement results in the reallocation of visual resources toward a new visual object, perhaps prompted by the waning relative attraction of the currently foveated image (e.g., Posner 1980). Our results suggest that these transitions are regulated by a single mechanism, regardless of whether the potential targets are stationary or moving.

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