
Slow eye movements to eccentric targets

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It is generally believed that a target offset from the direction of gaze can only be fixated with a saccadic jump in eye position. By preventing saccadic eye movements from fixating a target, we have observed slow eye movements to both stationary and moving eccentric targets. This supports the view that target offset plays a role in guiding slow eye movements.

Key words: slow eye movements, pursuit eye movements, target offset, retinal stabilization, open loop

To observe a smoothly moving object a person makes a smooth pursuit eye movement, i.e., a slow eye movement with approximately the same angular velocity as the object. Motion of a target (real or perceived) is usually thought to be the visual stimulus for smooth pursuit and for slow eye movements in general. In recent years, however, some evidence has suggested that in addition to target motion, target position (offset of the target from the direction of gaze) can also serve as a stimulus for slow eye movements. In particular, if a subject attempts to look at a target that is stabilized so it remains at a fixed eccentricity from the fovea (independent of the motion of the eye), vigorous slow eye movements directed toward the target often occur.¹⁻³ (The slow eye movements are interspersed with saccadic jumps in eye position, which apparently represent attempts by the saccadic system, as well as the slow movement system, to fixate the target.) There

are limitations on interpreting these findings, however, since during slow eye movements toward a target fixed at an eccentric retinal position the target moves smoothly along with the eye and thus moves (in head coordinates) with respect to the subject. Once the slow eye movement is underway it may be driven by both target position and the subject's perception of target motion.⁴ Therefore it is difficult to determine the extent to which target position is responsible for the movement.

To avoid this difficulty, perhaps the simplest experiment would be to ask a subject to make a slow eye movement to a stationary eccentric target (stationary in head coordinates). However, when most subjects elect to look at a stationary target substantially offset from the direction of gaze, they begin by making a saccadic eye movement toward the target. The saccade generally achieves fixation and the experiment is over. (If the target is stabilized, the saccadic attempt fails and the subjects subsequently make slow eye movements as well as saccades.) These findings suggest either that a substantially offset target in the real world cannot elicit slow eye movements, or that some built-in system strategy mandates a saccade for the first fixation attempt and slow eye movements can occur if the initial saccadic attempt fails. To see if the latter could be true, we have developed a target that is "open loop"

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(retinally stabilized) for saccadic eye movements but that is "closed loop" and stationary (fixed in head coordinates) for slow eye movements. By denying target acquisition to the saccadic system in this way, we have observed slow eye movements to stationary eccentric stimuli.

We have also asked subjects to visually track a constant velocity ("ramp") target. With this stimulus, Robinson⁵ found that subjects often make a saccade that falls short of the target, followed by a "catch-up" smooth pursuit eye movement faster than the target. Since retinal target velocity is opposite to eye velocity during catch-up movements, the occurrence of such movements suggests that slow eye movements can occur in response to target position under normal circumstances. To explore this possibility we used ramp target motion, but we stabilized the target during saccades with the same technique mentioned above for stationary targets. This increased the amount by which saccades fell short of the target and resulted in more vigorous and prolonged "catch-up" movements.

Methods and procedure

A 1.5 deg diameter round target was projected on a rear-projection screen 114 cm from the subject. Horizontal target position was controlled by a mirror on a penmotor galvanometer. Seated in a dark room, subjects viewed the screen monocularly with the left eye. Head position was held constant with the help of a dental impression bite-bar. A signal of horizontal position of the left eye was obtained with an infrared scleral reflection device (Narco Bio Systems, Inc.) and was differentiated electronically to provide an eye velocity signal. Target position, eye position, and eye velocity were recorded on a Grass polygraph. System bandwidth was about 0 to 75 Hz. Records shown are tracings of polygraph records.

We used a computer (Digital Equipment Corp.) to control the stimulus. The computer monitored eye velocity to determine the presence or absence of a saccade; for slow eye movements, eye velocity is nearly always less than about 25 deg/sec, whereas for saccades greater than 0.3 deg, eye velocity is greater than 30 deg/sec.^{6, 7} During a trial the stimulus remained stationary (or moved with constant velocity for some trials) in head coordinates as long as the subject used only slow

eye movements to achieve fixation. When a saccade started, the computer calculated the offset of the target from the fovea immediately prior to the saccade and jumped the target in the away-from-fovea direction by an amount equal to this offset. At the end of the saccade the actual saccade length was calculated and compared with the "assumed length," and the target position was corrected if necessary. This correction tended to be small, and our results did not differ significantly if the correction was omitted. The delay from saccade onset to target jump was less than 10 msec.

The eye position signal was calibrated before and after each trial. The subject fixated five equally spaced target positions along the horizontal meridian (straight ahead, ± 7.5 deg, and ± 15 deg) and signaled each fixation to the computer. During the trial the eye position signal was converted to angle with a four-segment piecewise linear fit through the five data points taken during the initial calibration. Trials were accepted if (1) mean-square deviation from linearity was less than 2% for both initial and final calibrations, (2) the slopes of the best linear fits to initial and final calibration data were within 5% of each other, and (3) the difference between the initial and final calibration values for the straight-ahead fixation point was equivalent to a difference of less than 0.3 deg. At least 20 trials were run in an experimental session, and size and direction of target steps were varied randomly. Subjects for these experiments were men and women between 20 and 40 years old.

Step stimuli. At the start of these trials the target assumed its central position and the subject fixated it, and after a short pause the target stepped horizontally away from the fovea. The subject's task was to attempt to look at the eccentric target, but whenever this attempt involved a saccade the target jumped by an amount equal to the saccade. The trial was initiated by the experimenter. Time of initiation was random within a 2 sec window, and many experiments were performed with direction of target motion randomized between left and right. In some of the experiments we varied the size of the target step (0.5, 1, 2, 4, or 6 deg). Large steps (>4 deg) usually made it necessary to use starting positions that were not at the center of the screen, in which case direction of motion was known before the start of the trial. This reduced variability but did not alter the main characteristics of the eye movements. These experiments were performed on 10 subjects, of whom seven were naive.

Ramp stimuli. These trials were run in the same

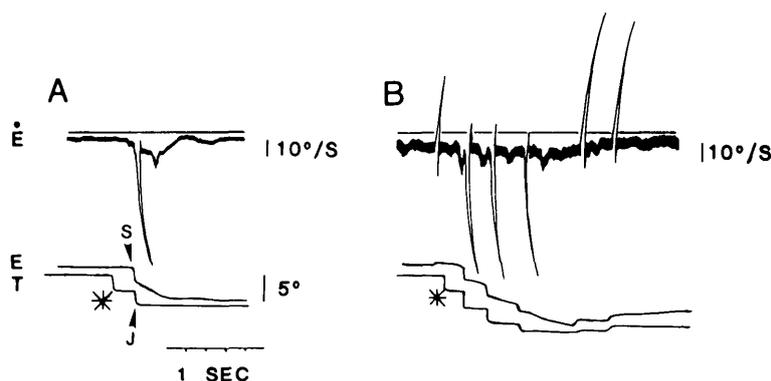


Fig. 1. A, Eye movement response to 3 deg target step off the subject's fovea, with target position on retina stabilized against saccadic fixation attempts. *T*, Target position; *E*, eye position; \dot{E} , eye velocity. Calibration marks at right, 5 deg for *T* and *E*, 10 deg/sec for \dot{E} . Asterisk marks initial target step. Subject responded with saccade (*S*), which was compensated for by stabilizing target jump (*J*). Smooth movement to target then commenced. Subject (J. P.) was experienced. B, First-time response of a naive subject tested under the same conditions as in A.

way as step stimulus trials, except that the stimulus was the sudden onset of constant velocity target motion. On some trials the target jumped to counteract saccadic attempts at fixation. Three types of trials were used, randomly mixed. (1) The stimulus was normal closed-loop ramp target motion and did not jump in response to saccadic eye movements (jump-saccade ratio = 0). (2) The stimulus was ramp target motion but the target jumped in response to a saccade by an amount equal to the saccade (jump-saccade ratio = 1). (3) The stimulus motion and jumps were as in (2), except that on the first saccade the compensatory jump was twice the size of the saccade (jump-saccade ratio = 2). (For subsequent saccades the target jump equaled saccade size.) The effect of the last condition was to exaggerate the target offset from the fovea after the first saccade (see Discussion). Trials were conducted with the subject initially fixating the target at one or the other side of the screen. The target started to move in ramp motion across the screen and disappeared at the far end of the screen. Subjects were urged to fixate the target before it disappeared. Ramp speed was 10 deg/sec. Target motion and eye movements were recorded on magnetic tape for subsequent computer analysis. (System bandwidth about 0 to 500 Hz.) This experiment was performed on four subjects.

Results

Responses to target steps. Fig. 1, A, shows a typical result from a trial in which the target

stepped 3 deg horizontally away from the fovea at the start of the trial and then remained stationary (except for a stabilizing jump when a saccade occurred). The bottom record shows stimulus position, the middle record shows eye position, and the top record shows eye velocity. The initial target step is marked with an asterisk. The subject made a saccade and this was compensated for by a target jump. After the saccade the subject achieved fixation in one continuous smooth movement, during which the target remained stationary.

We observed considerable intersubject variability in the responses to the "saccade-stabilized" stimulus of Fig. 1, A, with some subjects making more saccades, particularly for larger values of target offset. The degree of predictability of target behavior also affected the responses. In general, greater predictability tended to produce responses with shorter latency and higher smooth eye movement velocity. However, familiarity with target behavior was not a prerequisite for the occurrence of position-directed smooth movements. Fig. 1, B, shows a "first time ever" response by a naive subject to a stimulus like that of Fig. 1, A; smooth eye movements directed toward the stationary target are apparent. All 10 of our subjects showed some posi-

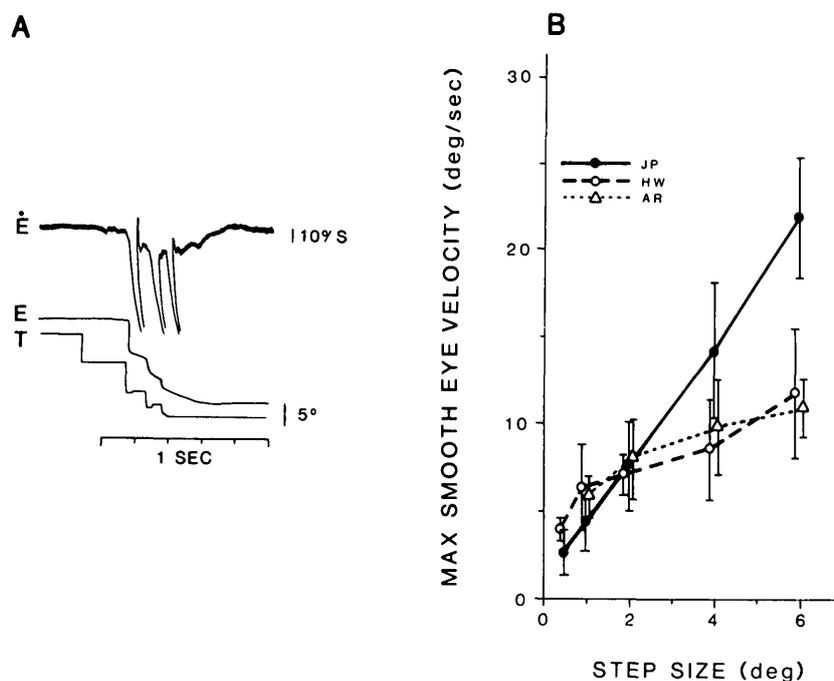


Fig. 2. A, Response to a 6 deg target step. Compare with Fig. 1, A. B, Peak smooth eye movement velocity as function of initial step size for subjects J. P. (\bullet), H. W. (\circ), and A. R. (Δ). Size and direction of steps were selected randomly. Error bars are standard deviations.

tion-directed slow eye movements; however, in the responses of two of the naive subjects these were often small or absent.

As we increased the size of the initial target step we observed that faster slow eye movements occurred. Fig. 2, A, shows the response to a 6 deg step, and the response may be compared with that of Fig. 1, A, where a smaller step elicited a slower smooth movement. The velocity records of Figs. 1, A, and 2, A, show increasing smooth eye movement velocity during the early part of the response and decreasing velocity during the late part. We have observed that this is a general feature of responses, whatever the initial step size. For five subjects we examined the effect of step size on the maximum smooth eye movement velocity in the responses, we varied step size from 0.5 to 6 deg in both directions and measured maximum velocity. Results for the three experienced subjects are shown in Fig. 2, B. The results lump together responses to leftward and rightward steps of each size and are the average of at

least six trials for each step size for one subject (J. P.) and at least four trials for the other subjects.

The responses of the five subjects tested systematically with different target step sizes all showed an increase in smooth eye movement velocity as step size increased. The best-fit slopes for the subjects shown in Fig. 2, B, are 3.3 (J. P.), 1.2 (H. W.), and 1.0 (A. R.), where units of slope are (deg/sec of maximum response velocity) per (deg of initial target offset). The two naive subjects had slopes of 0.5 and 1.0. The positive correlation between maximum velocity and step size was significant for all five subjects at confidence levels of greater than 95%.

Responses to target ramps. Responses to constant velocity target motion under normal closed-loop conditions and saccade-stabilized conditions are shown in Fig. 3. For the normal closed-loop ramp (Fig. 3, A) the subject usually made a pursuit movement followed by a saccade and then a "catch-up" pursuit (faster than the target) that achieved fixa-

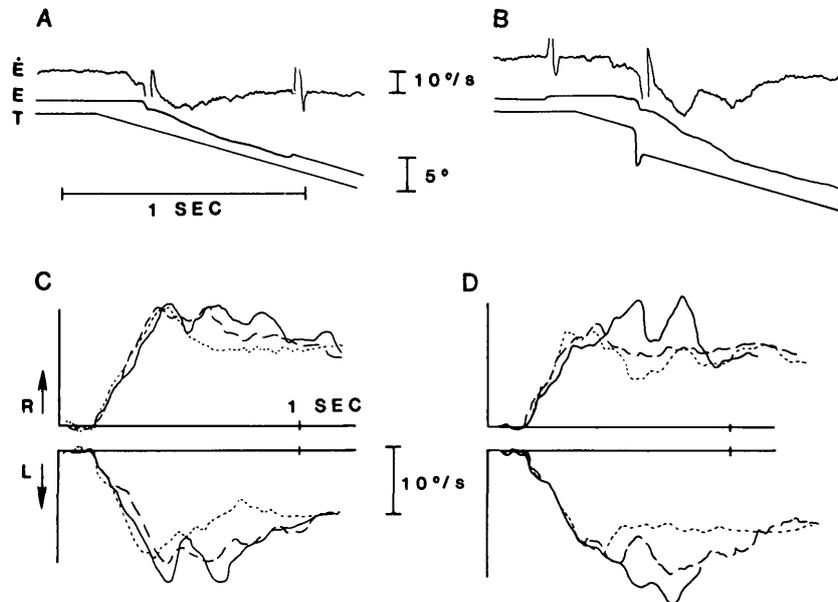


Fig. 3. Responses to ramp target motion. Target motion at 10 deg/sec began suddenly at the start of the trial. When subject made an initial saccade the target was jumped by an amount equal to the saccade length (jump-saccade ratio = 1) for saccade-stabilization as used with target steps. On other trials the first target jump was twice the saccade length and subsequent jumps were equal to saccade length (jump-saccade ratio = 2), or the target was not jumped at all; that is, it was a closed-loop ramp (jump-saccade ratio = 0). **A**, Response to a stimulus with ratio = 0. **B**, Response to a stimulus with ratio = 2. **C**, Average velocity records in responses to ramp stimuli. Computer-processed smooth eye velocity is plotted as a function of time after onset of ramp motion. Rightward velocities are shown in upper half of figure, leftward in lower half. *Dotted curves*, Ratio = 0; *dashed curves*, ratio = 1; *solid curves*, ratio = 2. **D**, Same as **C**, with responses from a second subject. Note that catch-up behavior is represented by overshoot of velocity curves above final value.

tion. Experiments with saccade-stabilization (jump-saccade ratio = 1 or 2, Fig. 3, *B*) elicited similar responses, except that the catch-up pursuits were faster and more prolonged. Oscillations in slow eye movement velocity were often observed, as seen in Fig. 3, *B*. Although only one saccade occurred in the response of Fig. 3, *B*, often two or more saccades occurred for jump-saccade ratios of 1 or 2. These later saccades often occurred near the positions of the maxima in the oscillatory velocity record of Fig. 3, *B*.

To see more clearly the differences between the slow eye movements to the closed-loop ramps and to saccade-stabilized ramps, we determined average slow eye movement velocities for the different conditions (Fig. 3,

C and *D*). Each of the average slow eye movement velocities was obtained for three to four responses recorded on magnetic tape. Saccadic spikes on the velocity records were removed and linear segments were inserted to close the gaps. The average was smoothed once (with a running 4-bin average, 5 msec binwidth), and the result was run out on a stripchart at the speed at which it was recorded, but with a high-frequency cutoff added at 15 Hz to reduce the contribution from 60 Hz noise.

It can be seen from Fig. 3, *C* and *D*, that as the jump-saccade ratio was increased from 0 (normal ramp) to 1 to 2, the slow eye movement velocity increased. The difference was only apparent after several hundred mil-

liseconds, corresponding to times after a first saccade. (Prior to the first saccade the target motion was a simple ramp regardless of the value of the jump-saccade ratio.) In examining Fig. 3, *C* and *D*, it should be kept in mind that the catch-up portion of the record is represented by the overshoot of the velocity above its final steady value.

Discussion

Responses to target steps. It is apparent from Figs. 1 and 2 that under the conditions of our experiments subjects can make slow eye movements that are directed toward a stationary target. Furthermore, these movements become more rapid when the target is farther from the fovea. These data support the view that target position relative to the fovea is a stimulus for slow eye movements.

Why does the simple experiment fail? Normal subjects always make a saccade when they choose to look at a stationary, substantially eccentric target. If target position can guide slow eye movements, then, since it is possible to choose to suppress saccades while maintaining fixation of a stationary target⁸ or following a ramp target,⁹ it might seem that subjects could choose to suppress saccades while making a slow movement to an eccentric target. We suggest that a built-in strategy initiates a saccadic response when a subject chooses to look at an eccentric target. Because saccades are very fast and because they do successfully fixate real-world targets, such a strategy would be teleologically sound.*

Responses to target ramps. We observed,

*It must be noted that one of us (J. P.) is capable of executing voluntary slow eye movements in the absence of a target. However, this requires a deliberate, conscious effort and was avoided for the purposes of this paper. Additionally, this subject has not been successful at using voluntary slow eye movements to achieve smooth fixation of eccentric targets, since the voluntary process is disrupted as the target is approached. The steep slope shown by J. P. in Fig. 2, *B*, may be of relevance to his voluntary capabilities. The other author (H. W.) cannot perform such eye movements voluntarily.

as did Robinson,⁵ catch-up pursuits in response to closed-loop ramp target motion. With such targets, offset of the eye from the target after a saccade was usually quite small—about 1 deg or less. The effect of our “saccade-stabilization” technique (with jump-saccade ratios of 1 or 2) was to create larger postsaccadic position errors. Like the smaller errors, these larger errors were eliminated by catch-up movements that were now more vigorous and more prolonged (Fig. 3).

Given the similarity between the catch-up pursuit movements under normal closed-loop circumstances (ratio = 0) and the catch-up slow eye movements in our ratio = 1 and 2 conditions, it seems reasonable to suggest that the two movements are produced by a common mechanism. Thus the greater velocity in the ratio = 1 and 2 conditions could result from larger postsaccadic offsets. This suggests that catch-up eye movements, including normal catch-up pursuits, could be accounted for by the relationship between slow eye velocity and target offset (Fig. 2).

Slow eye movements and saccades during pursuit. An interesting aspect of our results is that increases in slow eye movement velocity often appear quite suddenly at the end of a saccade (see Fig. 2, *A*). This might seem to suggest that the slow eye movements we have observed are “glissades,” a type of eye movement usually thought to result from mismatches between the pulse and the step of saccadic motor innervation.^{10–12} However, the time course of a glissade is a decreasing exponential as the globe shifts passively from the position to which the pulse took it to the position set by the step. In our experiments we have often observed increases in slow velocity after saccades during the early part of the response and decreases during the later part, as noted above and as seen in Figs. 1, *A*, and 2, *A*. Furthermore, oscillations in eye velocity are common (Fig. 3, *B*). Unless the “step” level of saccadic innervation is continuously adjustable in the absence of a pulse, which contradicts most views of the system, such responses cannot be explained as pulse-step mismatches. (This is not to say

that glissades are absent from our records; however, they are usually quite distinct from the slow eye movements under discussion.)*

Sudden increases in slow eye movement velocity after saccades occur frequently during normal tracking and have been interpreted in various ways. In particular, Westheimer¹³ suggested that discrete changes in the velocity of slow eye movements, often accompanied by saccades, are adjustments to tracking errors. Robinson's⁵ view was that changes in slow eye movement velocity, linked to saccades, represent a nonlinear interaction between the pursuit and saccadic systems. We suggest another possibility, perhaps related to these views, which is that the decision to "look at" a target activates a foveal position mechanism that employs *both* slow eye movements and saccades to achieve its goal. Support for this idea comes from experiments in which subjects tracked ramp target motion while avoiding "looking at" the target but attempting to match its velocity.⁹ These subjects did not make the usual saccades toward the target, but it was also the case that their slow eye movements were less vigorous than usual. (Their slow movements fell behind the target rather than catching up to it or even matching its velocity.) This si-

*We note that at least one other explanation besides the one that we have proposed could account for some of the slow eye movements during the "saccade-stabilized" trials. Because the target is stabilized during saccades, it jumps sequentially from one location in space to the next, according to the number of saccades that occur. This sequence of target jumps is perceived, to some extent, as target motion. It is possible that this perception of target motion activates the pursuit system and thus gives rise to some slow eye movements. However, a substantial number of responses occur with only a single saccade (as in Fig. 1, A), so that only one saccade-stabilized target jump occurs. This is too brief a "sequence" to generate much perception of motion, yet if anything the smooth movements on such trials are more vigorous than on trials with the same stimulus, where the responses show more saccades. A related point is that catch-up pursuit eye movements are seen with ordinary closed-loop ramp target motion, in which case there is *no* target jump and thus no jump-related percept of motion. In fact, we have occasionally observed catch-up pursuit responses with no saccades.

multaneous change in both saccades and slow movements could reflect the inactivation of a shared foveal position mechanism. We have proposed in previous reports that slow eye movements are governed by a position mechanism acting together with the traditionally recognized velocity mechanism.^{2, 3} It seems possible, then, that when saccades are "suppressed" the associated weakness of slow eye movements could represent the performance of the velocity mechanism acting by itself.

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