

Properties of Visual Inputs that Initiate Horizontal Smooth Pursuit Eye Movements in Monkeys¹

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Abstract

Smooth pursuit eye movements allow primates to fixate and track small, slowly moving objects. Pursuit usually requires visual targets; our aim was to determine the properties of the visual signals transmitted to the pursuit motor system. Rhesus monkeys were rewarded for tracking spots of light that underwent discreet changes in velocity under a variety of visual conditions. We measured the resulting smooth eye acceleration in a 100-msec interval that began with the initiation of pursuit and ended before there had been time for visual feedback. This approach allowed us to vary the parameters of visual stimulation and measure eye movement responses in a way that provides estimates of the properties of signals transmitted by visual pathways.

The initiation of pursuit showed different properties early and late in the interval we studied. In the first 20 msec of pursuit, eye acceleration was in the correct direction, but was independent of the initial position of the moving images, the velocity of the stimulus, or the presence or absence of background illumination. Thereafter, the initiation of pursuit depended strongly on all of the above parameters. Eye acceleration was highest when the moving images fell close to the fovea and decreased sharply as eccentricity was increased up to 21°. When the background was diffusely illuminated, eye acceleration showed velocity selectivity; it was highest for a middle range of velocities (30 to 60°/sec) and decreased for higher velocities. When the background was dark, eye acceleration increased as a function of target velocity up to 150°/sec.

We conclude that the initiation of pursuit has at least 2 visual components. The two components have different latencies and show quite different relationships to the visual

properties of the stimulus, suggesting two cell populations that could provide the visual inputs for pursuit.

Smooth pursuit eye movements are used by primates to track small objects that are moving across a stationary background. In general, pursuit is initiated by the smooth motion of a target (Rashbass, 1961) and is guided by continuous visual feedback (Robinson, 1965; Barmack, 1970) so that image motion across the retina is minimized. Recent work has begun to reveal brain structures that participate in pursuit. Lesion studies have shown that the visual cortex (Goldberg et al., 1982; Zee et al., 1982) and cerebellum (Westheimer and Blair, 1973; Zee et al., 1981) are important for pursuit, while anatomical experiments have begun to document cortico-ponto-cerebellar pathways that may be involved (Brodal, 1978; Brodal, 1979; Glickstein et al., 1980; Fries, 1981).

We assume that the visual cortex provides the visual inputs that drive pursuit, but it is not known which cortical cells are involved or what visual signals they transmit. Since pursuit is usually in the direction of target motion, its visual inputs probably originate in cortical cells that are direction-selective. However, this feature does not help to pinpoint the sources of visual inputs for pursuit, since many cortical areas contain direction-selective cells (Van Essen and Maunsell, 1983) and contribute to the cortico-ponto-cerebellar pathways (Brodal, 1978; Glickstein et al., 1980). Of cortical areas, the middle temporal visual area (MT) is particularly interesting because it seems to be specialized for analyzing image motion (Dubner and Zeki, 1971; Van Essen et al., 1981; Albright et al., 1984) and because small lesions in MT affect pursuit of targets in the area of visual field whose central representation has been destroyed (Newsome et al., 1985). However, more must be learned about pursuit before it will be possible to specify the signals which could be provided by MT and those which must originate from other visual areas.

The goal of our study was to measure pursuit eye movements in ways that would reveal properties of the visual signals transmitted to the pursuit motor system. We hope to provide a bridge between pursuit behavior and the burgeoning wealth of information about cells throughout the visual cortex of the monkey. To obtain this kind of information, we have used pursuit stimuli that provide precise, quantifiable visual inputs. Our approach should allow us to specify cell populations whose discharge properties are appropriate to provide inputs for pursuit, as well as those that show qualitatively or quantitatively inappropriate response properties. Our logic is like that of Dubois and Collewijn (1979a, b), who studied the visual properties of full-field images that evoke smooth tracking. Unfortunately, the relationship of such "optokinetic" tracking to pursuit of small targets is controversial. The few studies of the visual inputs that drive pursuit of small targets have provided only fragmentary information and only in humans (Winterson and Steinman, 1978; Haegerstrom-Portnoy and Brown, 1979; Barnes, 1983).

In this paper, we have studied the initiation of pursuit for step

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changes in target velocity. We have determined: (1) the extent to which visual inputs for pursuit emphasize the central retina; (2) the image velocities that are effective in activating pursuit; and (3) the effects of diffuse background illumination. Our data suggest that the initiation of pursuit has at least two components. One component has an amplitude that is affected by only one of the parameters we have studied. It seems to be driven by visual inputs that are direction-selective but otherwise unselective. The amplitude of the other components varies in relation to all of the above parameters and has properties that suggest it may originate from MT.

Materials and methods

Three rhesus monkeys (5 to 7 kg) were trained to perform visual tracking tasks for apple juice reinforcement. Initially, the monkeys were shaped to release a bar in response to the dimming of a visual target (Wurtz, 1969). Under Nembutal or halothane anesthesia, each monkey was then implanted with a scleral search coil to monitor eye position (Fuchs and Robinson, 1966; Judge et al., 1980). At the same time, bolts were implanted in the skull and were bridged with aluminum and dental acrylic to a cylindrical receptacle that was used to restrain the monkey's head (Miles and Eighmy, 1980). All surgery was done with sterile procedure.

Experiments were run daily and lasted about 2 hr. For these, the monkeys walked voluntarily from their home cages to a specially designed primate chair. After transport to the laboratory, the implant on the monkey's head was secured to the chair. A pair of 18-inch square field coils was bolted to the chair and the magnetic search coil technique was used to monitor horizontal and vertical eye position; the bandpass of the electronics was DC-330 Hz. The eye coil was calibrated by holding the target stationary at known positions while the monkey performed the behavioral task. One eye was patched in all experiments so that viewing was monocular through the eye carrying the search coil.

Stimulus presentation

Two moveable spots and one stationary spot served as targets. The stationary spot was red, circular, and $\frac{1}{4}^\circ$ in diameter. Unless otherwise stated, the moveable targets were white, circular, with a 6- to 12-min arc in diameter. They were moved by reflecting the light beam off a pair of servocontrolled mirror galvanometers (General Scanning, CCX-650) onto the back of a screen that was 114 cm from the mirrors and the monkey's eye. The moveable targets could be dimmed silently by reducing the voltage driving the light sources.

In different experiments, the screen and room were either dark or diffusely illuminated by incandescent lights. When the screen was illuminated, the monkey's entire visual field contained visible, stationary objects. The contrast between stimulus and background was defined by doing a psychophysical experiment on one of us (L. E. W.). A two-alternative, forced-choice method was used to define absolute threshold for a 100-msec flash of the stationary target 3° off the fovea. The intensity of the stimulus was varied according to the method of limits by inserting and removing neutral density filters. The values of contrast given in our figures indicate the number of log units of neutral density filters needed to reduce contrast to the threshold of our human subject. When the background was dark, the tracking target was 2.5 log units above our threshold for detection.

Our procedures had two problems that became apparent and were corrected during the study. First, the use of a tangent screen causes a substantial decrease in the brightness of the target at eccentricities of even 10 to 20° . Where necessary, we have done control experiments to verify which effects were caused by increased eccentricity and which by decreasing brightness of the stimulus. Second, the mirror galvanometers cause a perceptible sweep of the target when a step change in target position is executed. To eliminate any effects this may have on pursuit, we usually provided step changes in target position by switching between two targets at different positions.

Behavioral and stimulus control

Each presentation of a pursuit stimulus began with the monkey fixating a stationary target. At a randomized time, the fixation point went out and the monkey was required to change fixation and track a second target that began to move at constant velocity. This provided a step change in stimulus velocity that occurred at a retinal position defined by the initial separation between the stationary and moving targets; the resulting target motion is effectively the "step-ramp" of Rashbass (1961). In a given experimental session, we varied the initial retinal position of the target, the final velocity of

the target ramp and/or the visual conditions under which the target was presented. This was accomplished through an interactive computer program that presented up to 40 different "trials" in random order and directions. Each trial provided a step-ramp stimulus with a single step size and ramp velocity, and was presented many times in the course of a day's experiment. To keep the monkey from anticipating the direction of target motion, any step amplitude was always associated with two trials, where one trial provided image motion towards and the other away from the fovea. In some experiments, we randomly interspersed trials in which we imposed visual inputs that the monkey could not correct. Eye position was digitized by the computer and added to the desired visual stimulus to form a command for target position that could be used selectively in a specified part of the trial. This provided a means to open the visual feedback loop and to compare the monkey's responses in open-loop conditions to those in normal closed-loop tracking.

Most of our experiments used a fixation task to induce the monkeys to track the targets. Each trial began when the monkey brought his eye position within 1.5° of a stationary, flashing target. Usually, the red (stationary) and one of the white (moveable) targets flashed at different positions, and the trial could be initiated by fixating the red spot. The targets remained on steadily while the monkey maintained fixation for a random interval (600 to 900 msec). Next, the fixation target went out and the white target began to move. If the monkey initiated pursuit and tracked the target for an interval that varied randomly from 600 to 1500 msec, he received a reinforcement. The computer program suspended the fixation requirements for a grace period (usually 400 msec) after sudden changes in target motion, so that the monkey would not be penalized for failing to overcome the built-in latencies in his oculomotor system. In addition, larger errors between eye and target position were allowed during the more difficult trials. Except for the highest velocity target movements, we required that the eye position be within 2° of target position at the end of each trial.

To ensure that our results were not shaped by the size of the errors allowed in the fixation task, some experiments were repeated with a barpress task in which the reward was not directly contingent on pursuit performance. The monkey initiated a trial by pressing a bar after the fixation target began to flash. He was required to hold the bar down while the target underwent step-ramp motion and to release the bar within 600 msec after the target dimmed at some later and unpredictable time. To do this task, the monkeys fixated and tracked the spot. Our results did not depend on the behavioral task. Therefore, our graphs show data obtained with the fixation task, and the figure legends indicate which experiments were repeated with the barpress task.

When the monkey completed a trial, the eye and target voltages were displayed on a monitor and saved on the computer for later quantitative analysis. Trials designed only to prevent anticipation by the monkey were not saved. In addition, a small fraction of the experimental trials (5 to 10%) were discarded if there were substantial oscillations of eye velocity in the fixation period prior to the step-ramp or a saccadic eye movement occurred just before or within 50 to 100 msec after the onset of target motion. If the monkey failed to complete a trial, the timing and direction of the trial were randomized again and he was required to repeat it. Monkeys routinely performed 1500 to 2000 trials a day, completing more than 95% of them correctly.

Data acquisition and analysis

An eye velocity signal was obtained by passing the horizontal eye position voltage through a circuit that differentiated frequencies below 50 Hz, and rejected (-20 dB/decade) higher frequencies. The result had less than 1° /sec of noise and was digitized at 1 kHz along with signals proportional to horizontal eye and target position. Data were analyzed after the experiment using an interactive computer program. Each trial was displayed on a video screen (MATROX, MLSI-512). The user moved a cursor along the eye position records to mark the beginning and end of each saccadic eye movement. Another cursor was positioned on the eye velocity record to indicate the initiation of pursuit and the onset of the first rapid deflection associated with a saccade. If the interval before the first saccade was longer than 100 msec, the computer calculated the initial eye acceleration from the change in eye velocity in the first 100 msec of pursuit. The computer also calculated instantaneous eye acceleration by dividing the first 100 msec of pursuit into five intervals each 20 msec long and measuring the change in eye velocity (divided by 0.020) in each interval. If a saccade occurred before there had been 100 msec of pursuit, only the presaccadic pursuit was analyzed. Data from at least 20 identical stimuli were then pooled, and means and SDs calculated. In Figures 3, 4, 5, 8, and 10, we have shown the SDs as error bars to give an impression of the true variance of the monkeys' responses.

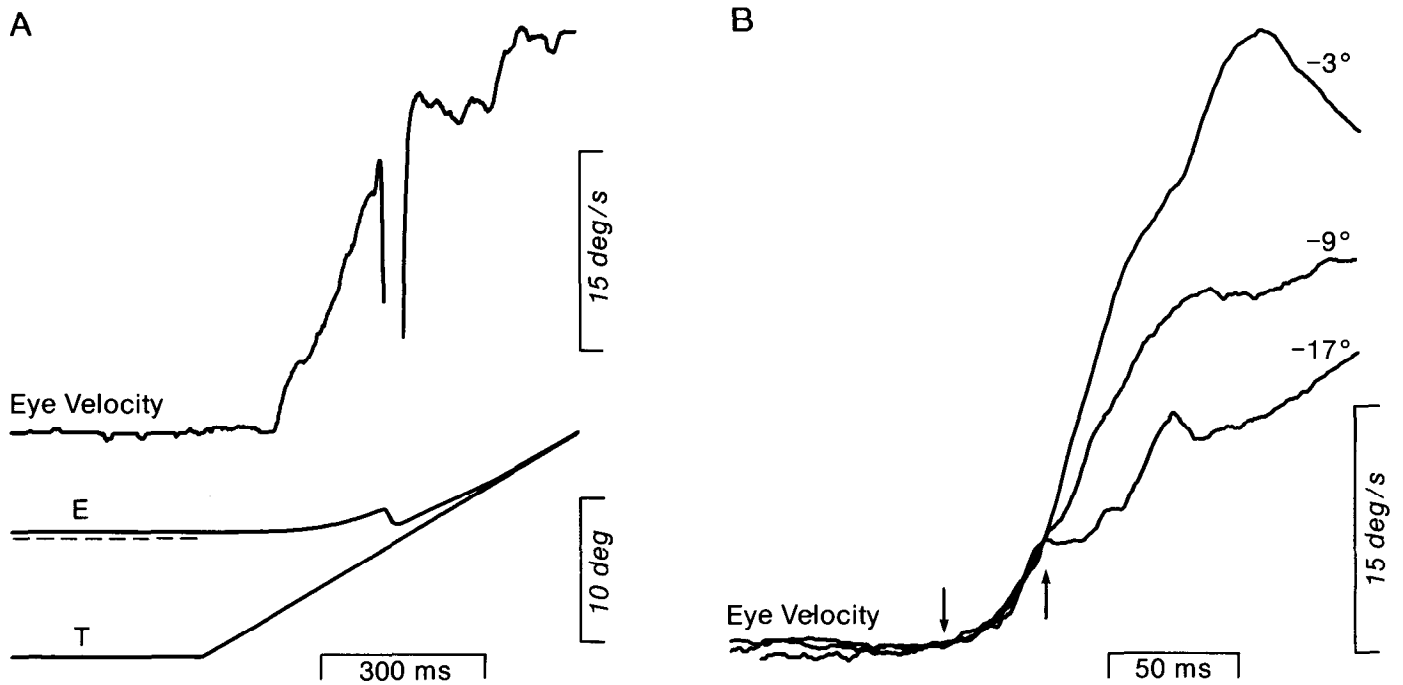


Figure 1. Effect of image position on the initiation of pursuit for rightward stimulus motion at 30°/sec. A, A representative trial that began with the fixation point at straight-ahead gaze and the tracking target on and stationary at 9° left. The horizontal dashed line indicates the position of the fixation point and the time interval when it was illuminated. E, eye position; T, target position. B, Averages of eye velocity for trials in which the target started at 3, 9, or 17° left and moved to the right at 30°/sec. The numbers next to each trace indicate the initial position of the tracking target, and negative numbers indicate leftward positions. The downward arrow shows the initiation of pursuit, and the upward arrow the time at which the traces separate. In this and subsequent figures, upward deflections represent rightward eye movement.

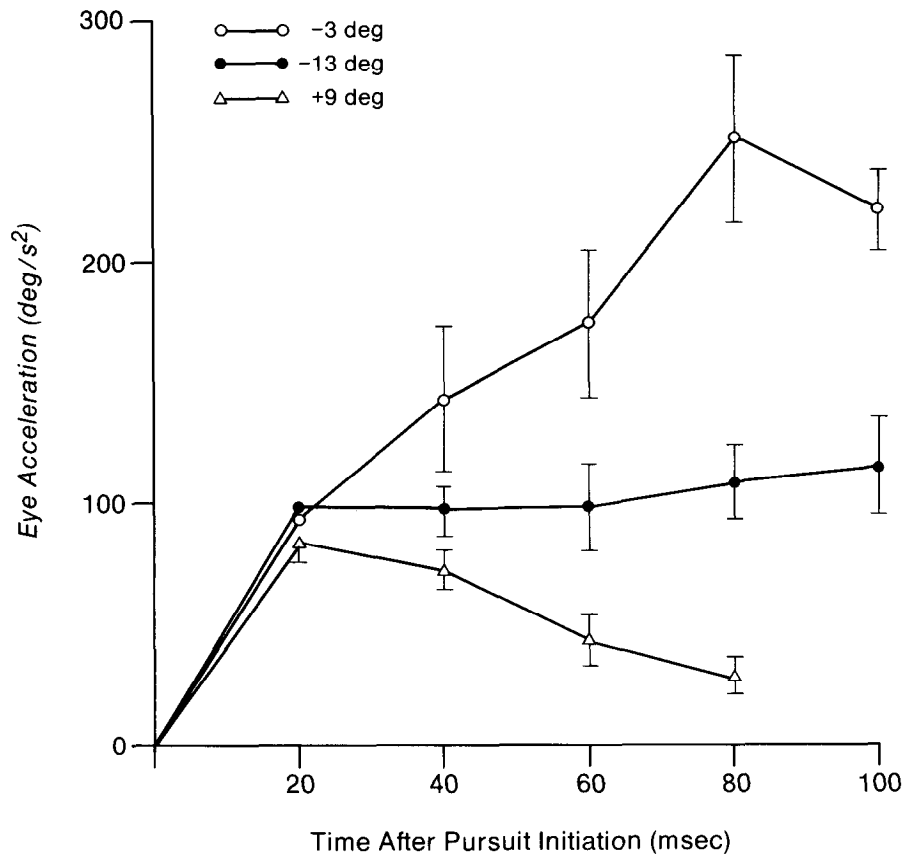


Figure 2. Quantitative analysis of the effect of image position on the initiation of rightward pursuit for target motion at 30°/sec. The data points show instantaneous eye acceleration in each 20-msec interval in the first 100 msec of pursuit. Points were plotted at times that represent the end of the interval over which accelerations were measured. Targets moved towards the fovea from 13° left (-13) or 3° left (-3), or away from the fovea from 9° right (+9). Each point is the average of measurements made on at least 10 identical trials; error bars indicate SEs of the mean.

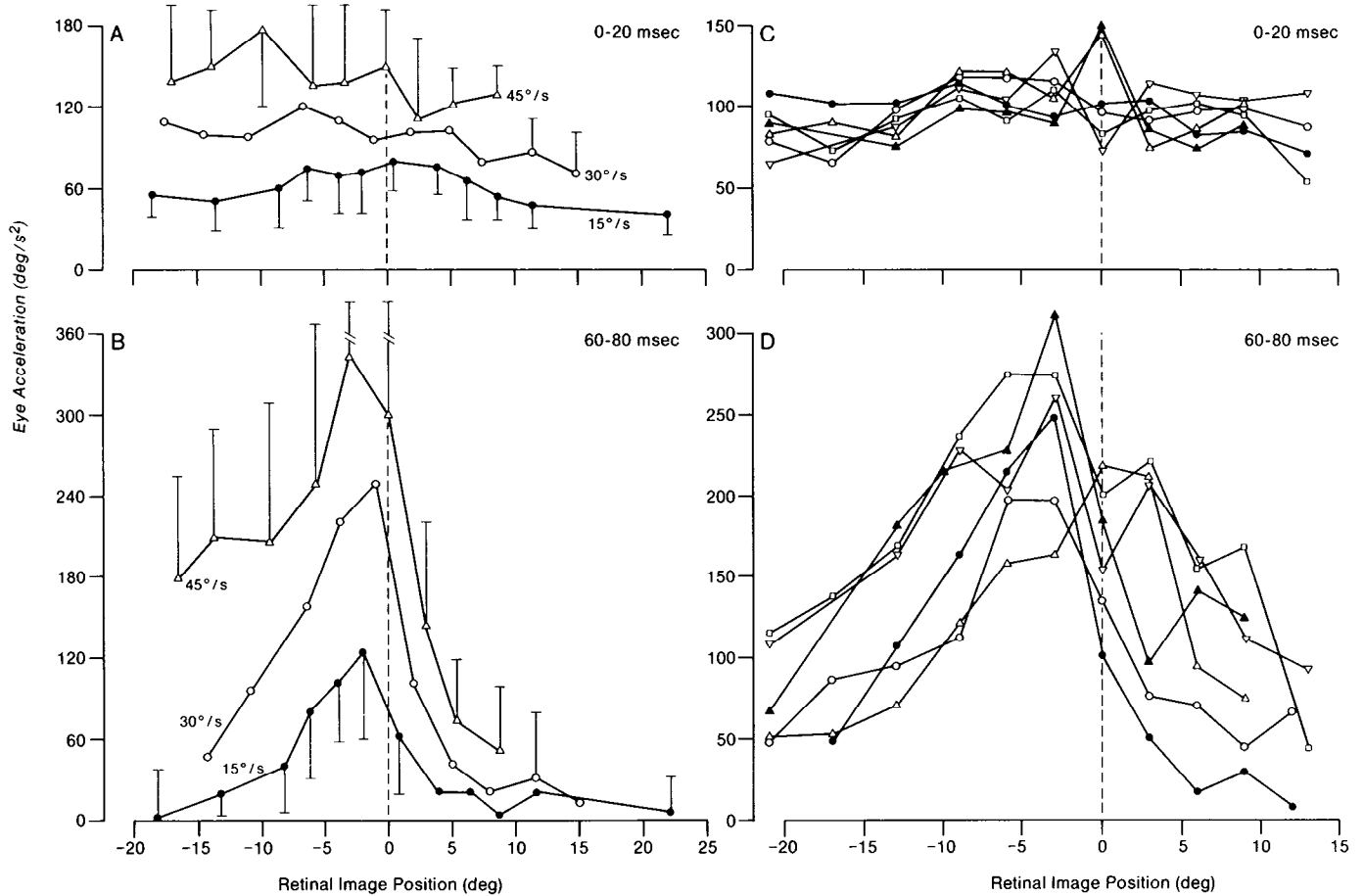


Figure 3. Effect of image position on the initiation of pursuit for target velocities of 15, 30, and 45°/sec. A, Instantaneous eye acceleration in the 0- to 20-msec interval for rightward pursuit in one monkey. B, Instantaneous eye acceleration in the 60- to 80-msec interval for the same trials used in A. In A and B, different symbols represent different velocities of target motion. Each point is the average of at least 10 trials; error bars indicate SDs. For A and B, points were plotted at a value that represented the average position of the moving stimulus in the time between the onset of target motion and the initiation of pursuit. C and D, Data for target motion at 30°/sec for both directions of target motion and all three monkeys. Points plotted to the left of zero retinal image position represent trials in which images moved towards the fovea. The experiments at 15 and 30°/sec were repeated in two monkeys with the barpress task; results were the same as shown here.

In Figures 2, 6, and 7, we have shown the SE of the mean to give an estimate of the statistical reliability of the averaged values.

The moment of pursuit initiation was usually unambiguous and analysis of the data did not require any subjective judgements by the operator. Trials were discarded if some ambiguity existed. Some of the experiments were analyzed independently by two investigators, yielding the same results. In addition, for many of our experiments we averaged eye velocity for at least 20 responses to a given stimulus. Averages were aligned on the onset of target motion; thus, the trial-to-trial variability in pursuit latency caused some ambiguity in the precise latency for pursuit initiation in the averaged records. Nonetheless, analyzing the latency and initial eye acceleration from the averaged records yielded results like those obtained by averaging the eye accelerations measured in individual trials.

Results

We begin by presenting the effects of various stimulus parameters on eye velocity during the first 100 msec after the initiation of pursuit in closed-loop conditions. At the conclusion of the "Results," we will show that the eye movements in this interval provide an accurate index of the open-loop pursuit response. Therefore, the relationships we have found should be direct reflections of the properties of the visual signals that are relayed to the pursuit system.

Effects of image position

Figure 1A shows an individual trial that illustrates how most of our data were obtained. The trial started with the monkey fixating a stationary target at straight ahead gaze (dashed line) and the

moveable target illuminated and stationary at an eccentric position (9° left in Fig. 1A). When the fixation point was extinguished, the target began to move to the right at 30°/sec along the horizontal meridian. The monkey always initiated pursuit before executing a saccade; thus, the smooth eye velocity before the saccade was a response to image motion across a retinal position that was determined by the initial position of the eccentric target.

For a given image velocity, the eye acceleration of pursuit initiation was more rapid when the images fell close to the fovea. Fig. 1B compares three averages of eye velocity for trials in which the moving images began at 3, 9, and 17° left and moved to the right at 30°/sec. Pursuit was initiated with a latency of 83 msec (downward arrow) and the first 40 msec of eye velocity was independent of initial image position (until the upward arrow). Thereafter, the eye velocity was highest when the images began 3° off the fovea and lowest when they began 17° off the fovea.

Figure 2 shows the time course of instantaneous eye acceleration for a similar experiment in which target speed again was 30°/sec. In this and most subsequent graphs, each point represents the mean eye acceleration in 20 msec bins for at least 10 to 20 individual responses to a given stimulus (see "Materials and Methods"); error bars show SEs of the mean. In the first 20 msec of pursuit, eye acceleration was independent of initial image position. Thereafter, eye acceleration was highest when the images started 3° eccentric and moved towards the fovea (open circles), intermediate when the images started at 13° and moved towards the fovea (filled circles),

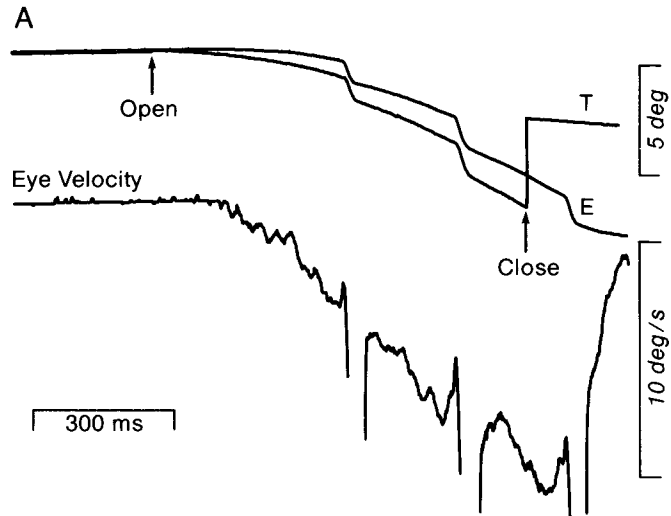
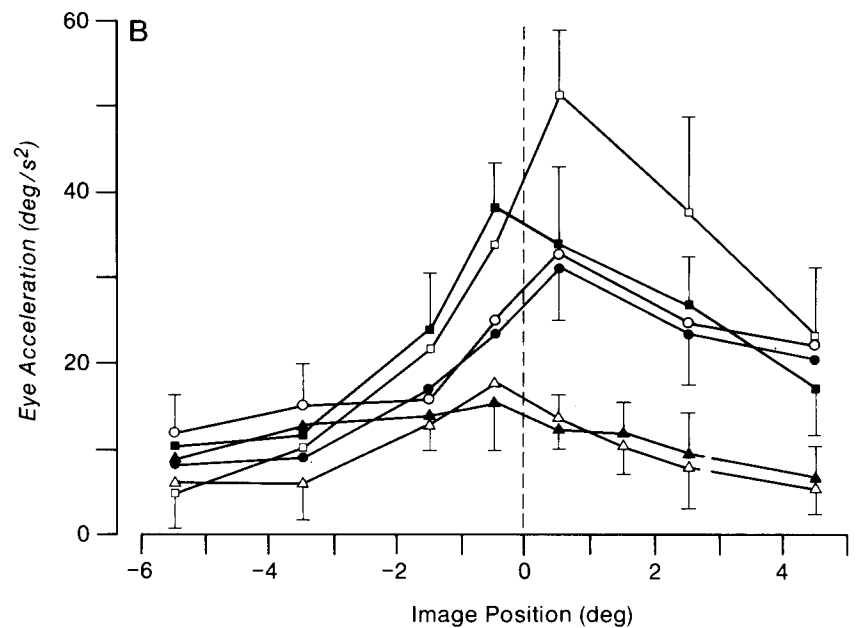


Figure 4. Effect of image position on the response to small image velocities. *A*, A single trial in which open-loop conditions were established for 800 msec between the two upward arrows. Image velocity was always $2^\circ/\text{sec}$ to the left and the target began on the fovea. *B*, Average eye acceleration as a function of image position for both directions of image motion in all three monkeys. Error bars represent SDs. This experiment was repeated with the bar-press task, yielding the same results shown here.



and lowest when the images started at 9° and moved away from the fovea (*open triangles*).

Figure 3, *A* and *B*, summarizes the effect of image position on the initiation of pursuit for rightward target motion at 15, 30, and $45^\circ/\text{sec}$ in one monkey. In this and subsequent figures, we have shown data for the first 20 msec of pursuit ("0- to 20-msec interval") and for 60 to 80 msec after the initiation of pursuit ("60- to 80-msec interval"). Values for the 20- to 40- and 40- to 60-msec intervals were generally intermediate. Image position had little effect on eye acceleration in the 0- to 20-msec interval (Fig. 3*A*), except at target motion of $15^\circ/\text{sec}$ when eye acceleration was slightly higher for images close to the fovea. For all three velocities, eye acceleration in the 60- to 80-msec interval (Fig. 3*B*) was highest when the images fell close to the fovea and decreased sharply as a function of increasing eccentricity. In addition, Figure 3*B* shows an asymmetry such that images moving towards the fovea (*negative values on abscissa*) across a given retinal position caused higher accelerations than those moving away from the fovea (*positive values of image position*). For example, image motion at a velocity of $45^\circ/\text{sec}$ and an eccentricity of 5° caused eye accelerations of $250^\circ/\text{sec}^2$ for motion towards the fovea and of $75^\circ/\text{sec}^2$ for motion away from the fovea.

Figure 3, *C* and *D*, show data for both directions of target motion

at $30^\circ/\text{sec}$ in all three monkeys; points to the left of 0 represent image motion towards the fovea. In five of the six curves, eye acceleration in the 60- to 80-msec interval (Fig. 3*D*) had the asymmetry of Figure 3*B*, and was higher for image motion towards the fovea. The remaining curve (*open triangles*) was an exception; eye acceleration was higher for image motion away from the fovea. One exception also occurs in Figure 3*C*. The monkey shown by *triangles* exhibited a peak in eye acceleration in the 0- to 20-msec interval at zero retinal image position. Background illumination did not affect the shapes of the relationships shown in Figures 1 to 3. In addition, the results were the same when target brightness was kept constant by starting the moveable target of the center of the screen and having the fixation target appear at various eccentric positions.

Two facts must be considered when interpreting our data. (1) There is substantial trial-to-trial variability in the monkey's performance, even for a given set of stimulus conditions in a single experimental session. The variability is shown by the *error bars* in Figure 3, *A* and *B*, which are SDs of eye acceleration and are representative of our data. (2) There can be systematic variations in pursuit gain and in the responses to a given stimulus in successive experimental sessions. For example, the three velocities shown in Figure 3, *A* and *B*, were studied one at a time in three experimental sessions on consecutive days. In addition, one or two trials at each velocity were

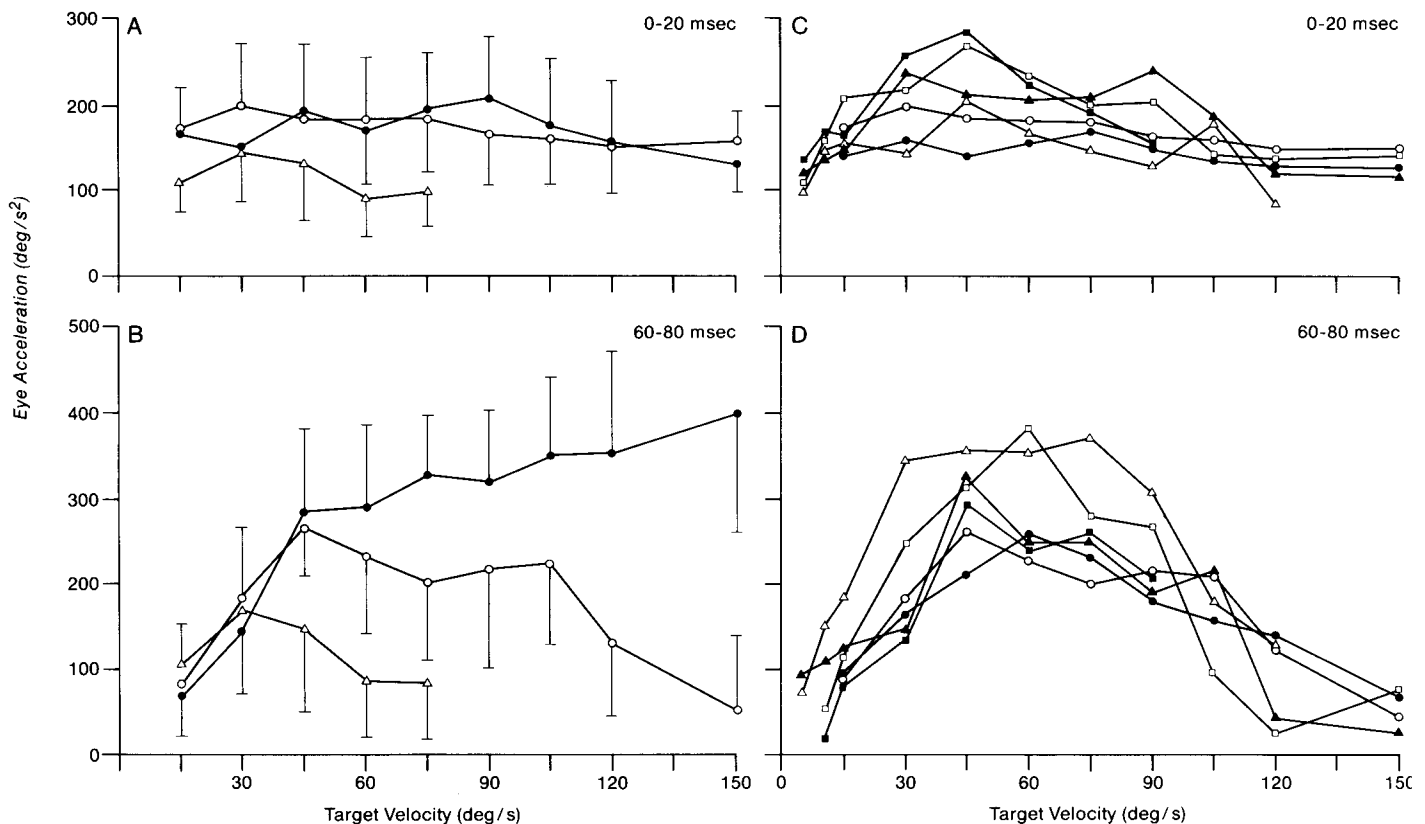


Figure 5. Effect of image velocity and background illumination on the initiation of pursuit. *A*, Instantaneous eye acceleration in the 0- to 20-msec interval; *B*, instantaneous eye acceleration in the 60- to 80-msec interval. In *A* and *B*, filled symbols show responses when the target was projected in otherwise dark surroundings; open circles show responses when the background was diffusely illuminated and the target was 2.2 log units above human perceptual threshold; open triangles show responses when the target was 1.2 log units above human perceptual threshold. *C* and *D*, Eye acceleration in the 0- to 20- and 60- to 80-msec intervals for both directions of image motion in all three monkeys. The background was dimly illuminated so that contrast between the target and background was 2.0 to 2.2 log units. Each point represents averages from at least 20 trials. Initial image positions were: 2° for motion of 15°/sec; 3° for 30 and 45°/sec; 4.5° for 60°/sec; 5.5° for 7.5°/sec; 6° for 90°/sec; 6.5° for 105°/sec; 7.5° for 120°/sec; 9° for 150°/sec. Image motion was always towards the fovea. In *A* and *B*, the error bars show SDs.

studied on all 3 days; a given stimulus caused eye accelerations that were highest on the day when most trials used target motion at 45°/sec and lowest on the day when most trials were at 15°/sec. Thus, the higher accelerations at higher target velocities in Figure 3, *A* and *B* should not be taken as an accurate estimate of the velocity selectivity of the pursuit system, since it exaggerates the effect of target velocity (see Fig. 5). All our monkeys increased pursuit gain by as much as 40% when the experiment required higher eye velocities. However, the shapes of the various relationships did not change.

The relationship between eye acceleration and image position also held at low image velocities. In Figure 4*A*, the monkey attempted to track a target that started at straight ahead gaze and began to move in true open-loop conditions to provide image motion to the left at 2°/sec for 800 msec. The monkey made both saccadic and smooth movements to catch the target. Figure 4*B* shows average eye acceleration during the 800-msec of open-loop stimulation for both directions of image motion at 2°/sec in all 3 monkeys. Initial retinal image position was up to 6° off the fovea; points to the left of zero represent image motion towards the fovea. Once again, eye acceleration was consistently larger when images were close to the fovea. Two of the monkeys showed an asymmetry with stronger responses for image motion away from the fovea. When we imposed the same image positions in open-loop conditions, but with image velocities of zero, the monkeys made saccadic but not smooth eye movements to track the target.

Velocity selectivity and the effect of background illumination

Figure 5, *A* and *B*, shows the effects of target velocity and background illumination for one monkey. Target velocity ranged from 15 to 150°/sec in 15°/sec increments and targets started at the retinal eccentricities that caused the largest eye accelerations. When the stimulus was presented against a dark background (filled circles), eye acceleration in the 0- to 20-msec interval (Fig. 5*A*) was independent of stimulus velocity, at least for velocities higher than 15°/sec. When the screen was illuminated diffusely so that the contrast between target and background was 2.2 log units (open circles), there was little change in the eye acceleration in the 0- to 20-msec interval. When the target was dimmed by one log unit (Fig. 5*A*, triangles) or the background illumination was increased by one log unit (not shown), eye acceleration in the 0- to 20-msec interval was smaller and showed slight decreases as target velocity was increased above 30°/sec.

Eye acceleration in the 60- to 80-msec interval depended strongly on both target velocity and background illumination. When the background was dark, (Fig. 5*B*, filled circles) eye acceleration increased as a function of stimulus velocity over the entire range we studied. Background illumination caused eye acceleration in the 60- to 80-msec interval to become selective for a middle range of target velocities. When the contrast between the target and background was 2.2 log units (open circles), eye acceleration in the 60- to 80-msec interval increased over the range 0 to 45°/sec, was maximal at 45°/sec, and decreased for higher velocities. When contrast was decreased by one log unit (Fig. 5*B*, triangles) eye acceleration in

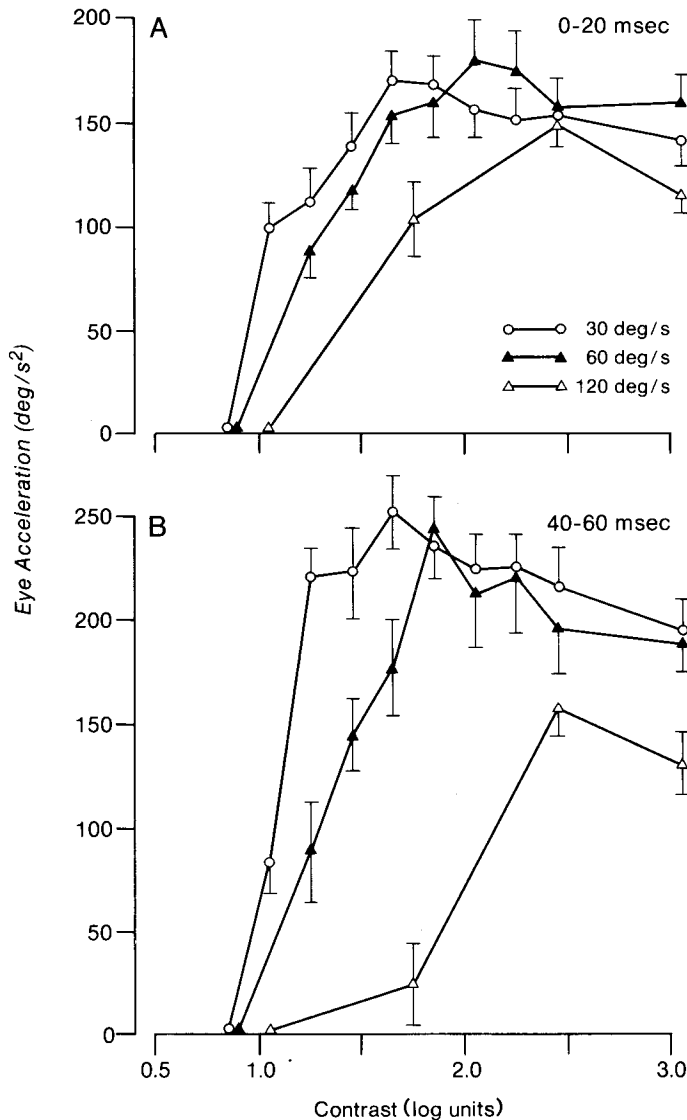


Figure 6. Effect of contrast on the initiation of pursuit. A, Eye acceleration in the 0- to 20-msec interval. B, Eye acceleration in the 40- to 60-msec interval; it was necessary to use the earlier interval because shorter latencies for pursuit implied that eye acceleration in the 60- to 80-msec interval could be affected by visual feedback, at least for high levels of contrast. Error bars show SE of the mean.

flash, the data were like those obtained in darkness with the brighter target.

Figure 5, C and D, show data for both directions of target movement in all 3 monkeys when the background was illuminated so that the contrast was 2.2 log units. Eye acceleration in the 60- to 80-msec interval was selective for velocities of 30 to 90°/sec (Fig. 5D), while eye acceleration in the 0- to 20-msec interval (Fig. 5C) remained independent of target velocity. In Figure 5C, one monkey (open and filled squares) was a minor exception to the general rule; eye acceleration in the 0- to 20-msec interval was somewhat selective for the middle range of target velocities.

Figure 6 documents the effect of contrast on the initiation of pursuit for a limited number of target velocities. When contrast was 0.8 log units or less, monkeys were unable to initiate pursuit for targets moving at 30, 60, or 120°/sec. Above this threshold, eye acceleration in the 0- to 20- and 40- to 60-msec intervals increased as a function of increasing contrast, reaching maxima at contrasts of 1.6 to 2.4. Further increases in contrast caused small but repeatable decreases in eye acceleration. In Figure 6B, we have plotted eye acceleration in the 40- to 60-msec interval because high contrasts caused the latencies for the initiation of pursuit to become less than 80 msec. In this instance, the 60- to 80-msec interval could include the first effects of visual feedback, and would not be a good estimator of the open-loop response of the pursuit system (see later).

Effects of stimulus size

The shape of the stimulus had little effect on the initiation of pursuit. Increasing the height of a 5-min square spot to a vertical bar 5 min of arc wide and up to 6° high caused no change in the shape of either the relationship between eye acceleration and image position or the relationship between eye acceleration and stimulus velocity. However, the height of the vertical bar did affect the magnitude of eye acceleration at all image positions and velocities. Increasing the height from 5 min to 1.5° caused a 25 to 50% increase in the eye acceleration throughout the first 100 msec of pursuit. Further increasing the height to 6° caused no further increase in eye accelerations. Systematic adjustments of target intensity showed that this increase was not caused by increases in the total amount of light; the results were the same whether bars of different heights contained equal flux or equal luminance.

Effect of target acceleration on eye velocity in the 0- to 20-msec interval

Figure 7 compares stimulus conditions in which the final target velocity was the same, but the rate of target acceleration was different. Figure 7B shows a single trial in which one spot was visible and moved at 15°/sec while the monkey viewed the fixation point (dashed line). When the fixation point was extinguished, the monkey was required to change targets and track the moving spot. Thus, Figure 7B provides a stimulus containing pure image velocity. Figure 7A shows another trial in which the final target velocity was 15°/sec, but the stimulus contained a step change in target velocity; this stimulus provides the pure velocity stimulus plus a target acceleration of 750°/sec². The eye velocity records in Figure 7, A and B, are representative of the averages for the two types of trials and show that the eye acceleration was more rapid and the latency for pursuit initiation shorter when the stimulus included target acceleration. Figure 7C compares the time courses of eye acceleration for these two stimuli. The responses were similar in the 60- to 80-msec interval, but the eye accelerations were larger in the earlier intervals of the response when the stimulus included target acceleration.

To further document the effect of target acceleration on eye acceleration on the initiation of pursuit, we measured the pursuit caused by target motion that accelerated at different rates to a final velocity of 5°/sec. Figure 7D shows the time courses of eye acceleration for three different target accelerations: 62.5, 125, and 500°/sec². Eye acceleration in the 0- to 20- and 20- to 40-msec intervals

the 60- to 80-msec interval remained selective for target velocity, but the maximum acceleration occurred at a lower target velocity of 30°/sec. At the lower contrast, monkeys were unable to complete trials at target velocities higher than 75°/sec; however, there was often short-lived smooth pursuit, suggesting that the response was still intact in the 0- to 20-msec interval, but not in the later intervals. It is worth noting that decreases in the contrast between the target and background affected primarily pursuit of high target velocities; there was little or no effect on the responses to target motion at 15 or 30°/sec.

We do not believe that the effects of background illumination on eye acceleration can be explained as a lack of effort by the monkey. For most of the target velocities, accurate tracking required a combination of smooth pursuit and saccades, and the latencies of the saccades were independent of background illumination. In addition, the effects cannot be explained by target brightness alone. When the target was presented in darkness, but dimmed so that it was 1.5 log units above our threshold for detecting a 100-msec

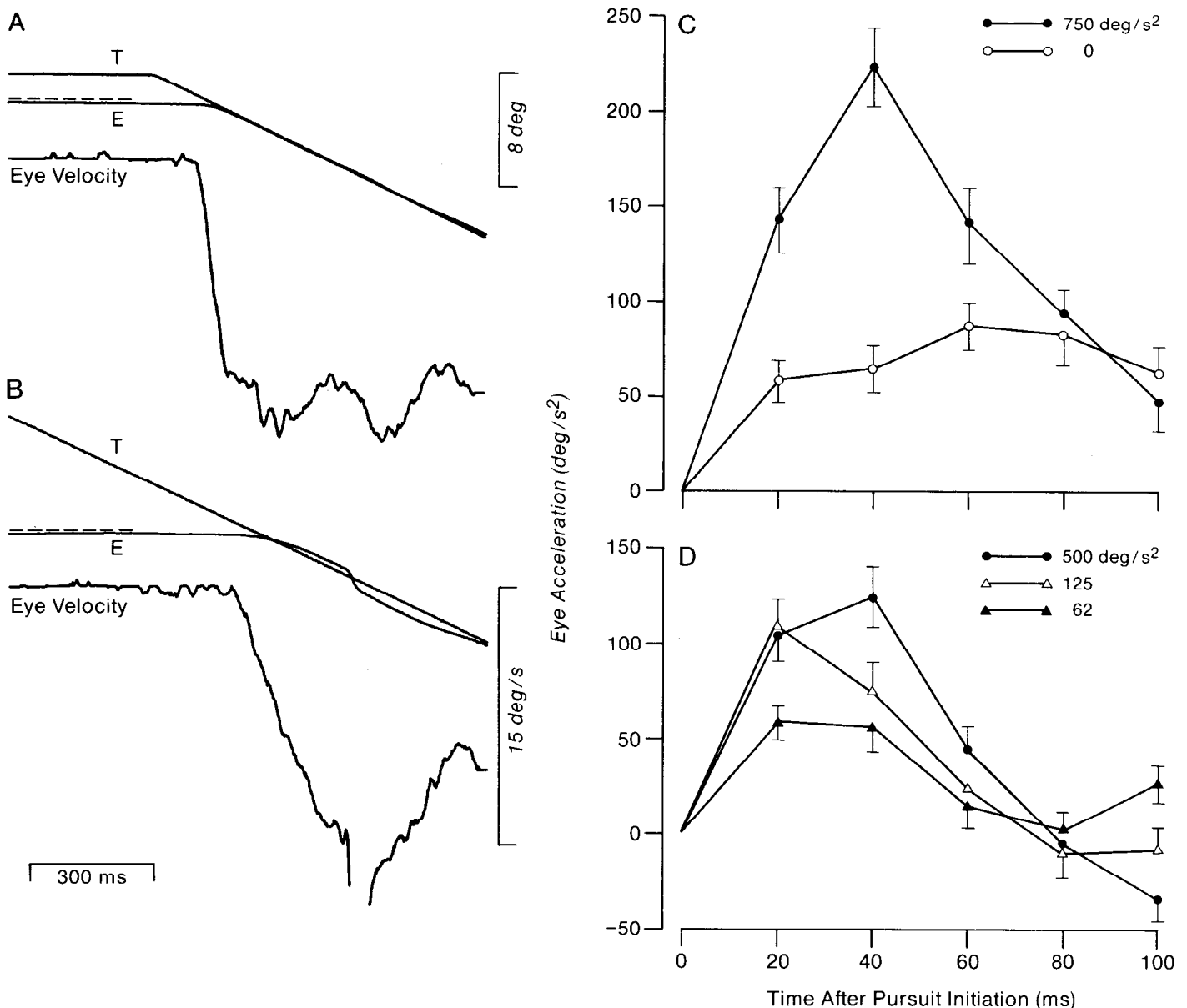


Figure 7. Effect of target acceleration on the initiation of pursuit. *A*, A single trial in which a combined target acceleration and velocity stimulus were provided by having the illuminated tracking target undergo a step change in target velocity (to 15°/sec) when the fixation point (horizontal dashed line) was extinguished. *B*, A pure target velocity stimulus was provided by requiring the monkey to change fixation from the stationary fixation point (dashed line) to a tracking target that was visible and moving to the left at 15°/sec. *C*, Time course of eye acceleration for the two types of trials shown in *A* and *B*; 750°/sec² refers to the trial that contains a step of target velocity up to 15°/sec (*A*), while 0°/sec² refers to the pure velocity stimulus (*B*). *D*, A family of curves showing the time course of eye acceleration as a function of the initial target acceleration (shown by the numerals in the legends). Final target velocity was 5°/sec. In *C* and *D*, each point represents the average of the eye accelerations measured from at least 20 trials. Points were plotted at times that represent the end of the interval over which accelerations were measured. Error bars show SEs of the mean.

depended on the rate of target acceleration, while eye acceleration in the later intervals did not.

Parameters affecting the latency of pursuit

At a given stimulus velocity, increases in contrast caused decreases in pursuit latency (Fig. 8*A*) to values that averaged 75 msec when the target was a small spot presented across an illuminated background. The latency averaged 60 msec when the pursuit stimulus was a very bright vertical bar 6° high and 5 min wide. Figure 8*A* also shows that stimulus velocity had only a small effect on pursuit latency, at least for high contrasts. Image position on the retina had a small effect that was more pronounced for target motion at 15 than at 30°/sec (Fig. 8*B*); more eccentric positions were associated with slightly longer latencies. To obtain the data in Figure

8*B*, the fixation point was moved to eccentric positions so that the tracking target always started at the center of the screen. Thus, the small effects on latency cannot be a secondary effect of the decreased intensity of the target at eccentric positions on our projection screen. Figure 8 shows data from one monkey, but all three monkeys had similar latencies.

Latency of visual feedback after pursuit initiation

Figures 9 and 10 show that the eye movements we measured to obtain Figures 1 to 8 (the first 100 msec after the initiation of pursuit) are the same as those that occur during true open-loop stimulation. In Figure 9*A*, the monkey tracked a target that underwent a 2° step to the left and simultaneously began to move to the right at 8°/sec. Open-loop tracking conditions were imposed at the time of the step-

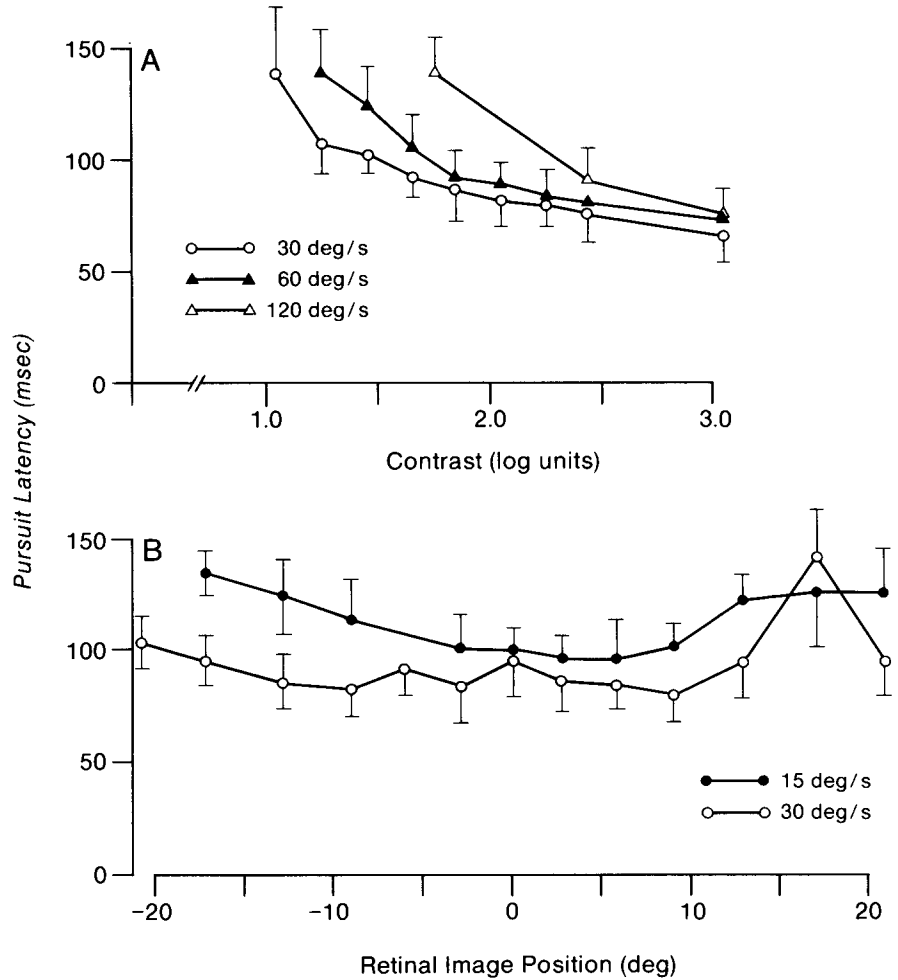


Figure 8. Parameters affecting the latency of pursuit. A, Effect of contrast at three velocities. B, Effect of image position at fixed contrast. Filled symbols show latencies for target motion at 15°/sec, open symbols target motion at 30°/sec. Each point represents averages of 10 to 20 trials. Error bars show SDs.

ramp to maintain image motion at 8°/sec. This caused eye velocity to increase nearly linearly throughout the 600 msec of open-loop tracking. In Figure 9A, the velocity record labeled "closed" is from a trial in which the target also underwent a 2° step to the left and motion at 8°/sec to the right, but in normal closed-loop conditions. The first 150 msec of the closed-loop record (up to the upward arrow) was the same as in the comparable open-loop trial.

In a single experimental session, open- and closed-loop trials with stimulus velocities ranging from 1 to 24°/sec were interspersed randomly; initial image positions were adjusted so that saccades were seldom made in the first 300 msec of pursuit. For closed-loop tracking (Fig. 10; filled circles), eye acceleration in the first 100 msec of pursuit was averaged for at least 20 trials at each velocity and plotted as a function of target velocity. For open-loop tracking (Fig. 10, open circles), eye acceleration was measured across the entire interval of open-loop stimulation, and the averaged values were plotted as a function of image velocity (which is different from target velocity in open-loop conditions). The relationship between eye acceleration and stimulus velocity was nearly the same for closed-loop and open-loop conditions.

Figure 9C shows trials used to determine the latency for the first visual feedback. When the fixation point went out, the target began to move at 5°/sec; at the time pursuit was initiated (vertical dashed line), target velocity was increased to 15°/sec. The latency at which the increase to 15°/sec affected pursuit should be the latency of the first visual feedback. We determined this time by comparing the resulting eye velocity record (labeled 5/15) to one from a trial in which target velocity remained at 5°/sec (labeled 5). For these examples, the change in target velocity from 5 to 15°/sec affected eye velocity with a latency of 127 msec (upward arrow).

We measured the latency for the first visual feedback from averages of eye velocity like those in Figure 9, B and D. For example, Figure 9D compares averaged eye velocity responses from the types of trials shown in Figure 9C. The latency of pursuit initiation averaged 104 msec, while the change in target velocity from 5 to 15°/sec affected eye velocity with a latency (upward arrow) averaging 90 msec (range, 77 to 112 msec in 3 monkeys). Figure 9B compares averaged responses to 5°/sec target motion in open- and closed-loop conditions. For the two monkeys that were studied, the latency of pursuit initiation averaged 100 msec and the averages from open- and closed-loop stimulation diverged (upward arrow) after an interval averaging 117 msec (range, 93 to 139). Thus, the latency for visual feedback during pursuit is equal to or just shorter than the latency for the initiation of pursuit, and is at least 80 msec.

Discussion

We have used step changes in target position and velocity to impose known retinal stimuli and obtain estimates of the open-loop response of the pursuit system. We have found a number of relationships between pursuit and the visual stimuli that we cannot attribute to properties of the motor pathways. During saccades, the vestibulo-ocular reflex (Lisberger, 1984) or even pursuit of sinusoidal target motion (Lisberger et al., 1981), monkeys can attain eye accelerations higher than those reported here. In fact, many of our findings represent a failure of the monkey to achieve smooth eye accelerations that he could attain if the visual properties of the stimulus or background were changed. Thus, we attribute the relationships documented here to the properties of the visual cell populations that provide inputs for pursuit. Later in the "Discussion,"

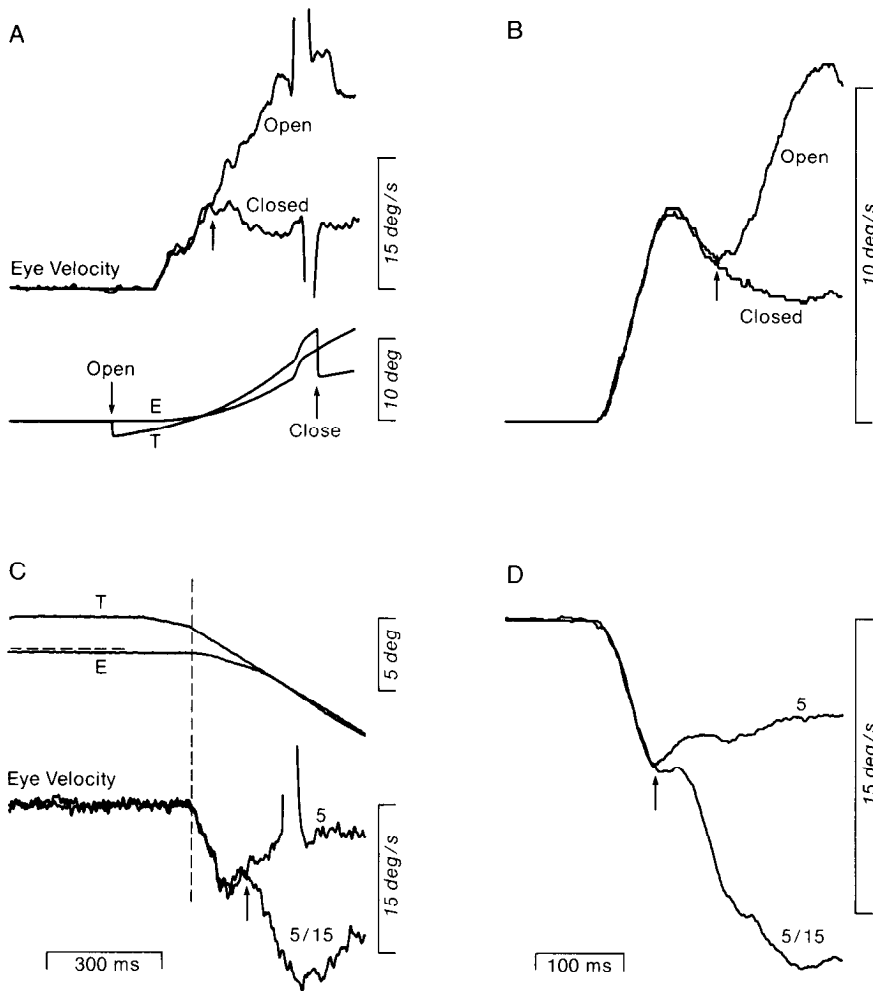


Figure 9. Absence of visual feedback in the first 100 msec of pursuit. *A*, The monkey tracked a target that underwent a 2° step to the left and moved at $8^\circ/\text{sec}$ to the right. The $8^\circ/\text{sec}$ stimulus was maintained by imposing open-loop conditions for 600 msec. The eye velocity record labeled "closed" is from a trial that started out like that shown here, but remained in closed-loop mode. *B*, Comparison of averaged eye velocity for 20 responses to target motion at $5^\circ/\text{sec}$ in open and closed-loop conditions. The upward arrow indicates the first visual feedback. *C*, A single trial in which the target began moving at $5^\circ/\text{sec}$ and underwent a further increase to $15^\circ/\text{sec}$ when pursuit was initiated (vertical dashed line). The resulting eye velocity record is labeled 5/15. The superimposed eye velocity record labeled 5 was taken from a trial in which target velocity remained at $5^\circ/\text{sec}$. Comparison of the two records shows the time (upward arrow) at which the $15^\circ/\text{sec}$ target motion had its first effect on eye velocity. *D*, Comparison of eye velocity averages for the two kinds of trial shown in *C*. Each average was made from at least 20 responses to identical stimuli. The upward arrow indicates the time at which eye velocity was affected by the increase in target velocity from 5 to $15^\circ/\text{sec}$.

we will argue that at least two visual cell populations play a role, and that they differ in their visual response properties.

The first 100 msec of pursuit as an estimate of open-loop responses

Most of our data were obtained during closed-loop conditions in which the monkey ultimately was able to catch and track the target. Nonetheless, we have been able to study the open-loop response by restricting our analysis to the first 100 msec of pursuit. Comparison of the initiation of pursuit in closed-loop and true open-loop conditions verified that the first 100 msec of pursuit do not rely on visual feedback (Figs. 9 and 10). In addition, we have shown that the latency for the first visual feedback was only a few msec shorter than the latency for the initiation of pursuit (Fig. 9).

It was essential to restrict our analysis to the first 100 msec of pursuit, since many of the most interesting features of our data would have been obscured if we had measured pursuit performance after feedback had occurred. For example, there is little or no relationship between eye velocity and initial image position at later times, since the combination of saccadic eye movements and visual feedback allow the monkey to look at the target and rotate his eyes at target velocity. An advantage of our approach is that it affords estimates of open-loop performance without imposing stimuli the monkey cannot track or intervening in his normal pursuit strategies.

Eye acceleration as a measure of pursuit gain

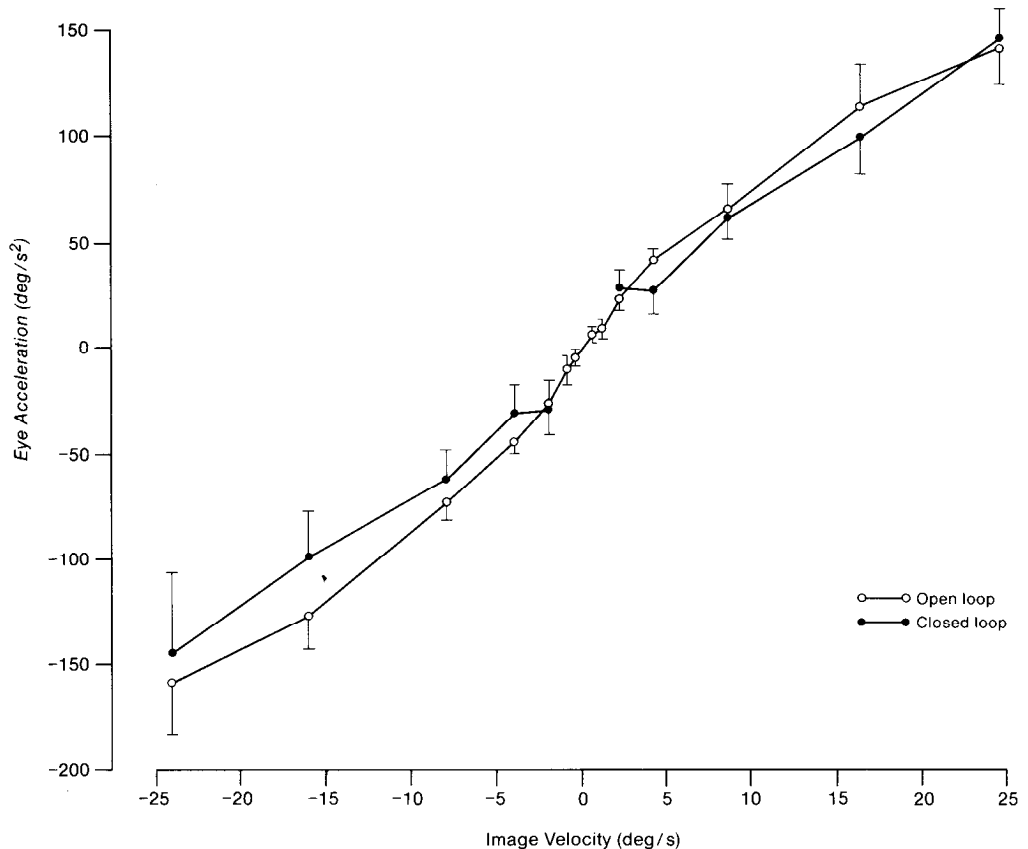
Several observations suggest that the pursuit system treats visual inputs as commands for eye accelerations, and that eye acceleration is therefore the best measure of the effectiveness of a given stimulus. (1) During tracking of sinusoidal target motion, eye acceleration is

the only parameter of eye movement that is consistently related to retinal image velocity (Lisberger et al., 1981). (2) Eye velocity is maintained when open-loop conditions are used to ensure zero retinal errors (Morris and Lisberger, 1983); therefore, visual inputs are needed only to change eye velocity. (3) True open-loop stimulation with constant retinal image velocity caused a constant eye acceleration that was sustained throughout the open-loop conditions (Fig. 9A) and that had a magnitude related to the imposed image velocity (Fig. 10).

Components underlying the initiation of pursuit

Subdividing the first 100 msec of pursuit into 20-msec intervals revealed qualitative differences in the effects of various visual parameters on eye acceleration in the early and late intervals. This suggests that there are at least two components underlying the initiation of pursuit. One component is most sensitive to sudden changes in image velocity (Fig. 7), receives inputs uniformly from at least the central 20° along the horizontal meridian, and is equally responsive over the range of velocities we studied. In our experimental situation, this component had a transient time course and was responsible for the eye acceleration measured in the 0- to 20-msec interval. The second component is stimulated by image velocity, receives inputs that emphasize the central retina, usually prefers motion towards the fovea, and is selective for a middle range of velocities when the surroundings are stationary and visible. This component has a sustained effect on eye velocity, and dominates the eye acceleration in the 60- to 80-msec interval. We assume that the eye accelerations in the 20- to 40-msec and 40- to 60-msec intervals reflect contributions from both components, although there may be other components not revealed by our experiments.

Figure 10. Quantitative comparison of eye acceleration in closed-loop and open-loop conditions. For closed-loop conditions (*filled symbols*), the graph plots average eye acceleration in the first 100 msec of pursuit as a function of the velocity of the target ramp. For open-loop conditions (*open symbols*), the graph plots average eye acceleration throughout the period of open-loop stimulation as a function of imposed image velocity. The duration of open-loop stimulation was 800 msec for image velocities of 4°/sec or less, 600 msec for image velocities of 8°/sec, and 400 msec for image velocities of 16 and 24°/sec. Each *point* is the average of measurements made on at least 20 trials, and *error bars* indicate SDs. Positive values indicate rightward and negative values leftward image velocities and eye accelerations.



We failed to find a large contribution from a third component that has been reported by Pola and Wyatt (1979). These authors have shown that human subjects can initiate pursuit in the direction of image position and opposite to the direction of image motion; we have only rarely seen this happen in monkeys. It seems unlikely that a separate input related to retinal position errors could be responsible for our observations on the effect of image position (Figs. 1 to 4). (1) Position errors should work together with velocity errors to enhance the response to images that moved away from the fovea; in fact that combination produced only weak initiation of pursuit. (2) Pursuit was not initiated (but saccades did occur) when open-loop conditions were used to impose small position errors without any image motion across the retina. We do not believe that our failure to produce pursuit in the direction of retinal position errors represents a failure to adequately motivate the monkeys, since we have been able to elicit reliable and large responses to retinal position errors during ongoing pursuit (Morris and Lisberger, 1983). The basis for this difference between our work and that of Pola and Wyatt (1979) will be resolved only if monkeys and humans can be tested using the same methodology and apparatus.

Neural basis of the components underlying the initiation of pursuit

The goal of our experiments was to measure oculomotor performance in a way that would define the receptive field properties of cell populations providing visual inputs for the initiation of pursuit. Because of the profound effect of cortical lesions on pursuit (Goldberg et al., 1982; Zee et al., 1982; Newsome et al., 1985), we believe that visual inputs utilize pathways through the visual areas of cortex. The distinct properties of the two components underlying the initiation of pursuit suggests that at least two different populations of cortical cells could be involved. For example, cells throughout the corticopontine projection system have properties that may be appropriate to drive eye velocity in the 0- to 20-msec interval. They show direction-selective responses, have large receptive fields, and respond over a wide range of stimulus speeds (Baker et al., 1976). In

addition, the projection from the cerebral cortex onto the pontine nuclei deemphasizes central retina (Cohen et al., 1981).

Similar logic suggests that cells in the MT may be appropriate to drive eye velocity in the 60- to 80-msec interval. The majority of the cells in MT are direction selective and tuned for velocity, with most preferred velocities between 2 and 128°/sec (Maunsell and van Essen, 1983; Van Essen et al., 1981). There is good agreement between the velocity selectivity of the initiation of pursuit in the 60- to 80-msec interval (Fig. 5D) and the ensemble average of firing rate in a large sample of MT cells that were studied in visual conditions similar to ours (Fig. 7B of Maunsell and Van Essen, 1983). In contrast, direction selective cells in the striate cortex are tuned for a 10-fold lower range of stimulus velocities (Fischer et al., 1981) and do not correspond as a population with our data (Fig. 5D). Finally, MT contains a topographic map of the visual field that has an expanded representation of the central 10° of retina (Van Essen et al., 1981). However, our data already show that at best a subset of cells in MT can be providing visual signals for the initiation of pursuit, since eye acceleration in the 60- to 80-msec interval is highest for images moving towards the fovea, while cells in MT as a population show no such preference (Maunsell and Van Essen, 1983; Albright et al., 1984).

The properties of the dorsolateral pontine nucleus are compatible with the scenario outlined above. Suzuki and Keller (1984) have shown that cells in this nucleus have direction selective responses to small moving stimuli. The responses appear to have two components, one that is activated uniformly across wide regions of retina and one that is activated only in central retina. Anatomical studies have shown that the dorsolateral pons receives inputs from the corticopontine projection (Brodal, 1978; Glickstein et al., 1980) as well as from MT (Fries, 1981). In turn, the dorsolateral pontine nucleus projects to areas of the vestibulo-cerebellum that are probably important for the generation and coordination of smooth pursuit (Brodal, 1979).

One of the most remarkable aspects of our findings is the

complexity of the relationships between eye acceleration and the visual parameters of our stimuli. We were surprised to find so many nonlinearities when the eye movement response to continuous target motion is so smooth and superficially linear. In retrospect, however, it seems reasonable to find such complexities, since microelectrode recordings have revealed some combination of these and other properties in every population of visual cells that has been studied. It appears that the pursuit system has made use of a wide variety of visual signals that may exist in species lacking good pursuit systems and that must subserve other motor and perceptual functions as well.

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