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A comparison of head-unrestrained and head-restrained pursuit: influence of eye position and target velocity on latency

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Abstract Horizontal step-ramp target trajectories were used to study the initiation of head-unrestrained and head-restrained pursuit in the monkey. In a first series of experiments, initial target position (0°, 5°, or 30°, contraversive to the direction of pursuit), fixation duration, target velocity (20°, 40°, 60° and 80°/s), and target direction were randomized in order to minimize predictive responses. Animals pursued the target either with their eyes alone (head-restrained: HR condition) or with a combination of eye and head movements (head-unrestrained: HU condition). Head motion onset consistently lagged pursuit onset (i.e., eye motion) by 50 ms or more in the HU condition, and was influenced by target velocity as well as by initial target position. Pursuit onset latencies did not vary systematically as a function of target velocity in either the HR or HU conditions. However, pursuit initiation latencies tended to be longer in the HU condition as compared to the HR condition when target motion started from the most contraversive position. A second series of experiments revealed that this difference in HR and HU pursuit onset latencies could be explained by the effects of initial eye-in-head position; more contraversive initial eye positions yielded shorter pursuit latencies in both conditions, and the monkeys generally moved their head towards the target in the HU condition, resulting in smaller eye-in-head eccentricities. Furthermore, we found that initial gaze and head positions had little or no effect on pursuit latencies. We conclude that the latency for pursuit initiation is similar irrespective of whether an animal is head-restrained or head-unrestrained, when initial eye position is held constant.

Key words Pursuit · Gaze · Eye movements · Head movements · Eye position

Introduction

Smooth pursuit eye movements allow primates to stabilize on the fovea an object that is moving across a stationary visual background. The smooth pursuit system is generally modeled as a negative feedback controller in which the difference between target velocity and eye velocity (i.e., a retinal velocity error signal) drives the pursuit eye movement (reviewed in Lisberger et al. 1987). Moreover, several studies have demonstrated that retinal position and acceleration error signals can also be effective stimuli during smooth pursuit (position error: Morris and Lisberger 1987; Segraves and Goldberg 1994; acceleration error: Lisberger et al. 1981, 1987; Morris and Lisberger 1987; Krauzlis and Lisberger 1994). In addition to visual error signals, non-visual mechanisms can influence smooth pursuit eye movements during sustained tracking. For example, it has been shown that the frequency response of smooth pursuit is enhanced by target predictability (Stark et al. 1962; Dallos and Jones 1963; Michael and Melvill-Jones 1966; Bahill et al. 1980; Collewijn and Tamminga 1984; Yasui and Young 1984; Barnes et al. 1987).

Although smooth pursuit eye movements have been well characterized when the head is restrained, only a small number of studies have characterized pursuit when the head is free to move (head-unrestrained). During natural behaviors, where the head can move freely, primates frequently generate smooth head as well as eye movements in order to follow a moving object (Gresty and Leech 1977; Lanman et al. 1978; Barnes 1981; Barnes and Lawson 1989; Cullen and McCrea 1990; Barnes and Grealy 1992; Smith et al. 1995; Wellenius et al. 1997). The resultant movement of the visual axis relative to space, termed gaze pursuit, is defined as the sum of the motion of the eye and head (gaze = eye-in-head + head-in-space). Prior studies of gaze pursuit using predictable

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target motion have reported little or no difference in the frequency response of gaze accuracy when compared to head-restrained smooth pursuit (Lanman et al. 1978; Barnes 1981; Leigh et al. 1987; Cullen and McCrea 1990). However, since predictive mechanisms are utilized by the pursuit system in the head-unrestrained as well as the head-restrained condition (Barnes and Grealy 1992), it is likely that these studies best demonstrated that predictive mechanisms similarly enhance the pursuit response in both conditions. Indeed, when target motion is unpredictable, pursuit gains (gaze velocity/target velocity) have been shown to be higher during head-unrestrained gaze pursuit than during head-restrained smooth pursuit (Cullen and McCrea 1990; Waterson and Barnes 1992; Smith et al. 1995); the improvement in tracking is most evident during pursuit of higher velocity target motion.

The maintenance of smooth eye-only pursuit and gaze pursuit has been studied during sustained tracking of a wide variety of target trajectories: sinusoidal, aperiodic pseudorandom and constant-velocity target movements. In contrast, the *initiation* of smooth pursuit has almost exclusively been studied during the initial phase (0–100 ms) of tracking of step-ramp target trajectories (Rashbass 1961; Robinson 1965; Lisberger et al. 1981; Lisberger and Westbrook 1985; Robinson et al. 1986; Tychsen and Lisberger 1986; Carl and Gellman 1987; Morris and Lisberger 1987; Lisberger and Pavelko 1989; Krauzlis and Lisberger 1994; Mann and Morrow 1997). Step-ramp target trajectories are a popular choice of stimulus in studies of pursuit initiation since, by choosing a step magnitude of the appropriate size, they can be used to initiate smooth eye movements that are free of corrective saccades (Rashbass 1961). In the head-restrained primate, the pursuit system responds to changes in target motion with a delay of 100 ms. Thus the first ~100-ms interval of pursuit is unique in that it operates in the absence of corrective visual feedback.

Several factors have been reported to affect the latency of pursuit initiation in head-restrained humans and monkeys. For example, visual properties of the target, such as size and contrast, can influence pursuit latency (Lisberger and Westbrook 1985; Tychsen and Lisberger 1986). The longest pursuit latencies are generally elicited by small, low-contrast targets. In addition, when step-ramp trajectories are used, pursuit latency tends to increase as a function of step size (Lisberger and Westbrook 1985; Tychsen and Lisberger 1986). Because of conflicting results, the effects of target velocity on pursuit latency are still unclear (Lisberger and Westbrook 1985; Carl and Gellman 1987; Morrow and Lamb 1996; Mann and Morrow 1997).

To date, all characterizations of pursuit initiation have been done with the head restrained. The goal of the present study was to investigate whether the latency of pursuit initiation differs when an animal is head-restrained compared to when it is free to move its head, as well as its eyes, to track the target. Specifically we: (1) compared pursuit onset latencies during head-unrestrained and head-restrained pursuit for the same step-ramp target

trajectories, (2) investigated whether initial gaze, eye, and/or head position influenced pursuit latencies, (3) determined the effect of target velocity (20–80°/s) on the latency of head-restrained versus head-unrestrained pursuit, and (4) characterized the influence of target eccentricity and velocity on the latency of the head motion component of the pursuit response during head-unrestrained pursuit.

Materials and methods

Animal preparation and experimental setup

Two monkeys (*Macaca mulatta*) were prepared for chronic recording of eye movements. All procedures were approved by the McGill University Animal Care Committee and were in compliance with the guidelines of the Canadian Council on Animal Care. The methods for surgical preparation of the animals were similar to those described by Cullen et al. (1991). Briefly, a scleral search coil was implanted in the right eye of each animal in order to monitor gaze position (Judge et al. 1980). To facilitate the immobilization of an animal's head, a stainless steel post was attached to the skull with stainless steel screws and dental acrylic. All surgeries were carried out under aseptic conditions.

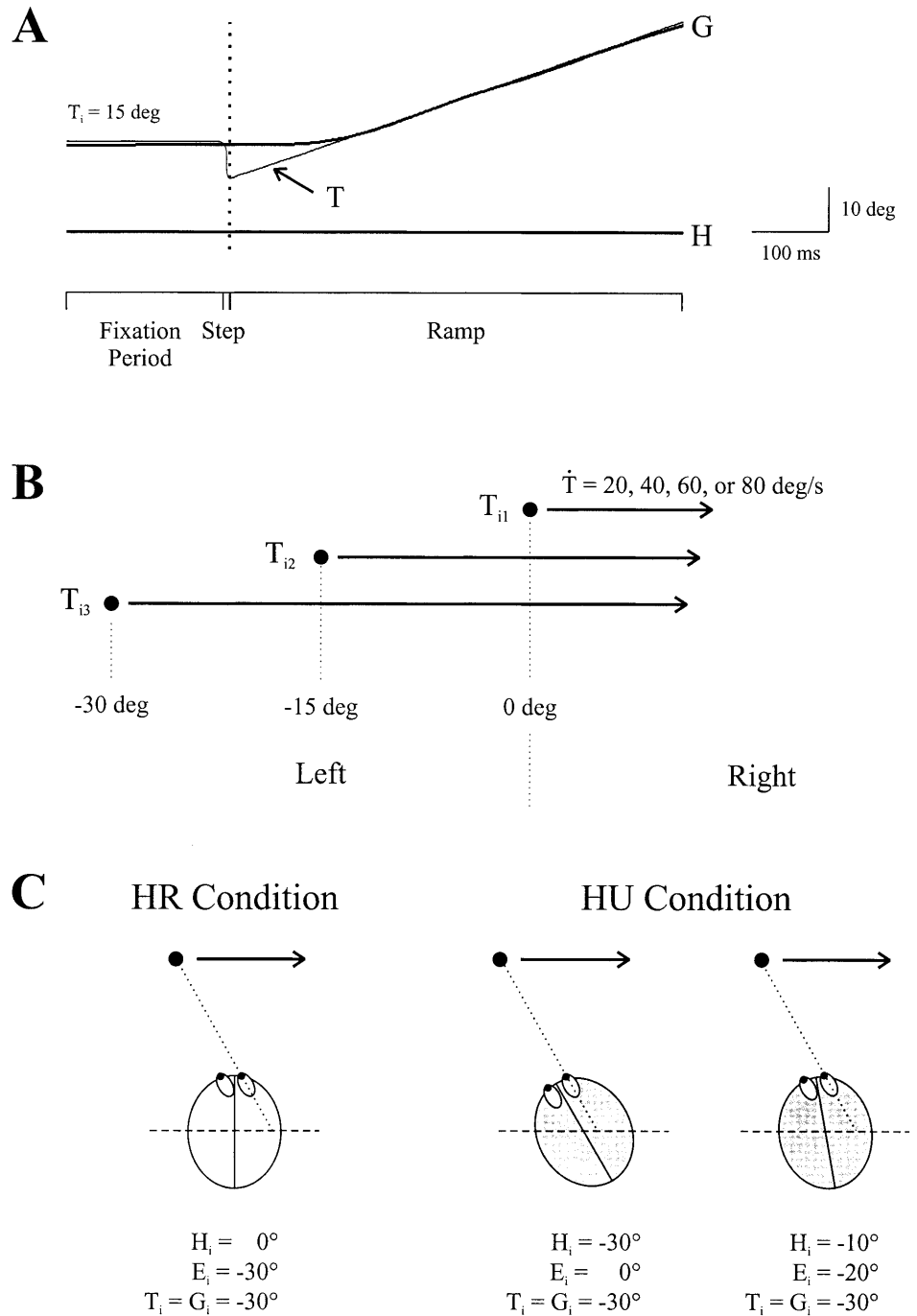
During training and experimental sessions, monkeys were comfortably seated in a stationary primate chair. The chair was placed in the experimental apparatus so that the animal's head was centered within a 1-m³ magnetic field coil system (CNC Engineering). Gaze and head positions were recorded using the magnetic search coil technique (Fuchs and Robinson 1966). A specially designed head-holder (Roy and Cullen 1998) enabled us to either completely immobilize the animal's head (head-restrained) or allow the animal full freedom of head motion (head-unrestrained). Monkeys were trained to track a small (0.3° in diameter) visual target for a juice reward. The target was generated by a HeNe laser and projected onto a white cylindrical screen, located 60 cm away from the monkey's eyes. The target was positioned on the screen by a pair of mirrors mounted on two computer-controlled galvanometers (General Scanning). Throughout experiments, target contrast was 3 log units above human perception, as measured by the method of Lisberger and Westbrook (1985). Since the visual properties of the target can affect the initial pursuit response (see "Introduction"), the size and contrast of the target were kept constant throughout these experiments.

Behavioral paradigms

Smooth pursuit was elicited by moving the target in a horizontal step-ramp trajectory (Rashbass 1961). A trial began when the animal fixated a stationary target. After a random fixation period (750–1500 ms) the target was stepped either towards the left or right, and then began moving at a constant velocity in the direction opposite to that of the step. By choosing the appropriate step size, it was possible to obtain smooth eye movements that were not preceded by corrective saccades (Rashbass 1961). The step size was initially adjusted for each target velocity in each animal such that the target spot crossed the initial target position after ~125 ms, and then remained fixed for subsequent target presentations in all experiments. Figure 1A shows an example trial of head-restrained pursuit made in response to step-ramp target motion. In this example, the target underwent a leftward position step which was immediately followed by a ramp in position (60°/s, constant velocity) towards the right. In turn, the monkey generated a smooth eye movement that was not preceded by a corrective eye saccade.

In the example in Fig. 1A, the initial step in target position was provided by quickly changing the position of a single target spot. This resulted in a brief target sweep in the direction opposite to

Fig. 1 **A** Example of a step-ramp target trajectory from monkey C. Initial target position was -15° and target velocity was $60^\circ/\text{s}$ towards the right. Because the head was restrained in the example shown, gaze position = eye position. Vertical dotted line indicates onset of the target ramp. **B** Illustration of the rightward ramp trajectories used in experiment 1. Initial target positions for these ramps were -30° , -15° , or 0° (T_{i3} , T_{i2} , and T_{i1} , respectively), and target velocities were 20° , 40° , 60° , or $80^\circ/\text{s}$. **C** In the HR condition, initial eye and gaze position were always identical. In contrast, in the HU condition, a given initial gaze position could be associated with a variety of initial eye positions and initial head positions. G_i , E_i , H_i , and T_i are initial gaze, eye, head, and target positions, respectively. G , E , H , and T are gaze, eye, head, and target position trajectory, respectively, and T' is target velocity



that of the ensuing ramp. Control trials were carried out using targets that began from center position (i.e., the target location at which the eye was centered in the orbit) and, following a step in target position, moved horizontally at 20° , 40° , 60° or $80^\circ/\text{s}$. In these control trials, two separate target spots were used. One spot was used for the initial fixation (fixation target), and the second was used for the position ramp (ramp target; constant velocity). The initial step was created by the disappearance of the fixation target and the simultaneous appearance of the ramp target (Lisberger and Westbrook 1985). Under these conditions, no qualitative differences were observed in either: (1) the dynamics of the target ramp motion or (2) the pursuit response of either monkey, as compared to the case where a single target was used. All subsequent experiments were carried out using a single target spot.

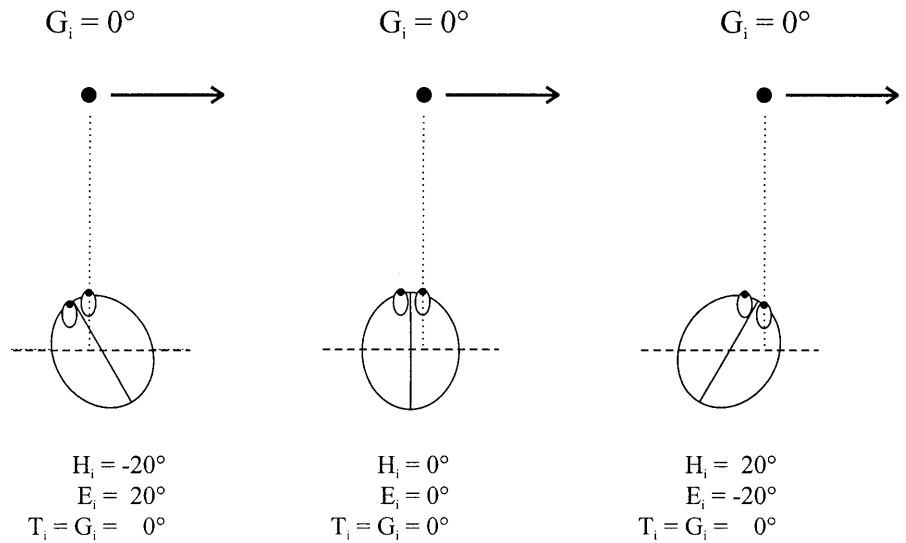
Experiment 1

Pursuit was elicited by horizontal step-ramp trajectories with a constant velocity of 20° , 40° , 60° , or $80^\circ/\text{s}$ towards the left or towards the right. A wide range of target velocities was used in order to determine whether pursuit latencies differed for combined eye-head pursuit versus smooth pursuit in a velocity-specific manner. In addition, initial target positions which were increasingly more contraversive with respect to the direction of pursuit were used. Rightward moving targets were initially presented at 0° , -15° , or -30° , where negative numbers indicate leftward positions relative to center position (0°). Leftward ramps began at 0° , 15° , or 30° , where positive numbers indicate rightward positions relative to center position. Rightward ramps terminated between 20°

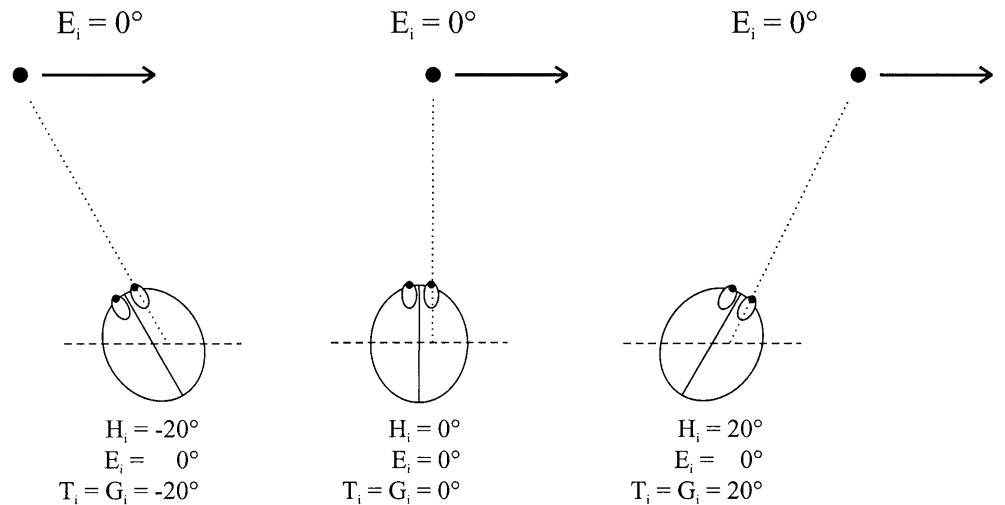
Fig. 2A, B Experiment 2.

A In the E_{var} condition, initial gaze (i.e., target) position was held constant and initial eye position was varied by statically placing the head in different positions. **B** In the G_{var} condition, initial gaze position was varied by statically placing the head in different positions and aligning initial target position with initial head position. Initial eye position was held constant in this condition (i.e., approximately centered in the orbit). Abbreviations are the same as those used in Fig. 1

A E_{var} Condition



B G_{var} Condition



and 25° . The exact end point was randomly chosen within this range for each target trajectory. Similarly, leftward ramps terminated between -20° and -25° . In all experiments, both leftward and rightward trajectories were presented. Since it was not the purpose of the present study to investigate differences between nasally and temporally directed pursuit, we elected to restrict our analysis to temporally directed movements (i.e., the responses of the right eye during rightward pursuit in both animals) during both head-restrained and head-unrestrained pursuit. Figure 1B illustrates example ramp trajectories towards the right. The initial starting positions are denoted by T_{i1} , T_{i2} , and T_{i3} and correspond to initial target positions of 0° , -15° , and -30° , respectively.

During the experiment, an animal's head was either: (1) completely immobilized so that pursuit was accomplished with the use of eye movements alone (head-restrained: "HR condition") or (2)

allowed full freedom of motion so that pursuit was accomplished with a combination of eye and head movements (head-unrestrained: "HU condition"). Each experimental session was divided into two to four separate HR and HU condition blocks. Within each block of trials, initial target position, target velocity, target direction, and fixation period were randomized. The order in which the HR and HU blocks were presented was varied on a daily basis.

In both the HR and HU conditions, initial gaze position (gaze = eye-in-head + head-in-space) approximated initial target position before a trial was initiated ($\pm 3.0^\circ$). In the HR condition, the head was held stationary at 0° , and therefore initial eye and gaze positions were equivalent (i.e., $H_i = 0^\circ$, $E_i = G_i = T_i$). Accordingly, both initial eye and initial gaze positions were under experimental control. Figure 1C (left panel) shows a schematic of a head-re-

strained trial where initial target position was -30° . In contrast, in the HU condition, a given initial gaze position could be associated with a wide range of initial eye and head positions. Figure 1C (middle and right panels) shows two possible schematics of head-unrestrained trials where initial target position was -30° . Initial gaze position was -30° in both examples, but initial eye position was 0° in one case and -20° in the other. These differences in initial eye position corresponded to differences in initial head position ($H_i = -30^\circ$ vs -10° , respectively). Under the HU condition, therefore, only initial gaze position was under experimental control; for a given initial target position, initial eye and head positions depended on the monkey's behavior. Consequently, further experiments were required to dissociate the effects of initial eye and gaze position on the initiation of head-unrestrained pursuit.

Experiment 2

In order to systematically examine the effects of initial eye, head and gaze positions on the initiation of pursuit eye movements, step-ramp trajectories were presented to a head-restrained monkey under two conditions (Fig. 2). In the first condition, initial gaze position (i.e., target position) was held constant ($0 \pm 2^\circ$), and different initial eye positions were elicited by statically placing the head in different positions ("E_{var} condition"). Figure 2A illustrates that if initial gaze position is constant ($G_i = 0^\circ$), different initial eye positions ($E_i = 20^\circ, 0^\circ$, and -20°) can be elicited by restraining the animal's head in different positions ($H_i = -20^\circ, 0^\circ$ and 20° , respectively). In the second condition, initial gaze/head position was varied by statically placing the head in different positions, and setting initial target position equal to that of the head in space ("G_{var} condition"). In this condition, initial eye position was effectively held constant ($0 \pm 2^\circ$). Figure 2B illustrates that if eye position is held constant ($E_i = 0^\circ$), different initial gaze positions ($G_i = -20^\circ, 0^\circ$, and 20°) can be elicited by restraining the animal's head in different positions ($H_i = -20^\circ, 0^\circ, 20^\circ$, respectively). In both the E_{var} and G_{var} conditions, target velocity was always $60^\circ/\text{s}$. Note that experiment 2 was, in effect, an extension of the HR condition of experiment 1. However, there was an important difference between these two experiments: in experiment 2 the head was statically placed in different positions, while in the HR condition of experiment 1 the head was always held stationary at a single position (0°).

Data collection and analysis

REX, a QNX-based, real-time data acquisition system (Hayes et al. 1982), was used to control target position, monitor performance, and collect data. Gaze, head, and target position signals were filtered (eight-pole Bessel, DC-250 Hz) and then digitized at 1000 Hz. Raw data files were transferred to a Pentium PC for subsequent analysis under Matlab (MathWorks). Eye position was calculated as the difference between the recorded gaze position and head position signals. Gaze, eye, head, and target velocity traces were obtained by digitally filtering (DC-55 Hz) and differentiating the corresponding position traces.

Gaze movement onset latencies were calculated in individual trials by the method of Carl and Gellman (1987). Briefly, as shown in Fig. 3, gaze onset latency was defined as the interval between: (1) the onset of the target ramp and (2) the point at which a regression line fit to the baseline gaze velocity trace intersected a regression line fit to the initial pursuit response. The baseline regression was calculated over the interval of -50 to 50 ms relative to target onset. The initial pursuit response regression was computed between the point where gaze (= eye) velocity deviated from the baseline by more than 2.5 SD, and the time 45 ms later. Figure 3 shows velocity traces for the same example trial shown in Fig. 1A (experiment 1, HR condition, -15° , $60^\circ/\text{s}$). Note that for simplification, in this and subsequent figures, target motion is illustrated as a step in target velocity. The latency of pursuit onset was estimated as 84 ms in this example. The same method was used to determine the latency of gaze and head movement onset during head-unrestrained trials.

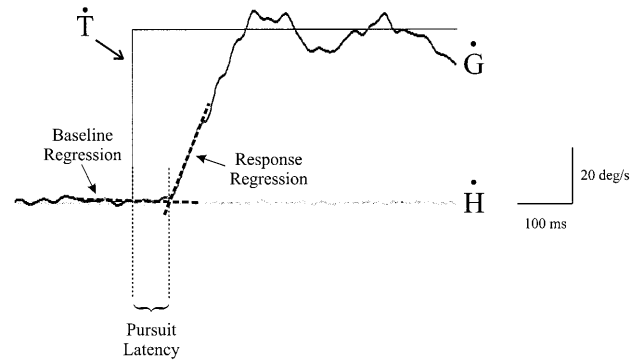


Fig. 3 Latency of movement onset was estimated from velocity traces as the intersection of a baseline regression and an initial pursuit response regression. The horizontal dashed line represents the baseline regression; the ascending dashed line represents the response regression. The left and right dotted vertical lines indicate the onset of target motion, and onset of the pursuit response, respectively. Note that, for the purpose of simplification, target motion is represented as a step in target velocity. In the example shown, the head was restrained such that gaze and eye velocity are equivalent. G' , H' , and T' are gaze, eye, head, and target velocity, respectively

To ensure that our measurements were not contaminated by saccades, we included only those trials that contained no saccades until at least 100 ms after gaze onset in the HR condition, and at least 100 ms after head onset in the HU condition. The latency of saccades was computed with respect to target onset using a gaze acceleration threshold ($>3500^\circ/\text{s}^2$). Each trial was visually inspected to ensure the accuracy of latency estimates. During head-unrestrained pursuit (experiment 1, HU condition), the distribution of head onset latencies for each of the stimulus conditions had a small number of outliers of unusually long latency (i.e., the median latency was less than the mean latency). For the purpose of statistical analysis, we normalized the distribution without shifting its location by eliminating values below the 5th and above the 95th percentile. Mean head latencies \pm SD provided in the "Results" were obtained from this data set.

In experiment 1, HR and HU conditions, average gaze onset latencies for each stimulus condition were computed from at least 20 responses to identical target presentations [mean (range) = 23 (20 – 28) and 31 (20 – 43) for monkeys B and C, respectively]. The following three comparisons were made between the 24 different experimental conditions (4 target velocities \times 3 initial target positions, head-restrained and head-unrestrained): (1) for each target velocity, a one-way analysis of variance (ANOVA) was carried out to determine whether pursuit onset latencies differed significantly across the three initial gaze positions. We then used a repeated-measures regression to determine whether pursuit onset latency was linearly related to initial gaze position. These two approaches yielded comparable levels of significance, and hence only the results of the regression analysis are reported in the results. (2) For each initial target position, a one-way ANOVA was used to determine whether gaze onset latencies differed significantly across the four target velocities. A repeated-measures regression was then used to determine whether gaze onset latency was linearly related to target velocity. Once again, these methods yielded comparable levels of significance and therefore only the results of the regression analysis are reported in the results. (3) In order to compare gaze onset latencies during head-restrained and head-unrestrained pursuit, data from the HR and HU conditions were compared for each stimulus condition. The significance of differences in gaze onset latencies in the HR and HU conditions was evaluated using Students' *t*-test. Comparable analyses were used to determine whether initial gaze position and/or target velocity influenced head motion onset latencies during head-unrestrained pursuit.

In the E_{var} condition of experiment 2, a total of 167 trials were collected at 8 different initial eye positions for monkey B, and 217 total trials at 10 different initial eye positions were obtained for monkey C. In the G_{var} condition, 102 total trials were collected at 5 different initial gaze positions for monkey B, and 310 total trials at 5 different initial gaze positions for monkey C. A repeated-measures linear regression was used to determine the strength of the relationship between either initial eye position (E_{var} condition) or initial gaze position (G_{var} condition) and gaze onset latency.

Results

The principal goal of the present study was to investigate whether the latency of initiation of head-unrestrained gaze pursuit differs from that of head-restrained smooth pursuit. Initial pursuit responses to the same step-ramp target stimulus are shown in Fig. 4 for monkey C in the HR (Fig. 4A) and HU conditions (Fig. 4B). In this example, initial position of the target was -30° (i.e., 30° to the left of center), and target velocity was $20^\circ/\text{s}$ in the opposite (i.e., rightward) direction. Figure 4A shows the gaze velocity responses for 22 individual trials (Fig. 4A, light lines) during head-restrained smooth pursuit of target motion. Individual gaze trials were aligned on gaze (= eye) movement onset to show the stereotyped nature of the initial pursuit response. The average gaze velocity trace (Fig. 4A, solid dark line) was superimposed on the individual trials (88 ± 8 ms, mean latency \pm SD). The results illustrated are typical in that gaze velocity lagged target velocity by ~ 100 ms.

Figure 4B shows the gaze velocity responses for 21 individual trials during head-unrestrained pursuit (HU condition: Fig. 4B, light lines) of the same step-ramp target stimulus shown in Fig. 4A. The average gaze and head velocity traces for these trials are also shown (solid lines). Gaze velocity lagged target velocity by 97 ± 13 ms, and head motion, in turn, significantly ($P < 0.005$) lagged gaze motion (328 ± 285 ms). Accordingly, the head movement response did not appear to contribute significantly to the initial pursuit response in the HU condition.

In the example shown in Fig. 4, the average pursuit response was faster in the HR condition as compared to the HU condition (Fig. 4B, compare dashed and solid dark lines). Indeed, at the most eccentric initial target position (-30°), average pursuit response latencies were consistently shorter for head-restrained pursuit than for head-unrestrained pursuit, for all four target velocities tested and in both animals (mean difference 5 and 6 ms for monkeys B and C, respectively), and these differences were significant ($P < 0.05$) for nearly half the cases tested. We decided to investigate this observation further, and postulated that at least two factors might contribute to such differences. First, during head-restrained pursuit, initial gaze, eye, and head position were experimentally controlled. However, this was not the case during head-unrestrained pursuit, where a given initial gaze position could be associated with a wide range of initial eye and head positions (see Fig. 1C). Since only initial gaze position was identical in Fig. 4A,B, it is possible that the ob-

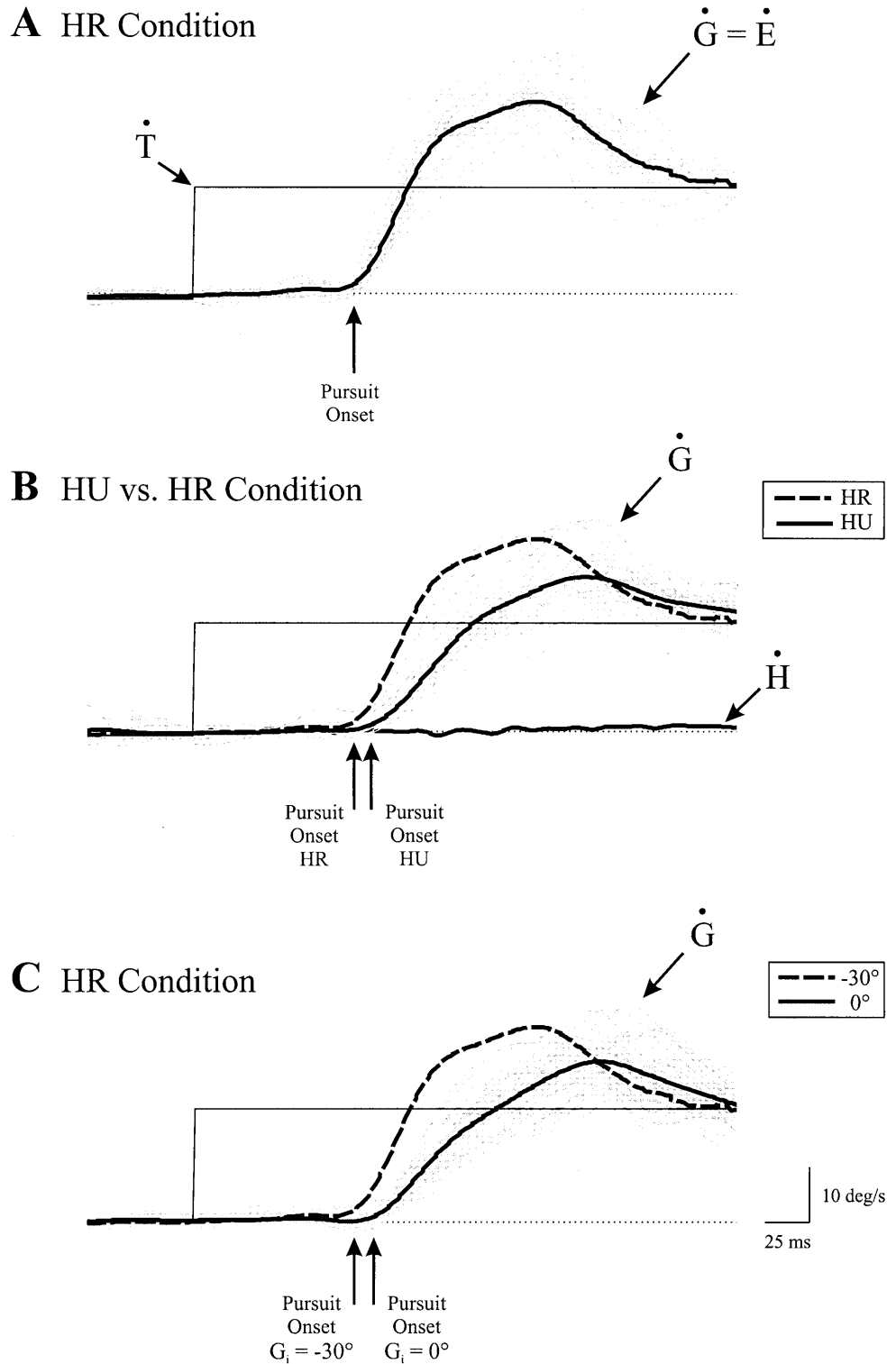
served difference in pursuit onset latencies could arise as a result of differences in initial eye or head positions during head-unrestrained versus head-restrained pursuit of the same target trajectory. Figure 4C shows that for head-restrained pursuit of $20^\circ/\text{s}$ target motion, the average response latency was significantly shorter for trials starting at the most contraversive eye position (-30°) than for trials starting at the central eye position (88 ± 8 ms vs 99 ± 9 ms, respectively, $P < 0.005$; Fig. 4C, compare dashed and solid dark lines). This suggests an influence of initial eye position on latency. Thus, the second goal of the present study was to investigate the effect of initial eye, gaze and head position on the latency of pursuit responses.

Effect of initial eye, gaze and head position

We first characterized the effect of initial eye position on pursuit latency during head-restrained pursuit (experiment 1, HR condition; Fig. 5). Because the head was held stationary at 0° during head-restrained pursuit, initial gaze and eye position were both equal to initial target position (see Fig. 1C). In Fig. 5A, the mean latency of pursuit is plotted as a function of initial gaze/eye position for the four target velocities tested. In this figure, and subsequent figures and tables, data for monkeys C and B are shown in the left and right panels, respectively. In both monkeys, mean head-restrained pursuit latency was inversely related to initial gaze/eye position. Histograms comparing the mean pursuit latencies for central (0°) and the most leftward initial gaze positions (-30°) highlight this effect (Fig. 5B, white vs solid bars, respectively). On average, a 30° shift in initial eye position resulted in a 17-ms decrease in pursuit latency for monkey B and a 10-ms decrease for monkey C. For each target velocity, in both animals, mean pursuit latencies decreased significantly for increasingly contraversive initial gaze positions. The level of statistical significance of this effect, based on regression analysis, is denoted by asterisks in Fig. 5B. Since during the HR condition of experiment 1, initial eye position equaled initial gaze position, the above results indicate that initial eye position *and/or* initial gaze position affected pursuit latencies.

We next investigated the effect of initial gaze position on the initiation of head-unrestrained pursuit, in order to determine whether the effect we observed in Fig. 5 was specific to head-restrained pursuit (i.e., where initial eye position was experimentally controlled). Figure 6A (experiment 1, HU condition) shows that during head-unrestrained pursuit, pursuit latency remained inversely related to initial gaze position. The effect of initial gaze position on pursuit latency during head-unrestrained pursuit is highlighted by the histograms of Fig. 6B, which presents the data in the same format as Fig. 5B. The response latencies elicited by more contraversive initial gaze positions tended to be shorter than those for more central initial gaze positions, for both monkeys, and for each of the four target velocities tested. On average, a

Fig. 4A–C Pursuit initiation in the HR and HU conditions of experiment 1. **A** Average gaze velocity (*dark line*) is superimposed on individual trials (*light lines*) during pursuit in the HR condition. **B** Average gaze velocity (*solid dark line*) is superimposed on individual trials (*light lines*) during pursuit in the HU condition. The average gaze velocity in the HR condition (*dashed dark line*) is shown for comparison. Average head velocity (*dark line labeled H'*) is also shown for the same trials, and significantly lags pursuit eye movement onset. Initial target position (-30°) and target velocity ($20^\circ/\text{s}$) was the same in the HU and HR conditions. **C** Average gaze velocity (*solid dark line*) is superimposed on individual trials (*light lines*) during pursuit of step-ramp target motion in the HR condition that began at the central (0°) target position. The average gaze velocity for step-ramp target motion that began at the most contraversive (-30°) target position is shown for comparison (*dashed dark line*). \dot{E} is eye velocity, and other abbreviations are the same as those used in Fig. 3. Note that the target velocity trace has been shifted by the mean response latency relative to the average gaze velocity response



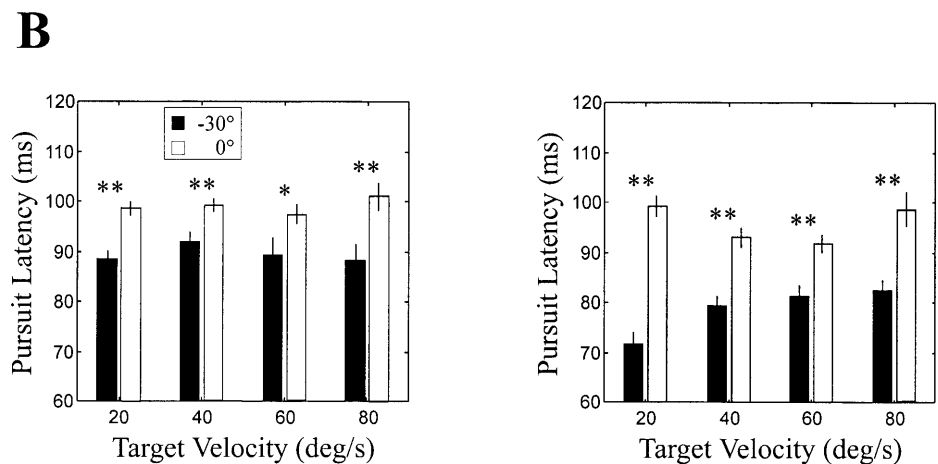
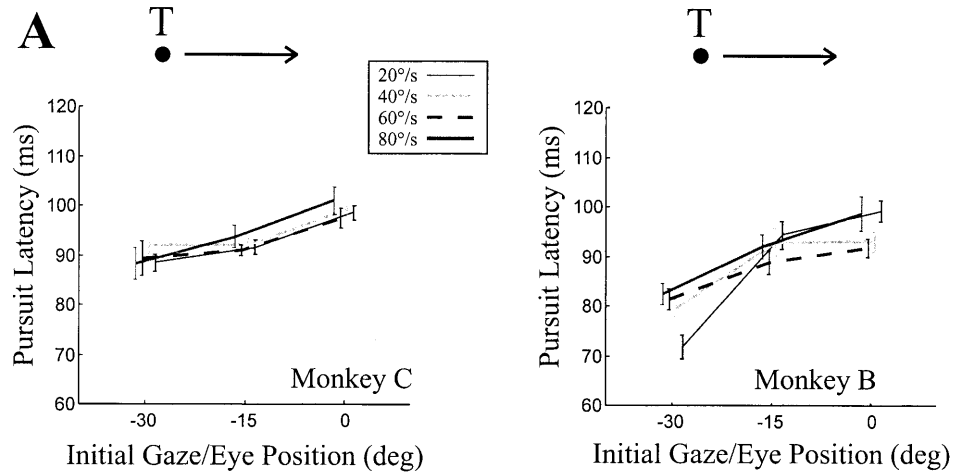
30° shift in initial eye position resulted in a 7-ms decrease in pursuit latency for monkey B and an 8-ms decrease for monkey C. The effect of initial gaze position on gaze onset latency was often, but not always, statistically significant (denoted by asterisks in Fig. 6B). Interestingly, while these results were similar to those obtained in the HR condition, the effect of initial gaze posi-

tion on pursuit latency was far less pronounced during head-unrestrained pursuit than during head-restrained pursuit (cf. Figs. 5B, 6B).

In the HU condition, only initial gaze position was under experimental control, while initial eye and head position were free to vary according to each animal's fixation strategy. Indeed, when fixating a target, our ani-

Fig. 5A, B Effect of initial gaze/eye position on pursuit latency during rightward pursuit in the HR condition. **A** Pursuit latency decreased for more contraversive initial gaze/eye positions. Each line type represents a single target velocity (20°, 40°, 60°, or 80°/s) (data points are offset slightly along the abscissa so that the error bars do not overlap). **B** Comparison of pursuit latency for central (0°, white bars) and the most contraversive (-30°, solid bars) initial gaze/eye positions. Statistical significance of the effect was determined using all three initial gaze/eye positions tested (* $P < 0.05$, ** $P < 0.005$; see “Materials and methods”). In this and subsequent figures, data are presented for monkey C on the left, and for monkey B on the right. Error bars represent SEM. Arrows indicate direction of the target (*T*) ramp motion

Experiment 1: HR Condition

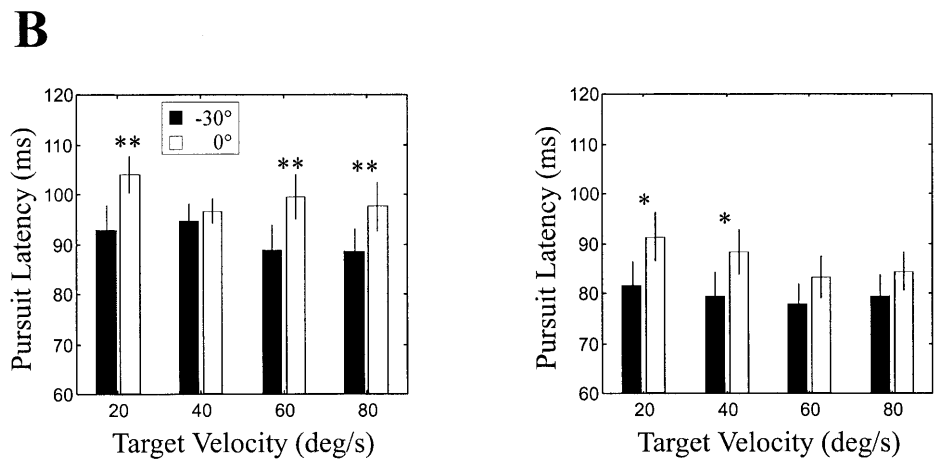
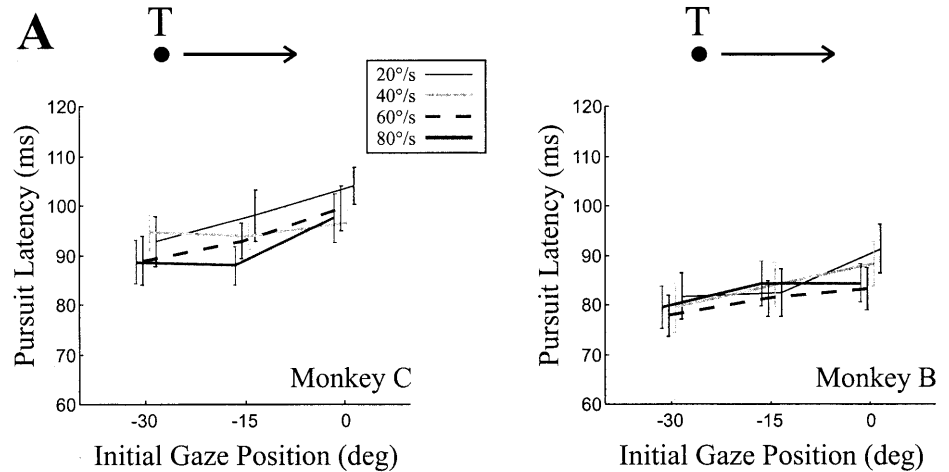


mals did not necessarily align their heads with the fixation target and center their eyes in their orbits, nor did they only move their eyes. Rather, in the HU condition, both animals used a combination of eye and head rotations in order to initially acquire the target. We found that although initial eye and gaze positions were not equal, they were well correlated ($r=0.79$ and 0.66 ; slope = 0.45 and 0.55 ; $n=265$ and 334 for monkeys B and C, respectively, when data from all target velocities were pooled). Likewise, initial head and gaze positions were also well correlated in both animals ($r=0.84$ and 0.59 ; slope = 0.55 and 0.45). Since initial eye position, initial head position, and initial gaze position did not vary independently in the HU condition, additional experiments were necessary to determine the effect of each parameter.

To dissociate the effects of initial eye, head, and gaze positions on pursuit latencies in the HU and HR conditions, we carried out a second series of experiments in which each of these parameters was independently controlled (see “Materials and methods”: experiment 2, E_{var} and G_{var} conditions). Recall that during this series of experiments the animal’s head was restrained. Figure 7A plots pursuit latency as a function of initial eye position, while initial gaze position was held constant (experiment 2, E_{var} condition) during pursuit of a constant velocity target (60°/s). For monkey C, the slope of the regression line fit to these data was $0.40 \text{ ms}/^\circ$, and the relationship was significant ($P < 0.005$; $r=0.40$). Thus, a 30° shift of initial eye position away from center in the contraversive direction resulted in an average decrease in pursuit latency of 12 ms. Initial eye position also had a significant ef-

Fig. 6A, B Effect of initial gaze position on pursuit latency in HU condition. **A** Latency decreased for more contraversive initial gaze positions. **B** Histograms showing pursuit latency for central (0° , white bars) versus the most contraversive (-30° , solid bars) initial gaze positions. This effect was less pronounced in the HU condition as compared to the HR condition (Fig. 5). Symbols as in Fig. 5

Experiment 1: HU Condition



effect on pursuit latency in monkey B; a similar 30° shift of initial eye position resulted in an 8-ms decrease in latency. The first line of Table 1 summarizes the results of the E_{var} condition of experiment 2 for both animals.

In contrast, when initial eye position was held constant and initial gaze position was varied (experiment 2, G_{var} condition), we observed few or no differences in mean pursuit latency (Fig. 7B). Although the regression through the data arising from the G_{var} condition was statistically significant for monkey C ($P < 0.05$; $r = 0.16$), the slope of the regression ($0.07 \text{ ms}/^\circ$) was very small in comparison to that obtained from the E_{var} condition (Table 1); a change of 30° in initial gaze position resulted in only a 2-ms difference in average pursuit latency. Initial gaze position had no significant effect on pursuit latency for monkey B (Table 1). Note that, in this para-

digm, initial gaze and head positions were equivalent. The results shown in Fig. 7 confirm that initial eye position had a pronounced effect on pursuit latency, while initial gaze position, and equivalently initial head position, had little or no effect.

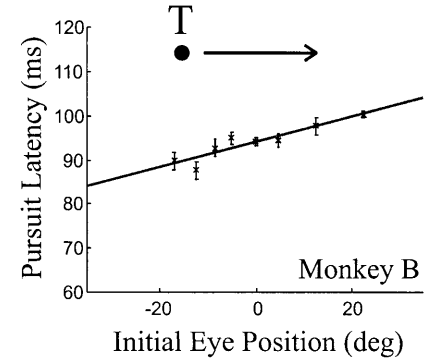
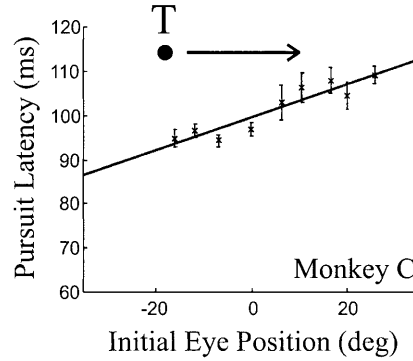
In order to directly compare the results of experiments 1 and 2, the effect of initial eye position on gaze onset latency found in experiment 1 was quantified with a linear regression, as in experiment 2. This allowed us to characterize the relationship between initial eye position and pursuit onset latency for both the HR and HU conditions of experiment 1, for trials in which target velocity was $60^\circ/\text{s}$ (the velocity used throughout experiment 2). The last two lines of Table 1 show the results of this analysis. The slopes of the regression through the HR data of experiment 1 were similar to the slope of the

Fig. 7A, B Effects of initial eye and gaze position on pursuit latency were dissociated using the E_{var} and G_{var} conditions of experiment 2.

A Pursuit latency decreased for more leftward (negative) initial eye positions during rightward pursuit. *Solid lines* indicate significant ($P < 0.05$) linear regressions. **B** Pursuit latency was not affected by initial gaze (or head) position

Experiment 2

A E_{var} Condition



B G_{var} Condition

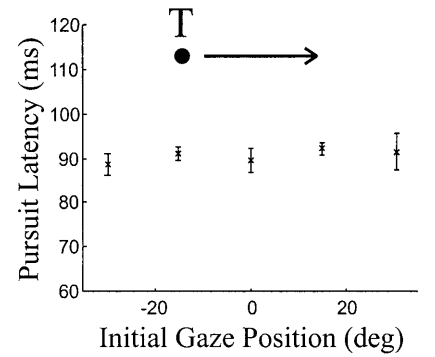
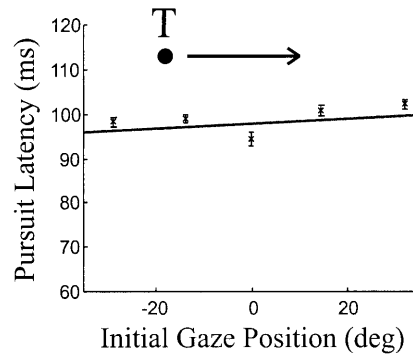


Table 1 Result of regression analysis for experiments 1 and 2. See text for details (T' target velocity, n number of observations, m, b slope and y-intercept of the regression, respectively, r correlation coefficient, P level of significance, *NS* not significant, * $P < 0.05$, ** $P < 0.005$)

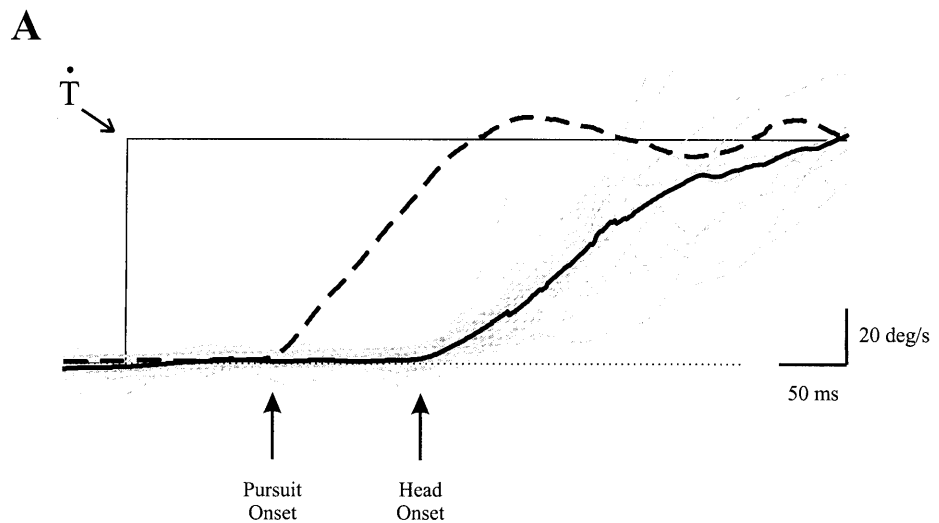
	Monkey C						Monkey B					
	T'	n	m	b	r	P	T'	n	m	b	r	P
Exp 2: E_{var}	60	217	0.40	99.51	0.40	**	60	167	0.27	93.98	0.32	**
Exp 2: G_{var}	60	310	0.07	99.14	0.16	*	60	102	0.04	90.82	0.09	NS
Exp 1: HR	60	93	0.30	96.69	0.30	**	60	74	0.34	92.26	0.40	**
Exp 1: HU	60	76	0.34	98.72	0.36	**	60	69	0.33	87.27	0.24	*

regression obtained from the E_{var} condition of experiment 2, suggesting that the relationship between initial eye position and pursuit latency was unaffected by variations in initial head position. Likewise, the slope of the regression through the HU data of experiment 1 was similar to the slope of the regression obtained from the HR condition of experiment 1, and the E_{var} condition of

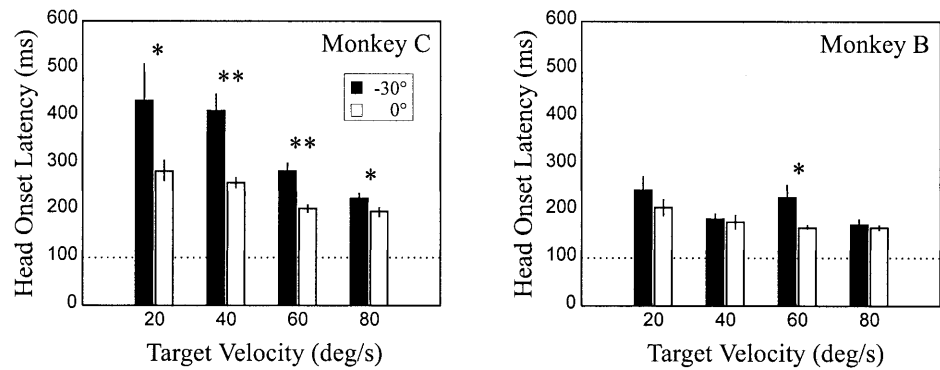
experiment 2. Thus, head-unrestrained and head-restrained pursuit onset latencies varied as a comparable function of initial eye position.

To further this conclusion, we carried out a multiple linear regression on the data set from the HU condition (pursuit latency as a function of initial eye and head position). Note that since gaze is an exact combination (i.e.,

Fig. 8A, B Head motion during the initiation of head-unrestrained pursuit. **A** Average head velocity (solid dark line) is superimposed on individual trials (light lines). Average gaze velocity from the same trials (dashed dark line) is superimposed for comparison. **B** Mean head onset latency for different target velocities and initial gaze positions. Even the shortest latency head movements significantly lagged the onset of gaze pursuit. A dashed line indicating typical pursuit latencies (i.e., 100 ms) is included for comparison. Error bars represent SEM. Symbols as in Fig. 5



B



the sum) of eye and head, it is impossible to carry out a regression that includes initial eye, head, and gaze positions. Initial eye position accounted for 92% and 87% of the variance accounted for (VAF) provided by a regression model for monkeys B and C, respectively. Furthermore, the contribution of initial head position was not significant either when added to initial eye position, or when examined alone. Taken together, the results of experiments 1 and 2 are consistent with the proposal that pursuit onset latency varies primarily as a function of initial eye position rather than initial gaze or initial head position.

Effect of head movements and head restraint

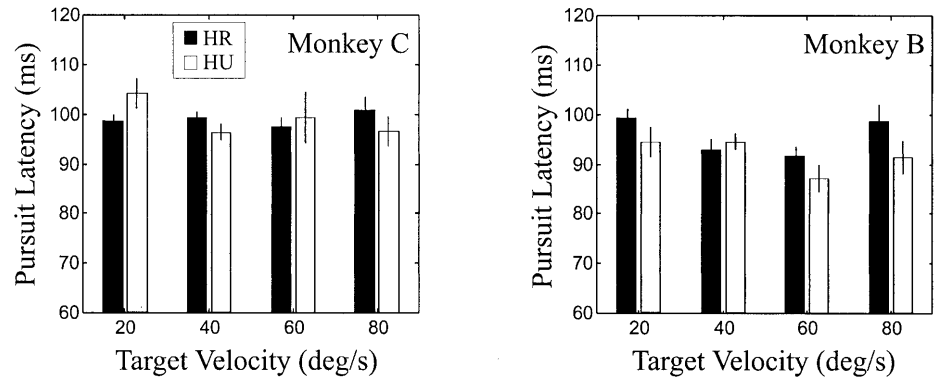
The above finding suggests that pursuit onset latencies are comparable during head-restrained and head-unrestrained pursuit initiation if initial eye position is held constant. This result is consistent with the long latency of the head move-

ment response. Figure 8A shows head velocity traces for 27 individual trials (Fig. 8A, light lines) of head-unrestrained pursuit for monkey C. In this example, target velocity was 60°/s and initial target position was 0°. The average head velocity trace (Fig. 8A, dark solid line) was calculated from individual trials aligned on head movement onset. This figure is typical of our data in that the onset of head motion consistently lagged the onset of gaze motion by ~50 ms or more. In both animals, slow, eccentric (−30°) targets yielded longer head onset latencies, as compared to fast, central targets, which yielded the shortest head onset latencies. The histograms of Fig. 8B highlight the effect of target velocity and eccentricity on head onset latency. In monkey C, initial gaze position significantly affected head onset latency for all target velocities (Fig. 8B, where the asterisks denote the level of significance obtained by regression analysis). Initial head onset latencies tended to be longer for more eccentric initial gaze positions in monkey B; however, the effect was only significant at 60°/s. In monkey C, head onset latency was also significantly influenced by target velocity for all

Fig. 9 Effect of head-restraint on gaze onset latency. For identical target motion and similar initial eye positions ($0 \pm 2^\circ$), gaze onset latencies were not significantly different during pursuit in the HU condition (white bars) as compared to the HR condition (solid bars)

Experiment 1: HU and HR Conditions

$$E_i = 0 \pm 3 \text{ deg}$$



initial gaze positions (0° , $P < 0.005$; -15° , $P < 0.05$; -30° , $P < 0.005$). In monkey B, the effect was only significant when initial gaze position was 0° .

To determine whether the strong influence of initial gaze position on head onset latency in monkey C was a result of variations in initial eye or head position, we carried out a multiple linear regression to determine how head onset latency varied as a function of target velocity, initial eye position, and initial head position in monkey C. Initial eye position and target velocity accounted for 99% of the total VAF provided by the regression model for this animal. Furthermore, the contribution of initial head position was not significant either when added to initial eye position and target velocity, or when examined alone. This suggests that head onset latency in monkey C varied primarily as a function of target velocity and initial eye position rather than initial head position.

Figure 8B also shows that average head onset latency was consistently longer than typical gaze latencies (i.e., ~ 100 ms, as denoted by the dashed line in Fig. 8B). Even during pursuit of fast ($80^\circ/\text{s}$), central targets, the onset of head movements still significantly lagged the onset of gaze movements ($P < 0.005$; 82 ± 43 and 99 ± 51 ms, mean latency of head movements \pm SD with respect to gaze onset for monkeys B and C, respectively). Thus, in the HU condition, head movements per se could not affect our measurements of gaze onset latency. Furthermore, as was shown above, pursuit onset latencies were not systematically related to initial head position immediately prior to pursuit in either the HR or HU condition. These observations indicate that initial pursuit responses were not significantly affected by either head motion or initial head position, thereby suggesting that pursuit initiation is comparable during head-restrained and head-unrestrained pursuit as long as initial eye position is held constant.

The data sets from experiment 1 (Figs. 5, 6) were used to directly address this proposal. In order to exam-

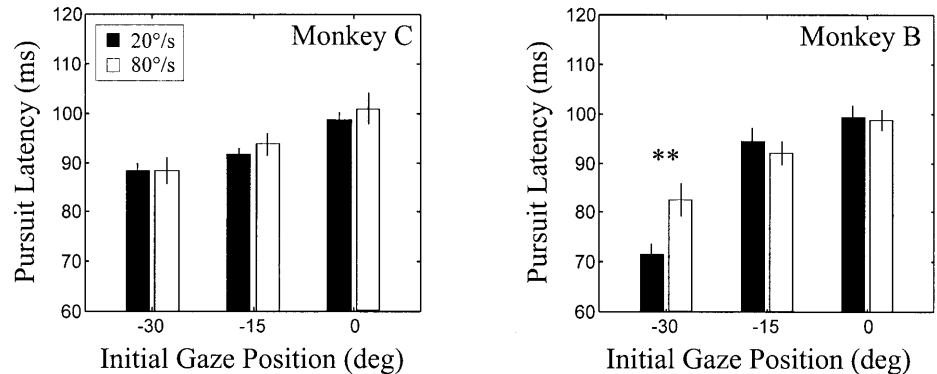
ine only the effect of restraining the animal's head, it was necessary to compare latencies from trials in the HR and HU conditions resulting from identical target presentations and where eye movements began from similar initial positions. To do so, we examined only those trials from experiment 1 in which initial gaze position was 0° and initial eye position was near the center of the orbit ($0 \pm 3^\circ$). The histograms of Fig. 9 show the mean latencies of pursuit in the HR and HU conditions (solid vs white bars, respectively) in this restricted data set. A comparison of the data in the HR and HU conditions shows that for identical target motion and independent of target velocity, pursuit latencies were not significantly different in either animal (t -test, $P > 0.05$). Therefore, we conclude that the act of physically restraining the head had no influence on pursuit onset latencies, when initial eye position was held constant.

Effect of target velocity

The majority of prior studies into head-restrained pursuit have been carried out with central initial gaze positions, such that during the initial fixation period the eye was approximately centered in its orbit (Lisberger and Westbrook 1985; Tychsen and Lisberger 1986; Carl and Gellman 1987; Lisberger and Pavelko 1989). The histograms in Fig. 9 illustrate that during both head-restrained and head-unrestrained pursuit, target velocity had no systematic effect on pursuit latency when the eye was initially centered in the orbit. We examined whether target velocity had an effect on head-restrained and head-unrestrained pursuit latencies for more contraversive initial eye positions. Figure 10 compares the latency of pursuit for the slowest ($20^\circ/\text{s}$) and fastest ($80^\circ/\text{s}$) target velocities during pursuit in the HR condition when initial eye position was 0° , -15° , and -30° . When initial eye position was 0° , target velocity had no significant effect on head-restrained pursuit latency. Similar results

Experiment 1: HR Condition

Fig. 10 Effect of target velocity on pursuit latency in the HR condition. Comparison of pursuit responses to the slowest (20°/s, solid bars) versus the fastest (80°/s, white bars) target velocities showed that target velocity had little or no effect on pursuit latency during pursuit in the HR condition



were obtained regardless of initial eye position, with only one exception; for monkey B, pursuit latency tended to increase with target velocity when initial eye position was -30° (Fig. 10). Therefore, in general, pursuit latency was not significantly affected by target velocity. Similar results were obtained for pursuit in the HU condition.

Discussion

The primary goal of this study was to investigate whether the latency of the initiation of a pursuit response differs during head-restrained versus head-unrestrained pursuit. In experiment 1, animals were trained to pursue step-ramp targets either with their eyes alone (head-restrained, HR condition), or with a combination of voluntary eye and head movements (head-unrestrained, HU condition). We found that during pursuit of targets starting at the most contraversive position tested (-30° from center), gaze pursuit onset tended to be slightly faster in the HR condition as compared to the HU condition. Accordingly, the second goal of this study was to characterize the effect of initial eye, gaze and head position on the latency of the pursuit response; initial eye position was equal to initial gaze position in the HR condition, but was a function of the animal's initial head position in the HU condition. Our results show that initial eye position influenced gaze onset latencies in both animals during both head-unrestrained and head-restrained pursuit. In contrast, varying initial gaze and initial head position had little or no effect on pursuit onset latencies. We also found that target velocity did not affect gaze onset latencies during either head-restrained or head-unrestrained pursuit. We conclude that, for identical target motion, there is no difference in the latency of the response of the pursuit system during head-restrained and head-unrestrained pursuit when the initial position of the eye in the orbit is comparable.

Effect of initial eye, gaze, and head position

The results from experiment 1 (HU and HR conditions) indicated that either initial eye position or initial gaze position, or both, had a significant influence on the latency of pursuit initiation. Because initial eye and gaze position did not vary independently of each other in either the HU or HR condition, we carried out additional experiments in order to establish the influence of each of these parameters.

We tried two approaches in order to successfully dissociate the effects of initial eye and gaze position on pursuit initiation. In a first approach, we trained one animal (not included in this study) to voluntarily align its head with a visual cue presented immediately before a trial. In this way, we could either: (1) keep initial gaze position constant (i.e., near zero) while varying initial eye position, or (2) keep initial eye position constant (i.e., near zero) while varying initial gaze position. Once the head was properly aligned, the cue was extinguished, and the pursuit trial proceeded as before. We found, however, that the training for this experiment made the animal conscious of its head position, and ultimately less likely to move its head. Consequently, the monkey's head movements during head-unrestrained pursuit became somewhat unnatural. Therefore, we abandoned this approach and excluded this monkey from the present study. In a second approach to separating the effects of initial eye and gaze position in this study, we statically placed the animal's head in different positions (Mann and Morrow 1997) and presented targets such that either initial gaze position or initial eye position were kept constant while the other was varied (experiment 2: E_{var} and G_{var} conditions, respectively). While this paradigm was artificial in its design, it did allow us to independently control initial eye and initial gaze/head positions in order to establish that initial eye position is the main factor that affects gaze onset latency.

The only other study to have specifically investigated the effect of initial eye position on pursuit initiation reported that pursuit latency was unaffected by initial eye position (Mann and Morrow 1997). Although those investigators used step-ramp trajectories, their experiment differed from ours in that for a given target velocity they randomized the size of the initial target step from trial to trial. Since the size of the step in a step-ramp trajectory can affect initial gaze dynamics (Lisberger and Westbrook 1985; Tychsen and Lisberger 1986; Carl and Gellman 1987), varying the step size in a random manner could have obscured the effect of eye position in that study. Observations by other investigators support the idea that pursuit eye movements are affected by the orbital position of the eye: (1) there have been reports that during *sustained* head-restrained sinusoidal tracking, smooth pursuit gain is decreased by increasing orbital eccentricity (Yee et al. 1983; Mann and Morrow 1997), and (2) it has been shown that orbital eye position influences the latency of *saccadic* eye movements in humans (Fuller 1992, 1996), monkeys (Tusa and Becker 1989), and during collicular stimulation in cats (McIlwain 1986; Guitton et al. 1980); more eccentric eye positions yield shorter latencies for saccades that take the eye towards the orbital midline. The findings of the present study are analogous to those from the saccadic literature; more contraversive initial eye positions with respect to the direction of target motion yield shorter latencies for pursuit of targets moving towards the orbital midline. However, the differences observed in our study of pursuit were slightly smaller than those observed in prior studies of the saccadic system. For example, a difference of 30° in initial eye position produced, on average, a 10-ms difference in pursuit onset latencies (target velocity = 60°/s, present study) versus a 26-ms difference in saccadic onset latencies (average of all subjects for 40° saccades; Fuller 1996).

It is possible that the effect of eye position on both saccade and pursuit dynamics arises in the cortical pathways that mediate these movements. In particular, the role of posterior parietal cortex in the generation of saccadic and pursuit eye movements has been extensively studied. Saccadic neurons whose activity is dependent on eye position have been described in several areas within the parietal cortex including the lateral intraparietal area (LIP) and area 7a (Andersen and Zipser 1988; Andersen et al. 1990; Brotchie et al. 1995). The activity of visual tracking sensitive neurons within these same areas has also been found to be influenced by eye position (Bremmer et al. 1997a). As well, the response of neurons within regions of the parietal cortex more typically associated with pursuit, such as the middle temporal (MT) and the medial superior temporal (MST) areas, is also modulated by eye position (Bremmer et al. 1997b; Squatrito and Maioli 1997). However, it seems improbable that the effect of orbital eye position on pursuit latency observed in the present study could have resulted from an eye-position-dependent motor command at the level of parietal cortex. Although eye position affects the discharge of individual neurons in parietal cortex, the

population discharge of any given area remains unaffected (Bremmer et al. 1997a, 1997b). Therefore, the net command to the downstream oculomotor structures is not likely to differ dramatically depending on current eye position. In addition, saccade latencies in cat differ significantly depending on initial eye position when the saccades are elicited by electrical stimulation of the superior colliculus (McIlwain 1986). Since the superior colliculus is downstream from parietal cortex in the saccadic pathway, this finding suggests that the effect of eye position on saccade dynamics is not completely cortical in origin.

The cerebellum is another possible source of the eye position effect that was observed in the present study. In particular, the floccular lobe of the cerebellum is critical for the generation of smooth pursuit eye movements. However, the discharges of Purkinje cells in the flocculus/ventral paraflocculus are only weakly correlated with eye position during fixation (Miles et al. 1980), and appear to contribute mostly to the dynamic (velocity and acceleration) rather than static (position) control of eye movements during pursuit (Krauzlis and Lisberger 1994).

It is more likely that the effect of eye position on the initial pursuit response reflects, in part, an effect of the eye's orbital mechanics rather than differences in the underlying neural command. The elastic properties of the extraocular muscles act asymmetrically, pulling the eyes towards the orbital midline (Robinson 1964, 1965). Thus, movements that start with the eye in an eccentric position and take the eye towards the orbital midline would have faster dynamics (and, thus, shorter measured latencies) than eye movements that take the eye away from the orbital midline. This schema is in agreement with the results of experiment 1 of the present study. In addition, it also explains why in experiment 2 we observed a continuation of the same trend, even once the orbital midline had been crossed (Fig. 7); gaze onset latencies are longer because the pursuit eye movement is now slowed by the elastic forces which will tend to pull the eye towards the orbital midline.

The effect of initial eye position on pursuit latency may be behaviorally advantageous to an animal during head-unrestrained pursuit. Fuller (1996) argued that the reduction in saccade latency that accompanies increasing contraversive initial eye position could be useful for the coordination of eye-head gaze shifts. In the HU condition, when the eye begins in a more contraversive position less ocular motor range is available for compensatory eye rotations made in response to the accompanying head movement. By expediting the initiation of eye movement, the eye can move further ipsiversively before a counterrotary eye movement is generated. We suggest that the dependence of pursuit latencies on initial eye position may serve a similar function in coordinating eye-head motion during active head-unrestrained pursuit.

Effect of target velocity

Our finding that gaze onset latency is unaffected by target velocity is in agreement with two recent studies of head-restrained pursuit that examined a comparable range of target velocities (Morrow and Lamb 1996; Mann and Morrow 1997). While a previous study by Lisberger and Westbrook (1985) reported that pursuit latency *increased* with increasing target velocity, the effect was most pronounced at low target contrasts and almost undetectable at high target contrasts, such as the one used in the present study. Additionally, in that study (Lisberger and Westbrook 1985), targets were presented in such a manner that increasing target velocities were associated with increasingly more ipsiversive initial eye positions. Thus, the effect of target velocity on pursuit latency reported by those investigators might have reflected an effect of initial eye position. In contrast, Carl and Gellman (1987) reported that pursuit latency *decreased* with increasing target velocity; however, this effect was only significant for target velocities below 20°/s (i.e., target velocities below those tested in this study). Finally, since step size can influence pursuit latencies (Lisberger and Westbrook 1985; Tychsen and Lisberger 1986; Carl and Gellman 1987), it is possible that the step sizes utilized in the present study obscured an influence of target velocity. However, at the target contrasts and step sizes which we used (10° and less), the effect of step size on pursuit latency is not significant (Lisberger and Westbrook 1985).

Effect of head movements and head-restraint

Once the effects of initial eye position were accounted for, head-restraint had no consistent effect on the latency of pursuit eye movements. In one regard, this finding was not surprising since head movements lagged eye movements by a minimum of approximately 50 ms (for the fastest target velocities), and therefore did not contribute to the initial pursuit response. As such, our measurements of gaze onset latency were not influenced by head movements. However, head restraint could have affected the monkey's pursuit strategy, state of attention, and/or willingness to perform the required tasks. For example, it is likely that the neck musculature was activated long before the head actually began to move in our head-unrestrained pursuit paradigms (see below). Hence, feedback from dynamic neck afferents to the brainstem oculomotor circuitry (Wilson 1992) could have differentially influenced initiation of head-restrained versus head-unrestrained pursuit. Nevertheless, the finding that pursuit latencies are indistinguishable in the HR and HU conditions when initial eye position was comparable indicates that the cumulative effect of these factors was not significant.

The apparent long latency of head movements in comparison to eye movements during head-unrestrained pursuit is partly attributable to the large inertia of the head as compared to the eye (Zangemeister et al. 1981,

or see Peng et al. 1996). The high inertia of the head system would result in a reduced head acceleration that would not be initially detected by our latency measurement method of pursuit responses. Studies of predictive combined eye-head tracking have shown that predictive mechanisms are able to at least partially compensate for the sluggish dynamics of the head. For example, during gaze pursuit of low-frequency predictable targets, head velocity may be in phase with, or even lead, target velocity (Gresty and Leech 1977; Lanman et al. 1978; Collewijn et al. 1982). Similarly, head movements may be synchronized with, or even lead, eye movements during gaze shifts to predictable targets (for example, see Bizzi et al. 1971; Dichgans et al. 1973; Zangemeister and Stark 1982b; Fuller 1992). However, during unpredictable gaze shifts, head movements typically lag eye movements (see Guitton 1992), as they did in our studies of gaze pursuit initiation.

Through the use of electromyographic (EMG) recordings, Zangemeister and Stark (1982a) have shown that, for unpredictable gaze shifts, the neural commands to the eyes and the head are, in fact, synchronous, although the actual head movement lags eye movement by more than 50 ms. Indeed, the long latency values that have been reported for the onset of detectable head movement response are not unexpected given the relatively large inertia of the head, which considerably damps the dynamics of the head movement response as compared to that of the eye. Neck EMG activity is also strongly coupled with eye movement dynamics during sustained pursuit and saccadic eye movements in the *head-restrained* human (André-Deshays et al. 1991), monkey (Bizzi et al. 1971; Lestienne et al. 1984), cat (Grantyn and Berthoz 1985), and rabbit (Fuller 1980), as well as during gaze shifts in the *head-unrestrained* human (Zangemeister and Stark 1982a) and monkey (Bizzi et al. 1971). We propose that, in both the head-restrained and head-unrestrained monkey, recordings of neck EMG activity would reveal that the eyes and head receive synchronous commands during the initiation of pursuit to fast, unpredictable, step-ramp target motion.

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