Temporal Properties of Visual Motion Signals for the Initiation of Smooth Pursuit Eye Movements in Monkeys

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SUMMARY AND CONCLUSIONS

1. Our goal was to assess whether visual motion signals related to changes in image velocity contribute to pursuit eye movements. We recorded the smooth eye movements evoked by ramp target motion at constant speed. In two different kinds of stimuli, the onset of target motion provided either an abrupt, step change in target velocity or a smooth target acceleration that lasted 125 ms followed by prolonged target motion at constant velocity. We measured the eye acceleration in the first 100 ms of pursuit. Because of the 100-ms latency from the onset of visual stimuli to the onset of smooth eye movement, the eye acceleration in this 100-ms interval provides an estimate of the open-loop response of the visuomotor pathways that drive pursuit.

2. For steps of target velocity, eye acceleration in the first 100 ms of pursuit depended on the "motion onset delay," defined as the interval between the appearance of the target and the onset of motion. If the motion onset delay was > 100 ms, then the initial eye movement consisted of separable early and late phases of eye acceleration. The early phase dominated eye acceleration in the interval from 0 to 40 ms after pursuit onset and was relatively insensitive to image speed. The late phase dominated eye acceleration in the interval 40–100 ms after the onset of pursuit and had an amplitude that was proportional to image speed. If there was no delay between the appearance of the target and the onset of its motion, then the early component was not seen, and eye acceleration was related to target speed throughout the first 100 ms of pursuit.

3. For step changes of target velocity, the relationship between eye acceleration in the first 40 ms of pursuit and target velocity saturated at target speeds > 10°/s. In contrast, the relationship was nearly linear when eye acceleration was measured in the interval 40–100 ms after the onset of pursuit. We suggest that the first 40 ms of pursuit are driven by a transient visual motion input that is related to the onset of target motion (motion onset transient component) and that the next 60 ms are driven by a sustained visual motion input (image velocity component).

4. When the target accelerated smoothly for 125 ms before moving at constant speed, the initiation of pursuit resembled that evoked by steps of target velocity. However, the latency of pursuit was consistently longer for smooth target accelerations than for steps of target velocity.

5. The eye movements evoked by smooth target acceleration were larger than those predicted by the relationship between eye acceleration and target velocity for the late component of pursuit elicited by steps of target velocity. The difference between the actual and predicted eye acceleration increased steeply for small target accelerations and then saturated for higher values of target acceleration.

6. Our data indicate that the visual inputs for pursuit cannot be thought of as a linear encoding of image velocity. We suggest that visual motion processing provides additional signals that can be represented as transient visual responses associated with the onset of image motion and/or sustained visual responses associated with smooth changes in image speed. Our behavioral observations provide a rationale, based on measurements of pursuit eye movements, for models of pursuit that use multiple visual motion inputs.

INTRODUCTION

During ocular tracking of small moving targets, monkeys and humans use a combination of saccadic and smooth pursuit eye movements to keep the retinal image of the target within the high acuity region near the fovea. Saccades are rapid eye movements that translate the images of visual targets from eccentric retinal locations onto the fovea. In contrast, pursuit is a continuous, smooth eye motion that normally is elicited by moving visual targets. Any mismatch between the motion of the target and the motion of the eye causes motion of the target's image across the retina. The resulting visual inputs alter smooth eye velocity in an attempt to reduce and ultimately minimize the image motion. Pursuit is configured as a negative-feedback system in which visual information about the motion of the target represents an error signal that drives corrective smooth eye movements. However, negative feedback, which arises from the physical link between the effector organ (the eyeball) and the sensory epithelium (the retina), is only part of the system that allows pursuit to achieve accurate tracking. The brain pathways from the retina to the eye muscles perform complex transformations that also form an integral part of the mechanisms that guide pursuit. Our goal is to reveal the temporal properties of the signals that result from those transformations.

Previous experiments on the pursuit eye movements of humans and monkeys have demonstrated that the internal organization of the pursuit system includes complexities beyond those of a simple negative-feedback system. If pursuit were a simple negative-feedback system, then eye movement would be driven directly by a visual error signal, and eye velocity would be related to image motion. In fact, eye acceleration, not eye velocity, is best related to image motion during smooth pursuit (Carl and Gellman 1987; Lisberger et al. 1981; Lisberger and Westbrook 1985; Tychsen and Lisberger 1986). If pursuit were a simple negative-feedback system, then perfect tracking would be impossible, because the elimination of image motion would remove the drive for pursuit, causing eye velocity to decay rapidly toward zero. In fact, eye velocity is sustained almost perfectly when image motion during pursuit is eliminated by stabiliz-
ing the target’s image on the retina (Morris and Lisberger 1987). These observations imply that the basic negative-feedback structure of the pursuit system is augmented by a form of internal memory that automatically maintains eye velocity. Because eye velocity is automatically sustained, the function of visual inputs is to produce smooth eye acceleration or deceleration that corrects differences between target and eye motion (Lisberger et al. 1981).

The neural substrate for pursuit consists of visual input pathways to the cerebral cortex, cerebrocerebellar pathways from the visual cortex to several regions of the cerebellum, and cerebellar output pathways through brain stem nuclei to ocular motoneurons. The importance of the visual cortex has been revealed by studying deficits in pursuit after lesions in extrastriate areas that are specialized for processing visual motion. For example, lesions in the extrastriate representation of the middle temporal area (MT) produce a transient decrement in the eye acceleration at the initiation of pursuit for targets that move through the lesioned part of the visual field (Newsome et al. 1985). Ablation of foveal MT or of the adjacent medial superior temporal area (MST) produces a more complicated syndrome consisting of a retinotopic deficit like that created by lesions of extrastriate MT as well as a directional deficit in which eye speed never matches target speed when the target moves toward the side of the lesion (Dursteler et al. 1987). More recently, lesion studies have demonstrated that a region of the arcuate sulcus near the frontal eye fields (FEF) also is important for normal pursuit (Keating 1991, 1993; Lynch 1987; MacAvoy et al. 1991). Studies with anatomic tracers have shown that these diverse cortical areas project to the dorsolateral and dorsomedial pontine nuclei (DLPN and DMPN) as well as to the accessory optic system (AOS). These nuclei, in turn, project to widespread regions of the cerebellum, including the ventral paraflocculus,\(^1\) the flocculus, and the vermis (Brodal 1978, 1979, 1982; Gereits and Voogd 1989; Glickstein et al. 1980, 1985; Huerta et al. 1986; Künzle and Akert 1977; Langer et al. 1985; Leichnetz 1982; May and Andersen 1986; Ungerleider et al. 1984). Neurons in the DLPN, AOS, ventral paraflocculus, flocculus, and vermis show activity related to smooth pursuit eye movements (Kase et al. 1979; Lisberger and Fuchs 1978; Miles and Fuller 1975; Miles et al. 1980; Mustari et al. 1988; Noda and Suzuki 1979; Stone and Lisberger 1990; Suzuki and Keller 1988a,b), and lesions in some of these regions also cause deficits in pursuit (e.g., May et al. 1988; Zee et al. 1981).

Despite the growing list of areas involved in pursuit, previous research has neither identified the signals that are used to initiate and guide pursuit nor ascertained how those signals are represented in the pathways that provide the neural substrate for pursuit. Beyond the general agreement that visual motion is an adequate stimulus for pursuit and that information about visual motion is evaluated by the extrastriate visual cortex, little is known about the temporal properties of the visual signals for pursuit. Available physiological data do not provide useful constraints on the many possible ways to configure a computer model that can emit realistic pursuit. For example, single-unit recordings from area MST and from the cerebellar vermis have been interpreted as supporting a model of the pursuit system (Robinson et al. 1986) in which signals related to image velocity and eye velocity are combined to construct a command for pursuit that encodes target velocity explicitly (Newsome et al. 1988; Suzuki and Keller 1988b). In contrast, recordings from Purkinje cells in the cerebellar flocculus have been interpreted as support for models in which raw visual signals lead directly to changes in eye velocity (Krauzlis and Lisberger 1989, 1991; Stone and Lisberger 1990).

In the present paper we use measurements of pursuit eye velocity to infer the temporal properties of the visual motion signals that drive pursuit. We examine the initiation of pursuit to steps of target velocity and target acceleration. Quantitative analysis shows that the eye acceleration in the first 100 ms of pursuit indicates that pursuit can be described by adding together three components of visual motion that have different temporal response properties. One component is related to image speed, as suggested by previous models of pursuit (e.g., Robinson et al. 1986), but the other two components are related to changes in image speed.

**METHODS**

**Preparation of animals**

Experiments were conducted on three male Rhesus monkeys weighing 5–8 kg. For behavioral training and experiments, monkeys were transferred from their home cages into specially designed primate chairs for a period of 2–3 h. After initial training on a reaction-time task modified from Wurtz (1969), each monkey underwent sterile surgery while anesthetized with halothane. A coil of wire was implanted on the sclera of one eye (Judge et al. 1980) so that eye movements could be monitored with the magnetic search coil technique. Three or four bolts were implanted in the skull to anchor a receptacle for head restraint. After recovery from the surgery, monkeys were conditioned to accept head restraint for all further training and experiments. The monkey was positioned with his head in the center of a pair of 18-in. square coils that were attached to the chair to generate the magnetic fields used to record eye position. The monkey’s eye monitor was initially calibrated by having him perform the reaction-time task with targets at known positions. Thereafter, the monkey performed a fixation-window task in which he received rewards every 1,500 ms as long as his eye position remained within 2–3° of the target.

**Presentation of visual stimuli**

Visual stimuli were provided by circular spots of light that were 0.1–0.5° diam and were projected onto the back of a tangent screen. A red, stationary target was provided by projecting the image of light-emitting diode (LED) directly onto the screen. White, moveable targets were generated by reflecting the beam from an optical bench off a pair of orthogonal, servo-controlled mirror galvanometers (General Scanning CCX650). Command signals for target position were provided by the digital-to-analog converter of a laboratory computer. Actual target position was monitored by recording the feedback signals from the mirror galvanometers. To eliminate possible nonlinearities introduced by using a flat tangent screen, both the mirror galvanometers and the monkey’s eyes were 114 cm from the screen. During experiments

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\(^1\) Many previous papers on the cerebellum have used the wrong terminology to refer to the flocculus and the ventral paraflocculus. In our paper we have reinterpreted the histological data in those papers and have used the corrected terminology to describe these previous results.
that shown in Fig. 1. Each trial started when the monkey fixated a stationary and moving spots. By using two targets at different positions, we selected this paradigm to provide a step of target position, we minimized the motion of monkeys, we extended the natural open-loop interval by driving the eye position within 2° of the stationary target and within 3–4° of the moving target throughout the trial. If his eye position strayed out of these windows, the trial was aborted and the monkey received no reward. The only exception to the fixation requirement was a grace period of 300–400 ms starting at the onset of target motion.

Experiments consisted of a series of 1,500–2,500 trials selected in random order from a list of up to 40 trials, each of which presented a different target motion. The randomization of trials was designed to minimize successful attempts by the monkey to anticipate how the target would move, because the first part of each trial did not contain enough information to cue the subsequent target motion. In addition, catch trials were inserted into the series at a lower frequency to eliminate anticipatory responses and to verify that anticipatory responses were not contaminating our data. The catch trials required the monkey to maintain fixation of the red spot as a white target flashed on for 300–500 ms at an eccentric location. For each type of trial, we initially set the starting position of the target so that it moved through the monkey’s fixation point as he initiated pursuit. During several practice sessions, we determined the size and direction of the saccades made by the monkey during each trial, and we made fine adjustments in the starting position of the target to eliminate the need for corrective saccades. As a result, saccades occurred at least 250 ms after the initiation of pursuit and often did not occur at all.

In standard trials the moveable target was visible and stationary at an eccentric position for 300–500 ms before the onset of target motion provided a step of target speed from zero to targets that ranged from 2.3 to 30°/s. In the remainder of the trials, we modified the presentation of target motion in one of three ways. In some experiments we presented step changes in target speed and systematically varied the duration of the interval when the moveable target was visible before it started to move. This interval, which we call the “motion onset delay,” ranged in duration from 0 to 1,000 ms. When the motion onset delay was zero, the white target appeared and began to move at the time when the fixation target was extinguished. In other experiments we altered the onset of target motion so that the target accelerated smoothly from rest for 125 ms before continuing ramp motion at the speed attained at the end of the period of acceleration. Target acceleration ranged from 45 to 400°/s² so that the final target speed ranged from 5.6 to 50°/s. In a final variation we studied the eye acceleration at the offset of pursuit by stopping the target at an unexpected time and requiring the monkey to fixate the stationary target for 300–500 ms. In these trials we eliminated the need for a corrective saccade at the offset of tracking by stepping the target forward as it stopped, in a manner complementary to the onset of target motion.

The latency of the pursuit system creates a natural open-loop interval in which the monkey’s eye movement is driven by the visual events that precede the onset of pursuit (Lisberger and Westbrook 1985). Even though the initiation of pursuit alters the motion of the target’s image across the retina, the changed visual events cannot affect eye velocity until the latent period later. Because the latency of pursuit is 80–100 ms in monkeys, the natural open-loop interval consists of the first 80–100 ms after the onset of pursuit. Most of our experiments have taken advantage of the natural open-loop interval for pursuit to describe the transformation of visual inputs into eye motion. In a few experiments on two monkeys, we extended the natural open-loop interval by driving the target motion with a signal that was created by adding a conditional version of the eye position signal obtained from the saccular search coil to the command for the desired target position. This prevented the monkey’s eye motion from altering the image mo-
tion and allowed us to examine longer intervals of the responses to constant image velocities of 5–30°/s and constant image accelerations of 45–120°/s². We used the procedures described by Morris and Lisberger (1987) to assess the quality of the open-loop tracking conditions and to correct for any nonlinearities in the system for monitoring eye position.

Two components in the initiation of pursuit

Systematic variation of the interval in which the target was visible and stationary dissociated two components in the first 100 ms of the pursuit evoked by the onset of target motion at constant velocity. Figure 2A shows schematically the target motion for two trials in which the motion onset delay or “MOD” was 300 or 0 ms. When the MOD was 300 ms, the red fixation light (R) was present for >600 ms, and the white, moveable target (W) was stationary but visible for 300 ms before the fixation light was extinguished and the target started to move. When MOD was 0 ms, the red fixation light was visible for >600 ms, but the moving white target did not appear until the fixation light was extinguished. Comparison of the dashed and solid traces in Fig. 2B shows the effect of changing the MOD on the average eye velocity evoked by target motion at 5, 15, and 30°/s.

For this monkey the latency for the initiation of pursuit was ~30 ms longer when MOD was 0 ms (dashed traces) than when MOD was 300 ms (solid traces). In addition, the initial rate of eye acceleration was larger, and there was some overshoot in the eye velocity when MOD was 300 ms (solid traces). In contrast, the initial rate of eye acceleration was lower, and there was no overshoot in the transition to accurate smooth tracking when the MOD was 0 ms (dashed traces). When MOD was 0 ms and target speed was 15 or 30°/s, eye velocity undershot target velocity and required a second phase of eye acceleration to bring eye velocity up to target velocity.

RESULTS

The top trace of Fig. 1 shows the mean and standard deviation of the eye velocity evoked by 22 presentations of a step change in target velocity from 0 to 25°/s to the right. After a latency of 80 ms, eye velocity increased smoothly, crossed target velocity, and then oscillated about a velocity that was close to the target velocity of 25°/s. The input to the visual system for the stimulus in Fig. 1 is shown by the trace labeled Image velocity, computed as target velocity minus eye velocity. The trajectory of image velocity emphasizes distinct initiation and maintenance phases in pursuit. Before the onset of pursuit, image motion was large and identical to target motion. During the maintenance of pursuit, image motion was small and reflected primarily fluctuations of eye velocity around target velocity.

Data acquisition and analysis

Experiments were conducted with the use of an interactive computer program that controlled the target motion, monitored the monkey's behavior, and sampled the data. Voltages related to eye position, eye velocity, and target position were digitized during the experiment at 1-ms intervals and stored on computer disk. The eye velocity signal was obtained by analog differentiation of the eye position voltage (band-pass DC to 50 Hz, 20 dB/decade).

Data were analyzed after the experiment with the use of MicroVAX II or DECstation 3100 computers. Records from each trial were displayed on a video screen with the use of an interactive program that allowed the user to place cursors on the data traces. We analyzed our data in two ways, depending on which features of the responses we wanted to examine. One analysis method provided measurements of latency and eye acceleration in individual trials. We inspected each response on the video screen and placed cursors on the eye velocity records at the initiation of pursuit and at the start of the first saccade. The computer calculated the latency to initiate pursuit and the eye acceleration in each of the first five 20-ms intervals after the initiation of pursuit. Data from identical target motions were pooled to obtain estimates of the mean and standard deviation of pursuit latency and initial eye acceleration for each stimulus condition. Intervals were not included in the averages if they overlapped the first saccade. A second method for data analysis provided averages of eye velocity aligned on the onset or offset of target motion. Each individual trial was again displayed on the screen and inspected. Approximately 3–10% of the trials were discarded because the pursuit response either began with a saccade or was interrupted by a saccade within the first 100 ms after the initiation of pursuit. For the remaining trials, we marked the beginning and end of each saccadic eye movement in the eye velocity trace. The computer removed the saccade and replaced it with a linear segment that connected the eye velocity at the beginning and end of the saccade. Responses to the same target motion were aligned on the onset or offset of target motion and averaged together to obtain the mean and standard deviation of eye velocity for each millisecond in the data.

Records of eye acceleration provided the clearest evidence of two separable components early (0–40 ms) and late (40–100 ms) in the initiation of pursuit. Figure 3, A and C, shows the eye acceleration traces obtained by using a digital filter to differentiate the six averages of eye velocity that appear in Fig. 2B. Figure 3, B and D, shows eye acceleration from identical experiments on a second monkey. When the motion onset delay was 300 ms (Fig. 3, A and B), the eye acceleration increased as a function of time throughout the early interval (0–40 ms, between the 1st and 2nd vertical dashed lines), but the value of eye acceleration at each time was nearly independent of target speed. In contrast, eye acceleration in the later interval (40–100 ms, between the 2nd and 3rd vertical dashed lines) was strongly related to target speed. In both monkeys, eye acceleration at the end of the early interval, 40 ms after the onset of pursuit, was almost as large as that later in the trial. When the MOD was 0 ms (Fig. 3, C and D), the early phase of eye acceleration was either small or absent. The response consisted primarily of a later phase of eye acceleration that was graded with target speed nearly from the onset of eye motion. The absence of the earlier component of the response caused a large increase in the latency for the initiation of pursuit in monkey O and only a small increase in monkey J.

Figure 4 quantifies the effect of MOD on eye acceleration early and late in the initiation of rightward (circles) and leftward (squares) pursuit for monkey J. Each graph plots eye acceleration in the intervals 0–40 and 40–100 ms after the onset of pursuit, measured from averages of eye velocity like those shown in Fig. 2. For these data, the measurement intervals were aligned with the onset of pursuit, not with the onset of target motion. Therefore each analysis interval was
MOD = 300 ms

MOD = 0 ms

FIG. 2. Effect of motion onset delay (MOD) on the initiation of pursuit. A: schematic diagram showing how we presented different MODs. In the top diagram, the MOD was 300 ms; both the red LED (R) and the white target light (W) were illuminated for 300 ms before the target started to move. In the bottom diagram, MOD was 0 ms. The shutter opened and the white target (W) became visible when the red fixation light (R) was extinguished. B: solid lines show averages of eye velocity for target motion at 5, 15, and 30°/s when the MOD was 300 ms. Dashed lines show averages of eye velocity for the same target motions in the same experiment when MOD was 0 ms. All records were taken from 1 day’s experiment. The downward arrow in B indicates the onset of target motion.

Eye velocity a few milliseconds later relative to the onset of target motion when MOD was 0 ms than when MOD was 300 ms. The graphs confirm the impression given by inspection of the eye acceleration traces in Fig. 3. When the MOD was 300 ms (Fig. 4A), the eye acceleration in the interval 0–40 ms after the onset of pursuit (open symbols) saturated for target speeds >10°/s. In contrast, the eye acceleration in the interval 40–100 ms after the onset of pursuit (filled symbols) increased monotonically as a function of target speed and did not saturate over the range of target speeds tested. When the motion onset delay was 0 ms (Fig. 4B), the eye acceleration increased as a function of target speed in both the early and later intervals, and none of the curves showed saturation.

We next examined the effect of MOD on the initiation of pursuit by varying the amount of time that the target was visible before it started to move. Figure 5, A and C, shows families of averaged eye velocity responses for a series of MODs in two monkeys. The traces are aligned on the onset of pursuit to highlight the effect of MOD on initial eye acceleration, even though aligning the traces in this way obscures the small effect of MOD on the latency of pursuit. The numbers to the left of the traces indicate the length of the interval between illumination of the target and the onset of its motion. As before, the initial eye acceleration was modest when the MOD was zero or small. As MOD increased, the initial eye acceleration was more brisk, and there was a tendency for eye speed to overshoot target speed. Figure 5, B and D, plots the magnitude of the average eye accelerations in the first 40 ms of pursuit as a function of the MOD. For both monkeys used in this experiment, the magnitude of the early eye acceleration was smallest when MOD was zero or small. Eye acceleration in the early interval of pursuit increased smoothly as MOD increased, reached a peak for delays of 100–300 ms, and decreased slightly for the largest values of MOD.

When open-loop tracking conditions were used to prolong the interval of controlled image velocity beyond the normal latency of pursuit, the later phase of eye acceleration was sustained at values that remained proportional to image speed. The solid traces in Fig. 6A show averages of the eye velocity evoked by steps of target velocity from 0 to 10 and 20°/s under normal closed-loop conditions. For comparison, the dashed traces show responses to prolonged image motion at the same speed in open-loop conditions. The eye velocity evoked in the interval from 40 to 100 ms after the onset of pursuit (between the 1st 2 arrows) was the same for open-loop and closed-loop target motion. In open-loop conditions the eye acceleration was maintained at a slightly lower rate for the subsequent 100-ms interval (between the 2nd and 3rd arrow). Figure 6B plots eye acceleration as a function of image speed for the late phase of pursuit. Eye acceleration in the interval from 40 to 100 ms after

FIG. 3. Effect of MOD on eye acceleration at the initiation of pursuit in 2 monkeys. Traces were obtained by differentiating the averages of eye velocity for MODs of 300 ms (A and B) and 0 ms (C and D) and target motion at 5, 15, and 25°/s in monkey O (B and D) and monkey J (C and D). Averages are aligned on the onset of target motion, which occurred at the beginning of each trace. For each monkey, the 1st vertical dashed line is placed at the time of the initiation of pursuit when MOD is 300 ms. The 2nd and 3rd vertical dashed lines are placed 40 and 100 ms after the 1st dashed line, respectively. The traces in A and B are differentiated versions of the traces in Fig. 2B.

Eye acceleration
the onset of pursuit of closed-loop target motion (filled symbols) was closely matched by measurements from the interval 40–200 ms after the onset of pursuit for trials in which the open-loop interval was extended (open symbols). The two lines in Fig. 6B show the results of linear regression on the two groups of individual measurements of eye acceleration that were averaged to obtain the open and filled symbols. The slopes of the lines were nearly identical for open-loop and closed-loop data, but the y-intercept for the closed-loop data was slightly lower than that for the open-loop data.

When the motion onset delay was 300 ms, the relationships between smooth eye acceleration and target velocity were different for the two components in the initiation of pursuit for steps of target velocity. In Fig. 7, the left column of graphs plots average eye acceleration in the interval 0–40 ms after the onset of pursuit as a function of target velocity. For each of the three monkeys, the amplitude of eye acceleration was near its maximum value for the lowest target speed used, 5°/s. For higher target speeds, there were either only small increases in the amplitude of eye acceleration (monkey J), or variable increases and decreases (monkeys O and N). The right column of graphs display measurements of eye acceleration taken over an interval 40–80 ms after the onset of pursuit. We have restricted this analysis to the first 80 ms of pursuit to be certain that our measurements were not contaminated by visual feedback in cases when the latency of pursuit was <100 ms. For the interval 40–80 ms after the initiation of pursuit, the relationship between eye acceleration and target velocity was nearly linear over the full range of velocities. This was true for each of the three monkeys, although there were differences among the monkeys in the steepness of the relationship between eye acceleration and target velocity.

**Pursuit of smooth target acceleration**

We examined the initial pursuit evoked by targets that accelerated smoothly in trials that began like our standard trials, with the red fixation spot at straight ahead gaze and the white tracking target visible and stationary at an eccentric position (e.g., Fig. 8A). When the fixation light was extinguished, the target illustrated in Fig. 8A accelerated smoothly at a constant rate of 120°/s² for 125 ms and then continued at 15°/s, which was the final velocity attained by the target at the end of the period of acceleration. The pur-
suit evoked by smooth target acceleration was qualitatively similar to that evoked by steps of target speed. In Fig. 8A, the latency to initiate pursuit was 120 ms. The eyes then accelerated smoothly for \( \sim 100 \) ms to reach a velocity that was close to the target velocity of \( 15^\circ/s \). The four traces in Fig. 8B display the average eye velocities measured during pursuit of targets that accelerated smoothly at rates of 45, 120, 180, and 320°/s\(^2\). The different amplitude of eye velocity achieved at the end of each trial reflects the different velocities attained by targets accelerating at these different rates for a fixed duration of 125 ms. Unlike the responses to steps of target velocity, the responses to different amplitudes of smooth target acceleration differed from the very beginning of the eye velocity response.

**FIG. 6.** Comparison of pursuit evoked by steps of velocity in closed-loop and open-loop conditions. A: averages of the eye velocity evoked by steps of target velocity from 0 to 10 or 20°/s. Solid traces show the responses under normal closed-loop tracking conditions, and dashed traces show the responses when electronic feedback of eye position was used to open the feedback loop and prolong by 100 ms the interval of controlled image velocity. The downward 3 arrows are placed 40, 100, and 200 ms after the onset of pursuit. Each trace starts at the time when the target started to move. B: average eye acceleration from traces like those shown in A is plotted as a function of target speed. Filled symbols show average eye acceleration over an interval from 0 to 40 ms after the onset of pursuit. Open symbols show average eye acceleration over an interval from 40 to 80 ms after the onset of pursuit. Error bars are not visible on most of the points because the size of the symbols was > 1 SE. Horizontal dashed lines indicate 0 acceleration.

The latency from the onset of target motion to the initiation of pursuit was consistently longer for smoothly accelerating targets than for steps of target velocity. We analyzed the latency of pursuit with a model in which the latency for initiation of pursuit is described as the sum of a fixed processing delay and the time required for the target to traverse a minimal displacement (Carl and Gellman 1987). For steps of target speed, latency can be related to speed by the equation as follows: latency = \( a + b \times (1/\text{speed}) \), where \( a \) gives the value of the fixed processing delay and \( b \), which has units of degrees, gives the minimum displacement. The graphs in the left-hand column of Fig. 9 plot latency as a function of inverse speed for the responses to steps of target velocity when MOD was 300 ms. Linear regression on the data shown in these graphs revealed that the value of \( a \) ranged from 67 to 72 ms and the value of \( b \) ranged from 0.033 to 0.068 (Table 1). For smooth target accelerations, latency can be related to acceleration by the equation as follows: latency = \( a + \left[ \frac{(2 \times b)}{\text{acceleration}} \right]^{1/2} \), where \( a \) again gives the value of the fixed processing delay and \( b \) gives the minimum displacement that must occur to initiate pursuit. The graphs in the right-hand column of Fig. 9 plot latency as a function of \( [2/\text{acceleration}]^{1/2} \) so that lin-
ear regression yielded values for $a$ and $b^{1/2}$. Table 1 shows that the values of $a$ (fixed delay) for smooth target acceleration tended to be larger than the values for steps of target velocity, whereas the values of $b$ (minimum displacement) tended to be smaller. Therefore some but not all of the differences in latency observed between steps in target velocity and smoothly accelerating targets can be attributed to the longer period of time needed for the accelerating target to exceed the postulated minimum displacement required for the initiation of pursuit.

We next asked whether the first 100 ms of the response to smooth target acceleration could be accounted for by the late component of the eye acceleration evoked by steps of target velocity. In Fig. 10, A–C, the solid traces labeled Eye acceleration show the first derivative of the averages of eye velocity evoked by smooth target acceleration at 45, 120, and $320^\circ/s$. The dashed eye acceleration traces show the eye acceleration predicted by the relationship between eye acceleration and target velocity for the late component of the response to steps of target velocity. To obtain these traces, cubic splines were fitted to curves like those in the right-hand column of Fig. 7. A cubic spline was used, rather than a simpler form of interpolation, to avoid abrupt changes in the slope of the functions. Eye acceleration then was predicted at each millisecond by evaluating the cubic spline for the target velocity in that millisecond. Finally, the predicted eye accelerations (dashed traces) were shifted to the right so that the predicted and measured responses began at the same time. For each magnitude of target accelera-

![Image](image_url)

**FIG. 8.** Initiation of pursuit for smooth target acceleration. *A:* records from a single trial in which the target accelerated from 0 to $15^\circ/s$ in 125 ms. Dashed line above the eye position trace indicates the interval when a fixation LED was illuminated at straight-ahead gaze. A small saccade in the eye position trace is responsible for the upward deflection in eye velocity ~250 ms after the onset of pursuit; the deflection has been cropped at $70^\circ/s$. *B:* averages of the eye velocity evoked by 20 presentations of targets accelerating at rates of 45, 120, 180, and $320^\circ/s$. Downward arrow indicates the onset of target motion.

**FIG. 9.** Analysis of the latency of pursuit for steps of target velocity and smooth target accelerations. In the *left column* the latency for steps of target velocity is plotted as a function of $1/(\text{target speed})$. In the *right column* the latency for smooth target acceleration is plotted as a function of $(2/\text{target acceleration})^{1/2}$. Each symbol shows data for 1 target speed or rate of target acceleration. Lines were obtained by linear regression, and the coefficients of the fitted lines are provided in Table 1.

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Values in Latency are means $\pm$ SD. Latency was modeled for each of the 4 monkeys as the sum of a fixed delay ($a$) and the time required to traverse a minimum displacement ($b$). For steps of target velocity, parameters were obtained by linear regression on the equation as follows: latency $= a + b(1/\text{speed})$. For smooth target acceleration, parameters were obtained from the equation as follows: latency $= a + [2b(1/\text{acceleration})]^{1/2}$. |
tion shown in Fig. 10, the actual eye acceleration was larger than the predicted eye acceleration. The differences between the pairs of traces, shown by the solid traces labeled difference in Fig. 10, D–F, represent a component of the measured eye accelerations that was evoked by smooth target acceleration but not predicted by the late component of the eye acceleration evoked by steps of velocity.

We summarized the results of this experiment by measuring average eye acceleration over the first 80 ms of the response (between the vertical dashed lines in Fig. 10). In Fig. 11, A, C, and E, the actual eye acceleration (filled symbols) was larger than the predicted eye acceleration (open symbols) for each value of smooth target acceleration in each monkey. Figure 11, B, D, and F, plots the difference between actual and predicted eye acceleration and demonstrates a consistent relationship in each monkey. The difference eye acceleration (Fig. 11, B, D, and F) had a steep slope around zero target acceleration and saturated for larger values of target acceleration. The saturation level for this "image acceleration" component of the eye acceleration evoked by smooth target acceleration is about one-half that in the early component of the pursuit evoked by steps of target velocity (Fig. 7, A, C, and E).

**Offset of pursuit**

Figure 12 shows an example of the trials we used to examine the offset of pursuit. The beginning of the trial presented a 2° step of target motion to the left and a ramp of target motion to the right at 10°/s. Target motion continued for 600 ms. Then the target stepped 2° forward, stopped, and remained visible at this final position for 400 ms. The monkey was required to fixate the stationary target at the end of the trial before receiving a reward. As shown by the trace labeled Image velocity, the onset of step-ramp-step-stop target motion provided image motion that started at a constant velocity and decreased toward zero as eye velocity increased and matched target velocity. The visual stimulus associated with the offset of target motion provided a similar pulse of image motion (in the opposite direction) that started at a constant velocity and again decreased toward zero as eye velocity approached zero.

The eye velocity evoked in our monkeys by step-ramp-

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**FIG. 10.** Demonstration that the initial eye movements evoked by smooth target acceleration cannot be predicted by the relationship between eye acceleration and target speed for steps of target velocity. Solid traces in the top row show the initial eye acceleration evoked by targets that accelerated at 45 (A), 120 (B), and 320°/s² (C). Eye acceleration traces were obtained from by differentiating traces representing average eye velocity with a 29-point finite impulse response filter that had a -3-dB roll-off at 94 Hz. Dashed traces in A–C show the eye acceleration predicted by using the velocity of the accelerating targets at each millisecond of the records as the input to cubic spline functions fitted to the data in the right half of Fig. 7 (details in text). Solid traces in the bottom row (D–F) show the difference between the measured acceleration of the eye and the predicted acceleration. The left vertical dashed line in each panel indicates the latency of the eye movement response. The right vertical dashed line indicates 80 ms after the onset of the response.

**FIG. 11.** Summary of eye accelerations measured from pursuit of smoothly accelerating targets. A, C, and E: filled squares plot the average eye acceleration over an interval from 0 to 80 ms after the onset of pursuit as a function of smooth target acceleration. Open circles show the values obtained by using the analysis described in the text to predict the eye acceleration that would have occurred if the initiation of pursuit were driven only by the late component of pursuit evoked by steps target velocity. B, D, and F: difference between actual and predicted average eye acceleration is plotted as a function of smooth target acceleration. Note that the y-axes in the right-hand columns are expanded compared with those in the left-hand column. The horizontal dashed lines indicate 0 eye acceleration.
from the onset of pursuit. Both the individual trace in Fig. 12 and the averages of eye velocity in Fig. 13, A and C, show that the initiation of pursuit included a brisk rise in eye velocity followed by overshoot before eye velocity settled on a value close to target velocity. During the offset of pursuit, the deceleration of the eye was also brisk, but there was no overshoot as the eye approached zero velocity. Further analysis of the responses to step-ramp-step-stop target motion reveal that the onset of pursuit was nonlinear while the termination of pursuit was linear. Figure 13, A and C, shows averages of eye velocity for the onset and offset of rightward and leftward target motion at 10 and 20°/s. Figure 13, B and D, shows the same traces after eye velocity had been normalized for target speed by halving each value of eye velocity in the averages for target motion at 20°/s without changing the averages for target motion at 10°/s. The nonlinear properties of the onset of pursuit appear in the failure of the rising phases of eye velocity to superimpose in Fig. 13, B and D. The eye velocity evoked by target motion at 10°/s had larger peaks at the initiation of pursuit because the early component of the response to steps of target velocity made a proportionately larger contribution to eye acceleration at lower image speeds. The linearity of the offset of pursuit appears as superposition of the normalized traces (Fig. 13, B and D) as eye velocity declined toward zero. As reported by Robinson et al. (1986), eye velocity during the offset of pursuit can be described as a decaying exponential with a single time constant. We estimated this time constant by measuring the interval between the time the target stopped and the time eye velocity declined to 1/e of its value just before the target stopped. In the monkey that was used for this experiment, the time constant of decay averaged 81.8 ± 3.8 (SD) ms for target motion at 10 and 20°/s and for both leftward and rightward pursuit.

**DISCUSSION**

*Eye movements as a probe for visual motion processing*

We have used the eye velocity measured during the initiation of pursuit as a probe to characterize the signals that are transmitted from the visual motion sensory system to the pursuit motor system. Several factors suggest that our measurements provide a good estimate of the inputs provided by the direct visuomotor pathways for pursuit. First, we have examined only the first 80–100 ms after the onset of pursuit, which is the portion of the response that is uncorrupted by visual feedback (Lisberger and Westbrook 1985). Second, stimuli of different speeds and directions were presented in a randomly interleaved sequence, making it unlikely that anticipatory effects and cognitive strategies introduced significant contaminants into our results (Kowler and Steinman 1979). Finally, the range of eye velocities and accelerations attained by the monkeys in our experiments was well below what is seen during saccadic eye movements, indicating that the nonlinear properties we have observed do not reflect limits imposed by the output motor pathways or the eyeball.

*A motion onset transient component in pursuit initiation*

The profile of initial eye acceleration elicited by a step of target velocity depended on how long the target was visible before it began to move (the MOD). The effects of varying
the MOD suggest that the visual inputs for pursuit eye movements can be described as at least two separable components of visual motion. One component is driven by a transient input that occurs at the onset of target motion and gets larger as the MOD increases from 0 to 200 ms. The other component is related to the speed of image motion, and its amplitude does not vary as a function of MOD. Previous studies have also found differences between the early and late phases of eye acceleration during the initiation of pursuit. Eye acceleration in the first 40 ms of pursuit is relatively unaffected by the speed, contrast, or size of the moving image (Lisberger and Westbrook 1985), and it is also isotropic across the visual field (Lisberger and Pavelko 1989). The magnitude of the later component of eye acceleration, 40–100 ms after the onset of pursuit, depends on target speed, target size, and the position of the moving target in the visual field (Lisberger and Westbrook 1985).

Carl and Gellman (1987) and Wyatt and Pola (1987) also have provided evidence that there are two components in the initiation of pursuit. The differences between the early and later components of the initiation of pursuit are similar in humans (Carl and Gellman 1987; Tychsen and Lisberger 1986; Wyatt and Pola 1987) and in monkeys (Lisberger and Pavelko 1989; Lisberger and Westbrook 1985), although the later component may have a relatively longer latency in humans than in monkeys.

Recent preliminary experiments have demonstrated that the image motion transient component is a significant component of the initiation of pursuit under natural conditions when the target is tracked across a brightly illuminated background (S. G. Lisberger and J. D. Schwartz, unpublished observations). However, these investigators also showed that the effect of MOD on the initiation of pursuit is related primarily to the background illumination. In the experiments reported in the present paper, the background was either dim or dark, and we observed a clear increase in early eye acceleration as MOD was increased from 0 ms. When the background and the target have the same high luminance, the effect of varying MOD is no longer observed, but the evoked eye velocity clearly expresses the early component that we have attributed to a motion onset transient (J. D. Schwartz and S. G. Lisberger, unpublished observations). Thus the MOD itself may not be an important functional parameter during pursuit in normal, brightly illuminated surroundings.

Variation of the MOD in the laboratory has provided a critical tool for establishing that the transient, early eye acceleration in the initiation of pursuit is a normal component of pursuit initiation and not simply a laboratory curiosity. Our data demonstrate that steps of target velocity cause a transient early component of eye acceleration in the initiation of pursuit when the visual background is bright or the MOD is 300 ms. Variation of the MOD demonstrated that the transient can be separated from a later, sustained component of eye acceleration. Recordings from anesthetized monkeys have demonstrated that a homologous transient is present in the responses of cells in MT when MOD is 300 ms (Movshon et al. 1990), that changes in the duration of MOD have parallel effects on the transient in MT cell firing and the initiation of pursuit when the visual background is dimly illuminated (Movshon et al. 1990), and that the transient response of MT cells is present even when MOD is zero if the visual background is brightly illuminated (S. G. Lisberger and J. A. Movshon, unpublished observations). These correlations suggest that the transient in the response of MT cells drives the transient, early component of eye acceleration seen in the initiation of pursuit for steps of target velocity.

A smooth image acceleration component in pursuit

Our analysis of the responses to smooth target acceleration provides evidence that the visual motion inputs for pursuit include a component related to smooth changes in image speed. This conclusion is based on the difference between the eye accelerations caused by smooth target acceleration and those predicted from the late component of the initiation of pursuit for steps of target velocity. It is unlikely that the augmented responses to smooth target acceleration can be attributed to systematic changes in the gain of visuomotor processing caused by a "range effect," because the trials that provided steps of target velocity were interleaved with those that presented smooth target accelerations.

Our predictions of the responses to smooth target acceleration did not include a possible contribution from the same source responsible for motion onset transient in the response to steps of target velocity. The possible contribution of the motion onset transient was omitted from the predictions because there was no way to infer how it would behave in the case of smooth target accelerations. Therefore it remains possible that the augmented responses to smooth target accelerations and the early component of the response to steps of target velocity are two manifestations of a single mechanism. Both phenomena, however, support the conclusion that pursuit receives visual inputs sensitive to changes in image speed. Previous studies have suggested that image acceleration plays a role in maintaining pursuit eye movements during tracking of ramp target motion, when eye velocity is large and image motion is small (Lisberger et al. 1987; Morris and Lisberger 1985). Our finding in the present paper (that image acceleration contributes to eye velocity during the open-loop interval in the initiation of pursuit) supports this suggestion and makes it unlikely that the previous observations documented the effects of a longer-latency feedback pathway.

Signals related to image acceleration have important consequences for the control of movement. Real objects rarely undergo step changes in speed or move at a constant speed. Their speed often fluctuates during continuous motion, and, because of inertia, their speed increases smoothly when real objects begin to move. The availability of visual motion signals related to image acceleration would improve the accuracy of motor performance in these cases by making it possible to change eye or limb velocity more quickly. Inputs related to smooth image acceleration also could play a role in maintaining the stability of pursuit. For example, we have shown previously how a sensitivity to image acceleration could account for the absence of uncontrolled overshoot in the transition from the initiation of pursuit to sustained tracking (Krauzlis and Lisberger 1989) and for the high frequency and low amplitude of the oscillations observed during pursuit of sustained target motion at...
constant velocity (Goldreich et al. 1992; Krauzlis and Lisberger 1989; Morris and Lisberger 1985). Although the use in pursuit models of signals called “image acceleration” and “motion onset transient” has illustrated that higher derivatives of image motion can help the models to emit realistic performance, the current descriptions of the signals must be considered temporary. It remains a problem for future models to describe the visual inputs for pursuit in a form that more nearly resembles signals recorded in the neural structures mediating pursuit.

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