Transitions Between Pursuit Eye Movements and Fixation in the Monkey: Dependence on Context

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SUMMARY AND CONCLUSIONS

1. We compared the visuomotor processing underlying the onset and offset of pursuit by recording the eye movements of three monkeys as they smoothly tracked a target that was initially at rest, started to move suddenly at a constant velocity along the horizontal meridian, and then stopped. We presented this sequence of target motions in two different contexts. In the first context, the target sometimes stopped after 500 ms, but on other interleaved trials the target either continued moving at a constant velocity, slowed down, speeded up, or reversed direction. In the second context, the target always stopped, but the duration of the preceding constant velocity was randomized from 500 to 700 ms.

2. The dynamics of the eye velocity during the offset of pursuit were markedly different in the two experiments. When the target stopped only sometimes, the decrease in eye velocity at the offset of pursuit often overshot zero, producing a brief, small reversal in the direction of pursuit before eye speed settled to zero. When the target always stopped, the decrease in eye velocity at the offset of pursuit followed a more gradual transition toward zero with no overshoot. Thus, the eye velocity profiles obtained in the first experiment were inconsistent, whereas those obtained in the second experiment confirm, previous characterizations of the offset of pursuit as an exponential decay toward zero eye speed.

3. To investigate the basis of the different eye velocity profiles obtained in the two experiments, we probed the state of transmission along the visuomotor pathways for pursuit with the use of small perturbations in the motion of the target. We used perturbations consisting of 1° step changes in target position superimposed on the constant velocity motion of the target, on the basis of previous findings that such perturbations elicited saccades during fixation but smooth changes in eye speed during maintained pursuit. Single perturbations were imposed at regularly spaced intervals on separate interleaved trials during the onset, maintenance, and offset of pursuit.

4. Perturbations imposed during the onset and maintenance of pursuit had similar effects regardless of whether the target stopped only sometimes or always. In both experiments, perturbations that stepped the target in the direction opposite to the constant velocity of the target produced decreases in eye speed; perturbations in the same direction produced negligible or inconsistent changes in eye speed. The changes in eye speed caused by perturbations were largest for those perturbations introduced within the first 100 ms after the start of target motion, before the onset of the smooth eye movement, and became progressively smaller as target motion continued. The largest changes in eye speed were therefore caused by those perturbations imposed during periods of large retinal slip and by those perturbations whose direction opposed that slip.

5. Perturbations imposed during the offset of pursuit had different effects depending on whether the target stopped only sometimes or always. When the target stopped only sometimes, forward perturbations produced large increases in eye speed, whereas backward perturbations produced negligible or inconsistent changes in eye speed. Thus the visuomotor processing underlying the offset of pursuit in this experiment strongly resembled that underlying the onset of pursuit: in both cases, those perturbations in the direction opposing large retinal slip produced the largest effects. In contrast, when the target always stopped, neither forward nor backward perturbations imposed during the offset of pursuit produced large changes in eye speed. This indicates that the visuomotor processing underlying the offset of pursuit in this experiment was different from the processing underlying the onset of pursuit.

6. Perturbations also produced changes in the frequency of saccades, although these effects were less consistent than the changes in pursuit eye speed. During the onset of pursuit, such effects as did occur were similar in the two experiments: perturbations in the same direction as the motion of the target increased the frequency of saccades, whereas perturbations in the opposite direction either decreased the frequency of saccades or had no effect. In contrast, during the offset of pursuit, perturbations had different effects on saccadic frequency, dependent on whether the target stopped only sometimes or always. When the target stopped only sometimes, backward perturbations increased the frequency of saccades, whereas forward perturbations decreased the frequency of saccades. However, when the target always stopped, there was little difference between the effects of forward and backward perturbations on saccades. Thus, the effects of the perturbations on the programming of saccades complemented the effects on smooth eye velocity.

7. Our data indicate that the visuomotor processing underlying the offset of pursuit can be either very similar to or very different from that underlying the onset of pursuit. These results raise doubts about the previous proposal that the onset and offset of pursuit are mediated by different mechanisms. For parsimony, we suggest that the onset and offset of pursuit are mediated by a single mechanism, but that the transmission of visual and motor signals through this mechanism can vary during pursuit. We present simulations to demonstrate that a model incorporating this suggestion can account for the variety of eye velocity profiles observed during the onset and offset of pursuit.

INTRODUCTION

As primates inspect their visual environment, the retinal images of objects are deftly manipulated through a combination of saccadic and pursuit eye movements intercalated by periods of fixation. Saccadic eye movements rapidly translate the images of targets from eccentric locations in the visual field to the fovea. Between successive saccades, fixation holds the eyes steady to keep the target's image near the fovea. If the target's retinal image should move, pursuit eye movements restore a nearly stationary retinal image by producing a slow rotation that keeps the eyes aligned on the target. Although the neural structures and systems responsible for saccades, fixation, and pursuit have been extensively studied (for reviews see Keller and Heinen 1991; Leigh and...
Zee 1991; Lisberger et al. 1987; Sparks and Mays 1990), the mechanisms responsible for coordinating the transitions between these components of oculomotor control have not. Because the neural processing underlying saccades, fixation, and pursuit appears to be very different, study of the functional differences between these modes can provide insights into another aspect of sensorimotor control—how the primary motor system coordinates the use of a single effector organ by different neural systems.

Previous studies of fixation and pursuit eye movements have shown that one distinction between these different oculomotor modes is their sensitivity to visual inputs. Robinson (1965) observed that changes in visual feedback had little effect when subjects fixated a stationary target, but that the same changes produced large oscillations in eye velocity when subjects tracked a moving target. Robinson therefore suggested that, contrary to a simple linear control system, there was a special significance to zero velocity and that fixation and pursuit were controlled by different mechanisms. More recent experiments have demonstrated differences between fixation and pursuit by imposing small movements of the visual target while it was either fixated or smoothly tracked. For example, high-frequency vibrations (1.5–15 Hz) imposed on a fixated stationary visual target do not evoke changes in eye velocity, but the same vibrations imposed on a pursued moving target evoke large oscillations in eye velocity (Goldreich et al. 1992). Similarly, discrete perturbations in the motion of a visual target can produce smooth changes in eye speed when introduced during pursuit, but not when introduced during fixation (Morris and Lisberger 1987; Schwartz and Lisberger 1994).

In addition to these differences between maintained pursuit and fixation, it has been further suggested that the mechanism that mediates the transition from fixation to pursuit (pursuit onset) may be different from the mechanism that mediates the transition from pursuit to fixation (pursuit offset). This distinction is based primarily on the profile of eye velocity commonly observed when subjects track a target, initially at rest, that moves at a constant velocity and then stops. At the onset of pursuit, as the subjects start to track the moving target, eye velocity tends to display overshoot and ringing before achieving a velocity that closely matches target velocity. In contrast, at the offset of pursuit, as the subject resumes fixation of the now stationary target, eye velocity tends to show an exponential decay toward zero. This behavior has been observed in both humans (Huebner et al. 1992; Luebke and Robinson 1988; Robinson et al. 1986) and monkeys (Krauzlis and Lisberger 1994a; Mohrmann and Thier 1995). These data have been taken to indicate that the onset of tracking is controlled by the pursuit system, whereas the offset of tracking is controlled by the fixation system (Luebke and Robinson 1988). In some computer models, specific mechanisms have been proposed to account for these differences between the onset and offset of pursuit (Huebner et al. 1992; Krauzlis and Lisberger 1994b). Although the models are substantially different, they both include a context-dependent input that prescribes that the oculomotor output is actively driven by visual inputs during the onset of pursuit, but returns to zero independent of visual feedback during the offset of pursuit. These models therefore predict that the sensitivity of the pursuit system to visual inputs should display an abrupt decrease at the offset of pursuit.

In this study we examined the onset and offset of pursuit by presenting targets for pursuit in two different experimental contexts. In the first experiment the target sometimes stopped after 500 ms, but on other interleaved trials, the target either continued moving at a constant velocity, slowed down, speeded up, or reversed direction. In the second experiment the target always stopped, but the duration of the preceding constant velocity was randomized from 500 to 700 ms. In both experiments we tested the prediction that the sensitivity of the pursuit system to visual inputs should decrease at the offset of pursuit by introducing perturbations at different times during the onset, maintenance, and offset of pursuit. Our results indicate that, depending on the experimental context, the system may respond to visual perturbations at the offset of pursuit just as it does during the onset of pursuit, or it may display a reduced sensitivity.

**Methods**

Data were collected from three adolescent rhesus monkeys (*Macaca mulatta*), weighing 4–9 kg. All experimental protocols were approved by the Institute Animal Care and Use Committee and complied with Public Health Service Policy on the humane care and use of laboratory animals. Under isoflurane anesthesia and aseptic conditions, the head of each monkey was fitted with a pedestal, secured to the skull with titanium screws and dental acrylic, which allowed the head to be fixed in the standard stereotaxic position. A scleral search coil was implanted around each eye, with the use of the technique of Judge et al. (1980). The coils were used to monitor eye position with the use of the electromagnetic induction technique (Fuchs and Robinson 1966). The AC voltages induced in the search coils were provided as inputs to a phase detector circuit that provided separate DC voltage outputs proportional to horizontal and vertical eye position, respectively, with a corner frequency (~3 dB) at 1 kHz (CNC Engineering). The coil output voltages were calibrated with respect to eye position by having the animal fixate small light-emitting diode targets at known eccentricities along the horizontal and vertical meridians.

**Stimulus presentation**

The monkeys viewed light-emitting diode stimuli that were projected as 0.1° spots onto a translucent tangent screen located 1 m in front of the animal. The monkeys were trained to maintain fixation of a central target spot until it moved. During this fixation period, which had a randomized duration of 1,000–1,500 ms, the monkeys were required to remain within 1.5° of the central target and to refrain from making saccades, which were detected on-line by the computer as any velocity >48°/s. If these requirements were not met, the target was extinguished and the paradigm reverted to the fixation period after a 2-s delay. If the fixation requirements were met, the target was stepped 1.5° to the right or left and started to move horizontally at a constant speed of 15°/s back toward the center of the screen. For the remaining 1,000–1,200 ms of the trial, the target speed either remained constant at 15°/s ("step-ramp"), or, after 500–700 ms, increased to 30°/s ("step-ramp/step-accelerate"), decreased to 0°/s ("step-ramp/step-stop"), or reversed direction and moved at 15°/s ("step-ramp/step-reverse"). The changes in target speed were accompanied by an additional step displacement that was proportional to the change in speed, according to the formula

\[ \Delta_{\text{position}} = (\Delta_{\text{speed}})(-0.1) \]
The purpose of the second step was the same as that of the initial step—to reduce the position error present when the monkey responded to the second ramp and thereby reduce the occurrence of corrective saccades. After changes in target speed, the monkey was provided with a grace period of 450 ms in which to get the eye position within 4.5° of the target position. If eye position strayed outside this window, the trial was aborted and followed by a new randomly selected trial. Controlled movements of the target spot were achieved with an X-Y mirror galvanometer system under negative feedback control (General Scanning, CCX101). The monkey was given a liquid reward at the end of each correctly performed trial. The luminances of the target and background were 3.8 and 0.04 cd/m², respectively.

On randomly interleaved trials we presented target motions that included an additional perturbation superimposed on the target motions described above. Each perturbation consisted of a 1° step displacement of the target either in the same direction as the ramp of target velocity (“forward” perturbation) or in the opposite direction (“backward” perturbations). On trials with perturbations, we introduced a single step displacement of the target at a randomized time either before or after the target began to move, or, in the case of step-ramp/step-stop trials, after the target stopped moving. As shown previously (Morris and Lisberger 1987), step changes in target position provide a sensitive probe of the state of the pursuit system because they produce smooth changes in eye speed during maintained pursuit but elicit saccades during fixation. We used a single amplitude of 1°, rather than a range of amplitudes, to reduce the number of conditions required and because, on average, 1° steps produced the largest changes in smooth eye speed during pursuit. Finally, step changes in target position have the advantage of occurring at a discrete point in time, a property that was especially well suited to the issues addressed in our experiments.

### Experimental paradigms

We recorded eye movements in two separate paradigms. In the first paradigm, each of the four target motions described above were presented (step-ramp, step-ramp/step-stop, step-ramp/step-acceleration, step-ramp/step-reverse), and the changes in target motion always occurred 500 ms after the onset of the target motion. In this experiment, the timing of the possible change in target motion was therefore predictable, but the amplitude and direction of the change were not. The set of trials included in this experiment consisted of four rightward and four leftward “control” trials in which no perturbations were presented, and an additional 106 trials with perturbations. Perturbations were imposed at 14 possible times: 33, 67, 100, 133, 167, 200, 300, and 400 ms after the beginning of target motion and 33, 67, 100, 133, 167, and 200 ms after the end of target motion.

In the second paradigm, only the step-ramp/step-stop target motion was presented, but the duration of the target motion presented before stopping was randomized between 500 and 700 ms. In this experiment, the occurrence of a change in target motion, as well as its direction and amplitude, were predictable, although the exact timing of the change was not. The set of trials included in this experiment consisted of rightward and leftward trials in which no perturbations were presented, and an additional 92 trials in which single perturbations were imposed. Perturbations were imposed at 23 possible times: 33, 67, 100, 133, 167, 200, and 300 ms before the beginning of target motion; 33, 67, 100, 133, 167, 200, 300, and 400 ms after the beginning of target motion; and 33, 67, 100, 133, 167, 200, 300, and 400 ms after the end of target motion.

### Data collection and analysis

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 and vertical components of eye position, and the horizontal and vertical mirror position provided by transducers in the galvanometer system, were low-pass filtered (6-pole Bessel filter, −3 dB at 180 Hz) and then digitized to a resolution of 12 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 with the use of Silicon Graphics workstations.

An interactive analysis program was used to filter, display, and make measurements from the data. Signals encoding horizontal and vertical eye velocity were obtained by applying a 29-point finite impulse response filter (−3 dB at 54 Hz) to the signals encoding horizontal and vertical eye position. Signals encoding eye acceleration were then obtained by applying the same finite impulse response filter to the signals encoding horizontal and vertical eye velocity.

We analyzed the eye movement data by first marking those segments containing saccadic eye movements, on the basis of a set of amplitude criteria applied to the eye velocity and eye acceleration signals. The analysis program scanned the eye velocity signals for each trial and flagged each data point with an absolute value >35°/s, a speed greater than that which was likely to be elicited by the motion of the target. The program then scanned the eye acceleration signals for each trial, but restricted its examination to the data points adjoining the segments already flagged on the basis of the velocity criterion. If an unflagged data point adjacent to a flagged data point had an absolute value >1.000°/s², it too was flagged. The acceleration criterion was thereby used to extend the boundaries of the flagged segments without identifying additional segments.

To quantify the eye movement performance, we first generated traces of average eye velocity with and without perturbations. We computed average eye velocity by aligning the responses to the same target motion on either the onset or the offset of the target motion and computed the mean and SD of eye velocity for each millisecond sample of the data. Within each millisecond sample, eye velocity values marked as residing within a saccade were not included in the calculation of mean and SD. For trials with no perturbations, we measured three features of the eye velocity traces in individual trials: 1) the peak eye velocity achieved in the time interval 0–300 ms after the beginning of target motion, 2) the average eye velocity in the interval 500–600 ms after the beginning of target motion, and 3) the trough in eye velocity reached in the time interval 0–300 ms after the end of target motion. These measurements were used to compare the dynamics of eye velocity in the two experimental conditions described above. Statistical significance of differences between measurements obtained in the two conditions was assessed with the Mann-Whitney rank-sum test, with the use of BMDP statistical software. For trials with perturbations, we determined the change in eye velocity caused by each perturbation. We measured the average value of eye velocity within a 100-ms interval starting 100 ms after the perturbation. We compared these values with a matching set of measurements from the same time intervals on trials without perturbations. Intervals that overlapped an interval marked as containing a saccade were excluded from analysis. Each of the measurements obtained from individual trials was saved in a file that was later accessed for performing statistical analyses. Statistical significance of differences between trials with and without perturbations was assessed with the Kruskal-Wallis test for multiple comparisons, with the use of BMDP statistical software.

For some experimental conditions, we also measured the latency of the change in eye velocity caused either by changes in target motion or by perturbations. For changes in eye velocity caused by the beginning or end of target motion, we measured latency on...
individual trials and report the values as means ± SD. For changes caused by perturbations, we first generated “difference” traces by subtracting the average eye velocity obtained with no perturbations from the average eye velocity obtained with a given perturbation. We then measured the latency on this difference trace and report the value without estimating its SD. Latency measurements were determined with the use of an algorithm adapted from Carl and Gellman (1987), similar to a technique originally devised by Williams and Fender (1977). With the aid of the analysis program, the investigator identified two intervals on the eye velocity trace. The first interval (“baseline”) had a duration of 80 ms and began with either the onset or the offset of the target motion, depending on whether we were measuring the latency of the onset or the offset of pursuit, respectively. The computer determined the mean and SD of the eye velocity data points within this interval. The second interval (”response”) had a duration of 64 ms and began at the first time point after the baseline interval when eye velocity exceeded 4 SD of the mean measured from the baseline interval.

The computer performed a linear regression on the eye velocity data points over the response interval and then determined when this linear function intersected the mean value of the baseline interval. The time corresponding to this intersection was marked as the latency of the change in eye velocity.

**RESULTS**

**Effect of experimental context on the dynamics of eye velocity**

The eye movements evoked by the step ramp/step stop target motion depended on the experimental context in which the target motion was presented. In Fig. 1A, the target could either stop, speed up, slow down, or reverse direction, but only the data obtained on trials when the target stopped are shown; in Fig. 1B, the target always stopped but the time of its stopping was randomized. As shown by the traces labeled “average eye velocity,” when the target stopped only sometimes, eye velocity tended to display a pronounced overshoot during both the onset (rightward-pointing arrows in Fig. 1A) and the offset (downward-pointing arrows in Fig. 1A) of pursuit. In addition, the eye velocity during steady-state pursuit was close to target speed. These points were quantified by measuring the average peak in eye velocity achieved in the 300 ms following the start of the target motion (shown in Fig. 1A above the rightward-pointing arrows), the average trough in eye velocity reached in the first 300 ms after the target stopped (downward-pointing arrows), and the average eye velocity during the first 100 ms after the target stopped (that is, before the end of target motion had any effect on pursuit). In contrast, when the target always stopped, eye velocity did not display much of an overshoot during either the onset or offset of pursuit (Fig. 1B). During steady-state pursuit, eye velocity tended to be appreciably lower than target speed. The paired sets of measurements in the two experiments shown in Fig. 1, A and B, were significantly different for each of the three monkeys. The complete set of measurements is listed in Table 1.

To probe the state of transmission along the visuomotor pathways for pursuit, we superimposed 1° step perturbations on the step-ramp/step-stop target motion, as illustrated by the example in Fig. 2. The solid trace labeled target position shows that the target underwent an additional 1° rightward displacement (indicated by ↑) 67 ms after the rightward motion of the target was stopped. This displacement appears as a discrete pulse in the trace labeled target velocity. Because the perturbation was in the same direction as the motion of the target on these trials, we called it a forward perturbation; we called perturbations in the opposite direction backward perturbations. In these sample data, taken from monkey 1 in the experiment in which the target stopped only sometimes, the perturbation produced a large change in eye velocity. As shown by the average eye velocity traces in Fig. 2, bottom, the effect of the perturbation was to increase eye velocity in the direction of the step displacement (black trace with SD shown in dashed lines) compared with the eye velocity obtained in trials without the perturbation (gray trace).

The effect of perturbations depended on the experimental context, the time that the perturbation was imposed, and the direction of the perturbation. We first present the results from the experiment in which the target stopped only sometimes, and describe how the effects of the perturbations depended on timing and direction. We then present the contrasting results obtained when the target always stopped.

**Effects of perturbations imposed when the target stopped only sometimes**

The traces in Fig. 3 summarize the effects of imposing either forward (A and C) or backward (B and D) perturbations during the onset of pursuit for monkey 1, in the experiment in which the target stopped only sometimes. In Fig. 3, A and B, each pair of traces shows average eye velocity aligned on the onset of target motion. Within each pair, the solid black trace (labeled “perturbation”) shows the average eye velocity obtained when a single perturbation was imposed at the time indicated by the upward arrows (Fig. 3A, denoting forward perturbations) or the downward arrows (Fig. 3B, denoting backward perturbations) and by the numbers at the left edge of each trace. The gray trace in each pair (labeled “control”) shows the average eye velocity obtained when no perturbation was imposed. In Fig. 3A, the eye velocities recorded during trials with and without perturbations nearly exactly superimpose, indicating that forward perturbations imposed during the onset of pursuit did not produce significant changes in eye velocity. In contrast, in Fig. 3B, the eye velocities recorded during trials with perturbations often display a deceleration at a fixed delay after the occurrence of the perturbation, suggesting that backward perturbations imposed during the onset of pursuit produced significant decreases in eye velocity. Comparison of the pairs of traces in Fig. 3B also indicates that perturbations were more effective when they were imposed soon after the onset of the target motion.

We illustrated the differences between forward and backward perturbations imposed during the onset of pursuit by subtracting the control eye velocity in each of the pairs shown in Fig. 3, A and B. These difference traces, which represent the changes in eye velocity caused by the perturbation, are labeled as “Perturbation minus control” in Fig. 3, C and D. In contrast to the traces in Fig. 3, A and B, which are aligned on the onset of the target motion, the difference traces in Fig. 3, C and D, are aligned on the time of the perturbation. The difference traces indicate even more
clearly that, during the onset of pursuit, forward perturbations produced only minor increases in eye velocity (Fig. 3C), whereas backward perturbations produced significant decreases in eye velocity (Fig. 3D). As indicated by the

individually labeled traces in Fig. 3D, the largest decreases in eye velocity were observed for backward perturbations imposed 33 and 67 ms after the beginning of the target motion, with smaller decreases observed for perturbations

| TABLE 1. Measurements of features of pursuit eye velocity when the target only sometimes stopped and when it always stopped |
|---------------------------------|-----------------|-----------------|-----------------|-----------------|
|                                 | Monkey 1        | Monkey 2        | Monkey 3        |
|                                 | Rightward       | Leftward        | Rightward       | Leftward        | Rightward       | Leftward        |
| Onset latency, ms               | 123.6 ± 13.2    | 121.6 ± 8.9     | 137.3 ± 12.3    | 132.0 ± 12.8    | 137.5 ± 13.3    | 138.6 ± 12.8    |
| Onset peak, deg/s               | 18.5 ± 2.5      | 19.0 ± 2.5      | 16.7 ± 3.2      | 14.0 ± 2.9      | 27.5 ± 6.7      | 22.6 ± 4.1      |
| Offset latency, ms              | 111.2 ± 14.3    | 106.9 ± 13.7    | 130.7 ± 16.5    | 130 ± 17.7      | 139.7 ± 19.8    | 131.9 ± 17.9    |
| Offset trough, deg/s            | 4.2 ± 3.2       | -4.6 ± 3.6      | -4.6 ± 4.3      | -2.9 ± 2.7      | -4.4 ± 3.4      | -4.3 ± 3.5      |
| Maintained, deg/s               | 14.8 ± 2.1      | 15.0 ± 1.7      | 16.1 ± 2.4      | 14.9 ± 1.7      | 14.2 ± 3.2      | 13.7 ± 2.2      |
| Onset latency, ms               | 104.1 ± 11.8*   | 116.2 ± 12.2*   | 111.3 ± 10.7*   | 110.2 ± 12.3*   | 104.5 ± 11.5*   | 107.4 ± 12.3*   |
| Onset peak, deg/s               | 14.2 ± 2.2*     | 14.8 ± 3.0*     | 14.5 ± 3.7*     | 13.9 ± 3.9      | 16.1 ± 2.7*     | 16.8 ± 4.9*     |
| Offset latency, ms              | 90.1 ± 17.7*    | 86.3 ± 14.3*    | 84.3 ± 13.2*    | 88.1 ± 13.4*    | 82.3 ± 12.7*    | 82.3 ± 9.9*     |
| Offset trough, deg/s            | -0.9 ± 0.9*     | -1.5 ± 1.3*     | -1.2 ± 1.6*     | -1.3 ± 1.6*     | -2.0 ± 1.0*     | -2.8 ± 1.2*     |
| Maintained, deg/s               | 13.0 ± 3.3*     | 11.9 ± 4.1*     | 10.3 ± 4.9*     | 11.5 ± 3.4*     | 12.3 ± 4.6*     | 14.3 ± 5.9      |

Values are means ± SD. * Significant difference from the corresponding set of measurements when the target sometimes stopped \((P < 0.001, \text{Mann-Whitney rank-sum test})\).
imposed at ≥100 ms. The measured latencies (see METHODS) of the largest decreases were 80, 74, and 79 ms for perturbations imposed at 33, 67, and 100 ms, respectively.

The relative efficacy of forward and backward perturbations was reversed for perturbations imposed during the offset of pursuit (Fig. 4, A and B). Unlike the results obtained with forward perturbations during the onset of pursuit (Fig. 3A), the eye velocity recorded during the offset of pursuit (Fig. 4A) displayed an acceleration at a fixed delay after the occurrence of some forward perturbations. In contrast, in Fig. 4B, the eye velocity recorded from trials with and without backward perturbations nearly exactly superimposed. The difference traces obtained from these data indicate that, during the offset of pursuit, forward perturbations produced significant increases in eye velocity (Fig. 4C), whereas backward perturbations did not produce significant decreases in eye velocity (Fig. 4D). The largest increases in eye velocity were observed with perturbations imposed at 33 and 67 ms after the end of the target motion, with smaller increases observed with perturbations imposed at ≥100 ms. The latencies of the largest increases were 75 and 63 ms for perturbations imposed at 33 and 67 ms.

Comparison of the effects of perturbations imposed during the onset (Fig. 3) and the offset (Fig. 4) of pursuit reveals several common features. First, perturbations had their largest effects when they were imposed within 100 ms after the target motion either started (Fig. 3B) or stopped (Fig. 4A). Because the latency of the onset and offset of pursuit was ~100 ms (Table 1), these time intervals corresponded to periods when the retinal image of the target was moving at relatively high speeds. Second, the reversal in the efficacy of forward and backward perturbations during the onset and offset of pursuit followed the reversal in the retinal image motion that accompanied the starting and the stopping of the target. During the 100-ms interval after the target started moving, there was forward retinal image motion, and backward perturbations produced larger effects. During the 100-ms interval after the target stopped moving, there was backward retinal image motion, and forward perturbations produced larger effects. For both the onset and the offset of pursuit, the more effective perturbations were therefore in the direction opposite to retinal image motion.

To quantify the effects of the perturbations, we measured the average eye velocity in the interval 100–200 ms after the perturbation on each trial. As shown by the shaded regions in Figs. 3, C and D, and 4, C and D, this interval included most of the changes in eye velocity caused by the perturbations. The measurements made for each of the three monkeys (Fig. 5) reiterated the pattern of changes in eye velocity shown graphically for monkey 1 in Figs. 3 and 4. During the onset of pursuit, backward perturbations produced significant decreases in eye velocity, as indicated in the graphs by the filled squares in the interval 0–300 ms after the beginning of target motion (vertical lines labeled "start") that lie closer to the baseline than the control measurements (thick dashed lines). In contrast, forward perturbations during pursuit onset did not produce significant changes in eye velocity, as indicated in the graphs by the circles in this interval, almost all of which are open and lie on top of the control measurements. During the offset of pursuit, the relative efficacy of forward and backward perturbations was reversed. Forward perturbations during pursuit offset produced significant increases in eye velocity, as indicated by the filled circles in the interval 0–300 ms after the end of target motion (vertical lines labeled "stop") that lie away from the control measurements. In contrast, backward perturbations during pursuit offset generally did not produce significant decreases in eye velocity, as indicated in the graphs by the squares in this interval, the majority of which are open and lie on top of the control measurements. As shown by the shaded regions in Fig. 5, the effects of forward perturbations imposed during the offset of pursuit were comparable with the effects of backward perturbations imposed during the onset of pursuit.

### Effects of perturbations imposed when the target always stopped

The traces in Fig. 6 summarize the effects of imposing either backward perturbations during the onset of pursuit (Fig. 6, A and C) or forward perturbations during the offset of pursuit (Fig. 6, B and D) for monkey 1, with the use of the same format as in Figs. 3 and 4. As was the case when the target stopped only sometimes, forward perturbations imposed during the onset of pursuit (cf. Fig. 3, A and C) and backward perturbations imposed during the offset of pursuit (cf. Fig. 4, B and D) did not produce significant changes in eye velocity; consequently, traces for these conditions are not shown. The effects of imposing backward perturbations during the onset of pursuit in this experiment were similar to the effects observed when the target stopped only sometimes. The eye velocity recorded from trials with perturbations (solid black traces in Fig. 6A) displayed a deceleration...
A: Forward Perturbations

B: Backward Perturbations

C: Perturbation minus control

D: Perturbation minus control

FIG. 3. Effect of perturbations during the onset of pursuit when the target stopped only sometimes. A: forward perturbations (↓) shift the target in the same direction as its constant velocity. B: backward perturbations (↑) shift the target in the direction opposite its constant velocity. Perturbations occurred at the times indicated by the numbers at the left of the traces (also see arrows). Traces show average eye velocity with (black line) and without (gray line) perturbations. Traces are aligned on the beginning of target motion (time = 0 ms, labeled "start"). C and D: difference traces obtained by subtracting the gray (control) trace from the black (perturbation) trace in each pair in A and B. Numbers in D identify the traces with the largest deflections resulting from perturbations imposed at 33, 67, and 100 ms with respect to the beginning of target motion. Shaded region: time interval over which measurements plotted in subsequent figures were taken. Difference traces are aligned so that the perturbation occurred at time = 0 ms.

ation at a fixed delay after the occurrence of the perturbation. In contrast, the effects of imposing forward perturbations during the offset of pursuit in this experiment were different from the effects observed when the target stopped only sometimes. In Fig. 6B, the eye velocities recorded from trials with (solid black) and without (gray) perturbations superimpose for all but the earliest two perturbations. The difference traces obtained from these data confirm that backward perturbations during the onset of pursuit produced large decreases in eye velocity (Fig. 6C), but forward perturbations during the offset of pursuit produced much smaller increases in eye velocity that were observed only for the earliest perturbations (Fig. 6D). The latencies of the largest decreases in Fig. 6C were 72, 71, and 71 ms for perturbations imposed at 33, 67, and 100 ms after the beginning of target motion, respectively. The latencies of the two detectable increases in Fig. 6D were 70 and 69 ms for perturbations imposed at 33 and 67 ms after the end of target motion, respectively.

To quantify the effects of perturbations, we again measured the average eye velocity in the interval 100–200 ms after the perturbation on each trial. The measurements made for each of the three monkeys are shown in Fig. 7, with the use of the same format as in Fig. 5. During the onset of pursuit, backward perturbations produced significant decreases in eye velocity, as indicated by the filled squares in the interval 0–300 ms after the beginning of target motion for both rightward (A, C, and E) and leftward (B, D, and F) pursuit that lie closer to the baseline than the control measurements (thick dashed lines). Forward perturbations during pursuit onset were less likely to produce significant changes in eye velocity, as indicated by the circles in this interval, more of which are open and which tend to lie closer to the control measurements. However, during the offset of pursuit, neither forward nor backward perturbations tended to produce large changes in eye velocity, as indicated by the circles and squares in the interval 0–300 ms after the end of target motion, which mostly lie on top of the control measurements. Forward perturbations were more likely to produce significant changes in eye velocity than backward perturbations during the offset of pursuit, as indicated by the presence of more filled circles than filled squares in this interval. However, as indicated by the shaded regions in Fig. 7, the effect of forward perturbations imposed during the offset of pursuit was much smaller than the effect of backward perturbations imposed during the onset of pursuit. In
this experimental condition, we also imposed perturbations at several times before the onset of target motion, producing the data points plotted in the interval from 0 to 400 ms before the beginning of target motion. Most of these data points lie near zero, confirming previous findings that position errors imposed during fixation are ineffective for eliciting smooth eye movements (Morris and Lisberger 1987).

Comparison between the two experimental conditions

To directly compare the results obtained when the target sometimes stopped and always stopped, we plotted the amplitude of the changes in eye velocity caused by the perturbations during the onset and offset of pursuit in the two experiments. For clarity, we present only the data from the more effective perturbations, namely, backward perturbations during the onset of pursuit and forward perturbations during the offset of pursuit. The changes in eye velocity were obtained by taking the difference between the experimental and control values plotted in Figs. 5 and 7, indicated graphically in these figures by the height of the shaded region in each graph. In Fig. 8, the measurements obtained from the onset (open symbols) and offset (filled symbols) of pursuit are shown on the same time axis, by considering either the beginning or the end of the target motion, respectively, as time zero. When the target only sometimes stopped (Fig. 8, A–C), forward perturbations imposed during the offset of pursuit (filled symbols) caused changes in eye velocity that were similar in amplitude to the changes caused by backward perturbations imposed during the onset of pursuit (open symbols). In contrast, when the target always stopped (Fig. 8, D–F), forward perturbations imposed during the offset of pursuit caused much smaller changes in eye velocity, compared with the changes in eye velocity caused by backward perturbations imposed during the onset of pursuit. In addition, there were also differences between the effects observed in the two experiments during the onset of pursuit: the changes in eye velocity were lower when the target always stopped (open symbols in Fig. 8, D–F) than when it only sometimes stopped (Fig. 8, A–C).

Effects of perturbations on the frequency of saccades

Perturbations of the target motion also had effects on the saccades produced during the step-ramp/step-stop trials in the two experiments. Consistent with the varying effects on smooth eye velocity described above, the introduction of a perturbation did not always produce a saccade, but instead
changed the likelihood that corrective saccades would occur during pursuit of the target. Because of the probabilistic nature of the effect on saccades, we could not distinguish between normal corrective saccades and those saccades caused by perturbations. We therefore could not analyze the metrics of individual saccades caused by the perturbations. Instead, we analyzed the changes in the frequency of saccades caused by the perturbations by counting the number of saccades that occurred on each trial.

In general, the effects of perturbations on saccades were less consistent than the effects on pursuit eye speed, but such changes as did occur formed a distinct pattern. The graphs in Fig. 9 summarize the changes in the number of saccades caused by perturbations during pursuit of the step-ramp/step-stop target motion when the target stopped only sometimes. During the onset and maintenance of pursuit (the interval between the dashed vertical lines), forward perturbations tended to increase the number of saccades, whereas backward perturbations tended to decrease the number of saccades. This is indicated in the graphs by the filled circles lying above, and the filled squares lying below, the horizontal dashed line. In four of the six cases, this trend reversed after the target stopped (right vertical dashed lines), indicating that during the offset of pursuit, backward perturbations were more likely to increase the number of saccades.

The pattern of effects on saccade number complements the effects on pursuit eye speed. During the onset and maintenance of pursuit, forward perturbations caused only small changes in pursuit eye velocity (cf. Figs. 3, A and C, and 5), but tended to increase the number of saccades. Similarly, during the offset of pursuit, backward perturbations caused only small changes in pursuit eye speed (cf. Figs. 4, B and D, and 5) but tended to increase the number of saccades. A somewhat different pattern of results was observed when the target always stopped (Fig. 10). During the onset and maintenance of pursuit (the interval between the dashed vertical lines), to the extent that there were any effects, forward perturbations again tended to increase the number of saccades, whereas backward perturbations tended to decrease the number of saccades. However, this pattern did not reverse after the target stopped (right vertical dashed lines). Instead, during the offset of pursuit, perturbations in both directions either increased the numbers of saccades (monkey 1) or had little effect (monkeys 2 and 3). This difference is consistent with the lack of a large effect of either forward or backward perturbations on pursuit eye velocity in this experiment (Figs. 6 and 7). The graphs also show the results of imposing perturbations at several times before the beginning of target motion, producing the data points plotted in the interval from −400 to 0 ms. Most of

FIG. 5. Summary of the effects of perturbations on eye velocity imposed when the target only sometimes stopped. A, C, and E: rightward pursuit. B, D, and F: leftward pursuit. Each of the three rows shows data obtained from 1 monkey. Each symbol plots the average eye velocity in the interval 100–200 ms after the occurrence of the perturbation for the subset of trials sharing the same perturbation timing. Measurements are plotted as a function of the time that the perturbations were imposed, with respect to either the beginning or end of target motion, as indicated by the dashed vertical lines labeled “start” and “stop.” Thick dashed line connects control measurements taken from trials with no perturbations, plus additional intervals before and after the target motion. Symbols indicate forward (circles) and backward (squares) perturbations. Filled symbols: measurements that were significantly different from the control measurements (P < 0.05, Kruskal-Wallis test). Shaded regions between 0 and 400 ms after the beginning of target motion: differences between values obtained from control trials and trials with backward perturbations. Shaded regions between 0 and 300 ms after the end of target motion: differences between values obtained from control trials and trials with forward perturbations. Asterisks: times for which >1 measurements are missing, because occurrence of saccades in the measurement interval excluded all but ≤3 trials from analysis. Error bars: SD.
these data points are significantly greater than zero, indicating that position errors imposed during fixation tend to elicit saccades rather than smooth changes in eye speed (cf. Fig. 7).

**DISCUSSION**

**Comparison with previous studies**

Our results provide additional constraints on how the primate oculomotor system accomplishes transitions between fixation and pursuit. The pattern of stimulus motion we have employed in the current experiments—namely, a target that is initially at rest, starts to move at a constant speed, and then stops—has been used in several previous studies to compare the dynamics of eye velocity during the onset and offset of pursuit. In those studies, it was observed that whereas the onset of pursuit was characterized by overshoot and ringing, the offset of pursuit consisted of a monotonic decay toward zero eye speed (Huebner et al. 1992; Krauzlis and Lisberger 1994a; Luebke and Robinson 1988; Mohrmann and Thier 1995; Robinson et al. 1986). Because of this difference, it has been proposed that the transition from fixation to pursuit is mediated by the pursuit system, whereas the transition from pursuit to fixation is mediated by the fixation system (Luebke and Robinson 1988). It was subsequently shown that the latency and initial deceleration at the offset of pursuit are not affected by the presence of a structured background (Mohrmann and Thier 1995), in contrast to the pronounced effects that backgrounds have on the onset of pursuit (Keller and Kahn 1986; Kimmig et al. 1992; Mohrmann and Thier 1995). The idea that separate mechanisms mediate the onset and offset of pursuit has also been incorporated into a recent model, which includes separate pathways for controlling the onset and the offset of pursuit (Huebner et al. 1992).

Only some of our present results are consistent with this prevailing interpretation of the offset of pursuit. In an experiment in which the target always stopped, but at a time that was randomized, we did find that the profile of eye velocity at the offset of pursuit returned smoothly to zero eye speed without any overshoot, consistent with previous studies. In addition, under the same conditions we found that small perturbations of the target motion had different effects during

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1 However, the retinal events are quite different in the two cases, with stationary background images associated with onset and moving ones associated with offset.
the onset and offset of pursuit—1° step displacements could produce large changes in eye velocity when they were imposed during the onset of pursuit, but not when they were imposed during the offset of pursuit. This result confirms the prediction made by some models of pursuit (Huebner et al. 1992; Krauzlis and Lisberger 1994b) that the sensitivity of the pursuit system to visual inputs should decrease at the offset of pursuit. However, we obtained very different results when the target did not always stop, but could also speed up, reverse direction, or simply slow down. In this experiment, we found that the profile of eye velocity at the offset of pursuit displayed an overshoot comparable with that observed at the onset of pursuit. In addition, perturbations imposed under these conditions produced similar effects during both the onset and offset of pursuit. Our current results therefore provide an additional clue about the transition from pursuit to fixation: the sensitivity to visual inputs during this period can be either the same as that during the onset of pursuit or much reduced, depending on the experimental context.

That the transmission of the visual inputs driving pursuit can be variable has also been demonstrated for other phases of pursuit. Some of this evidence for variable transmission is based on the effects of position errors similar to those used in this study. In the monkey, it has been shown that retinal position errors imposed on a visual target cause smooth eye accelerations if they are imposed during pursuit of a moving target, but not if they are imposed during fixation of a stationary target—they could modify but not initiate pursuit (Morris and Lisberger 1987). Our present results corroborate and extend this observation, because we found that perturbations imposed during pursuit could cause large changes in eye speed, whereas perturbations imposed during the periods of fixation immediately preceding and soon after pursuit did not (e.g., Fig. 7). We also observed changes in the frequency of saccades that complemented the effects on pursuit eye velocity. In general, perturbations that displaced the target in the same direction as its constant velocity tended to increase the frequency of saccades, whereas perturbations in the opposite direction tended to decrease the frequency of saccades. An interesting feature of this effect on saccadic frequency is that it too was affected by the experimental context: when the target only sometimes stopped, the effect continued during the offset of pursuit (Fig. 9), whereas when the target always stopped, the effect was absent during the offset of pursuit (Fig. 10).

There are several other examples of visual inputs that are unable to initiate pursuit, but that can influence pursuit after it has been initiated. For example, when presented with sine-wave target motions, the gain of pursuit in monkeys drops...
Pursuit Eye Movements and Fixation

Etiology and locus of effects

Our use of perturbations in the current study was an attempt to provide additional constraints on the functional structure of the visuomotor pathways for pursuit. We have found that step displacements of a target can cause effects of varying amplitudes, depending on the experimental context and the exact time during pursuit when the displacement was imposed. It is tempting to attribute both of these effects solely to changes in the gain of transmission along the visuomotor pathways specialized for pursuit. However, it has been suggested that, because of the spatiotemporal filtering within the visual system, step displacements of a visual target are interpreted as brief pulses of motion (Carl and Gellman 1987); thus a direct effect on lower-level motion detectors must also be considered. This is especially true in our experiments, because step perturbations were imposed at different times after changes in target speed that were themselves accompanied by a step displacement as part of a standard step-ramp paradigm designed to reduce the likelihood of catch-up saccades (Rashbass 1961). Thus the dependence on the exact time at which the perturbations were imposed is likely due in part to the varying degrees of interaction within each pair of step displacements. The dependence on context is less easily explained by an effect on motion detectors, because the steps were always applied at equivalent times regardless of context. However, during the offset of pursuit, because the eye velocity profiles were different when the target only sometimes stopped versus when it always stopped, the ambient retinal slip at the time the perturbations were applied was different in these two conditions. We therefore cannot rule out the possibility that this difference might have had a direct effect on motion detectors that could account for some of the effects of behavioral context we observed during the offset of pursuit. However, this possibility

![Figure 8](image-url)
cannot account for the admittedly smaller effects of behavioral context we observed during the onset of pursuit, before there was any ambient slip. We conclude that the varying effects obtained in the two experiments must be due at least in part to an influence of experimental context on transmission within the visuomotor pathways mediating pursuit.

The magnitude of the difference in the eye velocity achieved during maintained pursuit in the two experiments itself points to an effect of context beyond the motion detection stage. When the target only sometimes stopped, maintained eye speed was 95–107% of target speed (i.e., steadystate gain was 0.95–1.01), but when the target always stopped, maintained eye speed was 69–82% of target speed (i.e., steady-state gain was 0.69–0.82). Because pursuit is configured as a negative feedback system, changes in the gain of the visual input large enough to have such effects on the steady-state gain should also have had substantial impact on the initial eye acceleration during the onset of pursuit—and this was not observed. Furthermore, steady-state gains >1 cannot be achieved by increasing the gain of the visual input. However, in some models of pursuit, there are sites beyond the motion detection stage at which even modest decreases in transmission can cause considerable reductions in maintained eye speed and at which increases can cause steady-state gains >1. For example, in the model of Robinson et al. (1986) one such locus is the site at which an internal representation of target velocity is computed. Another such site in the model of Krauzlis and Lisberger (1994b) lies within a positive feedback loop used to maintain eye velocity. These considerations argue that the effects of context on visual sensitivity that we have observed were due at least in part to changes downstream of the lower-level motion detectors.

Physiological studies of several pursuit-related regions of the brain provide further evidence for a site or sites, downstream of those regions involved in visual motion processing, that can modulate the transmission of inputs for pursuit. For several of these regions, access to the pursuit output motor pathways is modulated in a context-dependent manner. For example, electrical stimulation applied within the medial superior temporal visual area (Komatsu and Wurtz 1989), the dorsolateral pontine nuclei (May et al. 1985), and the posterior vermis (Krauzlis and Miles 1994) produces changes in smooth eye velocity, but only if applied when the monkey is already engaged in pursuit. These structures lie anatomically at or downstream of those areas believed to process visual motion, yet they apparently lie upstream of a site at which behavioral context can influence transmission. In contrast, stimulation of the cerebellar flocculus or ventral paraflocculus (Belknap and Noda 1987; Ron and Robinson 1973) and the pursuit region within the frontal eye fields (Gottlieb et al. 1993) can elicit smooth eye movements even during fixation. These structures therefore appear to either lie downstream of, or bypass, the site at which transmission is modulated. A further possibility is that these areas help to define the gain of the modulation; this possibil-
ity is consistent with the evidence linking the frontal eye fields to anticipatory and predictive pursuit (Keating 1991, 1993; MacAvoy et al. 1991) and the recent suggestion that the dorsomedial frontal cortex may play a role in determining when pursuit is stopped (Heinen 1994).

**Functional significance**

It is not clear whether the effects of experimental context that we observed reflect normal operating modes of the system or are simply products of unusual laboratory conditions. It is admittedly unnatural for a subject to track the same target motion consecutively many hundreds of times, and this repetition may be a prerequisite for both the decreased sensitivity to visual inputs that we observed in the current experiments and the smooth decay in eye velocity that has been observed previously during the offset of pursuit. Conversely, under natural viewing conditions, subjects usually track targets within a rich visual environment, rather than across a featureless background like that used in the current study. When moving visual targets are presented against a textured background, eye acceleration is reduced during the onset of pursuit and eye velocity rarely overshoots target speed (Keller and Kahn 1986; Kimmig et al. 1992; Mohrmann and Thier 1995), presumably because of a direct effect on the decoding of the target’s motion. The overshoot in eye velocity commonly observed in the laboratory during the onset of pursuit may therefore be partly caused by impoverished viewing conditions.

Although in our experiments the effects we have observed may not reflect the typical operation of the pursuit system, they suggest to us that the use of visual inputs by the motor pathways for pursuit can be weighted in accordance with their potential value. When there is a large degree of uncertainty about how the target will move, visual inputs are important for determining both how and when to change eye velocity. Thus, when the target only sometimes stops, the sensitivity to visual inputs might be expected to remain elevated during the offset of pursuit. However, when it is certain that the target will stop, visual inputs may be important for determining when to change eye velocity, but the metrics of how eye velocity should be changed can depend on signals formulated independently of visual feedback. Consequently, when the target always stops, the impact of visual inputs might be expected to be reduced during the offset of pursuit. A similar mechanism might be deployed to stop tracking whenever the observer loses interest in the moving object and wishes to establish fixation on some other visual target.

**A model**

That the onset and offset of pursuit can have similar dynamics suggests they may be mediated by the same mechanism. However, our observation that the effects of perturba-
tions during pursuit can vary with context prompts us to suggest that the system can modulate the efficacy of transmission through this mechanism: when the gain of transmission is high, changes in eye velocity are brisk and accompanied by overshoot; when the gain is low, changes in eye velocity are more sluggish and monotonic. In this scheme, a single mechanism can account for the profiles of eye velocity exhibited during the onset and offset of pursuit, whether or not the transition involves overshoot.

To demonstrate the feasibility of this suggestion, we performed simulations of a proposed model, adapted from a model published previously (Krauzlis and Lisberger 1994b). Because the aim of the simulations was to reproduce the generic features of eye velocity during the onset and offset of pursuit, rather than to reproduce the details of particular eye velocity profiles, we used a model with a relatively simple structure. As shown in Fig. 11A, the visual input to the model is obtained by subtracting eye velocity from target velocity at the summing junction labeled “retina.” After being delayed by 80 ms (“delay”), the visual input is provided to two parallel pathways. The “image velocity pathway simply scales the visual input by a factor of 12. The “image acceleration” pathway first takes the derivative of the visual input and then applies a nonlinear scaling. The outputs from the two pathways are then summed with a scaled copy of the eye velocity output (“positive efferent feedback”) and provided as an input to a multiplicative junction (indicated by ×). The multiplicative junction modulates the amplitude of the summed inputs on the basis of the value of a second input, labeled “gain.” The modulated visuomotor signals are then provided as the input to a low-pass “filter,” which then produces the output of the model.

The placement of the multiplicative junction in the model is significant. As pointed out earlier, if the junction were placed in the visual pathways, changes in the gain input large enough to have the observed effects on the steady-state gain would have reduced the initial eye acceleration much more than we found. On the other hand, if the junction were placed in the efferent feedback pathway, changes in the gain input could not prevent visual inputs from causing...
changes in eye velocity, even during fixation. The junction is therefore located at a site that allows it to affect equally the gain of the visual motion inputs and the gain of positive efferent feedback, and is intended to represent a site in the visuomotor pathways specialized for pursuit.

We were able to reproduce the qualitative features of our data by making changes in the value of the gain input while keeping all other parameters fixed. The results of the simulations are shown in Fig. 11, bottom. In Fig. 11, B, D, F, and H, the black traces show the value of the gain input, which varied as a function of time during the trial; the gray traces show the 500-ms step of target velocity. In Fig. 11, C, E, G, and I, the black traces show the eye velocity output from the model, and the gray traces show target velocity again for comparison. When the value of the gain input ramped up to a value of 1.0 and remained there several hundred milliseconds after the target stopped (Fig. 11B), eye velocity displayed overshoot at both the onset and offset of pursuit (Fig. 11C). This simulation reproduces the profile of eye velocity we obtained when the target stopped only sometimes. Because the gain is elevated throughout the trial, perturbations would be expected to have large effects during the onset, maintenance, and offset of pursuit. In contrast, when the value of the gain input ramped up to a value of 0.8 and decreased again 100 ms after the target stopped (Fig. 11D), eye velocity did not overshoot target velocity at the onset of pursuit, although it did slightly overshoot maintained eye speed, and during the offset of pursuit eye velocity displayed a smooth transition to zero. This simulation reproduces the result we obtained when the target always stopped. In this case, because the gain reaches a lower value, perturbations would have smaller effects during the onset and maintenance of pursuit and, because the gain returns to zero earlier, the effects of perturbations would be further attenuated during the offset of pursuit.

We next grafted the first half of the gain signal shown in Fig. 11B onto the second half shown in Fig. 11D, producing the gain input shown in Fig. 11F. The eye velocity trace resulting from this simulation (Fig. 11G) displayed overshoot at the onset of pursuit, but a smooth decay at the offset of pursuit, reproducing the commonly observed difference between the two transitions. To complete the set of simulations, we grafted halves of the first two gain signals (Fig. 11, B and D) together again, but in the reverse order, producing the gain input shown in Fig. 11H. The eye velocity trace resulting from this simulation (Fig. 11I) shows no overshoot at the onset of pursuit, but displays an overshoot at the offset of pursuit. This profile of eye velocity has not yet been reported, but should be possible if the proposed mechanism is correct.

This simple model has obvious shortcomings. For example, we have made no attempt to describe the origin of the gain input, nor have we provided a biological description of the processing of visual motion. However, the aim of the simulations was not to provide an exhaustive description of the pursuit system but to demonstrate how a single mechanism could account for the qualitative features of the effect of context on the onset and offset of pursuit. Finally, it should be emphasized that although the model does not distinguish between transitions from fixation to pursuit and transitions from pursuit to fixation, it does respect the distinction between maintained pursuit and fixation. The difference between the two modes can be related to the value of the gain input: the “pursuit system” is the state of the model when the gain is near 1, and the “fixation system” is the state of the model when the gain is near zero. From this viewpoint, the structure of the proposed model is entirely consistent with Robinson’s original comment that “the smooth pursuit system is dormant until brought into play as an overlaying system by persistent retinal image velocity when, and only when, its peculiar dynamics may make themselves felt” (Robinson 1965, p. 589).

APPENDIX

The model shown in Fig. 11A was provided with two input signals. The first (target velocity) was defined as a pulse lasting 500 ms with an amplitude of 15°/s. The second (gain) remained at zero until time = 80 ms, at which point it ramped upward, reaching a value of 1.0 (Fig. 11, B and F) or 0.8 (Fig. 11, D and H) at time = 150 ms. The gain signal then either remained constant until time = 750 ms (Fig. 11B) or time = 600 ms (Fig. 11D), or changed smoothly to reach a value of 0.8 at time = 600 ms (Fig. 11) or a value of 1.0 at time = 750 ms (Fig. 11H). The gain signal then ramped downward, reaching a value of zero after an additional 150 ms.

The summing junction shown in Fig. 11A, top left, computed the difference between target velocity and the eye velocity output from the model. This difference signal was then delayed by 80 ms and provided as the input to two pathways. The pathway labeled “image velocity” scaled the difference signal by a factor of 12. The pathway labeled image acceleration first differentiated the difference signal and then applied a nonlinear scaling accomplished by the equation

\[ y = a \cdot \text{sgn} (x) \cdot e^{-|x| - b^2y^2} \]

where \(a = 90, b = 200,\) and \(c = 62.\) The sum of the image velocity, image acceleration, and positive efferent feedback pathways was then scaled by the current value of the gain signal and provided as the input to a first-order system with a time constant (80 ms) set to match the observed decay in eye velocity during the offset of pursuit. The gain of the first-order system (0.880) and the positive efferent feedback (12.5) were set so that the gain around this inner loop equaled 1 when the gain signal equaled 1. The output from the first-order system provided the “negative visual feedback” and “positive efferent feedback” within the model and the eye velocity output from the model.

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