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Gaze-, Eye-, and Head-Movement Dynamics During Closed- and Open-Loop Gaze Pursuit

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Dubrovsky, Alexander S. and Kathleen E. Cullen. Gaze-, eye-, and head-movement dynamics during closed- and open-loop gaze pursuit. *J Neurophysiol* 87: 859–875, 2002; 10.1152/jn.00447.2001. Horizontal step-ramp stimuli were used to examine gaze-, eye-, and head-movement dynamics during head-unrestrained pursuit in two rhesus monkeys. In a first series of experiments, we characterized and compared head-restrained (HR) and -unrestrained (HU) pursuit responses to unpredictable, nonperiodic, constant velocity (20–80°/s) stimuli. When the head was free to move, both monkeys used a combination of eye and head motion to initially fixate and then pursue the target. The pursuit responses (i.e., gaze responses) were highly stereotyped and nearly identical among the HR and HU conditions for a given step-ramp stimulus. In the HU condition, initial eye and initial head acceleration tended to increase as a function of target velocity but did not vary systematically with initial target eccentricity. In a second series of experiments, step-ramp stimuli (40°/s) were presented, and, ~125 ms after pursuit onset, a constant retinal velocity error (RVE) was imposed for a duration of 300 ms. In each monkey, HR and HU gaze velocity was similarly affected by stabilizing the target with respect to the monkey's fovea (i.e., RVE = 0°/s) and by moving the target with constant retinal velocity errors (i.e., RVE = ±10°/s). In the HU condition, changes in both eye and head velocity trajectories contributed to the observed gaze velocity responses to imposed RVEs. We conclude that eye and head movements are not independently controlled during HU pursuit but rather are controlled, at least in part, by a shared upstream controller within the pursuit pathways.

INTRODUCTION

Under natural conditions, primates use coordinated movements of their eyes and head to voluntarily align their axis of gaze (gaze = eye-in-head + head-in-space) with a target of interest. Accordingly, rapid orienting movements that involve the use of the eyes and the head have been termed gaze shifts, while the coordinated head and eye movements made to follow a slowly moving target are commonly referred to as eye-head gaze pursuit. Over the past two decades, considerable progress has been made toward characterizing behavioral responses during gaze shifts (see for example: Barnes 1981; Bizzi et al. 1971; Freedman and Sparks 1997; Guitton and Volle 1987; Tomlinson and Bahra 1986; Zangemeister and Stark 1982a,b; Zangemeister et al. 1981) as well as toward understanding neurophysiological mechanisms (reviewed in Sparks 2000) that mediate gaze shifts. In contrast, the control and coordination of eye and head movements during gaze pursuit has received far less attention. The vast majority of previous characterizations of the pursuit system have been carried out with the subject's head physically restrained so that only eye movements could be used to follow target motion. As a result, much is known about the processing of visual inputs and their use in generating smooth pursuit eye movements. However, less is known about how vestibular, proprioceptive, and central inputs are integrated with visual inputs to generate coordinated eye-head pursuit.

In *head-restrained* studies, the pursuit system has been typically characterized as a negative feedback controller that functions to reduce and minimize any discrepancy between the velocity of the target and that of the eye, defined as retinal velocity error (for review, see Lisberger et al. 1987). Although retinal velocity error is generally considered to be the main drive for pursuit eye movements, retinal position (Morris and Lisberger 1987; Pola and Wyatt 1980; Segraves and Goldberg 1994) and retinal acceleration (Krauzlis and Lisberger 1994; Lisberger et al. 1981, 1987; Morris and Lisberger 1987) errors can also serve as effective stimuli for pursuit eye movements. Furthermore, the amplitude of the initial eye acceleration depends on a number of target properties including velocity, luminance, size, and initial position. For example, faster moving step-ramp stimuli evoke a pursuit response in which the eyes accelerate more rapidly (Carl and Gellman 1987; Lisberger and Westbrook 1985; Lisberger et al. 1981; Mann and Morrow 1997; Morris and Lisberger 1987; Tychsen and Lisberger 1986), although this effect saturates for target velocities greater than ~50°/s (Carl and Gellman 1987; Lisberger and Westbrook 1985; Tychsen and Lisberger 1986). Moreover, nonvisual inputs have been reported to play an essential role during the maintenance phase of pursuit. For instance, it has been suggested that a copy of the pursuit eye motor command signal is used to maintain ongoing eye velocity once pursuit has been initiated (Lisberger and Fuchs 1978; Morris and Lisberger 1987; Robinson 1971; Robinson et al. 1986; Yasui and Young 1975; Young et al. 1968). Approximately 120 ms following the initiation of the pursuit response, eye velocity reaches that of the target and then oscillates around target velocity at a frequency of 4–6 Hz (Fuchs 1967; Goldreich et al. 1992; Robinson 1965; Robinson et al. 1986). It has been proposed that the oscillations result from the processing delay that is intrinsic to the visual feedback loop—i.e., the sum of

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retinal, cortical, and motor processing delays (Goldreich et al. 1992).

When the head is free to move, humans and monkeys commonly will move their heads as well as their eyes in a coordinated fashion to pursue a moving target that is well within their oculomotor range. As a result, it was suggested that the coordination of eye and head movements during gaze pursuit could be achieved by a common drive mechanism, whereby the same controller drives both the eye and head motor system with the vestibular system functioning to further couple the movements via the vestibuloocular reflex (Lanman et al. 1978). While we have recently shown that head-movement onset consistently lags eye-movement initiation by ≥50 ms during pursuit of step-ramp target trajectories in the head-unrestrained condition (Wellenius and Cullen 2000), it is not unexpected that the latency of onset of a detectable response to a common drive would be longer for the head than for the eyes because head dynamics are considerably more sluggish than eye dynamics (Peng et al. 1996; Zangemeister et al. 1981).

To date, all characteristics of the *dynamics* of pursuit initiation have been done with the head restrained. Furthermore, pursuit responses to step-ramp target trajectories have not been characterized during head-unrestrained pursuit maintenance. Most previous investigations of combined eye-head gaze pursuit have used stimuli such as periodic sinusoidal and/or triangular target trajectories to study the maintenance of gaze pursuit. The results of these studies have suggested that gaze accuracy is comparable during sustained eye-head pursuit and pursuit in the head-restrained condition (monkey: Cullen and McCrea 1990; Lanman et al. 1978; human: Barnes 1981; Leigh et al. 1987). A small number of studies have used unpredictable pseudo-random target trajectories, and their findings have been less conclusive. Improved pursuit gains (i.e., gaze velocity/target velocity) during eye-head pursuit as compared with eye-only pursuit have been reported for pseudo-random target trajectories with peak target velocities of >40°/s in squirrel monkey (Cullen and McCrea 1990). Similarly, it has been shown that gaze accuracy in humans is marginally improved for combined eye-head pursuit of higher velocity pseudo-random target motion (Waterston and Barnes 1992); however, this improvement is generally not significant.

The overall goal of the present study was to investigate the control of eye and head movements during head-unrestrained pursuit of nonperiodic, constant velocity, step-ramp target motion. First, we compared pursuit responses during the maintenance of pursuit in the head-unrestrained and -restrained conditions and examined whether it is behaviorally advantageous to recruit the head to pursue a faster moving target. Second, we compared the initial *gaze* pursuit responses made in the head-restrained and -unrestrained conditions to determine whether the additional vestibular, proprioceptive, and central signals that are present in the head-unrestrained condition might function to facilitate pursuit onset. Third, we characterized and compared the dynamics of the initial *eye*- and *head*-movement responses made during head-unrestrained pursuit. Finally, our fourth objective was to assess the effect of imposed retinal velocity errors on gaze, eye, and head movements during gaze pursuit.

METHODS

Animal preparation and experimental setup

Two adult male monkeys (*Maccaca 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 monkeys were similar to those described by Sylvestre and Cullen (1999). Briefly, under general anesthesia and aseptic conditions, a scleral search coil was implanted in the right eye in one monkey (*monkey C*) and in both the eyes in the other (*monkey J*) to monitor gaze position, and a stainless-steel bolt was attached to the skull for restraining the head.

During each experiment, a monkey was comfortably seated in a stationary primate chair that was placed in the center of a 1-m^3 magnetic field coil system (CNC Engineering). A specially designed lightweight aluminum head-holder (Roy and Cullen 1998) enabled us to either completely immobilize the animal's head or to allow the monkey to rotate its head through the natural range of motion in the yaw (horizontal), pitch (vertical), and roll (torsional) axes. Gaze position was recorded by using the magnetic search coil technique (Fuchs and Robinson 1966; Judge et al. 1980). Rotational head movements were recorded by way of a second search coil that was secured to the head-holder.

Monkeys were trained to track a small (0.3° diam) visual target for a juice reward that was delivered via a tube that was attached to the head-holder. The monkey received the reward every 500–1,000 ms only if its gaze was maintained within a precision window of 2.5° with respect to the position of the target. Target motion was generated using a HeNe laser spot that was projected on a white cylindrical screen, located 60 cm away from the monkey's eyes, by a pair of mirrors mounted on two computer-controlled galvanometers (General Scanning). The room was dimly lit and the intensity of the target was 3 log units above human perceptual threshold (see Wellenius and Cullen 2000).

Behavioral tasks

Monkeys were trained to pursue a horizontal step-ramp target trajectory (Rashbass 1961; see for example the top panel of Fig. 1*A*, trace labeled T). Each trial began when the monkey fixated a stationary target that was located at one of five initial target positions that were within a range of ±30° relative to the primary position (i.e., the position at which the eyes are centered in the orbit). After a random fixation period (750–3,000 ms), the target was stepped either toward the left or right and then immediately began to move at constant velocity (20–80°/s) in the direction opposite to that of the step. By choosing the appropriate step size for each target velocity, it was possible to obtain initial smooth eye movements that were not preceded by corrective saccades (Rashbass 1961). The target crossed the initial target position after an average of ∼110 and ∼120 ms in *monkeys C* and *J,* respectively.

During the experiments, the monkey's head was restrained (head-restrained, HR) such that the eyes and the head were aligned with the center of the cylindrical screen and pursuit was accomplished with the use of only the eyes. Alternatively, the monkey's head was unrestrained (head-unrestrained, HU) such that the monkey had full freedom of head motion and thus pursuit could be accomplished with any combination of eye and head movements (Roy and Cullen 1998). A typical 40- to 50-min experimental session consisted of 200–300 step-ramp target presentations, and each experimental session was divided into one or two separate HR and HU condition blocks. The order in which the HR and HU blocks were presented was varied on a daily basis. In addition to randomizing the target trajectories, the monkeys were given a number of breaks between trials during which they were either required to perform a number of different tasks (i.e.,

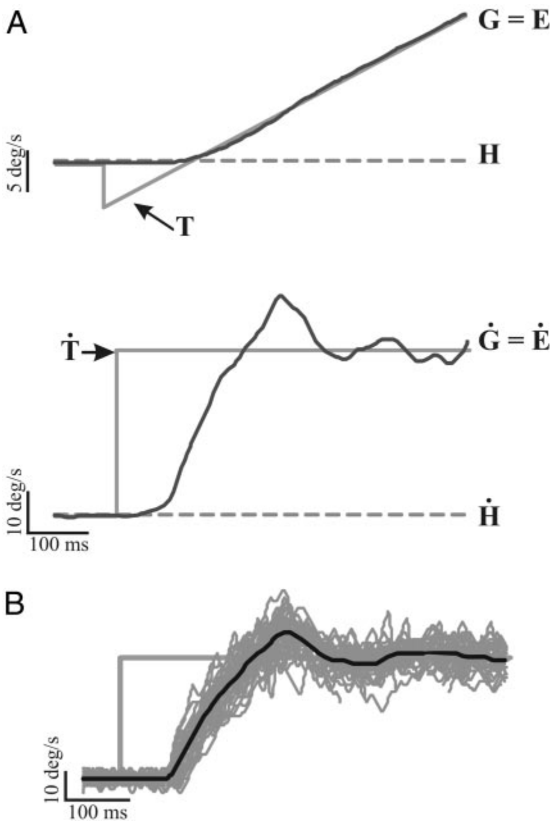


FIG. 1. *A*: example of a pursuit response to a step-ramp target trajectory in the head-restrained condition. The trial began with an initially centered target that underwent a leftward step immediately followed by a ramp in position (40°/s, constant velocity). *B*: average gaze velocity (dark line) is superimposed on individual trials (light lines). Note the stereotyped gaze responses. In this and subsequent figures, upward deflections represent temporally directed movements, and G, E, H, T, G′, E′, H′, and T′ are gaze, eye, head, and target position and velocity, respectively.

sinusoidal pursuit and/or a saccade task) or were simply allotted a "rest time" to prevent fatigue or loss of motivation.

EXPERIMENT 1: GAZE PURSUIT. A range of target velocities and eccentricities was used to characterize and compare the relationships between initial gaze, eye, and head acceleration with respect to target velocity and initial target position (i.e., initial gaze position) as well as to determine whether initial gaze accelerations differ for combined eye-head pursuit versus eye-only pursuit in a target velocity or initial target position specific manner. Pursuit responses were elicited using horizontal step-ramp target trajectories with constant velocities of 20, 40, 60, and 80°/s for *monkey C* and 20, 30, 40, 50, 60 and 70°/s for *monkey J*. For each velocity, we tested three different initial target positions. For *monkey C,* targets were initially presented at 0, 15, or 30° relative to primary position and contraversive to the direction of pursuit, and for *monkey J* targets were initially presented at 0, 10, or 20° because this monkey would not consistently look at more eccentric targets when its head was restrained. In all experiments, both leftward and rightward trajectories were presented, and all ramps terminated between 20 and 30°. Within each block of trials, fixation period, initial target position, target velocity, target direction, and the end point of the step-ramp were randomized to minimize predictive behaviors. Because it was not the purpose of the present study to investigate differences between nasally and temporally directed pursuit, we elected to restrict our analysis of gaze pursuit dynamics to temporally directed movements (i.e., the responses of the right eye during rightward pursuit in both monkeys).

EXPERIMENT 2: OPEN-LOOP GAZE PURSUIT. To investigate the effects of retinal velocity errors on pursuit responses in both the HR and HU conditions, we performed the following experiment. Pursuit was elicited by presenting horizontal step-ramp target trajectories of 40°/s that were initially positioned at ±10° with respect to primary position. Both rightward and leftward trajectories were presented. On a portion of trials (~15%), the target either was artificially stabilized relative to the monkey's fovea (i.e., gaze) or a constant velocity error was imposed (Morris and Lisberger 1987; Pola and Wyatt 1980; Segraves and Goldberg 1994). The onset of the open-loop interval occurred after a delay of ~125–150 ms after the monkey's gaze velocity crossed a threshold of 10°/s, thus allowing the monkey enough time to initiate and establish pursuit using both its eyes and head. The retinal velocity error was imposed for the duration of 300 ms, after which the target resumed moving at 40°/s. During the open-loop interval, the target velocity was controlled with a command signal representing the sum of ongoing gaze velocity and the desired horizontal retinal velocity error (RVE) of −10, 0, or +10°/s. Responses during the open-loop trials were compared with control trials in which the loop was not opened (closed-loop control trials). Within each experimental session, fixation period, target direction, and the end point of the step-ramp were randomized, and open-loop trials were randomly interleaved with closed-loop control trials.

It should be noted that small lagging retinal position errors (RPE), defined as the difference between the position of the target and that of gaze, were present at the onset of the open-loop interval (0.42 ± 1.00 and 0.37 ± 1.18°, averaged across all open-loop trials for *monkeys C* and *J*, respectively). However, the RPEs did not differ across conditions in which different RVEs were imposed ($P > 0.05$), with one exception for *monkey C*, in the HR condition when the imposed RVE $= -10$°/s, the average RPE (1.27 ± 0.89°) was larger than the RPE present when RVE $= 0$ or $+10$°/s ($P < 0.05$). Considering that the position errors did not vary across HU conditions, it is unlikely that they confounded the effects of imposing retinal velocity errors.

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 to collect data. Gaze, head, and target position signals were filtered (8-pole Bessel, DC-250 Hz) and then digitized at 1 kHz. Raw data files were transferred to a PC for subsequent analysis using custom algorithms developed in Matlab (MathWorks). Eye position was calculated as the difference between recorded gaze and head position signals. Gaze, eye, head, and target position traces were digitally filtered (DC-55 Hz) and differentiated to obtain the corresponding velocity traces.

To investigate the results of both *experiments 1* and *2*, desaccaded gaze velocity traces were averaged. Saccades were identified using a gaze acceleration threshold ($> \pm 3{,}500°/\text{s}^2$) and traces were then desaccaded as described by Wellenius and Cullen (2000). Unless otherwise stated, all averages were calculated by aligning individual traces on the onset of target motion in *experiment 1* and on the onset of the open-loop condition in e*xperiment 2.*

EXPERIMENT 1. The criteria for determining the onset of eye and head movements, defined as eye and head onset latencies, respectively, were similar to those described by Wellenius and Cullen (2000). Briefly, onset latency was defined as the point of intersection between a baseline regression and an initial response regression (Carl and Gellman 1987). The baseline regression was calculated over the interval of −25 to +75 ms with respect to the onset of target motion (target onset) for gaze onset, and between +50 and +150 ms with respect to target onset for head onset. The initial response regression was computed between the point where the eye or head velocity deviated from the baseline by 2.5 SD and the time 45 ms later. Each trial was visually assessed to ensure the accuracy of the latency estimates.

Initial pursuit dynamics were subsequently characterized by a method similar to that used in previous studies (Carl and Gellman 1987; Lisberger and Westbrook 1985; Tychsen and Lisberger 1986). Initial eye and head accelerations were quantified by applying a linear regression to the eye and head velocity traces over the interval of 0–80 ms from their respective motion onsets. The slope of the best-fit line was then used as an estimate of the mean acceleration in that interval.

Onset latencies and accelerations were calculated on a trial-by-trial basis. Average latencies and acceleration were calculated as the mean of the measurements obtained from ≥20 responses to identical stimuli. To ensure that our measurements were not contaminated by saccades, we included only those trials that did not contain saccades from 100 ms before target onset until ≥100 ms after gaze onset. Furthermore, trials were accepted for analysis only if gaze, eye, and head velocities were <3°/s during the 100-ms interval before target onset.

The relationship between target velocity or initial position and initial eye or head acceleration was quantified using a repeated-measures linear regression (Sokal and Rohlf 1995). To establish whether the average of two measured parameters were significantly different from each other, a Student's *t*-test was used ($P \leq 0.05$ considered significant).

The amplitude, frequency, and the time constant of the spontaneous oscillations in gaze velocity generated during pursuit were analyzed and compared between the HR and HU conditions. The individual gaze velocity records were subjected to two analyses. In the first method, oscillations were characterized as described previously by Robinson et al. (1986) and Goldreich et al. (1992). Briefly, a cursor was used to manually select the first and second peak of the oscillation, as well as the point at which the oscillations were no longer evident. The frequency was calculated as the reciprocal of the period between the two peaks, and the amplitude of the oscillation was determined by calculating the difference in the velocity between the first peak and the point at which the oscillations were no longer evident. In the second method, a cursor was used to select the segment of each trial to analyze by marking the time at which gaze velocity approximately reached target velocity (target velocity ±3°/s) and the time at which at least two cycles of the oscillation occurred as determined by visual inspection. A damped oscillation model of the form

$$(Ae^{kt})\sin(2\pi f(t)) \qquad (1)$$

was then fit through the selected portion of the velocity trace, where t is time, A is the initial amplitude, f is frequency, and k is the decay of the damped oscillation. The frequencies obtained from both methods were statistically identical ($P > 0.05$), and therefore we report only the frequencies calculated using the latter analysis. Because the damping of the oscillation was not calculated using the former method, we only report a value for k based on the latter analysis. Since the amplitude of the oscillations calculated using the first method estimated the magnitude of the initial overshoot of gaze velocity with respect to target velocity, whereas the latter method estimated the magnitude of the first oscillation, we report the amplitudes obtained from both methods.

Only trials that showed clear oscillations and showed a minimal decay of gaze velocity with respect to target velocity were analyzed, resulting in a data set which included ~85 and 40% of all trials for *monkeys C* and *J*, respectively. Note that an equivalent percentage of HR and HU trials were analyzed in each monkey. We observed that the magnitude of the HR oscillations, as previously reported (Fuchs 1967; Goldreich et al. 1992) as well as the HU oscillations, tended to decrease with training.

EXPERIMENT 2. We determined whether imposing a constant retinal velocity error during the maintenance of pursuit had an effect on the gaze, eye, and head responses by comparing average open-loop velocity trajectories to average closed-loop control trajectories. We considered the two conditions to differ only when the standard error of the mean velocities of the two conditions did not overlap for a period of ≥25 ms (Crane and Demer 2000). The onset of the difference was then defined as the open-loop response latency. This criterion tends to bias detection of the latencies toward later times than they actually occur, especially for the head traces because they showed a greater degree of variability (see RESULTS).

We also quantified the observed effects of imposing constant RVEs on the gaze, eye, and head responses. On a trial-by-trial basis, the gaze, eye, and head velocity over the 50-ms interval following the offset of the open-loop interval were measured and subsequently averaged across trials. To compare the open-loop responses with the closed-loop control responses, we calculated and averaged the control gaze, eye, and head velocities over a comparable 50-ms interval (i.e., ~450–500 ms after the onset of pursuit).

RESULTS

Eye-head pursuit strategy

Figure 1*A* shows an individual trial that illustrates a typical HR pursuit response from *monkey C*. Figure 1*A*, *top*, shows the position profile of the target and of the eye (=gaze) response; the *bottom panel* shows the accompanying target and eye velocity profiles. The target underwent a leftward step followed by a ramp in position (i.e., constant velocity of 40°/s) toward the right. The stereotyped nature of the HR pursuit responses is demonstrated in Fig. 1*B*. Pursuit latencies for this 40°/s step-ramp target trajectory were 86 ± 10 and 106 ± 10 ms (average ± SD) for *monkeys C* and *J*, respectively, and the monkeys' pursuit responses were such that they accelerated, exceeded target velocity, and then oscillated around the velocity of the target.

During HR trials, the gaze response was accomplished entirely by the use of the eyes alone because the head was immobile. However, in HU trials, the monkey was free to use any eye-head strategy desired to acquire initial fixation of the target and subsequently pursue it. Figure 2*A* shows a few of the infinite number of potential strategies a monkey could have used to acquire fixation of a target initially located at a position of −30° with respect to primary position. As in the HR trials, the monkey may have chosen to keep its head centered at 0° and used only its eyes to fixate the target (*left*), or may have used any number of combinations to align its axis of gaze (line of sight) with the target (*middle* and *right*). The actual strategies used by the two monkeys to acquire initial fixation of the target is shown in Fig. 2*B*, where the mean initial position of the gaze, eye, and head is plotted for the three initial target positions tested (see METHODS). The data were pooled across all velocities because the data were not significantly different across velocities. Each monkey oriented its axis of gaze toward the target and used a combination of both its eyes and head to accomplish this. Furthermore, both monkeys used statistically identical ($P > 0.05$) eye-head strategies to fixate eccentric targets. On average, 60% of the gaze redirection was accomplished by rotation of the head, while 40% of the gaze redirection was accomplished by rotation of the eyes. Note that the percents of initial head and eye contributions did not vary across initial target eccentricities ($P > 0.05$).

While both monkeys used similar strategies to acquire fixation of the target, they employed different eye-head pursuit strategies. Figure 3*A* shows superimposed gaze, eye, and head

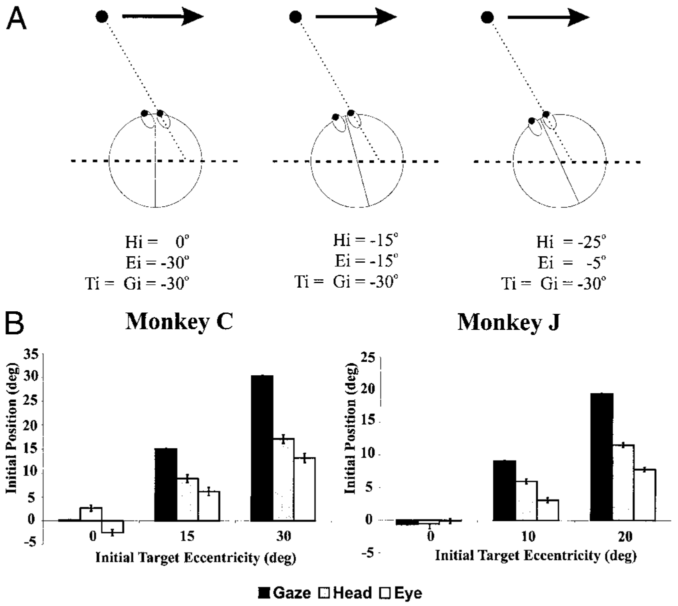


FIG. 2. Head-unrestrained initial fixation strategies. *A*: in the head-unrestrained (HU) condition, any number of different combinations of eye and head movements can be used to acquire initial fixation of the target. *B*: average initial gaze, head, and eye positions used to acquire initial fixation targets at different eccentricities. In this and subsequent figure, error bars represent SEs of the mean.

velocity movements made by the two monkeys in response to an initially centered target that was moved at a constant velocity of 40°/s. Individual trials (light lines) were aligned with respect to their own onset, and the average velocity traces were superimposed (solid dark lines). Despite the different *eye-head* strategies used by each monkey, the resulting HU *gaze* responses were highly stereotyped, analogous to the HR gaze responses. The individual trials shown in Fig. 3*A* were aligned with respect to target onset to calculate the average gaze, eye, and head position and velocity traces shown in Fig. 3*B*, *top* and *bottom*, respectively. Each monkey's gaze pursuit strategy was similar to that observed in the HR condition; gaze initially accelerated to match target velocity and then continued to oscillate around the velocity of the target for *monkey C* and oscillated yet steadily decayed from target velocity for *monkey J*. Furthermore, each monkey began pursuing the step-ramp target trajectory with its eyes at statistically identical pursuit latencies as in the HR conditions (HU pursuit latencies: 83 ± 9 and 104 ± 12 ms for *monkeys C* and *J*, respectively). The head-movement onset latencies (238 ± 72 and 182 ± 30 ms for *monkeys C* and *J*, respectively) were significantly longer than the eye latencies ($P > 0.05$). Note that although both monkeys employed different eye-head pursuit strategies, both monkey's eyes did not deviate far from primary position (i.e., within ~10° from primary position).

The effects of target velocity on the gaze-, eye-, and head-movement gains during sustained HU pursuit at all initial target eccentricities tested are shown in Fig. 4. The average movement gains were calculated by dividing gaze, eye, and head velocity by target velocity over the interval of 300–400 ms after target onset. Although the monkeys' eye (dashed lines)- and head (light solid lines)-movement gains varied in different directions as a function of velocity, their pursuit gains (i.e., gaze gains; dark solid lines) decreased as target velocity increased ($P < 0.005$) and did not vary as a function of initial target position ($P > 0.05$). Additionally, note that *monkey C* tended to match target velocity better than *monkey J* [compare *monkey C*'s average pursuit gain of 0.95 ± 0.08 with *monkey J*'s pursuit gain of 0.84 ± 0.07 ($P < 0.005$)]. Similar findings were obtained when the average movement gains were calculated over a later interval of 400–500 ms after target onset.

Is there a head-unrestrained advantage?

To determine whether the monkeys natural use of both their eyes and head to pursue moving targets is advantageous as compared with using the eyes alone, we first investigated whether pursuit accuracy was improved by comparing HU with HR pursuit gains (i.e., gaze velocity/target velocity). Figure 5 shows a plot of the relationship between HU and HR pursuit gains and target velocity for each monkey, calculated over the interval of 300–400 ms after target onset. For each monkey, HU and HR pursuit gains similarly decreased as velocity increased at all initial target positions with the exception that for *monkey J*, for initially centered targets at higher velocities (>50°/s), HU pursuit gains were significantly greater than HR pursuit gains ($P < 0.05$). Similar results were obtained when the pursuit gains were calculated over the interval of 400–500 ms after target onset with the exception that for *monkey J*, low HU pursuit gains were observed at lower velocities (<40°/s)

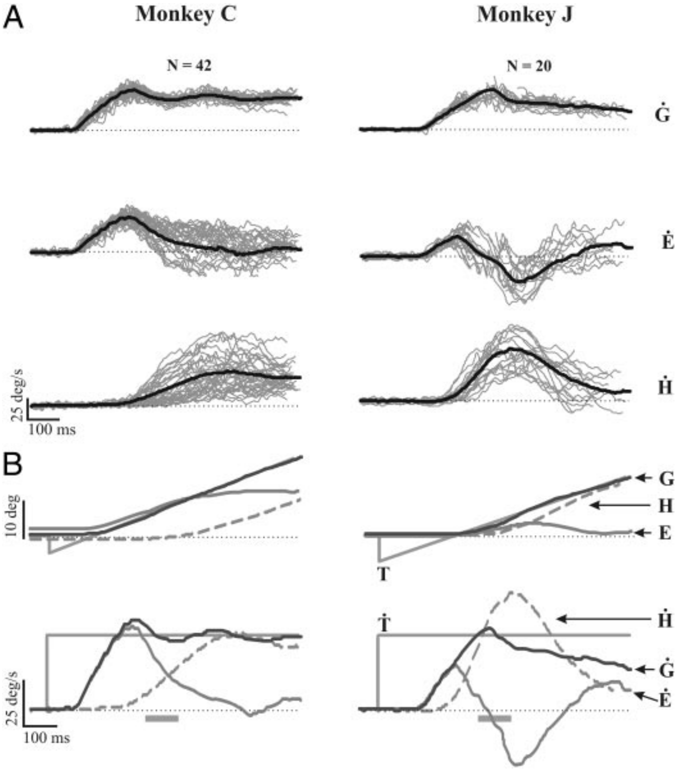


FIG. 3. Gaze pursuit strategy. *A*: average gaze, eye, and head velocity trajectories (dark lines) superimposed on individual trials (light line) made in response to a 40°/s step-ramp target trajectory that was initially centered are aligned on their respective movement onsets. Note the stereotyped gaze responses. *B*: average gaze, eye, and head position (*top*) and velocity (*bottom*) traces for traces shown in *A*. Note that although not shown, these response profiles are typical of what we observed in response to all target trajectories tested. Bar denotes the interval over which gaze, eye, and head movement gains were calculated.

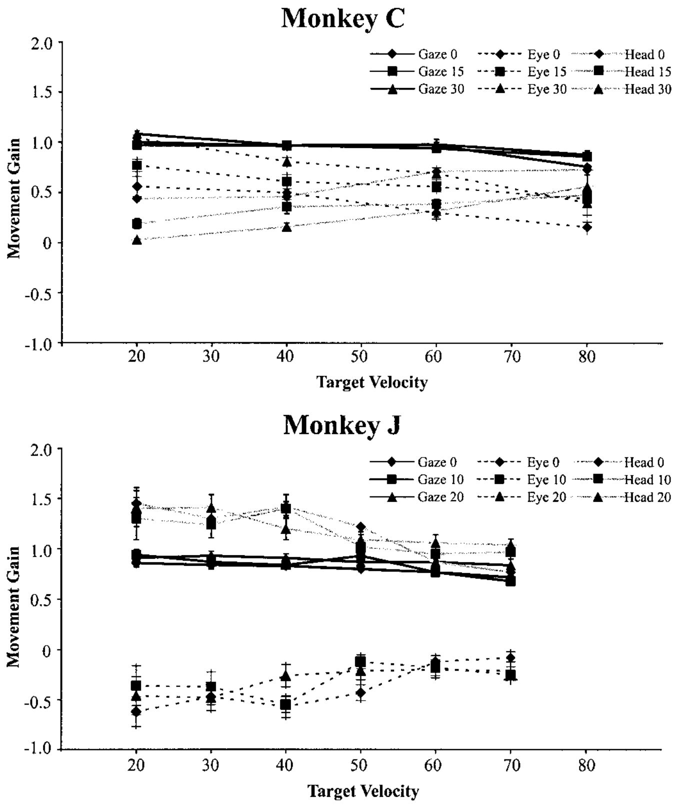


FIG. 4. Comparison of gaze, eye, and head movement gains during head-unrestrained pursuit. Gains were defined as the average velocity over the 300- to 400-ms interval following target onset divided by the target velocity over that interval. Note that the numbers in the *insets* indicate the initial target eccentricity.

for initially eccentric targets as compared with HR pursuit gains ($P < 0.05$). Hence it appears that there is no general advantage in terms of tracking performance for using both the eyes and the head.

A well-documented feature of HR pursuit is that the gaze velocity trajectory oscillates around target velocity when a constant target velocity is used (Fuchs 1967; Goldreich et al. 1992; Robinson et al. 1986). We therefore investigated whether similar oscillations in gaze pursuit were observed during HU pursuit, and, if so, whether they were reduced in amplitude such that pursuit accuracy was improved. Figure 6, *A* and *B*, illustrates examples of *monkey C*'s HR and HU response profiles, respectively, during gaze pursuit of an initially centered target moving at 20°/s. Also shown is the model fit used to characterize the oscillations (see METHODS). In the HR trial, the gaze velocity trajectory initially overshot and then oscillated around target velocity with each subsequent period being reduced in amplitude. In the HU trials, we observed similar oscillations. Table 1 shows the analysis results for all trials in which the target was initially centered and then moved at 20 and 40°/s. There were no consistent differences between the overshoot, frequency, amplitude, and/or the damping coefficient of the oscillation in the HR versus the HU conditions, suggesting that recruitment of the head did not alter the oscillations. Furthermore, no significant differences were observed between oscillation parameters for initially centered targets and targets initially presented eccentrically ($P > 0.05$, data not shown).

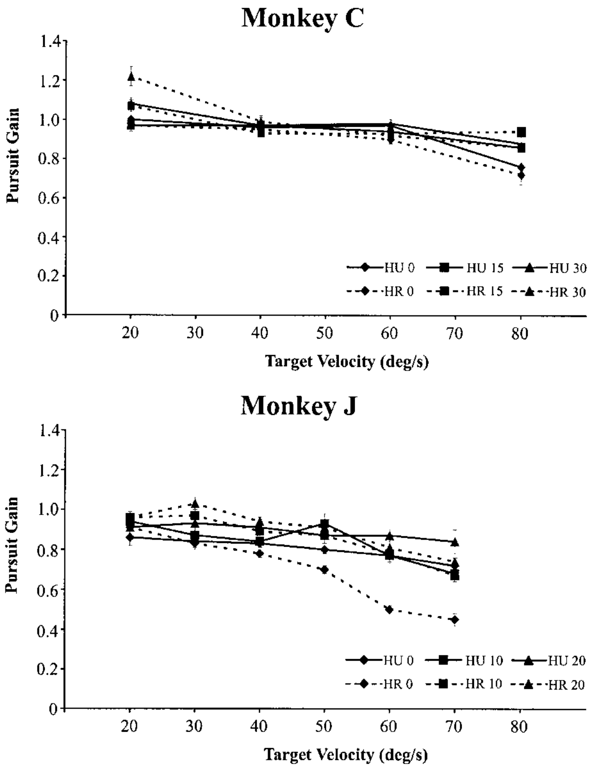


FIG. 5. Comparison of pursuit gains in the head-restrained and head-unrestrained conditions during sustained tracking. Pursuit gains were nearly identical in both the head-restrained (HR) and HU conditions for both monkeys.

As illustrated in Fig. 7*A*, both monkeys tended to make a saccade some time after the first 100 ms of pursuit. The possibility that head motion altered the timing of the first corrective saccade was also examined. For example, the initiation of the first corrective saccade might be facilitated in the

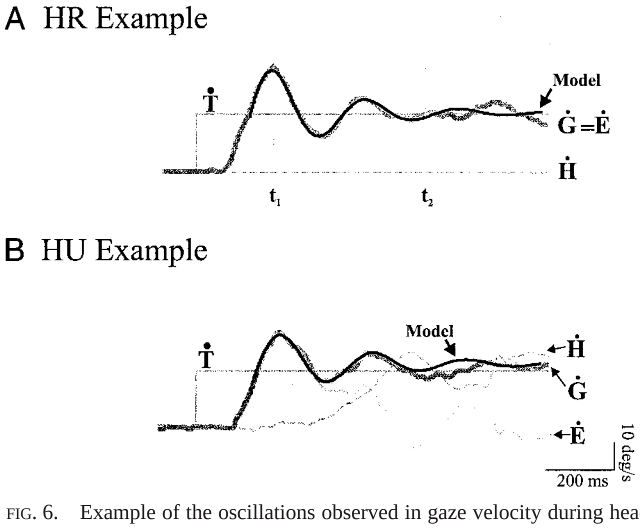


FIG. 6. Example of the oscillations observed in gaze velocity during head-restrained (*A*) and head-unrestrained (*B*) pursuit of a step-ramp target trajectory at 20°/s for *monkey C.* In both the HR and HU conditions, a damped oscillation model (dark trace, see METHODS) provided a good estimate of gaze velocity. The frequency of the oscillation was comparable in both conditions (3.7 and 3.5 Hz for the HR and HU example trials, respectively). Additionally, the amplitude of the gaze velocity overshoot (re: target velocity) was calculated from the difference in velocity at time *t*1 (peak velocity) and *t*2 (the velocity at which the oscillations were no longer evident). For the example HR and HU trials, the overshoot was 16.7 and 12.7°/s, respectively.

TABLE 1. *Comparison between head-restrained and -unrestrained oscillation characteristics*

	20°/s			40°/s		
	HR	HU	*P*	HR	HU	*P*
Monkey C						
Calculated						
Overshoot, deg	8.2 ± 3.0	7.9 ± 2.7	ns	7.2 ± 3.6	8.0 ± 3.6	ns
Model						
Frequency, Hz (*f*)	4.1 ± 1.4	3.4 ± 1.0	*	4.3 ± 0.6	4.2 ± 0.8	ns
Amplitude, deg (*A*)	12.6 ± 6.6	14.4 ± 8.8	ns	9.7 ± 6.2	11.9 ± 7.4	ns
Damping coefficient (*k*)	−5.1 ± 2.8	−5.5 ± 4.0	ns	−3.5 ± 4.3	−4.1 ± 3.1	ns
Monkey J						
Calculated						
Overshoot, deg	9.9 ± 3.6	7.9 ± 2.7	ns	14.7 ± 2.0	14.1 ± 8.6	ns
Model						
Frequency, Hz (*f*)	4.7 ± 1.0	3.8 ± 1.7	ns	5.5 ± 2.1	4.9 ± 1.3	ns
Amplitude, deg (*A*)	16.0 ± 8.3	9.6 ± 3.3	*	20.5 ± 10.2	18.2 ± 12.9	ns
Damping coefficient (*k*)	−7.6 ± 4.1	−4.2 ± 2.4	*	−6.7 ± 3.9	−5.5 ± 4.0	ns

Values are means ± SD. A Student's *t*-test was used to determine whether the means differed from each other. ns = $P > 0.05$; * $P < 0.05$; ** $P < 0.005$, where P is the probability that the difference between the means is not significantly different from zero. HR and HU, head restrained and unrestrained.

HU condition relative to the HR condition, possibly via vestibular quick phase mechanisms. We thus compared the time at which the first saccade occurred, relative to pursuit onset, for the HU and HR conditions. Figure 7*B* shows the average time for the first saccade for target trajectories of 40°/s for each of the initial target eccentricities tested. Again, no systematic difference was observed between the timing of the saccade between HU and HR trials for either monkey; the use of the head did not facilitate the onset of the first saccade nor did it alter the variability of its timing. In fact, the only condition in which we observed a large significant difference was for *monkey C*, for targets initially presented at a position of 30°, in which the saccade occurred later during combined eye-head pursuit in the HU condition, as compared with when only the eyes were used in the HR. In addition, the timing of the saccade did not vary as a function of target velocity or target eccentricity, nor was it related to the onset of head motion ($P > 0.05$, data not shown). Moreover, its timing was also not systematically related to tracking errors (i.e., RVE and RPE). The timing of *monkey J*'s first saccades were more stereotyped across all target trajectories as compared with *monkey C*. In general, *monkey J* generated an early saccade ~160 ms following the onset of pursuit, whereas *monkey C* generated saccades much later in the pursuit response (>320 ms). Therefore we did not observe any advantage during sustained tracking of a moving target for using the head as well as the eyes as compared with using the eyes alone.

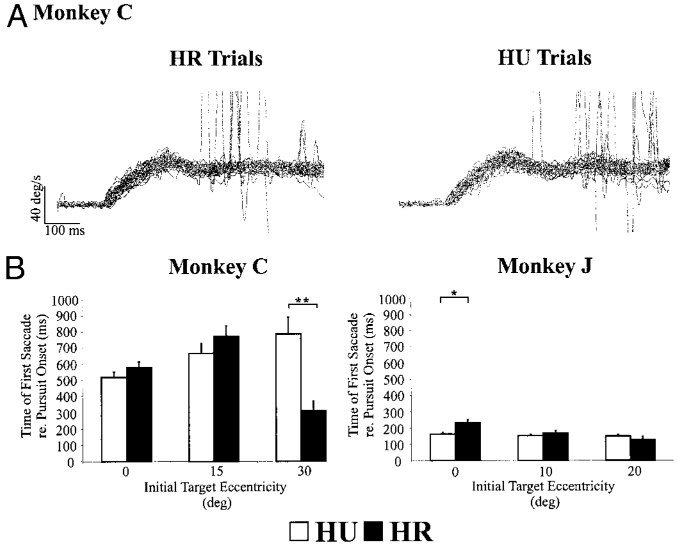


FIG. 7. *A*: superimposed HR and HU individual trials of *monkey C*'s pursuit responses to 40°/s step-ramp target trajectories that were initially centered. *B*: the time of the occurrence of the 1st corrective saccade, relative to pursuit onset, for HR and HU trials for 40°/s step-ramp target trajectories. Symbols as in Table 1.

Characterization of initial movement dynamics

Previous studies have shown that the first 80 ms of HR pursuit is free of any feedback of the visuomotor pathways that drive pursuit (see for example Krauzlis and Lisberger 1994; Lisberger and Westbrook 1985) and thus describes the system's output in response to a purely visual input. By characterizing initial eye (=gaze)-movement dynamics over the first 80-ms interval from movement onset, we were able to first compare HR and HU eye dynamics to determine whether an effect of head-restraint was present during this feedback-free period. Second the initial head dynamics (i.e., the first 80 ms of the response) were characterized to determine whether the signals that initially drove the head shared similar relationships with stimulus parameters, as did the signals that initially drove the eyes. Note that because the head began to move 180 ± 100 and 83 ± 30 ms (averaged across all trials for *monkeys C* and *J*, respectively) after gaze onset and because we only analyzed trials in which the gaze, eye, and head were immobile (0 ± 3°/s) at target onset, initial gaze and eye dynamics were generally equivalent during the first 80 ms and will thus be referred to as initial eye dynamics.

The average HR eye velocity accelerations are plotted as a function of target velocity for each of the initial target positions tested in Fig. 8*A* and Table 2 provides a summary of the results obtained from a repeated-measures linear regression of acceleration as a function of target velocity. For *monkey C*, eye acceleration tended to increase as a function of target velocity for all initial target positions tested. However, at the most eccentric initial target position, the regression analysis did not

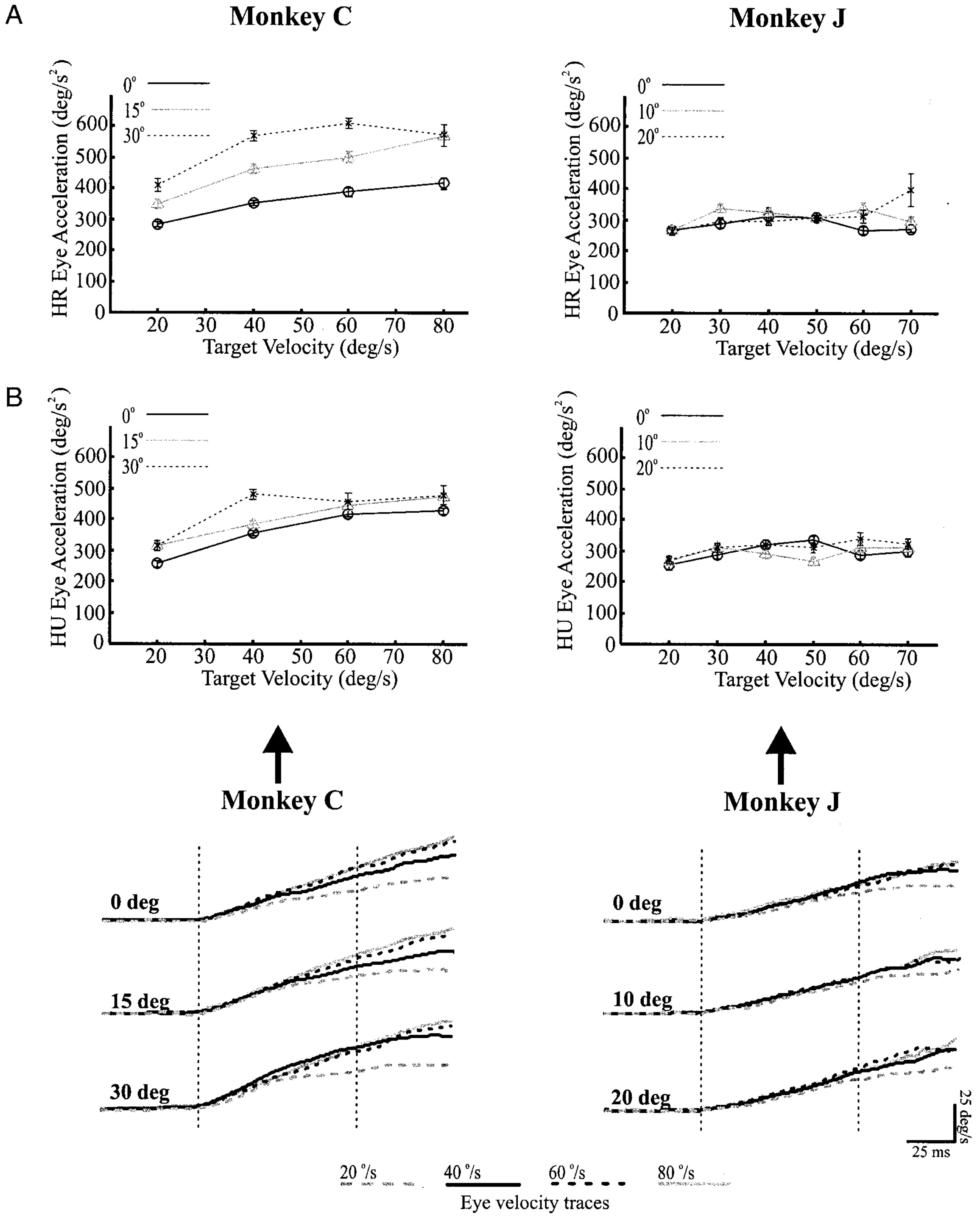


FIG. 8. Effect of target velocity on initial eye (=gaze) acceleration. *A*: effect of target velocity on initial HR eye acceleration for all eccentricities tested. *B*, *top*: effect of target velocity on initial HU eye acceleration for all eccentricities tested. *Bottom*: average eye velocity traces in response to target motion at different velocities in the HU condition aligned on eye movement onset. Dotted vertical lines denote the 80-ms interval over which acceleration was quantified.

show statistical significance; possibly as a result of the saturation of initial eye acceleration at ~600°/s^2 observed in response to the faster velocity step ramps. For *monkey J*, there was also an increasing trend for initial target positions of 0 and 20°, which then appeared to saturate at velocities >50°/s. However, only when the target motion began from the most eccentric (i.e., 20°) position was this trend significant. Figure 8*A* also illustrates the relationship between eye acceleration and initial target position. For *monkey C*, eye acceleration systematically increased as a function of initial target eccentricity ($P < 0.05$). In contrast, for *monkey J*, average eye acceleration showed only a small increase with target eccentricity at higher target velocities (>50°/s), and the trends were not statistically significant ($P > 0.05$).

TABLE 2. *Initial eye (HR and HU) and initial head (HU) acceleration versus target velocity*

	T	*n*	*m*	*R*	*P*
Monkey C					
HR eye	0	117	2.19	0.57	**
HU eye	0	160	2.77	0.65	**
HU head	0	160	6.47	0.56	**
HR eye	15	110	3.56	0.66	**
HU eye	15	133	2.7	0.64	**
HU head	15	133	5.12	0.64	**
HR eye	30	81	2.92	0.51	ns
HU eye	30	89	2.06	0.35	ns
HU head	30	89	6.11	0.63	**
Monkey J					
HR eye	0	173	−0.21	0.05	ns
HU eye	0	131	0.69	0.16	ns
HU head	0	131	2.98	0.26	*
HR eye	10	145	0.44	0.11	ns
HU eye	10	125	0.62	0.15	ns
HU head	10	125	5.79	0.43	**
HR eye	20	149	2.08	0.29	**
HU eye	20	133	0.99	0.22	*
HU head	20	133	4.52	0.31	**

T = initial target position (deg); n = number of trials; m = slope of regression; R = correlation coefficient; ns = $P > 0.05$; * $P < 0.05$; ** $P < 0.005$, where P is the probability that the regression slope is not significantly different from zero.

Figure 8*B* (*bottom*) illustrates the average eye velocity traces during HU pursuit in response to target motion at four different target velocities and for each of the initial target positions tested. In both monkeys, the eye velocity traces tended to diverge within the first 80 ms such that targets with faster velocities resulted in larger eye accelerations. This relationship is quantified in Fig. 8*B* (*top*) and in Table 2. For *monkey C*, eye acceleration significantly increased as a function of target velocity for initial target positions of 0 and 15°. For *monkey J*, similar to the HR condition, initial eye acceleration tended to increase as a function of target velocity; however, only when the target began from the most eccentric positions was this trend statistically significant. We thus also compared the average initial eye acceleration for 20 versus 50°/s in both the HR and HU condition for all initial target positions for *monkey J* and found a significant increase ($P < 0.05$) for all but one condition (HU, initial target position = −10°). In addition, for *monkey J*, no significant difference was found when HR and HU average initial eye accelerations were directly compared across all conditions ($P > 0.05$). For *monkey C*, HR and HU average initial eye accelerations were statistically identical only when initial target position was presented at an initial position of 0° ($P > 0.05$).

Interestingly however, the effect of initial target position on eye acceleration in the HU condition observed for *monkey C* was markedly reduced as compared with its effect in the HR condition, especially at high velocities (>60°/s; compare Fig. 8, *A* and *B*). Although initial gaze positions in the HU and HR conditions were similar, initial eye and head positions were not. We therefore investigated whether the reduced effect of eccentricity on eye acceleration in the HU condition was due to an effect of initial eye or head position by performing a regression analysis of acceleration as a function of initial eye or head position (analysis not shown). We found that initial eye acceleration significantly increased for more eccentric initial eye positions in the HR and HU conditions in response to 60°/s step-ramp stimuli (Table 3) and was not significantly related to initial head position ($P > 0.05$). These results are consistent with our previous finding that pursuit latencies are influenced by eye position (Wellenius and Cullen 2000) and the results of Mann and Morrow (1997) who reported that head position had no effect on HR pursuit responses. Thus the reduced effect of target eccentricity on average initial eye accelerations observed in the HU condition compared with the HR condition could largely be accounted for by the effect of initial eye eccentricity.

To determine whether initial *head* dynamics shared similar relationships to stimulus parameters as initial *eye* dynamics, we next compared average head velocity trajectories made in response to step-ramp target trajectories at four different velocities and for all initial target positions tested (Fig. 9, *bottom*). In each monkey, the head velocity trajectories strikingly diverged as target velocity increased within the first 80 ms of the movement response. This is further illustrated in Fig. 9, *top*, and is quantified in Table 2. Head acceleration increased as a function of target velocity at all initial target positions tested. In addition, initial head acceleration was not systematically related to initial target position in either monkey ($P > 0.05$).

Characterization of open-loop gaze pursuit responses

Several studies have shown that RVEs are effective stimuli for eliciting smooth eye accelerations during HR fixation and for altering eye velocity during HR pursuit (Morris and Lisberger 1987; Segraves and Goldberg 1994). Recall that *experiment 1* was designed so that both the eyes and the head were motionless at target onset (see METHODS) such that the target and its initial image on the retina moved at the same velocity. It then follows that as target velocity increased, so did initial retinal velocity error as well as both initial eye and head acceleration. Accordingly, we explored in *experiment 2* whether the gaze, eye, and/or head velocity trajectories are similarly altered in response to RVEs imposed during the maintenance of the pursuit responses.

The effects of imposing different RVEs on gaze, eye, and head velocity trajectories were investigated by comparing the average velocity trajectories during closed-loop control and open-loop trials in the HR and HU conditions. As discussed in METHODS, we considered the two conditions to differ only when the standard error of the mean velocities of the two conditions did not overlap for a period of ≥25 ms. The HR and HU average responses for *monkeys C* and *J* are shown in Fig. 10, *A* and *B*, respectively. The trials started with the monkey

TABLE 3. *Initial eye acceleration versus initial eye position (target velocity = 60°/s)*

	T′	*n*	*m*	*y* intercept	*R*	*P*
Monkey C						
HR	60	78	6.97	399.42	0.66	**
HU	60	109	4.04	421.98	0.41	*
Monkey J						
HR	60	67	3.95	274.59	0.41	**
HU	60	63	6.44	287.09	0.39	**

ns = $P > 0.05$; * $P < 0.05$; ** $P < 0.005$.

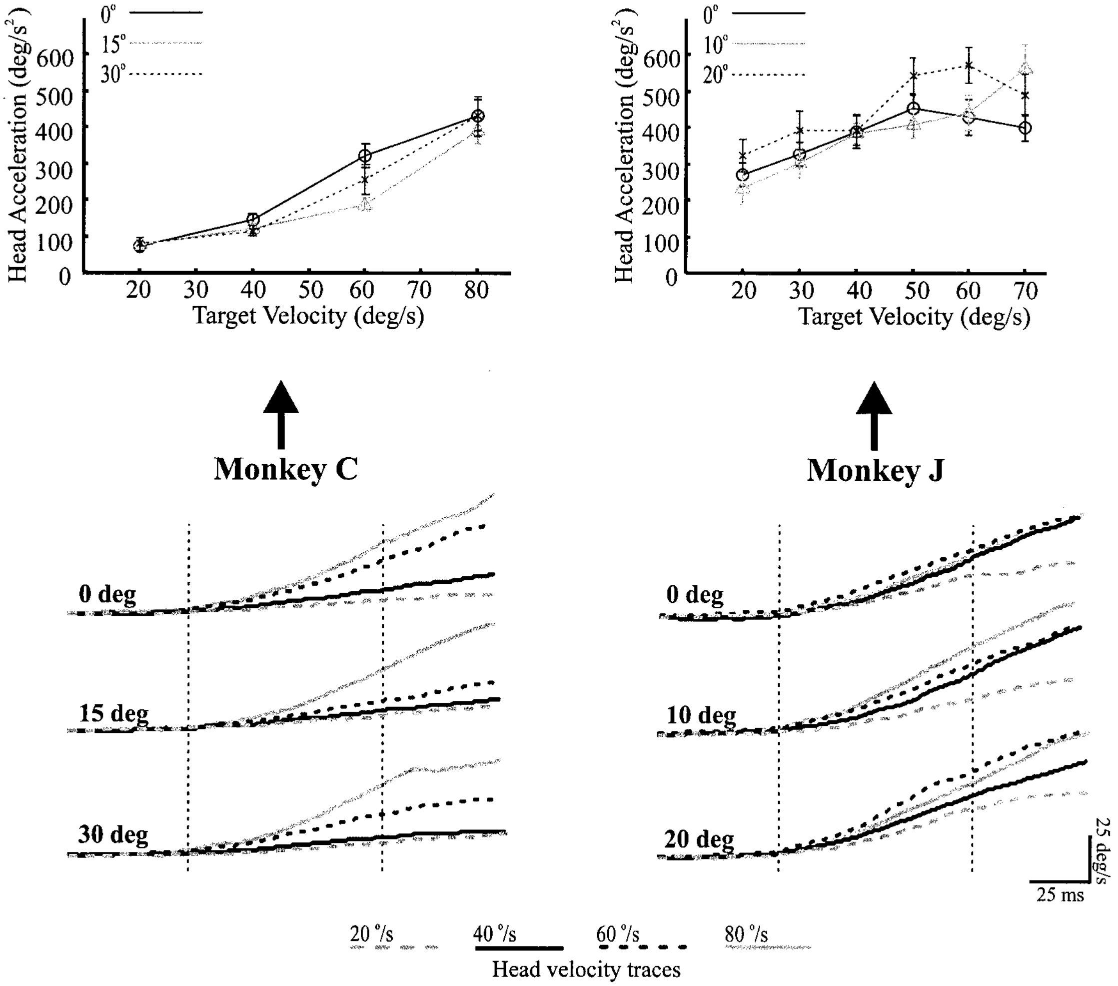


FIG. 9. Effect of target velocity on initial head acceleration during HU pursuit. *Top*: effect of target velocity on initial head acceleration for all eccentricities tested. *Bottom*: average head velocity traces in response to target motion at different velocities in the HU condition aligned on head movement onset. Dotted vertical lines denote the 80-ms interval over which acceleration was quantified.

initiating a pursuit response to a 40°/s step-ramp stimulus. In the open-loop trial, following a ~125 ms delay from gaze movement onset, the loop was opened and a RVE of 0 (*left*), −10 (*middle*), or +10°/s (*right*) was applied. In *monkey J*, because positive error always evoked saccades within 100 ms after the loop was opened, we were only able to study the effects of imposing negative errors. For *monkey C*, when the target was artificially stabilized with respect to the fovea such that RVE = 0°/s (*left*), the open-loop HR average eye (=gaze) trajectory was slightly greater than the average closed-loop control trajectory. Moreover, HR eye velocity decreased for the imposed negative errors (*middle*) and increased for the positive error (*right*), relative to the average closed-loop control trajectory. For *monkey J*, in the absence of any visual input (*left*), HR eye velocity diverged slightly from the average closed-loop control trajectory such that its velocity was less than that of the control, and when RVE = −10°/s (*right*), the HR eye velocity decreased even more relative to the control. The gaze response latencies (see METHODS), illustrated by the arrows, occurred ~110–120 ms following the onset of the open-loop interval.

Figure 10, *A* and *B*, also illustrates that for *monkey C*, when RVE = 0°/s, the average HU gaze velocity trajectory did not differ from the average closed-loop control trajectory, and analogous to the HR responses, when RVE = −10 or +10°/s, the trajectories decreased and increased, respectively, relative to the average closed-loop control responses. For *monkey J*, when RVE = 0°/s, the average HU gaze velocity trajectory decreased slightly compared with the closed-loop control trajectory and decreased even more when RVE = −10°/s. The HU open-loop gaze response latencies were also similar to those obtained in the HR condition (i.e., ~110–120 ms).

We next examined whether the effects of RVE were mediated by altering the velocity of the eyes alone, the head alone, or by altering the velocity of both the eyes and the head. When RVE = 0°/s, neither the eye nor the head trajectory differed from their respective closed-loop control trajectories for *monkey C* (Fig. 10*A*), whereas both the eyes and the head trajectories decreased compared with closed-loop control for *monkey J* (Fig. 10*B*). When we imposed a negative velocity error to both monkeys' foveae, both the eye and the head velocity trajectories responded by decelerating (i.e., decreasing their velocities); and for *monkey C*, when a positive error was imposed both the eye and the head accelerated (i.e., increasing their velocities) relative to their closed-loop control responses.

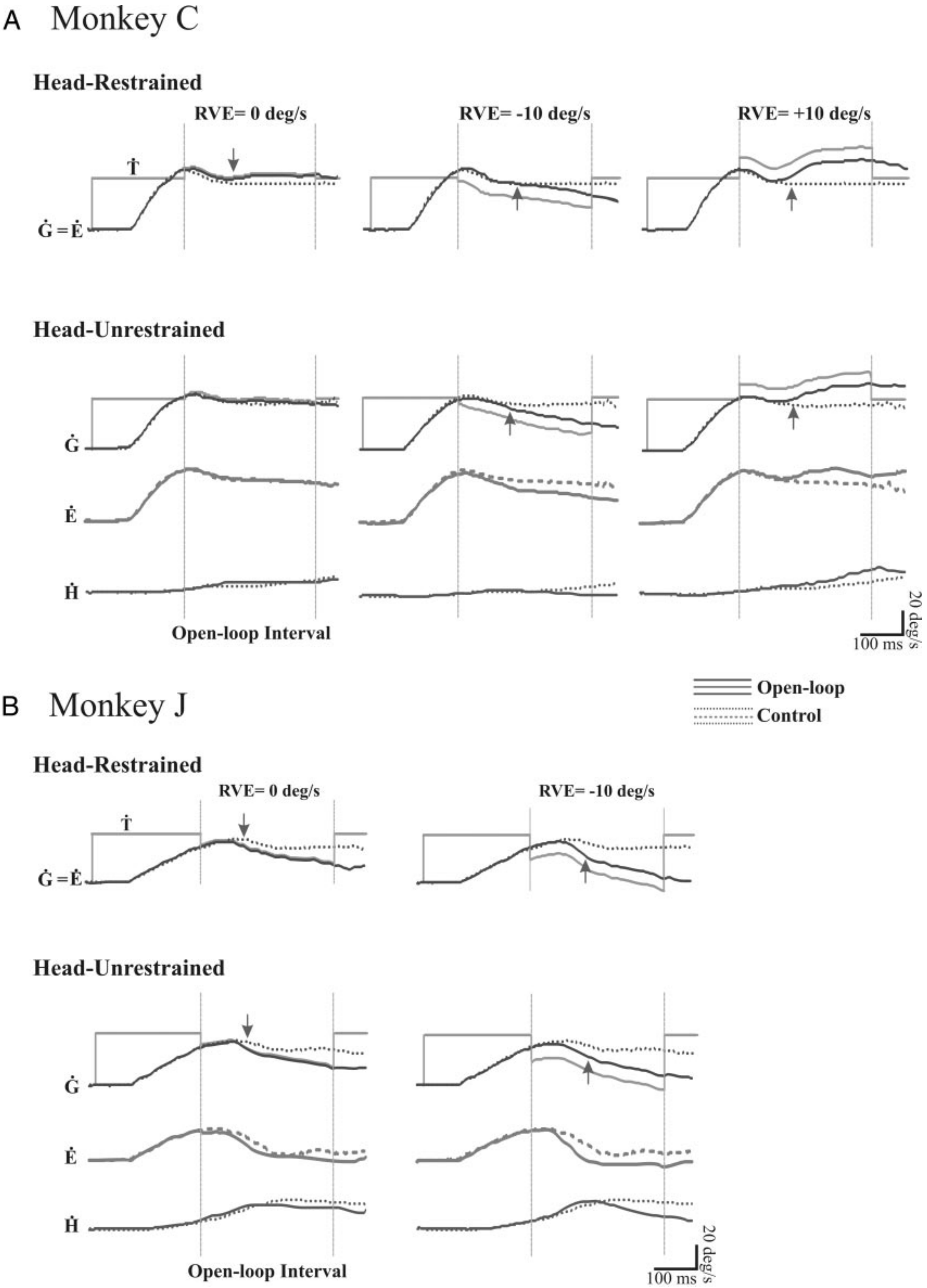


FIG. 10. Comparison of open-loop response vs. closed-loop control responses in the HR and HU conditions. The average HR eye and HU gaze, eye, and head velocity traces during open-loop trials (solid line) are superimposed on their respective average velocity traces during closed-loop control trials (dashed line) for *monkeys C* (*A*) and *J* (*B*). During the open-loop interval, the target was either artificially stabilized with respect to the animal's fovea such that the retinal velocity error was equal to 0°/s (*left*), or a retinal velocity error of −10 or +10°/s was imposed (*middle* and *right*, respectively). Downward arrows indicate the time at which the standard error of the open-loop response diverged from that of the closed-loop control response (i.e., 0°/s vs. control). Upward arrows indicate the time at which the standard error of the open-loop trace with an imposed error of 10°/s diverged from that of the response to a stabilized target (i.e., ±10 vs. 0°/s). Dashed lines represent onset and offset of the open-loop interval, which was 300 ms in all open-loop experiments.

Note that the open-loop head responses lagged the eye response by ~50–100 ms.

We quantified the effect of imposed RVE on the gaze, eye, and head responses by comparing the average velocity of the gaze, eye, and head in the 50-ms interval following loop offset to a comparable interval in the closed-loop control trials (see METHODS). The effect of stabilizing the target relative to the subject's axis of gaze (RVE = 0°/s) compared with closed-loop control trials is quantified for each monkey in Table 4. In *monkey C*, no significant effect was observed in the HU gaze, eye, or head, although HR gaze was slightly faster than control when RVE = 0°/s. In contrast to *monkey C,* stabilizing the target on *monkey J*'s fovea resulted in a significant effect such that HR and HU gaze responses decreased with respect to the closed-loop control trials. However, although both the eyes and the head responded by altering their velocity trajectories in the same directions so that the resultant gaze response (i.e., gaze = eye + head) decreased significantly, neither the eye nor the head responses were themselves significantly different from their closed-loop control responses.

The effect of stabilizing the target on the retina (RVE = 0°/s) was compared with the effect of imposing negative (RVE = −10°/s) or positive (RVE = +10°/s) velocity errors (Table 5). In *monkey C*, gaze, eye, and head responses were significantly different between conditions; negative errors evoked decelerations and positive errors evoked accelerations. Analogous to *monkey C,* in *monkey J*, negative errors evoked significant decelerations in both HR and HU gaze velocity. Although the eye and the head responded in the same direction as did gaze, neither responses showed a statistically significant deceleration in this interval. Nevertheless, in each monkey, the gaze, eye, and head responses toward imposed retinal velocity errors were qualitatively similar.

The results of *experiment* 2 provide evidence that the pursuit system possesses some form of velocity storage that drives gaze to continue at its current (or damped) velocity. Recent models of the pursuit system have proposed that velocity memory arises from an efference copy of the eye velocity command (Krauzlis and Lisberger 1991, 1994; Robinson et al. 1986; Zee et al. 1981). Since gaze velocity is no longer equivalent to eye velocity in the HU condition, we postulated that during eye-head pursuit the storage of velocity information arises from an efference copy of the gaze velocity command. To further probe this hypothesis, we examined the results from the HU condition of *experiment* 2 for *monkey J*, whose eye movements were not equivalent to the gaze movements at the onset of the open-loop interval, and compared them to the results obtained from the HR condition. Figure 11*A* shows *monkey J*'s average HR and HU closed-loop control gaze responses for *experiment 2.* Note that the two responses are statistically indistinguishable, illustrating once more the lack of a head-restraint effect on gaze pursuit. Figure 11*B* shows, for trials in which the target was artificially stabilized, *monkey J*'s average HR and HU pursuit responses as well as the average HU eye response. Once more, the pursuit (i.e., gaze) trajectories superimpose almost perfectly. On the other hand, unlike the gaze trajectories, the HU eye trajectory actually diverges from the HU gaze trajectory ~50 ms before the loop is opened due to the contribution of the head to the pursuit movement (see Fig. 11*B*) and does not superimpose with the HR gaze trajectory. Therefore we suggest that the stored velocity information was better related to the gaze trajectory than to the eye trajectory at the time the loop was opened.

TABLE 4. *Comparison of velocities when the target was artificially stabilized with respect to the monkey's fovea (i.e. RVE = 0°/s) and closed-loop control trials*

RVE =	Control	0°/s	*P*
Monkey C			
HR gaze	38.5	45.0	**
HU gaze	37.9	35.7	ns
HU eye	29.2	28.0	ns
HU head	8.6	7.8	ns
Monkey J			
HR gaze	30.5	18.8	**
HU gaze	28.8	17.2	**
HU eye	4.7	0.6	ns
HU head	22.5	17.0	ns

ns = $P > 0.05$; * $P < 0.05$; ** $P < 0.005$.

TABLE 5. *Comparison of velocities when the target was artificially stabilized with respect to the animal's fovea (i.e. RVE = 0°/s) and trials with imposed retinal velocity errors (RVE = ±10°/s)*

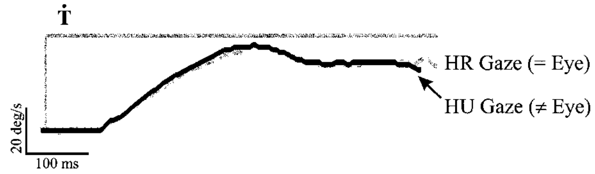
RVE =	0°/s	−10°/s	*P*	+10°/s	*P*
Monkey C					
HR gaze	45.0	26.7	**	55.5	**
HU gaze	35.7	21.8	**	50.5	**
HU eye	28.0	20.4	**	37.5	**
HU head	7.8	2.3	**	15.7	**
Monkey J					
HR gaze	18.8	9.1	**	—	—
HU gaze	17.2	12.8	**	—	—
HU eye	0.6	−1.7	ns	—	—
HU head	17.0	12.3	ns	—	—

ns = $P > 0.05$; * $P < 0.05$; ** $P < 0.005$.

DISCUSSION

The main purpose of this study was to characterize initial gaze, eye, and head dynamics during combined eye-head pur-

A Closed-loop Control Responses



B Open-loop Responses

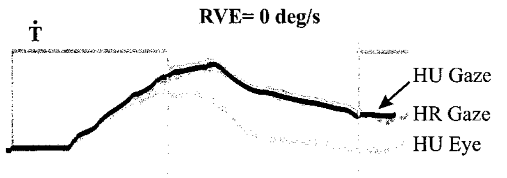


FIG. 11. *A*: superimposed average closed-loop control HR and HU gaze responses in *experiment 2*. *B*: superimposed average HR gaze with HU gaze and HU eye responses during the open-loop interval in *experiment 2* when RVE = 0. Note how well the HU gaze trajectory superimposes on the average HR gaze trajectory during both the control and open-loop trials, suggesting that the stored velocity information reflects an efference copy of the gaze movement rather than of the eye movement.

suit in responses to step-ramp stimuli in the HU condition. The principal findings were that the pursuit responses (i.e., gaze responses) were highly stereotyped and nearly identical among the HR and HU conditions in response to identical step-ramp stimuli such that there was no HU advantage; initial eye and initial head acceleration tended to increase as a function of target velocity; HR and HU gaze similarly responded to targets that were stabilized with respect to the monkey's fovea or that were moved with constant retinal velocity errors; and the observed HU gaze responses to imposed RVEs were generally mediated by the eyes and the head.

Why use both the eyes and the head to pursue a moving target?

The results from *experiment 1* showed that in the more natural HU condition, monkeys use both their eyes and their head to pursue a step-ramp target trajectory, although different pursuit strategies could be employed. What our experiments failed to reveal was the existence of any apparent difference between the HR and HU conditions that would be advantageous to the monkey's pursuit response during either the initiation or the maintenance of pursuit. Our findings using step-ramp trajectories confirm previous studies that have reported little or no advantage during the maintenance of pursuit, in terms of pursuit accuracy, for using both the eyes and the head to pursue predictable (i.e., sinusoidal and/or triangular) and unpredictable periodic (i.e., pseudorandom) target trajectories (Barnes 1981; Barnes and Grealy 1992; Barnes and Lawson 1989; Barnes et al. 1987; Gresty and Leech 1977; Lanman et al. 1978; Leigh et al. 1987; Smith et al. 1995).

If pursuit could be accomplished with equivalent accuracy with the use of the eyes alone, why rotate the head when it requires a larger force, as compared with the eyes, to overcome its large viscous-inertial load (Zangemeister et al. 1981; or see Peng et al. 1996)? We propose that an inherent advantage for the use of the head during pursuit is to keep the eyes somewhat centered in the orbit (i.e., with respect to the head) and far from the mechanical limits of ocular motor motility. In fact, as shown in Fig. 3*A*, the eye positions throughout the pursuit responses in both monkeys ($\pm 15°$) were generally close to the primary position (within 15°) and thus were well within the physical and mechanical limits of ocular motor motility ($\sim \pm 50°$) (Cullen and Guitton 1997; Freedman and Sparks 1997; Lauritis and Robinson 1986; Tomlinson and Bahra 1986), a finding that has also been previously reported in monkey eye-head pursuit responses to periodic target trajectories (Lanman et al. 1978).

Prior investigations have shown that primates use both their eyes and their head to rapidly reorient their line of sight with a target (referred to as a gaze shift; see for example: Barnes 1981; Bizzi et al. 1971; Freedman and Sparks 1997; Guitton and Volle 1987; Roy and Cullen 1998; Tomlinson and Bahra 1986; Zangemeister and Stark 1982a,b; Zangemeister et al. 1981). Interestingly, these studies have shown that head motion accomplishes a greater percentage of the gaze shift for larger amplitude target displacements ($>40°$), such that the eyes remain within $\sim 25°$ of their primary position. Hence, both gaze shift and gaze pursuit systems, which are mediated by two distinct neural pathways (reviewed in Leigh and Zee 1999), employ similar eye-head strategies to redirect the visual axis to an object of interest. Such eye-head gaze-reorientation strategies possess the teleological advantage of ensuring that when a second object of interest appears in the vicinity of the object (i.e., more eccentrically) being pursued, the subject will be able to more rapidly align its line of sight in any direction with the new object of interest given that a smaller effort is required to rapidly rotate the eyes as compared with the head (Zangemeister et al. 1981; or see Peng et al. 1996).

Initial eye- and head-movement dynamics

In contrast to the striking effect of target velocity observed on the initial head dynamics in both monkeys, we found that the effects of target velocity on initial HR and HU eye acceleration were more subtle in *monkey J* as compared with *monkey C* (compare slopes for HU eye of 2.7 vs. 0.7 for *monkeys C* and *J*, respectively, for initially centered targets, as seen in Table 2). Several factors may have contributed to the differential effect of target velocity on initial eye acceleration observed between the two monkeys. First, as seen in Fig. 5, *monkey J*'s performance during the maintenance of pursuit declined at higher velocities ($>50°/s$), as indicated by pursuit gains that were below unity. It is possible that this resulted because *monkey J* had less experience with pursuit tasks than did *monkey C.* Alternatively, it is possible that the eyes and the head might have different preferred ranges of target velocities and that eye acceleration saturates for lower target velocities than head acceleration, consistent with the increasing recruitment of the head as the velocity of the target is increased (see Fig. 9). Moreover, these preferred ranges may differ across subjects such that *monkey J*'s eye acceleration saturated earlier and at lower target velocities than *monkey C*'s eye acceleration (see Fig. 8).

Second, *monkey J* rotated its head earlier and more rapidly to initially acquire and pursue the target (see Fig. 3*A*). For example, for initially centered 40°/s step-ramps, head latency was 182 and 238 ms ($P < 0.005$) and head acceleration was 389 and $143°/s^2$ ($P < 0.005$) for *monkeys J* and *C*, respectively. Considering that gaze velocity is equivalent to the sum of eye and head velocities and because the head moved more rapidly in response to faster moving targets (see Fig. 9), *monkey J*'s eyes did not accelerate as rapidly as compared with *monkey C*'s eyes. We propose that in the HU condition, a modification of the premotor drive to the eyes may have occurred via an interaction with vestibular signals that arose from the self-generated head motion as has been reported to occur during gaze-reorienting movements (Barnes 1981; Belton and McCrea 2000; Freedman and Sparks 1997; Lanman et al. 1978; Roy and Cullen 1998). Similarly, other inputs could have contributed to modifying the premotor drive to the eyes in both the HR and HU conditions. Electromyography recordings have revealed that neck muscle activity is strongly coupled with eye-movement dynamics during ongoing pursuit and saccadic eye movements in the *HR* 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 HU human (Zangemeister and Stark 1982a) and monkey (Bizzi et al. 1971). Given that *monkey J* moved its head earlier, it is possible that inputs from a neck motor efference command and/or neck proprioceptors to the eye-motor system contributed to masking the effect of target velocity on initial eye acceleration in this animal, even before vestibular inputs came into play in both the HU and HR conditions.

In both the HR and HU conditions, initial eye-movement dynamics showed some degree of saturation at target velocities >50°/s. These results are in general agreement with those of previous studies, which have used similar, yet not identical, step-ramp stimuli to characterize HR pursuit responses in primates (Carl and Gellman 1987; Lisberger and Westbrook 1985; Mann and Morrow 1997; Suzuki et al. 1999). The finding that initial eye and initial head-movement responses shared similar relationships with target velocity, regardless of the different eye-head pursuit strategies used by each monkey, provides evidence for the existence of an upstream shared-controller within the pathways that drive pursuit (see following text).

Gaze, eye, and head responses to retinal velocity errors

The results from *experiment 1* revealed the similar relationships that both the eyes and the head share with stimulus parameters during the initiation of the pursuit responses. Additionally, by opening the visual feedback loop ~125–150 ms after pursuit had been initiated (see METHODS), we examined the effects of imposing constant retinal velocity errors on the gaze, eye, and head responses during the maintenance of pursuit, which have been shown to be mediated, at least in part, by different mechanisms than those that mediate pursuit initiation (Morris and Lisberger 1987). Our HR data revealed, in agreement with previous studies (see for example: Becker and Fuchs 1985; Carl and Gellman 1987; Morris and Lisberger 1987; Newsome et al. 1988), that eye velocity is roughly maintained in the absence of retinal velocity errors and that RVEs are effective stimuli for modifying eye velocity to correct for errors in tracking. A novel finding in our study was that during HU pursuit, gaze velocity was also generally maintained in the absence of retinal velocity errors, and both the eyes and the head mediated the changes in gaze velocity that were observed in response to RVEs. It should be noted that although a small RPE was present at the onset of the open-loop interval, it was always in the same direction (i.e., lagging the target) and it did not generally differ across conditions and thus did not bias the effects of imposing different velocity errors. Accordingly, we suggest that both responses indicate that the pursuit system possesses some form of velocity storage that drives gaze to continue along its current or at a damped velocity until the pursuit system receives an input that indicates the current ongoing gaze velocity should be appropriately corrected.

Gaze pursuit velocity memory

Although many previous studies have reported that the pursuit system has the ability to store velocity information (see for example Barnes and Asselman 1991; Barnes and Grealy 1992; Barnes et al. 1995, 1997; Becker and Fuchs 1985; Collins and Barnes 1999; Keller and Johnsen 1990; Morris and Lisberger 1987), the source of these signals remains contentious. For instance, Morris and Lisberger (1987) have suggested that the stored velocity signal, or velocity memory as they termed it, is derived from the corollary discharge of eye velocity. These investigators suggested that velocity memory is the principal drive during the maintenance of pursuit and that visual inputs cause corrective changes in eye velocity. In contrast, Barnes and collaborators (Barnes and Asselman 1991; Barnes and Grealy 1992; Barnes et al. 1995, 1997; Collins and Barnes 1999) have performed a number of studies using targets with repetitive trajectories to investigate the characteristics of anticipatory (or predictive) smooth eye movements. They proposed that anticipatory eye movements are driven by signals that reflect stored information related to the velocity of the target, which they argue is not derived from an efferent copy of the eye movement but more likely from a more central gaze-related signal (i.e., gaze = eye + head). Moreover, Barnes and collaborators have recently shown that both the eyes and the head show evidence of such anticipatory movements and have recently found that both the eyes and the head receive the velocity memory signal (Barnes and Grealy 1992; Collins and Barnes 1999). Although all these studies present evidence that velocity information is being stored, none were able to distinguish whether the source of the stored velocity information was of an afferent or of an efferent source. Furthermore, it is also not known whether velocity memory and anticipatory movements arise from the same neural mechanisms.

The results from *experiment 2* also do not allow us to discriminate whether the source of the stored velocity information arises from a visual afferent source or an efference copy of the gaze velocity command. However, in agreement with Barnes and collaborators (Barnes and Grealy 1992; Collins and Barnes 1999), our data do suggest that the response to the stored velocity information is better related to gaze velocity than to eye velocity (see Fig. 11). Our general hypothesis is therefore that the stored information is encoded in gaze- not eye-based coordinates.

Our results indirectly address the question of whether gaze responses to targets stabilized on the fovea might arise from the same neural mechanisms as do predictive gaze movements that occur in response to periodic target presentations (Barnes and Asselman 1991; Barnes and Grealy 1992; Barnes et al. 1995, 1997; Collins and Barnes 1999). Interestingly, *monkey C*, whose pursuit response to stabilized targets showed the strongest evidence for velocity memory, was highly experienced in pursuing step-ramp and sinusoidal target trajectories (i.e., >5 yr training). In contrast, *monkey J*, whose pursuit responses showed less striking support for the existence of velocity memory was relatively inexperienced to pursuit tasks (i.e., <1 yr training). Thus it appears as though the pursuit system's ability to accurately store velocity information is dependent on the amount of training and/or practice that the subject receives. Becker and Fuchs (1985) similarly proposed that the magnitude of the "predictive" responses that they observed after the disappearance of a target moving at constant velocity could be affected by training. Taken together, it appears that the storage of velocity information is mediated by a neural substrate that drive to both the eye and neck motor plants.

Eye-head coordination—evidence for a shared-controller

An important implication of the findings presented here is that the primate pursuit system has the ability to use and store information about the motion of a visual stimulus to drive the initiation and the maintenance of *both* the eyes and the head during gaze pursuit. Thus it appears as though the coordination of eye and head movements during pursuit is achieved by a common drive mechanism, whereby a shared-controller drives both the eye and neck motor systems.

Although the neural substrate of the shared controller for pursuit is not known, one possible candidate is the cerebellar flocculus and/or ventral paraflocculus (herein referred to as the floccular lobe). Patients with cerebellar disease generally show comparable deficits during combined eye-head and ocular only pursuit of pseudorandom targets (Waterston et al. 1992). Furthermore, electrical stimulation of the floccular lobe elicits smooth eye movements in the HR primate (Belknap and Noda 1987; Ron and Robinson 1973) and combined smooth eye-head movements in the HU rabbit, suggesting that the structure may be involved in eye-head gaze control (De Zeeuw and Koekkoek 1997). Single-unit studies (Lisberger and Fuchs 1978; Miles and Fuller 1975; Miles et al. 1980; Noda and Suzuki 1979a,b; Stone and Lisberger 1990b), including the one by Stone and Lisberger (1990a) in which they employed a very similar open-loop stabilization procedure to the one used in our study, have revealed that the floccular lobe receives information related to retinal error, eye motion, and head motion. Thus the floccular lobe appears to receive and transmit all the signals necessary for it to adequately perform the role of a shared-controller within the pathways that mediate both the initiation and the maintenance of gaze pursuit.

Conversely, Belton and McCrea (1999) have recently argued that the output of the floccular lobe is not adequate to perform this role. They showed that after muscimol inactivation of the floccular lobe, eye-only pursuit and not combined eye-head pursuit was impaired in squirrel monkeys. However, there are two points to consider in the analysis of their data. First, the monkeys in their study primarily used their heads to pursue a periodic target trajectory in the HU condition. It is possible that the periodicity of the target led their monkeys to adopt a strategy that recruited additional and/or different pathways to specifically generate rhythmic head motion. This would explain why their monkeys' head motions routinely led target motion. Moreover, it was recently demonstrated that while eye and head movements are normally coupled during gaze pursuit, they can be controlled independently when subjects are engaged in a highly predictive tracking task (Collins and Barnes 1999), such as the one employed in Belton and McCrea's (1999) study. Second, in contrast to floccular Purkinje cells in rhesus monkey that have similar sensitivities to eye and head velocity (Lisberger and Fuchs 1978; Miles et al. 1980; Stone and Lisberger 1990a), squirrel monkey neurons are, on average, preferentially sensitive to horizontal eye velocity. Thus experiments using nonperiodic targets are needed to determine whether the floccular lobe can be attributed the role of a shared controller during gaze pursuit in rhesus monkeys.

Another possibility, although not a mutually exclusive one, is that the coordination of the eyes and the head during pursuit emerges more centrally. For example, neurons in the medial superior temporal sulcus (MST) of the parietal cortex and in the frontal eye fields (FEF) of the prefrontal cortex have signals related to retinal velocity errors (Fukushima et al. 2000; Kawano et al. 1984; Komatsu and Wurtz 1988, 1989; Newsome et al. 1988; Sakata et al. 1983) and gaze velocity (Fukushima et al. 2000; Kawano et al. 1984; Komatsu and Wurtz 1988; Newsome et al. 1988; Sakata et al. 1983). Furthermore, neurons in area MST and in the FEF continue to respond even in the absence of visual inputs (Fukushima et al. 2000; Newsome et al. 1988; Tanaka and Fukushima 1998). Given that FEF and MST are reciprocally connected (Stanton et al. 1993, 1995; Tian and Lynch 1996a,b; Tusa and Ungerleider 1988), it has been proposed that FEF and MST form positive feedback circuits for the calculation of a target-velocity-in-space and/or a gaze-velocity command signal (Fukushima et al. 2000; Newsome et al. 1988; Tanaka and Fukushima 1998). Because FEF and MST efferents project to the dorsal lateral pontine nuclei (Glickstein et al. 1980), which in turn project to the floccular lobe (for review, see Keller and Heinen 1991), they are well situated within a neural network that could function to coordinate combined eye-head gaze pursuit.

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REFERENCES

André-Deshays C, Revel M, and Berthoz A. Eye-head coupling in humans. II. Phasic components. *Exp Brain Res* 84: 359–366, 1991.

Barnes GR. Visual-vestibular interaction in the coordination of voluntary eye and head movements. In: *Progress in Oculomotor Research*, edited by Fuchs A and Becker W. Amsterdam: Elsevier, 1981, p. 299–308.

Barnes GR and Asselman PT. The mechanism of prediction in human smooth pursuit eye movements. *J Physiol (Lond)* 439: 439–461, 1991.

Barnes GR, Donelly SF, and Eason RD. Predictive velocity estimation in the pursuit reflex response to pseudo-random and step-displacement stimuli in man. *J Physiol (Lond)* 389: 111–136, 1987.

Barnes GR, Goodbody S, and Collins S. Volitional control of anticipatory ocular pursuit responses under stabilized image conditions in humans. *Exp Brain Res* 106: 301–317, 1995.

Barnes GR, Grealy M, and Collins S. Volitional control of anticipatory ocular smooth pursuit after viewing, but not pursuing, a moving target: evidence for a re-afferent velocity store. *Exp Brain Res* 116: 445–455, 1997.

Barnes GR and Grealy MA. Predictive mechanisms of head-eye coordination and vestibulo-ocular reflex suppression in humans. *J Vestib Res* 2: 193–212, 1992.

Barnes GR and Lawson JF. Head-free pursuit in the human of a visual target moving in a pseudo-random manner. *J Physiol (Lond)* 410: 137–155, 1989.

Barnes GR and Ruddock CJS. Factors affecting the predictability of pseudo-random motion stimuli in the pursuit reflex of man. *J Physiol (Lond)* 408: 137–165, 1989.

Becker W and Fuchs AF. Prediction in the oculomotor system: smooth pursuit during transient disappearance of a visual target. *Exp Brain Res* 57: 562–575, 1985.

Belknap DB and Noda H. Eye movements evoked by microstimulation in the flocculus of the alert macaque. *Exp Brain Res* 67: 352–362, 1987.

Belton T and McCrea RA. Contribution of the cerebellar flocculus to gaze control during active head movements. *J Neurophysiol* 81: 3105–3109, 1999.

Belton T and McCrea RA. Role of the cerebellar flocculus region in the coordination of eye and head movements during gaze pursuit. *J Neurophysiol* 84: 1614–1626, 2000.

Bizzi E, Kalil RE, and Tagliasco V. Eye-head coordination in monkeys: evidence for centrally patterned organization. *Science* 173: 452–454, 1971.

Carl JR and Gellman RS. Human smooth pursuit: stimulus dependent responses. *J Neurophysiol* 57: 1446–1463, 1987.

Collins CJS and Barnes GR. Independent control of head and gaze movements during head-free pursuit in humans. *J Physiol (Lond)* 515: 299–314, 1999.

Crane BT and Demer JL. Effect of adaptation to telescopic spectacles on the initial human horizontal vestibuloocular reflex. *J Neurophysiol* 83: 38–49, 2000.

Cullen KE and Guitton D. Analysis of primate IBN spike trains using system identification techniques. II. Relationship to gaze, eye, and head movement dynamics during head-free gaze shifts. *J Neurophysiol* 78: 3283–3306, 1997.

Cullen KE and McCrea RA. Gaze pursuit of predictable and unpredictable moving targets compared to smooth pursuit and vestibulo-ocular reflex cancellation. *Soc Neurosci Abstr* 16: 373.6, 1990.

De Zeeuw CI and Koekkoek SKE. Signal processing in the C2 module of the flocculus and its role in head movement control. In: *Progress in Brain Research. The Cerebellum: From Structure to Control,* edited by De Zeeuw CI, Strata P, and Voogd J. Amsterdam: Elsevier, 1997, vol. 114, p. 299–320.

Freedman EG and Sparks DL. Eye-head coordination during head-unrestrained gaze shifts in rhesus monkeys. *J Neurophysiol* 77: 2328–2348, 1997.

Fuchs AF. Saccadic and smooth pursuit eye movements in the monkey. *J Physiol (Lond)* 191: 609–631, 1967.

Fuchs AF and Robinson DA. A method for measuring horizontal and vertical eye movement chronically in the monkey. *J Appl Physiol* 21: 1068–1071, 1966.

Fukushima K, Sato T, Fukushima J, Shinmei Y, and Kaneko CRS. Activity of smooth pursuit-related neurons in the monkey periarcuate cortex during pursuit and passive whole-body rotation. *J Neurophysiol* 83: 563–587, 2000.

Fuller JH. Linkage of eye and head movements in the alert rabbit. *Brain Res* 205: 363–381, 1980.

Glickstein M, Cohen JL, Dixon B, Gibson A, Hollins M, LaBossiere E, and Robinson F. Corticopontine visual projections in macaque monkeys. *J Comp Neurol* 190: 209–229, 1980.

Goldreich D, Krauzlis RJ, and Lisberger SG. Effect of changing feedback delay on spontaneous oscillations in smooth pursuit eye movements of monkeys. *J Neurophysiol* 67: 625–638, 1992.

Grantyn A and Berthoz A. Burst activity of identical tectoreticulo-spinal neurons in the alert cat. *Exp Brain Res* 57: 417–421, 1985.

Gresty M and Leech J. Coordination of the head and eyes in pursuit of predictable and random target motion. *Aviat Space Environ Med* 48: 741–744, 1977.

Guitton D and Volle M. Gaze control in humans: eye-head coordination during orienting movements to targets within and beyond the oculomotor range. *J Neurophysiol* 58: 427–459, 1987.

Hayes AV, Richmond BJ, and Optican LM. A UNIX-based. multiple process system for real-time data acquisition and control. *WESCON Conf Proc* 2: 1–10, 1982.

Judge SJ, Richmond BJ, and Chu FC. Implantation of magnetic search coils for measurement of eye position: an improved method. *Vision Res* 20: 535–538, 1980.

Kawano K, Sasaki M, and Yamashita M. Response properties of neurons in posterior parietal cortex of monkey during visual-vestibular stimulation. I. Visual tracking neurons. *J Neurophysiol* 51: 340–351, 1984.

Keller EL and Heinen SJ. Generation of smooth-pursuit eye movements: neuronal mechanisms and pathways. *Neurosci Res* 11: 79–107, 1991.

Keller E and Johnsen SD. Velocity prediction in corrective saccades during smooth-pursuit eye movements in monkey. *Exp Brain Res* 80: 525–531, 1990.

Komatsu H and Wurtz RH. Relation of cortical areas MT and MST to pursuit eye movements. I. Localization and visual properties of neurons. *J Neurophysiol* 60: 580–603, 1988.

Komatsu H and Wurtz RH. Modulation of pursuit eye movements by stimulation of cortical areas MT and MST. *J Neurophysiol* 62: 31–47, 1989.

Kraulis RJ and Lisberger SG. Visual motion commands for pursuit eye movements in the cerebellum. *Science* 253: 568–571, 1991.

Kraulis RJ and Lisberger SG. Temporal properties of visual motion signals for the initiation of smooth pursuit eye movements in monkeys. *J Neurophysiol* 72: 150–162, 1994.

Lanman J, Bizzi E, and Allum J. The coordination of eye and head movements during smooth pursuit. *Brain Res* 153: 39–53, 1978.

Lautitis VP and Robinson DA. The vestibulo-ocular reflex during human saccadic eye movements. *J Physiol (Lond)* 373: 200–233, 1986.

Leigh RJ, Sharpe JA, Ranalli PJ, Thurston SE, and Hamid MA. Comparison of smooth pursuit and combined eye-head tracking in human subjects with deficient labyrinthine function. *Exp Brain Res* 66: 458–464, 1987.

Leigh RJ and Zee D. *The Neurology of Eye Movements* (3rd ed.). New York: Oxford Univ. Press, 1999.

Lestienne F, Vidal PP, and Berthoz A. Gaze changing behaviour in head-restrained monkey. *Exp Brain Res* 53: 349–356, 1984.

Lisberger SG, Evinger C, Johanson GW, and Fuchs AF. Relationship between eye acceleration and retinal image velocity during foveal smooth pursuit in man and monkey. *J Neurophysiol* 46: 229–249, 1981.

Lisberger SG and Fuchs AF. Role of primate flocculus during rapid behavioral modification of vestibuloocular reflex. I. Purkinje cell activity during visually guided horizontal smooth-pursuit eye movements and passive head rotation. *J Neurophysiol* 41: 733–763, 1978.

Lisberger SG, Morris EJ, and Tychsen L. Visual motion processing and sensory-motor integration for smooth pursuit eye movements. *Annu Rev Neurosci* 10: 97–129, 1987.

Lisberger SG and Westbrook LE. Properties of visual inputs that initiate horizontal smooth pursuit eye movements in monkeys. *J Neurophysiol* 5: 1662–1673, 1985.

Mann CA and Morrow MJ. Effects of eye and head position on horizontal and vertical smooth pursuit. *Invest Opthalmol Vis Sci* 38: 773–779, 1997.

Michael JA and Melvill-Jones G. Dependence of visual tracking capability upon stimulus predictability. *Vision Res* 6: 707–716, 1966.

Miles FA and Fuller JH. Visual tracking and the primate flocculus. *Science* 189: 1000–1002, 1975.

Miles FA, Fuller JH, Braitman DJ, and Dow BM. Long-term adaptive changes in primate vestibuloocular reflex. III. Electrophysiological observations in flocculus of normal monkeys. *J Neurophysiol* 43: 1437–1476, 1980.

Morris EJ and Lisberger SG. Different responses to small visual errors during initiation and maintenance of smooth pursuit eye movements in monkeys. *J Neurophysiol* 58: 1351–1369, 1987.

Newsome WT, Wurtz RH, and Komatsu H. Relation of cortical areas MT and MST to pursuit eye movements. II. Differentiation of retinal from extraretinal inputs. *J Neurophysiol* 60: 604–620, 1988.

Noda H and Suzuki DA. The role of the flocculus in fixation and smooth pursuit eye movements. *J Physiol (Lond)* 294: 335–348, 1979a.

Noda H and Suzuki DA. Processing of eye movement signals in the flocculius of the monkey. *J Physiol (Lond)* 294: 349–364, 1979b.

Peng GC, Hain TC, and Peterson BW. A dynamical model for reflex activated head movements in the horizontal plane. *Biol Cybern* 75: 309–319, 1996.

Pola J and Wyatt HJ. Target position and velocity: the stimulus for smooth pursuit eye movements. *Vision Res* 20: 523–534, 1980.

Rashbass C. The relationship between saccadic and smooth tracking eye movements. *J Physiol (Lond)* 159: 326–338, 1961.

Robinson DA. The mechanics of human smooth pursuit eye movement. *J Physiol (Lond)* 180: 569–591, 1965.

Robinson DA. Models of oculomotor neural organization. In: *The Control of Eye Movements,* edited by Bach-y-Rita P. New York: Academic, 1971.

Robinson DA, Gordon JL, and Gordon SE. A model of the smooth pursuit eye movement system. *Biol Cybern* 55: 43–57, 1986.

Ron S and Robinson DA. Eye movements evoked by cerebellar stimulation in the alert monkey. *J Neurophysiol* 36: 1004–1022, 1973.

Roy JR and Cullen KE. A neural correlate for vestibulo-ocular reflex suppression during voluntary eye-head gaze shifts. *Nat Neurosci* 1: 404–410, 1998.

Sakata H, Shibutani H, and Kawano K. Functional properties of visual tracking neurons in posterior parietal association cortex of the monkey. *J Neurophysiol* 49: 1364–1380, 1983.

Segraves MA and Goldberg ME. Effect of stimulus position and velocity upon the maintenance of smooth pursuit eye velocity. *Vision Res* 34: 2477–2482, 1994.

Smith WAD, Segal B, and Cullen KE. Eye and head coordination during head-free gaze pursuit in the rhesus monkey: predictable vs. unpredictable stimuli. *Soc Neurosci Abstr* 21: 470.6, 1995.

Sokal RR and Rohlf FJ. *Biometry* (3rd ed.). New York: Freeman, 1995, p. 476–486.

Sparks DL. Conceptual issues related to the role of the superior colliculus in the control of gaze. *Curr Opin Neurobiol* 9: 698–707, 2000.

Stanton GB, Bruce CJ, and Goldberg ME. Topography of projections to the frontal lobe from the macaque frontal eye fields. *J Comp Neurol* 330: 286–301, 1993.

Stanton GB, Bruce CJ, and Goldberg ME. Topography of projections to posterior cortical areas from macaque frontal eye fields. *J Comp Neurol* 353: 291–305, 1995.

Stark L, Vossius G, and Young L. Predictive control of eye tracking movements. *IRE Trans Hum Factors Electron* 3: 52–57, 1962.

Stone LS and Lisberger SG. Visual responses of purkinje cells in the cerebellar flocculus during smooth-pursuit eye movements in monkeys. I. Simple spikes. *J Neurophysiol* 63: 1241–1261, 1990a.

Stone LS and Lisberger SG. Visual responses of purkinje cells in the cerebellar flocculus during smooth-pursuit eye movements in monkeys. II. Complex spikes. *J Neurophysiol* 63: 1262–1275, 1990b.

Suzuki DA, Yamada T, Hoedema R, and Yee RD. Smooth-pursuit eye-movement deficits with chemical lesions in macaque nucleus reticularis tegmenti pontis. *J Neurophysiol* 82: 1178–1186, 1999.

Sylvestre PA and Cullen KE. Quantitative analysis of abducens neuron discharge dynamics during saccadic and slow eye movements. *J Neurophysiol* 82: 2612–2632, 1999.

Tanaka M and Fukushima K. Neuronal responses related to smooth pursuit eye movements in the periarcuate cortical area of monkeys. *J Neurophysiol* 80: 28–47, 1998.

Tian J and Lynch JC. Functionally defined smooth and saccadic eye movement subregions in the frontal eye field of Cebus monkeys. *J Neurophysiol* 76: 2740–2753, 1996a.

Tian J and Lynch JC. Corticocortical input to smooth and saccadic eye movement subregions in the frontal eye field of Cebus monkeys. *J Neurophysiol* 76: 2754–2771, 1996b.

Tomlinson RD and Bahra PS. Combined eye-head gaze shifts in the primate. I. Metrics. *J Neurophysiol* 56: 1542–1557, 1986.

Tusa RJ and Ungerleider LG. Fiber pathways of cortical areas mediating smooth pursuit eye movement in monkeys. *Ann Neurol* 23: 174–183, 1988.

Tychsen L and Lisberger SG. Visual motion processing for the initiation of smooth pursuit eye movements in humans. *J Neurophysiol* 56: 953–968, 1986.

Waterston JA and Barnes GB. Visual-vestibular interaction during head-free pursuit of pseudorandom target motion in man. *J Vestib Res* 2: 71–88, 1992.

Waterston JA, Barnes GB, and Grealy MA. A quantitative study of eye and head movements during smooth pursuit in patients with cerebellar disease. *Brain* 115: 1343–1358, 1992.

Wellenius GA and Cullen KE. A comparison of head-unrestrained and head-restrained pursuit: influence of eye position and target velocity on latency. *Exp Brain Res* 133: 139–155, 2000.

Yasui S and Young LR. Perceived visual motion as effective stimulus to pursuit eye movement system. *Science* 190: 906–908, 1975.

Young LR, Forster JD, and Van Houtte N. A revised stochastic sampling model for eye tracking movements. In: *Fourth Ann Nasa-Univ Conf Manual Control.* Washington, DC: NASA, 1968, p. 489–508.

Zangemeister WH, Jones A, and Stark L. Dynamics of head movement trajectories: main sequence relationships. *Exp Neurol* 71: 76–91, 1981.

Zangemeister WH and Stark L. Gaze latency: variable interactions of head and eye latency. *Exp Neurol* 75: 389–406, 1982a.

Zangemeister WH and Stark L. Types of gaze movement: variable interactions of eye and movements. *Exp Neurol* 75: 389–406, 1982b.

Zee DS, Yamazaki A, Butler PH, and Gücer G. Effects of ablation of flocculus and paraflocculus on eye movements in primate. *J Neurophysiol* 46: 878–899, 1981.