Effect of Stimulus Position and Velocity Upon the Maintenance of Smooth Pursuit Eye Velocity

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The relative contributions of retinal slip velocity and position errors to the generation of smooth pursuit eye movements were examined in three rhesus monkeys. Recognizing the unlikelihood of producing a pure retinal slip velocity or position error signal, these two stimulus parameters were combined under open-loop conditions. Both slip velocity and position error were used by the monkey to maintain an established eye velocity. Both parameters had the greatest effects upon eye velocity when they were in the same direction, enabling the monkey to maintain an established pursuit velocity. When slip velocity and position error were in the direction opposite to the initial pursuit, eye velocity reversed direction and moved very quickly towards zero. When the two parameters were in opposite directions, their effect upon eye velocity was minimized.

Oculomotor Smooth pursuit Eye movements Macaca mulatta

INTRODUCTION
Smooth pursuit eye movements minimize visual target movement on the retina by matching eye movements to target motion in space. Both target motion on the retina (retinal slip) and position offset of the target from the fovea might drive smooth pursuit movements, and there is evidence that the smooth pursuit system responds to each of these stimulus parameters (Robinson, 1965; Pola & Wyatt, 1980; Morris & Lisberger, 1987). In the laboratory, one can easily produce and monitor changes in retinal slip, demonstrating the pursuit system's response to motion of targets on the retina. However, it has been more difficult to study the effect of position offset on pursuit. One common technique is to stabilize the location of a visual target on the retina by continually adding a measure of eye position to target position (Pola & Wyatt, 1980; Morris & Lisberger, 1987; Segraves, Goldberg, Deng, Bruce, Ungerleider & Mishkin, 1987). In this way, when the eye moves, the target moves with it, and its position will, ideally, remain fixed on the retina. In this experimental situation, the subject frequently makes saccades in an attempt to foveate the target. Unfortunately, the response of the target movement system is never perfect. As a result, target motion during saccades may lag retinal movement, resulting in brief movements of the target on the retina. This introduction of retinal slip velocities confounds the interpretation of how the pursuit system responds to positional offsets. The following experiments were designed to examine the contributions of retinal slip and position offset to the generation of pursuit movements, not by attempting to produce stimuli with purely motion or positional components, but by combining the two stimulus parameters in both agonistic and antagonistic ways and examining the pursuit system's response to targets whose direction of motion implied by retinal slip was sometimes the same and sometimes opposite to the direction implied by position offset from the fovea. A preliminary report of these experiments has been published elsewhere (Segraves & Goldberg, 1988).

MATERIALS AND METHODS
Pre-operative training
Three adult rhesus monkeys (Macaca mulatta) were trained preoperatively to do a simple visual fixation task using established techniques (Wurtz, 1969). The monkey was seated in a primate chair, and began a trial by pressing a metal bar in front of him. This resulted in the onset of a target light on a screen in front of the monkey. The monkey was required to detect the dimming of the light, and signal this detection by releasing the metal bar to receive a liquid reward.
Surgery

Surgery was performed under aseptic conditions. The monkey was anesthetized with ketamine hydrochloride (10 mg/kg i.m.) followed by sodium pentobarbital to effect and supplemented through an i.v. catheter as needed. During the surgical procedure, a subconjunctival wire coil for the measurement of eye position with the magnetic search coil technique was implanted in one eye (Judge, Richmond & Chu, 1980; Robinson, 1963). Two to three trephine holes were made through the skull at sites where recording cylinders would be located. Recording cylinders were used in neurophysiological experiments performed after the behavioral experiments described in this report. Small stainless steel bolts to strengthen the bond of dental acrylic to the skull were fastened in slots cut through the skull and extending away from the edges of the trephine holes. The recording cylinders, a stainless steel receptacle to fix the monkey’s head during recording sessions, and the connector for the eye coil were fixed in place and bonded to the skull with dental acrylic. At the completion of surgery, the monkey was given the analgesic pentazocine (Talwin, 1.5–3 mg/kg i.m.) to relieve pain. Gentamicin sulfate (5 mg/kg i.m.) was given immediately after surgery and in daily dosages for 1 week post-operatively as a prophylactic measure against infection. Post-operative training was begun between 1½ and 2 weeks after surgery.

Post-operative training

After surgery, each monkey received additional training in several visual and eye movement tasks. The computer hardware and software used to monitor and control the monkey’s behaviour has been described in detail elsewhere (Goldberg, 1983). The monkey was seated in a primate chair with its head fixed, and centered within horizontal and vertical magnetic field coils. Visual stimuli presented to the monkey included stationary and moveable light stimuli originating from red light-emitting diodes rear-projected onto a tangent screen 86 cm in front of the monkey. Each projected stimulus was about 0.25 deg in diameter with a brightness 1.4 log units above a background of 0.18 cd/m². The moveable stimulus was positioned by a pair of servo-controlled mirror galvanometers (General Scanner Inc.) driven by analog signals synthesized by 12 bit digital to analog converters under the control of a PDP 11/73 computer (Digital Equipment Co.). Stimulus position was updated at a rate of 1 kHz. Since, after surgery, it was possible to accurately measure eye position, the monkey was no longer required to detect the dimming of the stimulus. Instead, the monkey had to meet predetermined criteria for eye position relative to target position, and for saccade amplitude and direction in order to receive a liquid reward. Eye position was measured by the magnetic search coil system (C.N.C. Engineering) using a phase-sensitive detector. Eye position measurement was accurate to 15 min arc within a range of 20 deg from the center of gaze, and was not corrected for cosine error. Mirror position was measured from the position feedback signal of the mirror galvanometer. Both horizontal and vertical eye and mirror position were sampled at a rate of 1 kHz.

Behavioral trials used for this study began with the monkey pursuing a target moving horizontally at 10 20 deg/sec. At an unpredictable time the target jumped to a position calculated by adding a step ranging from −1 to +3 deg to eye position. Thereafter, each millisecond, target position was calculated by adding an amount to eye position sufficient to provide the target with a retinal slip velocity of −2 to +2 deg/sec. The net effect being that the target was stepped to a location near the fovea and then began to move slowly towards or away from it. Because the monkeys were rewarded for maintaining eye position within a window surrounding the target, a criteria that was always met in open-loop trials, open-loop trials were intermixed as needed with closed-loop trials to maintain the monkeys’ performance. The initial starting point of the target was adjusted, so that stabilization would occur at about the time when the eyes were crossing the primary position. Figure 1 illustrates the correspondence between horizontal eye and target position when eye position feedback is used to stabilized the target on the retina. For purpose of illustration, a 2 deg rightward position offset was subtracted from the target trace so that it could be superimposed on the eye trace. No intentional retinal slip velocity was introduced during this trial. Note that during the saccade in the middle of the figure, target position lags behind eye position. This lag in the ability of the mirror galvanometer to update target position produces an initial leftward deceleration of the target as the eye moves toward the target during the saccade followed by rightward acceleration as the target moves further ahead of the eye near the end of the saccade.

FIGURE 1. Target lag during saccades to stabilized images. To facilitate the comparison, target position has been superimposed upon eye position by shifting the target’s location 2 deg to the left. Although the eye never catches up to the target, the lag in target position results in an initial backward movement of the target toward the fovea at the beginning of the saccade followed by a forward movement of the target away from the fovea near the end of the saccade. The lag in target position behind eye position during a rightward saccade results in a brief leftward movement of the target on the retina. This and all subsequent figures use the convention that movement to the right is plotted upward and positive, and movement to the left is plotted downward and negative.
FIGURE 2. Measuring eye velocity 200 msec after the start of target stabilization. (A) Using acceleration criteria, data analysis software placed vertical cursors at the beginning and end of the first saccadic velocity profile occurring after the target was stabilized. The position of these cursors could also be adjusted manually by the investigator. The saccadic velocity was then deleted by drawing a straight line between the two cursors. (B) First vertical cursor on the velocity trace marks the beginning of target stabilization. Second and third vertical cursors mark points 200 and 225 msec after target stabilization. Pursuit velocity was measured at the 200 msec point, and mean pursuit velocity was computed for the interval between 200 and 225 msec. For Figs 2 and 3, the y-axis calibration for eye velocity (deg/sec) is identical to the calibration for eye and target position (deg).

DATA ANALYSIS

Eye velocities were calculated using a 51 component finite impulse response differentiating digital filter with a 3 dB roll-off at 9 Hz. The filter did not induce a phase lag but broadened velocity peaks.

To assess the effect of different combinations of position offsets and retinal slip velocities upon pursuit maintenance, pursuit velocities were sampled at 200 msec after target stabilization. Since saccades often occurred during this interval, saccadic velocities were removed during the time period following target stabilization (Fig. 2). Saccades were located by computer using an acceleration criterion, and confirmed by one of the investigators. Eye velocity attributable to the saccade was then removed from the record by linear extrapolation between points on the velocity trace before and after the saccade.

RESULTS

Four examples of single trials with different combinations of position error and retinal slip velocity are illustrated in Fig. 3. In each of these trials, the monkey began by tracking a target moving to the right at 10 deg/sec. At time zero, the target was stabilized with position error of ±2 deg, and a retinal slip velocity of ±2 deg/sec was introduced. The initial rightward tracking velocity was affected least when the position error and retinal slip velocity were also directed to the right [Fig. 3(A)]. The greatest decrement in velocity occurred when both position error and retinal slip velocity were in the direction opposite to the initial tracking velocity [Fig. 3(D)]. With position error to the right and a leftward slip velocity [Fig. 3(B)], the initial tracking velocity was maintained for about 300 msec. At this point, the retinal slip velocity appeared to become the more salient stimulus, causing eye velocity to reverse, and begin moving to the left. Note that for the first 1000 msec, the monkey was pursuing a target that was drifting towards the fovea. From approximately the 500 msec time-mark onward, the monkey generated leftward pursuit to a target that was actually moving towards the fovea until about 100 msec after stabilization. With a leftward position error and slip velocity to the right [Fig. 3(C)], eye velocity slowed to near zero and then began to accelerate towards the right at about 500 msec, following the direction of the retinal slip. As was the case for Fig. 3(B), the eyes were moving rightward before the rightward moving target crossed the fovea.

We used both instantaneous velocity 200 msec after stabilization and mean velocity in the interval from 200 to 225 msec after the beginning of stabilization as a parameter to indicate the effect of target position and velocity on smooth pursuit. Figure 4 illustrates the effect of changing position error for three different retinal slip velocities. For these trials, the monkey was pursuing to the left at 20 deg/sec. For retinal slip velocities of 0 deg and 2 deg left or right, position error in the on-direction (-1 to -3 deg) increases pursuit velocity to as much as 40 deg/sec for a combination of 2 deg/sec leftward slip velocity with a 2 deg leftward position error. Position error in the off-direction (+1 to +3 deg) decreases pursuit velocity to as much as 40 deg/sec for a combination of 2 deg/sec rightward slip velocity with a 2 deg rightward position error. Position error in the off-direction (+1 to +3 deg) decreased pursuit velocity. Increasing position error increased the effect upon velocity for both directions, with the exception that -3 deg was less effective in increasing leftward eye velocity than was -2 deg.

In a similar series of data taken from a different monkey, a combination of rightward slip velocity and position error enabled the monkey to maintain a rightward pursuit velocity (top half of Fig. 5). All other combinations of slip velocity and position error resulted in decreases from the initial rightward velocity. Combining leftward slip velocity with leftward position error caused eye velocity to approach 0 deg/sec. For initial pursuit towards the left (bottom half of Fig. 5), leftward position error combined with leftward slip velocity evoked pursuit velocities that were greater than
the initial velocity. Rightward slip velocities in combination with leftward position error enabled the monkey to maintain velocity near the initial level. A combination of rightward slip velocity with rightward position error brought eye velocity to a level near 0 deg/sec. We noted the same effects when we examined the instantaneous velocity 200 msec after image stabilization.

FIGURE 3. Examples of single trials where position errors and slip velocities were introduced while the monkey was tracking to the right at 10 deg/sec. Target stabilization and retinal slip velocities were introduced at time 0. When initial position error and slip velocity were in the same direction (A, D), the position error increased. When initial position error and slip velocity were in opposite directions (B, C), position error decreased, with the target moving towards and eventually crossing the fovea.

FIGURE 4. The effect of target position on eye velocity. Position error was varied in 1 deg intervals from 3 deg left to 3 deg right for slip velocities of 2 deg left, 0, or 2 deg right. At the time that the target was stabilized, the monkey was tracking to the left at 20 deg/sec (horizontal dotted line). Vertical bars indicate the SEM.

DISCUSSION

In these experiments we sought to establish the contribution of position error to the monkey smooth pursuit system. Because humans can generate smooth pursuit eye movements in response to an extrafoveal afterimage, target position error itself must be able to sustain and initiate pursuit (Heywood & Churcher, 1971). Monkeys, however, do not initiate pursuit to an extrafoveally stabilized image (Morris & Lisberger, 1987). We have established that the velocity of maintained smooth pursuit can be affected by a stabilized position error.

Recognizing the technical problems encountered in producing a purely position error stimulus, we have incorporated both position errors and retinal slip velocities into our stimuli. This enabled us to compare the effects of different combinations of position error and slip velocity upon the maintenance of smooth pursuit velocity. It should be noted that both stimulus parameters were present in every trial using image stabilization, including trials when the nominal values for position error and retinal slip velocity were zero. When position error was zero at the start of image stabilization, retinal slip produced its own position offset from the fovea. When retinal slip velocity was zero at the start of image stabilization, lag of the stimulus movement system during saccades resulted in transient retinal slip velocities (Fig. 1). By comparing the effects of different combinations of position error and slip velocity, it is clear that the monkey smooth pursuit system uses both parameters for the generation of smooth pursuit eye velocity. These two parameters make independent contributions to the maintenance of smooth pursuit velocity. Combinations of slip velocity and position error mitigated each other's effect when they were
of opposite sign, and produced the most substantial effects upon velocity when they were of the same sign. Background movement during pursuit is an additional signal that has been identified as contributing to the maintenance of pursuit (Pola & Wyatt, 1989). However, our ability to reverse the direction of pursuit velocity by changing the sign of position error and slip velocity indicates that these parameters can overcome the influence of background motion. One possible confounding issue is that the act of stabilization at a given position error involves a target step. Robinson, Gordon and Gordon (1986) have proposed that the initial step in position of the stimulus when it is stabilized produces a signal that is interpreted to be a velocity signal, as in the phi phenomenon. This target step might be construed by the cortical motion detection system as a velocity pulse (Mikami, Newsome & Wurtz, 1986). However, if this were the only effect of the position error we would expect the effect to be transient, but instead it was quite sustained. In fact, it has been shown that the human response to a target step is very brief, beginning about 100 msec after the step and ending about 100 msec later (Carl & Gellman, 1987). Another potential flaw is the presence of saccades during the period of image stabilization. This also could only have a transient influence. As illustrated in Fig. 1, target movement lags that of the eye during saccades producing retinal slip, however the resultant signal is ambiguous since equivalent movements both toward and away from the fovea are produced. Several additional observations suggest that the presence of saccades had little influence upon the pursuit eye movements the monkeys made in our experiments. Trial to trial variation in the pattern of saccades generated did not appear to affect pursuit eye movements, and very different pursuit movements were made in the presence of nearly identical sequences of saccades [cf. Fig. 3(A) and (B)].

Our findings concerning the importance of position error in the generation of pursuit velocity are in agreement with previous reports for both humans (Pola & Wyatt, 1980; Carl & Gellman, 1987) and monkeys (Morris & Lisberger, 1987). The present results demonstrate that position errors twice the size of those employed by Morris and Lisberger (1987) can be effective in maintaining pursuit velocity. It should be emphasized that our findings pertain to the maintenance of an existing smooth pursuit velocity. The present findings are also in agreement with models of the smooth pursuit system that include retinal slip velocity and position error as inputs used for the maintenance of pursuit velocity (Lisberger, Morris & Tychsen, 1987). Future experimental studies and models of the smooth pursuit system must account both for retinal slip velocity and position error as the visual inputs to the smooth pursuit system.

REFERENCES


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