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**Gaze, eye, and head movement dynamics  
during closed- and open-loop  
gaze pursuit**

by

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of the requirements of the degree of Master of Science.

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## ABSTRACT

Horizontal step-ramp stimuli were used to examine gaze, eye, and head movement dynamics during *head-unrestrained* pursuit with and without imposed retinal velocity errors (RVE; i.e. open- and closed-loop, respectively) in two rhesus monkeys. In the closed-loop experiment, pursuit was elicited by step-ramp stimuli with a constant velocity of 20-80 deg/s. Each monkey used a combination of eye and head motion to initially fixate and then pursue the target. Additionally, we found that initial eye and head acceleration increased as a function of target velocity. In the open-loop experiment, step-ramp stimuli (40 deg/s) were presented and ~125 ms after pursuit onset, a constant RVE was imposed for a duration of 300 ms. In each monkey, when RVE= 0 deg/s, gaze, eye, and head velocity trajectories were maintained at their current or at a damped velocity. Moreover, the head as well as the eyes mediated the observed increase and decrease in gaze velocity when RVE was +10 and -10 deg/s, respectively. Based on our findings we conclude that the pursuit system uses visual and non-visual signals to drive coordinated eye-head pursuit.

## RÉSUMÉ

Des stimuli de type Rashbass (1961) furent utilisés afin de caractériser les dynamiques des mouvements de l'axe visuel, des yeux, et de la tête chez les singes rhésus ayant la tête *non-immobilisée*. De plus, la vitesse de l'image sur la rétine (VIR) fût artificiellement contrôlée ou non-contrôlée (i.e. expérience 2 et 1, respectivement). Lors de l'expérience 1, le stimulus Rashbass fut produit à une vitesse constante de 20-80 deg/s. Les deux sujets ont utilisé leur tête et leurs yeux afin de poursuivre la cible. De plus, nous avons observés que l'accélération du mouvement de la tête et des yeux augmentait en fonction de la vitesse de la cible. Dans l'expérience 2, le stimulus Rashbass fut produit à une vitesse de 40 deg/s, et ~125 ms après le début de la poursuite nous avons imposé une VIR constante pour une durée de 300ms. Chez les deux singes, lorsque la VIR = 0 deg/s, les vitesses de l'axe visuel, des yeux et de la tête sont demeurées constantes ou ont diminué faiblement. Aussi, lorsqu'une VIR de +10 ou -10 deg/s a été imposée, les vitesses de l'axe visuel, des yeux, et de la tête ont augmenté et diminué, respectivement. Nos données démontrent que des signaux visuels et non-visuels sont utilisés pour accomplir une poursuite coordonnée yeux-tête.

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## **CHAPTER 1: Literature Review**

Sense organs link organisms with the outside world and allow them to receive information about the environment. Vision allows animals to detect changes in the environment and begins when the image of an object falls on the retina. Although animals detect objects over the entire retina, images focused on the fovea, a small and highly specialized area of the retina, are seen with greatest acuity. In order to maintain the image of an object on the fovea, the eyeball must be able to move. An important function of the ocular motor system is therefore to bring targets of interest onto the fovea and keep them there as the animal, or the object of interest, moves through the environment (reviewed by Goldberg et al. 1991).

The ocular motor system can be separated into five movement systems, each of which are mediated by the same three pairs of skeletal muscles that are attached to the eyeball. The five systems can be divided into two that stabilize the eye during head movements and three that voluntarily reorient the fovea (i.e. the line of sight) to a new target of interest. Stabilizing eye movements are the vestibulo-ocular reflex (VOR) and the optokinetic reflex, both of which compensate for movements of the head. Reorienting eye movements include saccadic, smooth pursuit, and vergence eye movements. Saccadic eye movements shift the fovea rapidly to a new target spotted at the periphery; smooth pursuit eye movements keep the image of a moving target aligned with the fovea; and vergence movements move the eyes in opposite directions so that the image of an object is positioned on both foveae, thereby allowing for depth perception (reviewed by Goldberg et al. 1991).

Under natural conditions, many animals (e.g. humans, monkeys) use a combination of both their eyes and head to voluntarily reorient their line of sight (for review see Guitton 1992). The behavioral goal is then to align the axis of gaze (gaze = eye-in-head + head-in-space) with the target of interest. Accordingly, saccades that involve the use of both the eyes and the head are termed gaze shifts, while combined eye-head smooth pursuit movements are referred to as gaze pursuit. In the past two decades, many investigators have characterized the control of head-unrestrained gaze shifts (see for example: Bizzi et al. 1971; Barnes 1981; Zangemeister et al. 1981, 1982a,b; Tomlinson and Bahra 1986; Guitton and Volle 1987; Freedman and Sparks 1997). However, even though eye-head pursuit is a common natural behavior, the vast majority of previous characterizations of the pursuit system have been carried out with the subject's head physically restrained such that only the eyes were used to follow the moving target. As a result, a great deal is known about the processing of visual inputs and their use in generating smooth eye movements while very little is known about how visual inputs, as well as vestibular, proprioceptive, and central inputs, are processed and used to generate eye-head pursuit. The goal of the present study was therefore to characterize the control of coordinated eye-head pursuit movements. We begin by providing a review of the literature describing smooth pursuit eye movements in which the subjects' heads were restrained, followed by a description of the known neural pathways that generate pursuit eye movements.

## **I. Smooth Pursuit**

When a small moving visual stimulus appears in the visual field, primates can stabilize the object's image on the fovea by matching eye velocity to that of the target.

However, smoothly moving targets often evoke a combination of both smooth and saccadic eye movements. Although saccadic eye movements do play a role in maintaining accurate pursuit, they are mediated by a separate neural system from the one that mediates pursuit eye movements (see for example: Rashbass 1961, Robinson 1965, Fuchs 1967, Newsome et al. 1985) and pursuit is thus defined as the smooth component of the response.

Traditionally, the pursuit system has been thought of as a negative feedback system which acts to minimize the difference between the velocity of the target and the velocity of the eye, defined as retinal velocity error (Rashbass 1961; Robinson 1965; Fuchs 1967; Lisberger and Westbrook 1985; Robinson et al. 1986; Tychsen and Lisberger 1986; Carl and Gellman 1987; Lisberger et al. 1987; Morris and Lisberger 1987; Lisberger and Pavelko 1989; Segraves and Goldberg 1994). It has been convincingly shown that small retinal velocity errors imposed either during fixation (Morris and Lisberger 1987) or during ongoing pursuit results in smooth eye accelerations (Lisberger et al. 1981; Morris and Lisberger 1987; Segraves and Goldberg 1994). In addition, retinal position (Pola and Wyatt 1980; Morris and Lisberger 1987; Segraves and Goldberg 1994) and retinal acceleration (Morris and Lisberger 1987; Lisberger et al. 1987) errors imposed during ongoing pursuit, but not during fixation, would result in smooth eye accelerations. The pursuit system therefore uses signals related to retinal velocity errors to initiate pursuit, and signals related to retinal position, retinal velocity, and retinal acceleration errors to maintain accurate ongoing pursuit.

Pursuit eye movements generally begin between 80 and 130 ms after the onset of target motion and are fairly stereotyped for a given stimulus (Carl and Gellman 1987;

Wellenius and Cullen 2000). However, pursuit latencies have been shown to depend on a number of visual parameters, including the target's luminance, size, velocity, and position in the visual field (Lisberger and Westbrook 1985; Tychsen and Lisberger 1986a). The initiation of pursuit encompasses the period of pursuit within the first visual feedback latency (~100 ms). The most commonly used stimulus for the study of pursuit initiation has been the step-ramp target trajectory (Rashbass 1961; Robinson 1965; Lisberger and Westbrook 1985; Robinson et al. 1986; Tychsen and Lisberger 1986; Carl and Gellman 1987; Lisberger and Pavelko 1989; Wellenius and Cullen 2000) which entails having the target stepped in one direction and then immediately moving at a constant velocity in the direction opposite to that of the step. The initial response to a step-ramp stimulus consists of a smooth acceleration of the eyes in order to match the velocity of the target, instead of the usual catch-up saccade in response to a ramp stimulus (Rashbass 1961). Similar to pursuit latencies, the initial acceleration of the eyes during pursuit initiation has also been reported to be highly stereotyped and to depend on a number of target parameters such as target luminance, size, velocity, and initial target position. For example, the eyes accelerate more rapidly in response to faster moving step-ramps (Lisberger et al. 1981; Lisberger and Westbrook 1985; Tychsen and Lisberger 1986; Morris and Lisberger 1987; Carl and Gellman 1987; Mann and Morrow 1997), although this effect saturates for target velocities greater than ~50 deg/s (Lisberger and Westbrook 1985; Tychsen and Lisberger 1986; Carl and Gellman 1987).

The maintenance of pursuit begins when the eyes have approximately matched the velocity of the target. In response to step-ramp targets, pursuit maintenance generally occurs ~120 ms after the onset of the pursuit response and consists of the eyes oscillating

at approximately 4-6 Hz around the velocity of the target (Fuchs 1967; Robinson 1965; Robinson et al. 1986; Goldreich et al. 1992). These studies have proposed that the oscillations in eye velocity during ongoing pursuit are a result of the intrinsic delay of the visual feedback loop (i.e. the sum of retinal, cortical, and motor processing delays).

Although visual inputs do provide the main stimulus for pursuit eye movements, cognitive factors also play a role. For example, a moving target must be volitionally selected in order to generate a pursuit response since moving targets can easily be ignored (Kowler et al. 1984). Moreover, the pursuit system is capable of prediction such that pursuit of a periodic target trajectory (i.e. sinusoidal trajectory) is more accurate than pursuit of a non-periodic target trajectory (Stark et al. 1962; Michael and Melvill Jones 1966). Smooth eye movements can also anticipate changes in the position or velocity of predictable targets (see for example: Kowler and Steinman 1979; Becker and Fuchs 1985; Barnes and Asselman 1991). Furthermore, in addition to visual signals correcting for errors in tracking, it has been postulated that a non-visual signal related to ongoing eye velocity keeps the eyes moving at nearly a constant velocity in order to accurately pursue a moving stimulus (Young et al. 1968; Robinson 1971; Yasui and Young 1975; Lisberger and Fuchs 1978; Robinson et al. 1986; Morris and Lisberger 1987). It is therefore important to bear in mind the influences of extraretinal factors for the interpretation of data and when designing models of the pursuit system.

## **II. Neural Pathways of the Pursuit System**

Visual information originating from the retina is transmitted, via the thalamus, to the primary visual cortex (area V1). From area V1 (figure 1-1), information related to the motion of the image is relayed to the middle temporal visual area (MT), the medial

superior temporal sulcus (MST), and area 7a of the posterior parietal cortex, all areas that are important for the perception of motion and the generation of pursuit eye movements (for review, see Lisberger et al. 1987). In turn, efferent signals from MT, MST, and area 7a, as well as from the frontal eye fields (FEF) of the prefrontal cortex which is reciprocally connected to area MST (Tusa and Ungerleider 1988; Stanton et al. 1993, 1995; Tian and Lynch 1996a,b), converge on the dorsolateral pontine nucleus (DLPN) (Brodal 1978; Glickstein et al. 1980). The DLPN projects to the areas of the cerebellum that are involved in the control of pursuit eye movements; primarily the flocculus and vermal lobules-VI and VII (Brodal 1979, 1982; Langer et al. 1985a). A second parallel pursuit pathway consists of projections from the FEF to the nucleus reticularis tegmenti pontis (NRTP) (Kunzle and Akert 1977; Leichnetz et al. 1984; Huerta et al. 1986; Stanton et al. 1988). NRTP projections, similar to DLPN projections, transmit pursuit-related signals to the cerebellum (Brodal 1978; 1979, 1982; Yamada and Noda 1987; Thielert and Their 1993). Moreover, additional pathways from the superior colliculus have also been shown to play a role in the generation of pursuit eye movements (Basso et al. 2000; Krauzlis et al. 2000).

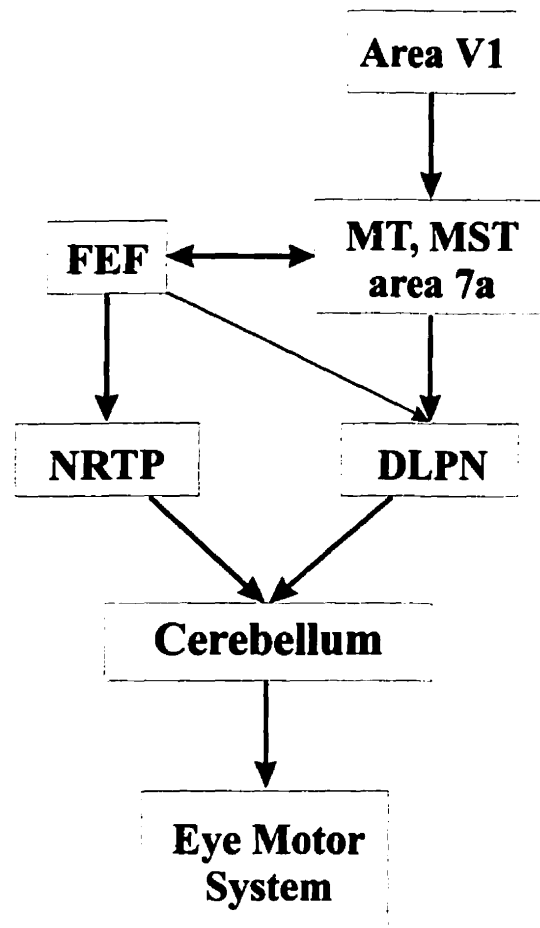
Lesion studies in the posterior parietal cortex (Newsome et al. 1985; Dürsteler and Wurtz 1988), FEF (Lynch 1987; Keating 1991, 1993; MacAvoy et al. 1991; Shi et al. 1998), DLPN (Suzuki and Keller 1984; May et al. 1988a,b), NRTP (Suzuki et al. 1999), and in the cerebellum (Westheimer and Blair 1973; Takemori and Cohen 1974; Zee et al. 1981; Takagi et al. 2000) have shown that both pathways are necessary for normal functioning of pursuit even though there is some redundancy of function (Suzuki et al. 1999). For instance, bilateral ablation of the DLPN does not permanently impair the

ability of monkeys to accurately pursue moving stimuli (May and Keller 1988a,b). In addition, microstimulation and unit recording studies have helped elucidate the specific roles of each the regions within the parallel pathways for the control of pursuit. For example, microstimulation of certain portions of area MST evoke smooth eye movements during ongoing pursuit, but not during fixation (Komatsu and Wurtz 1989). On the contrary, microstimulation of the FEF evokes continuous slow eye movements both during fixation and ongoing pursuit (Bruce 1985; Keller and Heinen 1991; MacAvoy et al. 1991; Gottlieb et al. 1994; Tian and Lynch 1996a). Taken together, it has been proposed that the neurons in the FEF, which have long been known to control purposive saccades (for review see Goldberg and Segrave 1989), are involved in the control of both pursuit initiation and maintenance while neurons in area MST play a role in the generation of the motor command for the maintenance of ongoing pursuit.

Moreover, although most studies investigating the different components of the pursuit pathways have done so with the animal's head physically restrained and have thus characterized the control of smooth pursuit eye movements, there is a wealth of emerging evidence that these areas could be involved in the control of coordinated eye-head pursuit as well. For example, neurons in area MST (Komatsu and Wurtz 1988, 1989; Newsome et al. 1988; Their and Erickson 1992; Shenoy et al. 1999), area 7a (Kawano et al. 1980, 1984), FEF (Fukushima et al. 2000), and the cerebellum (Lisberger and Fuchs 1978; Kase et al. 1979; Miles et al. 1980; Suzuki and Keller 1988b; Stone and Lisberger 1990a) have all been shown to carry signals related to the motion of the head as well as of the eyes.

Much is known about the visual and non-visual inputs to the pursuit system and the sensory-motor transformations that take place in order to generate smooth eye movements. However, primates will generate combined smooth eye-head movements in order to pursue a moving target when the head is not restrained (Gresty and Leech 1977; Lanman et al. 1978; Barnes 1981; Barnes and Lawson 1989; Cullen and McCrea 1990; Smith et al. 1995; Barnes and Grealy 1992; Collins and Barnes 1999; Wellenius and Cullen 2000). To date, little is known about how eye and head movements are coordinated to align the fovea with a moving target of interest. In this thesis, I address the question of whether smooth eye and head pursuit movements are generated by a shared mechanism, or whether they are independently controlled.





**Figure 1-1: Schematic of the pursuit pathway.** Information related to the motion of the target is relayed from the primary visual cortex (area V1) to the middle temporal visual area (MT), the medial superior temporal sulcus (MST), and area 7a of the posterior parietal cortex. Area MST is reciprocally connected to the frontal eye fields (FEF) of the frontal cortex. In turn, efferent signals from MT, MST, area 7a, and FEF converge on the dorsolateral pontine nucleus (DLPN). A second parallel pursuit pathway consists of projections from the FEF to the nucleus reticularis tegmenti pontis (NRTP). Neurons from both DLPN and NRTP project to the cerebellum which in turn transmits pursuit-related signals to the eye motor system.

## **CHAPTER 2: Gaze, Eye, and Head Movement Dynamics During Closed- and Open-loop Gaze Pursuit**

### **I. Introduction**

The pursuit system generates smooth eye movements in order to stabilize the image of a moving object on the fovea. Typically, the system has been characterized as a negative feedback controller which 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, several studies have shown that retinal position (Pola and Wyatt 1980; Morris and Lisberger 1987; Segraves and Goldberg 1994) and retinal acceleration (Lisberger et al. 1981, 1987; Morris and Lisberger 1987; Krauzlis and Lisberger 1994) errors can also serve as effective stimuli for pursuit eye movements. Moreover, non-visual inputs have been reported to play an essential role during ongoing (i.e. steady-state) pursuit eye movements. For instance, whereas visual signals correct for errors in tracking, it has been suggested that a non-visual signal, which encodes a copy of the pursuit eye motor command, is used to maintain ongoing eye velocity (Young et al. 1968; Robinson 1971; Yasui and Young 1975; Lisberger and Fuchs 1978; Robinson et al. 1986; Morris and Lisberger 1987).

Smooth pursuit eye movements have been extensively studied with the subject's head physically restrained. However, only a small number of studies have characterized the pursuit responses in the head-unrestrained condition. Naturally, primates generate a combination of smooth eye and head movements, referred to as gaze pursuit, in order to align their line of sight (i.e. gaze = eye-in-head + head-in-space) with a moving stimulus

(Gresty and Leech 1977; Lanman et al. 1978; Barnes 1981; Barnes and Lawson 1989; Cullen and McCrea 1990; Barnes and Grealy 1992; Smith et al. 1995; Collins and Barnes 1999; Wellenius et al. 1997, 1998; Wellenius and Cullen 2000). Previous investigations that have used predictable targets, such as periodic sinusoidal and/or triangular target trajectories, to characterize gaze pursuit have reported no significant difference in pursuit accuracy between eye-head and eye-only steady-state pursuit responses (monkey: Lanman et al. 1978; Cullen and McCrea 1990; human: Barnes 1981; Leigh et al. 1987). Furthermore, the accuracy of the eye-head and eye-only pursuit responses were similar across a range of target frequencies of 0.1-3.5 Hz, as well as for peak target velocities up to ~20 deg/s. However, results from studies using unpredictable pseudo-random target trajectories with peak target velocities of ~40 deg/s have been less conclusive. For example, investigations in squirrel monkeys have reported improved steady-state pursuit gains (i.e. gaze velocity/target velocity) during eye-head pursuit as compared to eye-only pursuit (Cullen and McCrea 1990), while in humans pursuit accuracy was only marginally improved during eye-head pursuit, although the improvements were generally not significant (Waterson and Barnes 1992). One possible explanation for these differences may be the fact that squirrel monkeys have a relatively small oculomotor range ( $\sim \pm 20$  deg, Cullen et al. 1991) as compared to humans and rhesus monkeys ( $\sim \pm 50$  deg, Lauritis and Robinson 1986; Tomlinson and Bahra 1986; Guitton and Volle 1987; Freedman and Sparks 1997; Cullen and Guitton 1997) and therefore would not be able to follow a visual target that was moving at even a modest speed (e.g. 40 deg/s) for very long without moving their heads. Accordingly, it is possible that the pursuit system, particularly in squirrel monkeys, was developed so that any moving visual target could

be tracked by a combination of both eye and head movements. It still remains to be determined whether eye-head tracking of unpredictable stimuli in humans and rhesus monkeys is similarly advantageous, in terms of steady-state pursuit accuracy, for the subjects, especially at high target velocities ( $>40$  deg/s).

Moreover, in a recent study of head-unrestrained pursuit of unpredictable, non-periodic target trajectories, Wellenius and Cullen (2000) reported that pursuit onset latencies were similar regardless of whether the monkey's head was restrained or unrestrained, when initial eye position was held constant. Additionally, Wellenius and Cullen (2000) demonstrated that the onset of the head movement consistently lagged the onset of the eye movement by at least 50 ms. They attributed the longer latencies of the head to its relatively larger moment of inertia as compared to that of the eyes (Zangmeister et al. 1981; or see Peng et al. 1996) and suggested that the eyes and the head synchronously receive a shared pursuit command in order to initiate visual pursuit of a moving target.

To date, the results from studies of head-unrestrained pursuit have not been sufficient to address the mechanism by which the eye and head movements are coordinated during the initiation and during steady-state gaze pursuit. One hypothesis is that eye and head pursuit movements are driven by two independent controllers (Belton and McCrea 2000). Alternatively, the coordination of eye and head movements during gaze pursuit may 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 coordinate the movements (Lanman et al. 1978). Such a mechanism has been proposed to coordinate eye and head movements that reorienting the visual axis

rapidly in order to look at a target of interest that, for example, had just appeared in the peripheral visual field (for review see Guitton 1992; Galiana and Guitton 1992).

In order to investigate whether eye-head pursuit movements are generated by two independent controllers or by a common drive mechanism, we characterized gaze, eye, and head movement dynamics during pursuit of unpredictable, non-periodic, constant velocity stimuli in the natural head-unrestrained condition. In particular, we 1) compared head-unrestrained and head-restrained pursuit accuracy, 2) characterized and compared initial eye and head movement dynamics during head-unrestrained pursuit, and 3) examined whether the signals that drove the head movements were similarly responsive to imposed constant retinal velocity errors as those that drove the motion of the eyes during ongoing pursuit. The results of these studies revealed two main features of the pursuit system. First, there was no difference between gaze responses when pursuit was accomplished with the use of the eyes alone or with a combination of the eyes and the head. Second, during the natural HU condition, the pursuit system appears to use a gaze velocity command signal, at least in part, to drive both the eyes and the head in order to track a moving target.

## **II. Materials and Methods**

### **A. 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 anaesthesia 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*) in order to monitor gaze position, and a head holder 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<sup>3</sup> magnetic field coil system (CNC Engineering). Gaze and head positions were recorded by using the magnetic search coil technique (Fuchs and Robinson 1966; Judge et al. 1980). Monkeys were trained to track a small (0.3 deg in diameter) visual target for a juice reward. Target motion was generated using a HeNe laser spot that was positioned 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 perception (see Wellenius and Cullen 2000).

### **B. Behavioral tasks**

Monkeys were trained to perform pursuit of a horizontal step-ramp target trajectory (Rashbass 1961) as illustrated in figure 2-1. 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  $\pm 30$  deg relative to the primary position (i.e. the position at which the eyes are centered in the orbit). After a random fixation period (750-3000 ms), the target was stepped either towards the left or right and then immediately began to move at constant velocity (20-80 deg/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  $\sim 110$  and  $\sim 120$  ms in monkeys C and J, respectively. Figure 2-1A shows an example trial of a pursuit eye movement made by monkey C in response to a step-ramp target trajectory when its head was restrained. In this example, the target underwent a leftward step that was immediately followed by a ramp in position (40 deg/s, constant velocity) towards the right.

### ***1. Experiment 1: Gaze Pursuit***

A wide range of target velocities and eccentricities were used in order 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 acceleration differs 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 deg/s for monkey C and 20, 30, 40, 50, 60 and 70 deg/s for monkey J. Three different initial target positions were also used. For monkey C, targets were initially presented at 0,  $\pm 15$ , or  $\pm 30$  deg relative to primary position and for monkey J, targets were initially presented at 0,  $\pm 10$ , or  $\pm 20$  deg,

where positive and negative numbers refer to nasal and temporal positions, respectively. Less eccentric initial fixation targets were presented to monkey J because this monkey would not consistently look at more eccentric targets when its head was restrained. This was most likely due to a decreased familiarity with pursuit tasks as compared to monkey C and did not reflect the eyes reaching the physical limits of their rotation (see DISCUSSION). In all experiments, both temporally and nasally directed trajectories were presented and all ramps terminated between 20 and 30 deg. The exact end point was randomly chosen within this range for each target trajectory. For the purpose of the present study, we restricted our analysis of gaze pursuit dynamics to temporally directed movements (i.e. the responses of the right eye during rightward pursuit in both monkeys).

During the experiment, the monkey's head was either 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 40-50 minute 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. Within each block of trials, fixation period, initial target position, target velocity, target direction, and the end point of the step-ramp were randomized in order to minimize predictive behaviors. 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. sinusoidal pursuit and/or a saccade task), or were simply allotted a "rest-time" in order to prevent fatigue or loss of motivation.

## ***2. Experiment 2: Open-loop Gaze Pursuit***

In order 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 deg/s that were initially positioned at  $\pm 10$  deg with respect to primary position. Both temporally and nasally directed trajectories were presented. On a portion of trials (~30% of temporally directed targets) the target was either artificially stabilized relative to the monkey's fovea (i.e. gaze) or a constant velocity error was imposed (Pola and Wyatt 1980; Morris and Lisberger 1987; 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 deg/s and remained open for a duration of 300 ms, after which the target resumed moving at 40 deg/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 deg/s. The visual feedback loop was thus opened (**open-loop trials**) and the resulting responses were compared to control trials in which the loop was not opened (**closed-loop control trials**). During open-loop and control trials, the monkey's head was either completely immobilized (**HR**) or allowed full freedom of motion (**HU**). Each experimental session lasted between 40-50 minutes and typically consisted of one block of HU trials and one block of HR trials, the order of which was varied on a daily basis. Within each session, fixation period, target direction, and the end point of the step-ramp were randomized, and

open-loop trials were randomly interleaved with control trials. Experiment 2 was performed only after Experiment 1 had been entirely completed (i.e. >6 months later).

### **C. 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 (eight-pole Bessel, DC-250 Hz) and then digitized at 1 KHz. Raw data files were transferred to an Athlon 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, eye, and head velocity traces were averaged. Saccades were identified using a gaze acceleration threshold ( $> \pm 3500$  deg/s) 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 Experiment 2.

#### ***1. 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 a 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 movement response regression was computed between the point where the eye or head velocity deviated from the baseline by more than 2.5 standard deviations 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 (Lisberger and Westbrook 1985; Tychsen and Lisberger 1986; Carl and Gellman 1987). 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 at least 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 at least 100 ms after gaze onset. Furthermore, trials were accepted for analysis only if gaze, eye, and head velocity were stable at  $0 \pm 3$  deg/s during the 100 ms interval before target onset. It should also be noted that, although rare, HU trials in which the monkey did not move its head ( $0 \pm 3$  deg/s) were not included in our analysis.

The effect of target velocity or initial target position on initial eye or head acceleration was established using a repeated-measures linear regression (Sokal and

Rohlf 1995). In order to establish whether the average of two measured parameters were significantly different from each other, a Student's *t*-test was used.

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 condition. The individual gaze velocity records were subjected to two analyses. The first method used to characterize the oscillations was similar to the methods used by both Robinson et al. (1986) and Goldreich et al. (1992). Briefly, a cursor was used to manually select the time and position of the first and second peak of the oscillation, and the position of the steady-state gaze velocity. The frequency was then 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 steady state. The second method entailed using a cursor to select the segment of each trial to analyze by selecting the time at which gaze velocity approximately reached target velocity (target velocity  $\pm 3$  deg/s) and the time at which a steady-state gaze velocity occurred. A damped oscillation model of the form

$$(A e^{kt}) \sin(2\pi f(t)) \quad (1)$$

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 time-constant. The frequencies obtained from both methods were statistically identical ( $p > 0.05$ ) and therefore we report only the frequencies calculated using the latter analysis. The time-constant was not calculated using the former method and we thus report only a time constant estimate based on the latter analysis. Because the amplitude of the oscillations calculated using the former method estimated the magnitude of the initial overshoot of gaze velocity with respect to

target velocity while the latter method estimated the magnitude of the first oscillation, we report the amplitudes obtained from both methods since they are in fact measures of different oscillation characteristics.

In addition, 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 both over days with increased training and within each session as the monkey's motivation and/or attention decreased and as training increased. However, we analyzed all trials that showed clear oscillations, which resulted in ~85 and 40% of trials being analyzed for monkey C and J, respectively. Note that an equivalent percentage of HR and HU trials were analyzed in each monkey.

## ***2. 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 at least 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 since 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. In order to compare the open-loop responses with the closed-loop control responses, we calculated and averaged the control gaze, eye, and head velocities over an analogous 50 ms interval (i.e. ~450-500 ms after the onset of pursuit). The following two questions were then addressed: 1) Do the gaze, eye, and/or head responses differ for open-loop trials with no imposed error (i.e.  $RVE = 0$  deg/s) compared to the closed-loop control responses? And 2) do the gaze, eye, and/or head responses differ for open-loop trials with no imposed error (i.e.  $RVE = 0$  deg/s) as compared to those trials with imposed errors ( $RVE = \pm 10$  deg/s)?

### III. Results

The principal goals of this study were 1) to investigate whether combined eye-head pursuit of a step-ramp target trajectory differed as compared to eye-only pursuit 2) to characterize and compare initial gaze, eye, and head dynamics in response to step-ramps, and 3) to examine the effects of retinal velocity errors on gaze, eye, and head responses. We begin by characterizing the HU strategy used by each monkey to acquire initial fixation and subsequently pursue the step-ramp stimulus.

#### A. Eye-Head Pursuit Strategy

Figure 2-1A shows an individual trial that illustrates a typical HR pursuit response from monkey C. The top panel of figure 2-1A 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 deg/s) towards the right. The stereotyped nature of the HR pursuit responses is demonstrated in figure 2-1B. Pursuit latencies for this 40 deg/s step-ramp target trajectory were  $86 \pm 10$  and  $106 \pm 10$  ms (average  $\pm$  std) for monkey 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 since the head was immobile. However, in HU trials, the monkey was free to use any eye-head strategy desired in order to acquire initial fixation of the target and subsequently pursue it. Figure 2-2A shows potential strategies a monkey could have used to acquire fixation of a target initially located at a position of -30 deg with respect to

primary position. As in the HR trials, the monkey may have chosen to keep its head centered at 0 deg and used only its eyes to fixate the target (left panel), or may have used any number of combinations in order to align its axis of gaze (line of sight) with the target (center and right panels). The actual strategies used by the two monkeys to acquire initial fixation of the target is shown in figure 2-2B, where the mean initial position of the eye, head, and gaze is plotted for the three initial target positions tested (see METHODS). The data were pooled across all velocities since the monkeys could not predict the velocity of the target and were therefore unable to form any velocity-dependent strategies. Each monkey oriented its axis of gaze toward the target and used a combination of both its eyes and head to accomplish this. Furthermore, as illustrated in the insets of figure 2-2B, both monkeys used similar eye-head strategies to fixate eccentric targets; 55-65% of the gaze redirection was accomplished by rotation of the head while 35-45% of the gaze redirection was accomplished by rotation of the eyes.

While both monkeys used similar strategies to acquire fixation of the target, they employed different eye-head pursuit strategies. Figure 2-3A shows superimposed gaze, eye, and head velocity profiles from individual trials that were aligned on their respective movement onset. Despite the different and relatively less stereotyped eye-head strategies used by both monkeys, and analogous to the HR gaze responses, the HU gaze responses were highly stereotyped. In addition, although not shown, both monkeys tended to make a saccade some time after the first 100 ms of pursuit (see BELOW). Figure 2-3B shows the average gaze, eye, and head position (top panel) and velocity (bottom panel) profiles used by the two monkeys in response to an initially centered target that was moved at a constant velocity of 40 deg/s. Each monkey's gaze pursuit strategy was similar to that



observed in the HR condition; gaze initially accelerated and then continued to oscillate around the velocity of the target. 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:  $83 \pm 9$  and  $104 \pm 12$  ms for monkey C and J, respectively). However, the head and eye strategies used by the two monkeys differed. On the one hand, monkey C accelerated its head (head movement onset latency was  $238 \pm 72$  ms) until it reached target velocity and subsequently maintained pursuit primarily by maintaining the velocity of its head at approximately the same velocity as that of the target. Monkey C's eyes began to decelerate early after the onset of the head movement until the head reached target velocity, at which point the eyes remained virtually motionless with respect to the head at an orbital position of approximately 10 deg. On the other hand, monkey J tended to accelerate its head earlier (head movement onset latency was  $182 \pm 30$  ms) and much faster than monkey C such that it substantially overshot target velocity and then decelerated. Monkey J's eyes began to decelerate early after head motion onset, actually reversed direction, and subsequently accelerated in nearly an equal but opposite manner with respect to the head movement, such that the eyes did not deviate far from primary position.

The effects of target velocity on the gaze, eye, and head movement gains during steady-state HU pursuit at all initial target eccentricities tested are shown in figure 2-4. 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 steady-state 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  $0.95 \pm 0.08$  with monkey J's pursuit gain of  $0.84 \pm 0.07$  ( $p < 0.005$ )).

### **B. Head-unrestrained Advantage**

The preceding results indicate that rhesus monkeys naturally use both their eyes and their head to pursue targets moving at constant velocities. We subsequently hypothesized that the use of both the eyes and the head is advantageous for the monkey as compared to using the eyes alone. We first investigated whether pursuit accuracy was improved in the HU condition as compared to the HR condition by comparing steady-state pursuit gains (i.e. gaze velocity/target velocity). Figure 2-5 shows a plot of the relationship between HU and HR pursuit gains and target velocity for each monkey. For each monkey, HU and HR pursuit gains show similar gains that decrease as velocity increases at all initial target positions. One exception is in monkey J, where low HR pursuit gains were observed at higher velocities ( $> 50$  deg/s) for initially centered targets as compared to HU pursuit gains ( $p > 0.05$ ). Thus, 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; Robinson et al. 1986; Goldreich et al. 1992). 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 2-6A and B illustrate examples of monkey C's HR and HU response profiles, respectively, during

gaze pursuit of an initially centered target moving at 20 deg/s. Also shown is the model fit used to characterize the oscillations (see METHODS). In the HR trial, the clear oscillation is typical of what we observed. The gaze velocity trajectory initially overshoot and then oscillated around target velocity with each subsequent period being reduced in amplitude. In the HU trials, we observed similar oscillations. Table 2-1 shows the average data for all trials that were analyzed for initially centered targets that moved at 20 and 40 deg/s. In general, we observed no difference between the overshoot, frequency, amplitude, and/or the time-constant of the oscillation in the HR versus the HU conditions, suggesting that the use of both the eyes and the head does 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).

We also examined the possibility that head motion altered the timing of the first corrective saccade. For example, the initiation of the first corrective saccade could be facilitated in the 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 2-7 shows the data for 40 deg/s target trajectories for each of the initial target eccentricities tested. Again, no systematic increase or decrease was observed between the timing of the saccade between HU and HR trials for either monkey. Thus, the use of the head did not facilitate the onset of the first saccade. This is further exemplified by observing that in monkey C, the timing of the saccade occurred much later during combined eye-head pursuit in the HU condition, as compared to when only the eyes were used in the HR condition for targets

initially presented at a position of 30 deg. 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). As can be seen by examining the means and the error bars in figure 2-7, the timing of monkey J's first saccades were more stereotyped across all target trajectories as compared to monkey C. In general, monkey J generated an early saccade  $\sim 160$  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, in terms of steady-state pursuit responses, for using the head as well as the eyes, as compared to using the eyes alone, to pursue a moving target. Furthermore, the timing of the first saccade was not systematically related to prior tracking errors. We then proceeded to investigate whether there were differences in the initial pursuit responses between the head-unrestrained and head-restrained conditions.

### **C. 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 Lisberger and Westbrook 1985; Krauzlis and Lisberger 1994) 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. Secondly, by also characterizing initial head dynamics in the first 80 ms of its responses, we were able 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 since the head began

to move  $180 \pm 100$  and  $83 \pm 30$  ms (averaged across all trials for monkey C and J, respectively) after gaze onset, and since we only analyzed trials in which the gaze, eye, and head were stable ( $0 \pm 3$  deg/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.

Figure 2-8A illustrates average eye velocity traces during HR 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 is characterized in figure 2-8B where average eye acceleration is plotted as a function of target velocity. Table 2-2 provides a summary of the results obtained from a repeated-measures linear regression of acceleration as a function of target velocity. In 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 show statistical significance; possibly as a result of the saturation of initial eye acceleration at  $\sim 600$  deg/s<sup>2</sup> observed in response to the faster velocity step-ramps. Similarly, for monkey J, there was also an increasing trend at all initial target positions tested, which then showed evidence of saturation at velocities greater than 50 deg/s. Note, in monkey J, eye acceleration varied significantly as a function of target velocity only when the target motion began from the most eccentric (i.e. 20 deg) position. We also characterized the relationship between initial eye acceleration and initial target position. As is evident in figure 2-8B, eye acceleration also increased as a function of initial target eccentricity for monkey C ( $p < 0.05$ ). In monkey J,

average eye acceleration showed a small increase with target eccentricity at the higher target velocities ( $>50$  deg/s), although the trends were not statistically significant ( $p>0.05$ ).

Analogous to the HR condition, initial eye velocity trajectories in the HU condition tended to diverge as velocity increased for all eccentricities tested (Figure 2-9A). This relationship is quantified in figure 2-9B and in table 2-2. For monkey C, eye acceleration increased as a function of target velocity for all initial target positions. In 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.

Interestingly, the effect of initial target position on eye acceleration in the HU condition was markedly reduced as compared to its effect in the HR condition, especially at high velocities ( $>60$  deg/s) (compare figures 2-8B and 2-9B). Although initial gaze positions in the HU and HR conditions were similar, initial eye and head positions were not. We subsequently 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. We found that initial eye acceleration significantly increased with increasingly contraversive initial eye positions in the HR and HU conditions in response to 60 deg/s step-ramp stimuli (table 2-3) and was not significantly related to initial head position ( $p>0.05$ , analysis not shown). These results are in accord with those of previous investigations that have reported a similar effect of eye position on pursuit onset latencies (Wellenius and Cullen 2000) and no effect of head position on HR pursuit responses

(Mann and Morrow 1997). Thus, the reduced effect of target eccentricity on average initial eye accelerations that were observed when HU and HR eye acceleration were compared could largely be accounted for by the effect of initial eye eccentricity, which Wellenius and Cullen (2000) suggest reflects an effect of the eye's orbital mechanics rather than differences in the underlying neural command.

Since one of our principal goals was to investigate whether initial eye dynamics differed between HR and HU conditions, we compared HR and HU initial eye acceleration for each target velocity. We restricted this analysis to responses to targets that were initially centered in order not to obscure the effect of head-restraint on eye acceleration with the effect of initial eye position. Our rationale was that at this initial target eccentricity, the conditions between HR and HU trials were similar since each monkey's HU strategy was to keep their eyes and their head centered (as shown in figure 2-2B). In fact, we found no difference in initial eye accelerations in the HU as compared to the HR condition for all target velocities tested when the target was initially centered in either monkey ( $p > 0.05$ ).

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 (figure 2-10A). In each monkey, the head velocity trajectories strikingly diverged as velocity increased. This is further illustrated in figure 2-10B and is quantified in table 2-2. The 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 ( $p > 0.05$ ).

#### **D. Characterization of Open-loop Gaze Pursuit Responses**

Several studies have shown that retinal velocity errors (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). The results of Experiment 1 indicate that initial eye and initial head acceleration tended to increase with increasing target velocity. Recall that Experiment 2 was also devised 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. Put another way, both initial eye and head acceleration tended to increase as RVE increased. 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 as they were during the initiation of their responses.

Example HR and HU open-loop trials from monkey C are illustrated in figure 2-11A, B. The trials started with the monkey initiating a pursuit response to a nasally directed 40 deg/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 panel), -10 (center panel), or +10 deg/s (right panels) was applied. Approximately one visual feedback latency after the onset of the open-loop interval (~100 ms, as shown by the downward arrow), gaze decelerated when a negative velocity error was imposed and accelerated when a positive error was imposed in both the HR and HU conditions. At the end of the



open-loop interval, the target resumed moving at its initial velocity of 40 deg/s and the monkey continued to pursue the target. Note the monkey's gaze, eye, and head responses at the end of the open-loop interval in the trials in which both positive and negative errors were imposed. Approximately one visual feedback latency (as shown by the upward arrow) after the target resumed its initial velocity, the monkey's gaze, generated by the movement of the head as well as the eyes, accelerated and decelerated for negative and positive errors, respectively, in order to match that of the target.

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 (see METHODS). The HR average responses for monkey C and J are shown in figure 2-12A and B, respectively. In monkey J, because we restricted our analysis to study the effects of imposed velocity errors on the pursuit system alone, we were only able to study the effects of imposing negative errors since positive error always evoked saccades within ~100 ms after the loop was opened, and thus employed the saccadic system as well. For monkey C, when the target was artificially stabilized with respect to the fovea such that  $RVE = 0$  deg/s, the open-loop HR average eye (=gaze) trajectory was slightly greater than the average closed-loop control trajectory (left panel). Moreover, HR eye velocity decreased for the imposed negative errors (middle panel) and increased for the positive error (right panel), relative to the average closed-loop control trajectory. For monkey J, in the absence of any visual input (left panel), eye velocity diverged slightly from the average closed-loop control trajectory such that its velocity was slightly less than the control's, and when  $RVE = -10$  deg/s (right panel), the eye velocity decreased even more

compared to the control. The open-loop gaze response latencies (see METHODS), illustrated by the arrows, were an average of ~110-120 ms with respect to the onset of the open-loop interval.

Figure 2-13A and B illustrates the results of Experiment 2 for monkey C and J, respectively, in the HU condition. For monkey C, when  $RVE = 0$  deg/s, the average gaze velocity trajectory did not differ from the average closed-loop control trajectory, and analogous to the HR responses, when  $RVE = -10$  or  $+10$  deg/s, the trajectories decreased and increased, respectively, relative to the average closed-loop control responses. For monkey J, when  $RVE = 0$  deg/s, the average gaze velocity trajectory decreased slightly compared to the closed-loop control trajectory and decreased even more when  $RVE = -10$  deg/s. The HU open-loop gaze response latencies were similar to those obtained in the HR condition (i.e. ~110-120 ms).

In the HU condition the head was free to move and therefore gaze velocity was no longer equivalent to eye velocity; it was equal to the sum of eye and head velocities. We thus 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  $RVE = 0$  deg/s, neither the eye nor the head trajectory differed from their respective closed-loop control trajectories for monkey C (figure 2-13A), whereas both the eyes and the head trajectories decreased compared to closed-loop control for monkey J (figure 2-13B). Remarkably, when we imposed a negative velocity error to the 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. Note that the open-loop head responses lagged the eye response by ~50-100 ms.

We quantified the open-loop effect 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). In table 2-4, we first compared whether stabilizing the target relative to the subject's axis of gaze ( $RVE = 0$  deg/s) had an effect as compared to closed-loop control trials in each monkey. In monkey C, no significant effect was observed in the HU gaze, eye, or head, although HR gaze was slightly faster than control when  $RVE = 0$  deg/s. In contrast to monkey C, stabilizing the target on monkey J's fovea resulted in a significant effect such that HR gaze 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, the differences during the interval following loop offset were not statistically significant.

The effect of imposing negative or positive errors to the monkeys' foveae was examined by comparing their responses to those obtained when the target was stabilized on the fovea (i.e. when  $RVE = 0$  deg/s), as seen in table 2-5. In monkey C, the effects (i.e. gaze, eye, and head responses) were statistically significant; negative errors evoked decelerations and positive errors evoked accelerations. Analogous to monkey C, monkey J showed a significant decrease in both HR and HU gaze velocity as compared to responses to a stabilized target. 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 monkeys, the gaze, eye, and head responses towards 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 (Zee et al. 1981; Robinson et al. 1986; Krauzlis and Lisberger 1991, 1994). 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 this proposal, we examined the results from our 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 2-14A shows monkey J's average HR and HU closed-loop control pursuit responses for Experiment 2. Note that the two responses are virtually identical, illustrating once more the lack of a head-restraint effect on gaze pursuit. Figure 2-14B shows monkey J's average HR and HU pursuit responses, as well as the average HU eye response, for trials in which the target was artificially stabilized. 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 approximately 50 ms before the loop is opened due to the contribution of the head to the pursuit movement (see figure 2-13B) and does not superimpose with the HR gaze trajectory. Therefore, we suggest that the stored velocity information (i.e. velocity

memory) is better related to the gaze trajectory than to the eye trajectory at the time the loop was opened.

#### **IV. Discussion**

The main purpose of this study was to characterize initial gaze, eye, and head dynamics during combined eye-head pursuit in responses to step-ramp stimuli in the head-unrestrained condition. The principal findings were that 1) 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; 2) initial eye and initial head acceleration tended to increase as a function of target velocity; 3) 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 4) the observed HU gaze responses to imposed RVEs were generally mediated by the eyes and the head. These findings, their relationships to previous work, and their implications for hypotheses about the control of coordinated eye-head pursuit are discussed below.

##### **A. 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 either the monkey's initial or steady-state pursuit response of a non-periodic target trajectory. Our findings using step-ramp trajectories confirm and compare with 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. pseudo-random) target trajectories (Gresty and Leech 1977; Lanman et al. 1978; Barnes

1981; Leigh et al. 1987; Barnes et al. 1987; Barnes and Lawson 1989; Smith et al. 1995; Barnes and Grealy 1992).

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 to the eyes, in order to overcome its large viscoinertial load (Zangmeister 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 figure 2-3A, the eye positions throughout the pursuit responses in both monkeys ( $\pm 15$  deg) were generally well within the physical and mechanical limits of ocular motor motility ( $\sim \pm 50$  deg, Lauritis and Robinson 1986; Tomlinson and Bahra 1986; Freedman and Sparks 1997; Cullen and Guitton 1997), a finding that has also been previously reported in monkey eye-head pursuit responses to periodic target trajectories (Lanman et al. 1978).

Interestingly, 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: Bizzi et al. 1971; Barnes 1981; Zangemeister et al. 1981, 1982a,b; Tomlinson and Bahra 1986; Guitton and Volle 1987; Freedman and Sparks 1997; Roy and Cullen 1998). These prior studies showed that head motion accomplishes a greater percentage of the gaze shift for larger amplitude target displacements ( $>40$  deg), such that the eyes remain within  $\sim 25$  deg of their primary position. Hence, both gaze shift and gaze pursuit systems, which are mediated by two distinct neural pathways (reviewed in Lisberger et al. 1987), employ similar eye-head strategies in order 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 reveals itself 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 since only a small viscoelastic effort is required to rapidly rotate the eyes as compared to the head (Zangmeister et al. 1981, or see Peng et al. 1996).

We also showed that both initial eye and head movement dynamics tend to increase with the velocity of the target such that the magnitude of their initial accelerations increased as the velocity of the target increased. This is obviously advantageous as well for the subject because the faster an object of interest is moving, the faster the target will exceed the ocular motor limit, and then exceed the visual limit as well. The behavioral advantage of accelerating both the eyes and the head faster in order to acquire faster moving objects is therefore to minimize the likelihood that the subject will lose sight of the object.

#### **B. 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 to monkey C (compare slopes for HU eye of 2.7 versus 0.7 for monkey C and J, respectively, for initially centered targets, as seen in table 2-2). 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 figures 2-4 and 2-5, monkey J's steady-state performance was poor, especially at higher velocities, as indicated by pursuit gains well below unity. It is possible that monkey J, who was less experienced in pursuit tasks as compared to



monkey C, was unable to adequately pursue the target at these higher velocities. In fact, when we performed a repeated-measures linear regression through monkey J's initial eye acceleration data for trials in which the pursuit gain was greater than 0.8, the slopes of both the HR and HU gaze acceleration slopes increased by an average of  $\sim 3.5$  times and reached statistical significance ( $p < 0.05$ , data not shown).

Secondly, monkey J rotated its head earlier and more rapidly in order to initially acquire and pursue the target (see figure 2-3A). For example, for initially centered 40 deg/s step-ramps, head latency was 182 and 238 ms ( $p < 0.005$ ) and head acceleration was 389 and 143 deg/s<sup>2</sup> ( $p < 0.005$ ) for monkey J and C, respectively. Considering that gaze velocity is equivalent to the sum of eye and head velocities, and since the head moved more rapidly in response to faster moving targets (see figure 2-10), monkey J's eyes did not accelerate as rapidly as compared to monkey C's eyes. We propose that the modification of the pre-motor drive to the eyes may have occurred, at least in part, via an interaction with vestibular signals that arose from the self-generated head motion, as has been reported to occur during gaze reorienting movements (Lanman et al. 1978; Barnes 1981; Freedman and Sparks 1997; Roy and Cullen 1998; Belton and McCrea 2000). Additionally, since electromyography recordings have revealed that neck muscle activity is strongly coupled with eye movement dynamics during ongoing pursuit and saccadic eye movements in the *head-restrained* human (André-Deshays et al. 1991), monkey (Bizzi et al. 1971; Lestienne et al. 1984); cat (Grantyn and Berthoz 1985), and rabbit (Fuller 1980), as well as during gaze shifts in the head-unrestrained human (Zangemeister and Stark 1982a) and monkey (Bizzi et al. 1971), it is also possible that in monkey J, inputs from neck proprioceptors to the eye-motor system contributed to

masking the effect of target velocity on initial eye acceleration in both the HR and HU conditions.

Nonetheless, it is apparent from Experiment 1 that initial eye movement dynamics in the HR and HU conditions tended to increase with target velocity in each monkey. In addition, HR and HU initial eye movement dynamics showed some degree of saturation at target velocities greater than 50 deg/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 (Lisberger and Westbrook 1985; Carl and Gellman 1987; Mann and Morrow 1997; Suzuki et al. 1999). The finding that initial eye and initial head movement responses shared similar relationships with stimulus parameters, 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 BELOW).

### **C. 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; Morris and Lisberger 1987; Carl and Gellman 1987; Newsome et al. 1988), that eye velocity is

roughly maintained in the absence of retinal errors and that RVEs are effective stimuli for modifying eye velocity in order to correct for errors in tracking. A novel finding of our data was that during HU pursuit, gaze velocity was also generally maintained in the absence of visual feedback and was modified in response to RVEs such that both the eyes and the head mediated the changes in gaze velocity that were observed in response to RVEs. 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.

#### **D. Gaze pursuit velocity memory**

Although many previous studies have reported that the pursuit system has the ability to store velocity information (see for example Becker and Fuchs 1985; Morris and Lisberger 1987; Keller and Johnsen 1990; Barnes and Asselman 1991; Barnes and Grealy 1992; Barnes et al. 1995, 1997; Collins and Barnes 1999), 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 a positive 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 that could be measured as eye accelerations. 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 the gradual build-up of stored velocity information, which they argue is not an efferent copy of the eye movement, but more likely a corollary discharge from the pre-motor drive signal. Moreover, Barnes and collaborators have recently shown that both the eyes and the head show evidence of such anticipatory movements and have suggested 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 does suggest that the response to the stored velocity information is better related to gaze velocity than to eye velocity (see figure 2-14). Our general hypothesis is therefore that the stored information is charged by an efference copy of the gaze movement command and/or by a build-up of afferent visual information; not by an efference copy of the eye movement.

Our results only indirectly shed light as to whether the gaze responses to targets stabilized on the fovea 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 years 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 year training). 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 is capable of 1) storing velocity information, 2) improving its ability to store and/or access the information, and 3) conveying the stored velocity information to both the eye and neck motor plants.

#### **E. 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 in order to drive the initiation and the maintenance of both the eyes and the head during gaze pursuit. The model shown in figure 2-15 is a simplified, adapted version of previously described models (Barnes and Grealy 1992; Barnes et al. 1997). In this model, the pursuit system compares the target velocity with the eye and head velocity (junction A) in order to obtain an accurate representation of the current retinal velocity error. This error signal is then used to generate the pre-motor drive to both the eyes and the head while the storage of velocity information is achieved through a positive feedback loop that relays an efference copy of the gaze command and/or visual afferent

information (junction B) through a variable gain element (VGE). The retinal velocity error signal and the stored velocity information are continuously sampled, stored, and added together in order to generate the required coordinated eye-head gaze pursuit movement. Thus, junction B performs the role of a shared-controller in that it sums available information to generate a gaze pursuit command that is used by both the eyes and the head. At the same time, the neck and eye motor systems continuously interact, possibly via activation of the vestibular system (Galiana and Guitton 1992), such that both the eyes and the head work together to contribute to the gaze pursuit movement and to ensure that the eyes remain near primary position. Moreover, it is likely that both the eye and neck motor system also receive other inputs, for example predictive inputs (Stark et al. 1962, Michael and Melvill-Jones 1966; Gresty and Leech 1977; Becker and Fuchs 1985; Barnes and Ruddock 1989; Barnes and Asselman 1991; Barnes and Grealy 1992; Barnes et al. 1987, 1995, 1997; Collins and Barnes 1999), that have been shown to play a role in the generation of visual pursuit.

Although the neural substrate of the shared-controller is not known, one possibility is the cerebellar flocculus. Electrical stimulation of the flocculus in the HR primate elicits smooth eye movements (Ron and Robinson 1973; Belknap and Noda 1987) while in the HU rabbit, electrical stimulation of the flocculus elicits a combined smooth eye-head movement (De Zeeuw and Koekkoek 1997). Single-unit recordings (Miles and Fuller 1975; Lisberger and Fuchs 1978; Noda and Suzuki 1979a,b; Miles et al. 1980; Stone and Lisberger 1990a,b) have revealed that the flocculus receives information related to retinal error and information related to the motion of the eyes as well as to the motion of the head. In addition, Stone and Lisberger (1990a) have shown

that the firing rates of many Purkinje cells are sustained in the absence of visual inputs (i.e. during target stabilization on the retina). The flocculus thus 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.

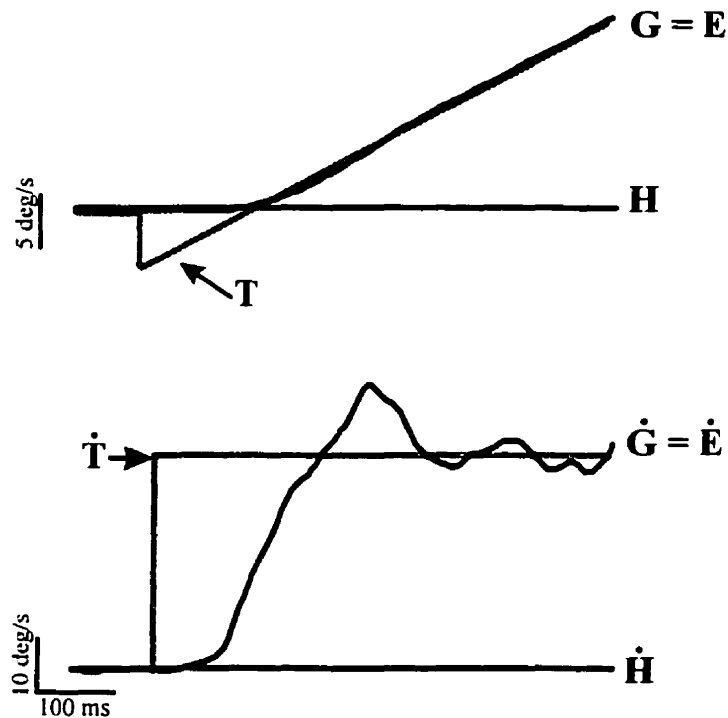
Conversely, Belton and McCrea (1999) argue that the output of the flocculus is not adequate to perform this role. They showed that after muscimol inactivation of the flocculus, eye-only pursuit and not combined eye-head pursuit was impaired in squirrel monkeys. However, there are two points to consider in the analysis of their data. First, the monkeys used in their study primarily used their heads to pursue a periodic target trajectory in the HU condition. It is possible that their monkeys utilized additional and/or different pathways to activate the neck motor plant and generate the rhythmic head motion, especially considering that the strategy utilized by their monkeys to pursue the sinusoidal target trajectories was one in which the head *led* the target. Second, in contrast to previous neuronal recording studies in rhesus monkeys (Lisberger and Fuchs 1978; Miles et al. 1980; Stone and Lisberger 1990a), the floccular Purkinje cells in squirrel monkeys have different sensitivities to horizontal eye and head velocity. Thus, future experiments should utilize non-periodic targets in rhesus monkeys to determine whether the flocculus can be attributed the role of a shared-controller during gaze pursuit.

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

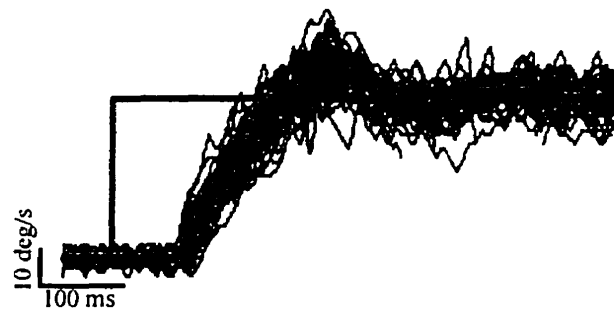
velocity errors (Sakata et al. 1983; Kawano et al. 1984; Komatsu and Wurtz 1988, 1989; Newsome et al. 1988; Fukushima et al. 2000) and gaze velocity (Sakata et al. 1983; Kawano et al. 1984; Komatsu and Wurtz 1988; Newsome et al. 1988; Fukushima et al. 2000). Furthermore, neurons in area MST and in the FEF continue to respond even in the absence of visual inputs (Newsome et al. 1988; Tanaka and Fukushima 1998; Fukushima et al. 2000). Given that FEF and MST are reciprocally connected (Tusa and Ungerleider 1988; Stanton et al. 1993, 1995; Tian and Lynch 1996a,b), 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 (Newsome et al. 1988; Tanaka and Fukushima 1998; Fukushima et al. 2000). Since FEF and MST efferents project to the DLPN (Glickstein et al. 1980), which in turn project to the cerebellar flocculus (for review see Keller and Heinen 1991), they are well situated within a neural network that appears to have an important role in coordinating eye-head pursuit.



**A.**

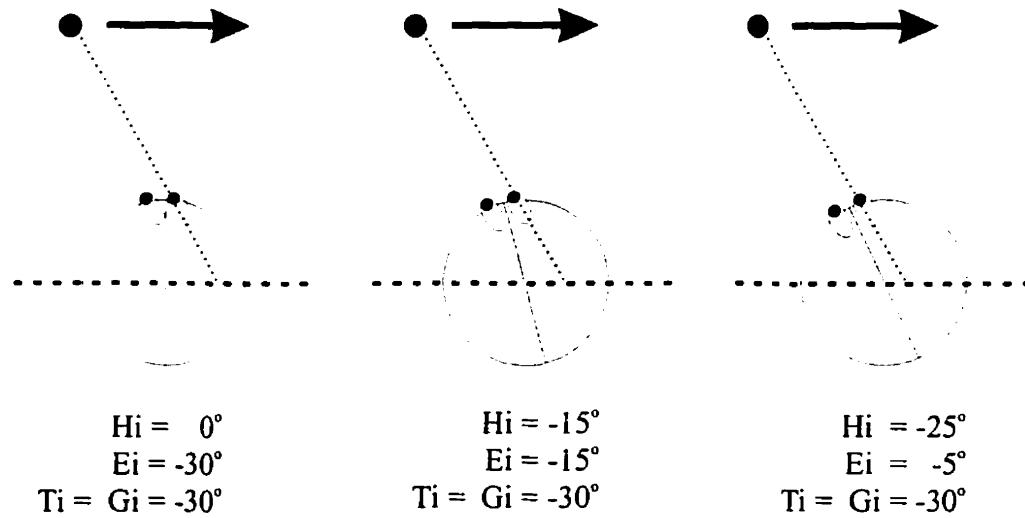


**B.**

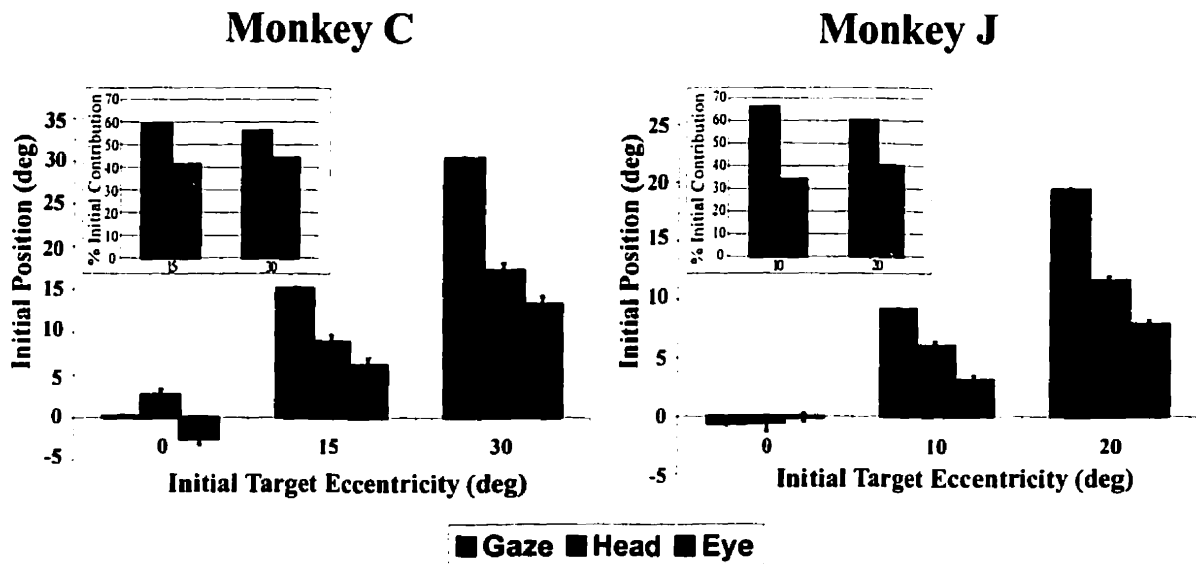


**Figure 2-1:** **A.** Example of a pursuit response to a step-ramp target trajectory in the *head-restrained* condition. The trial began with an initially centered target that underwent a leftward step immediately followed by a ramp in position (40 deg/s, constant velocity). **B.** Average gaze velocity (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  $G$ ,  $E$ ,  $H$ ,  $T$ ,  $\dot{G}$ ,  $\dot{E}$ ,  $\dot{H}$ , and  $\dot{T}$  are gaze, eye, head, and target position and velocity, respectively.

**A.**

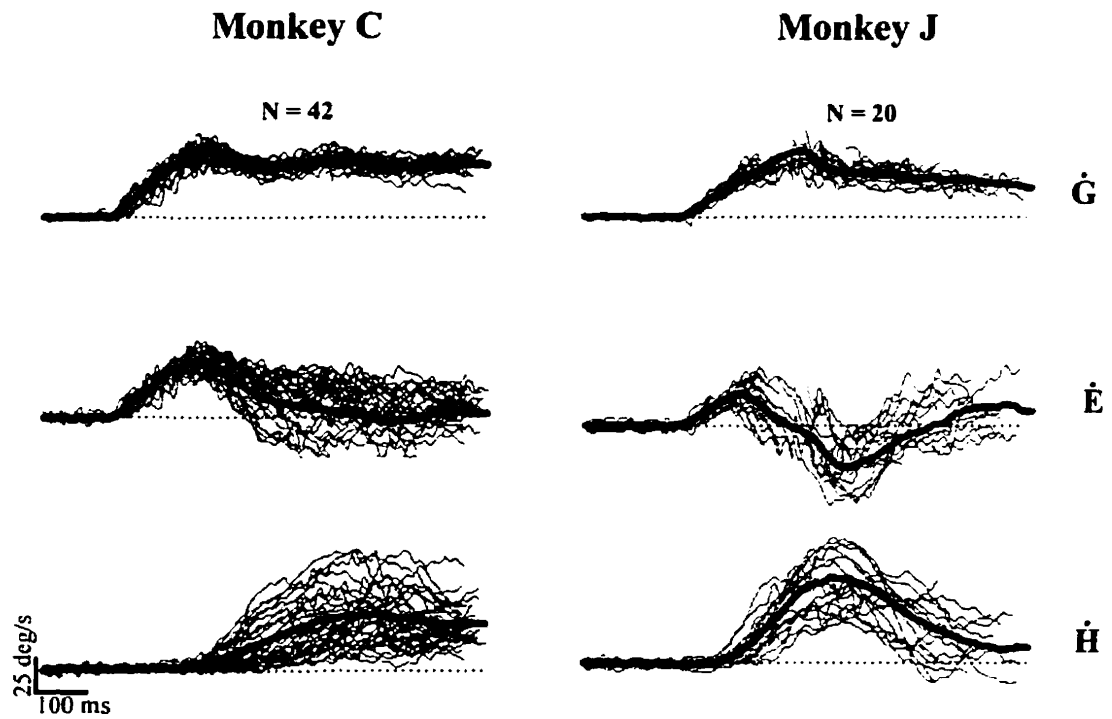


**B.**

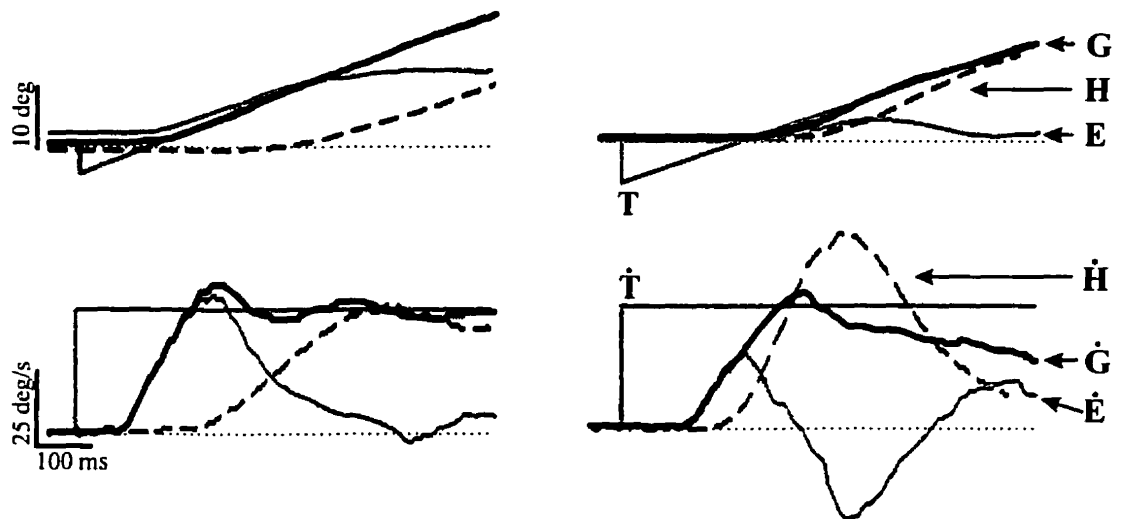


**Figure 2-2: Head-unrestrained initial fixation strategy.** **A.** In the HU condition, any number of different combinations of eye and head movements can be used to acquire initial fixation of the target. **B.** Average initial gaze, head, and eye positions used to acquire initial fixation targets at different eccentricities. *Inset:* Relative contribution of the head and the eye, relative to gaze position, used to acquire initial fixation of eccentric fixation targets. In this and subsequent figure, *error bars* represent SEs of the mean.

**A.**

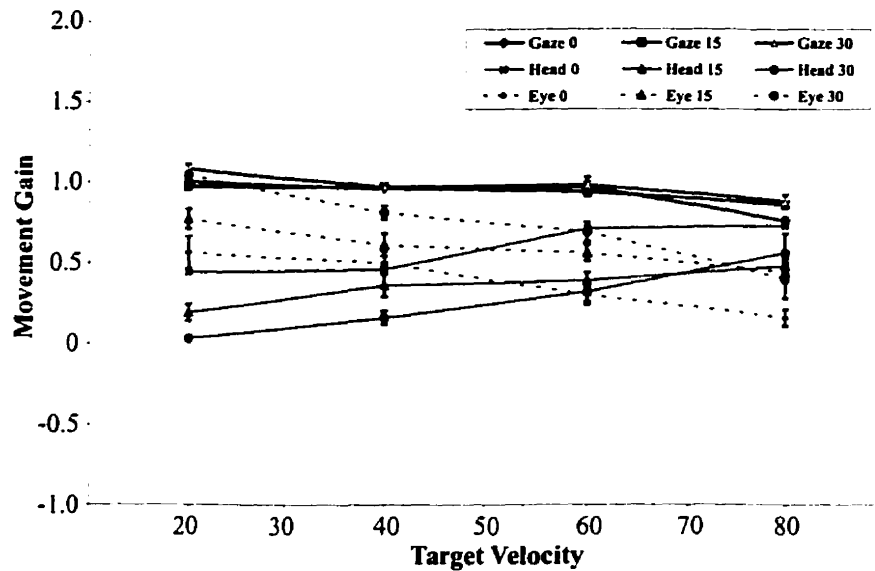


**B.**

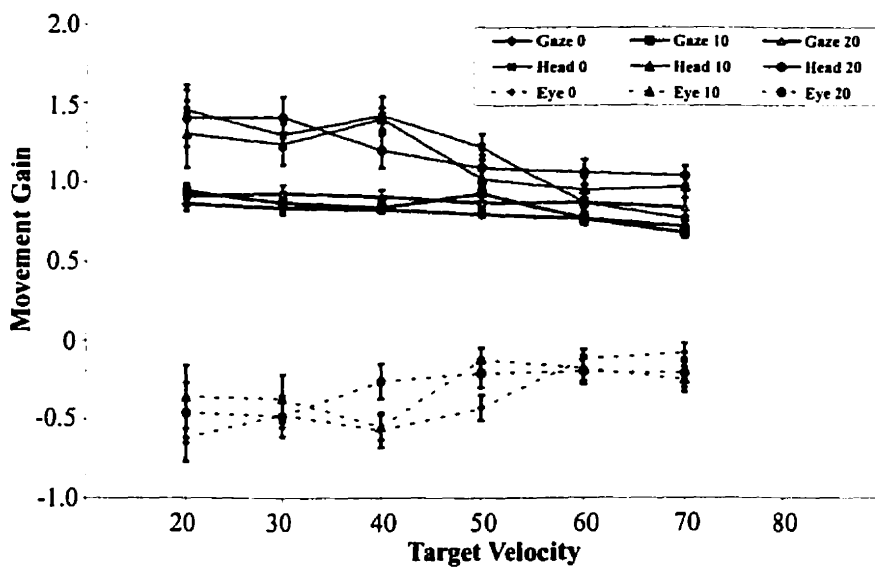


**Figure 2-3: Gaze pursuit strategy.** **A.** Average gaze, eye, and head velocity trajectories (dark lines) superimposed on individual trials (light line) aligned on their respective movement onsets. Note the stereotyped gaze responses. **B.** Average gaze, eye, and head position (top panel) and velocity (bottom panel) traces in response to a 40 deg/s step-ramp target trajectory that was initially centered. Note that although not shown, these response profiles are typical of what we observed in response to all target trajectories tested.

### Monkey C

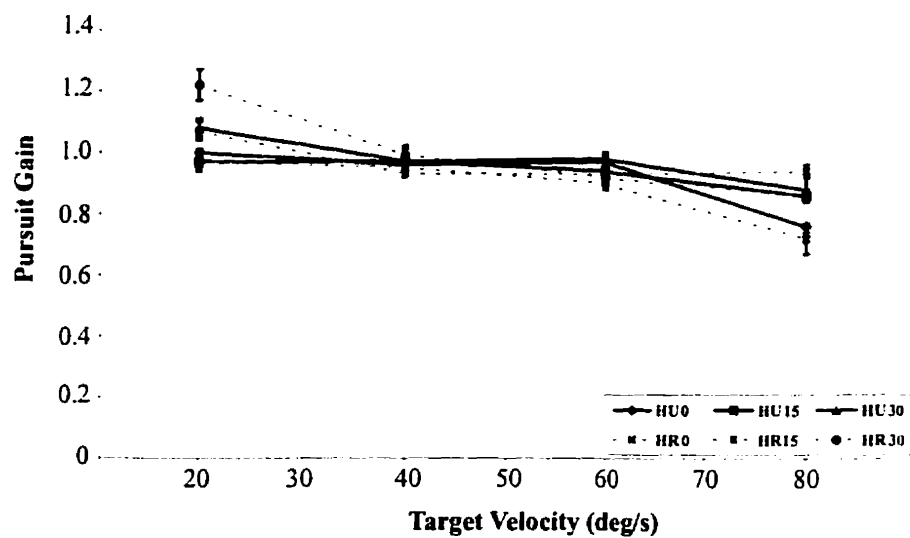


### Monkey J

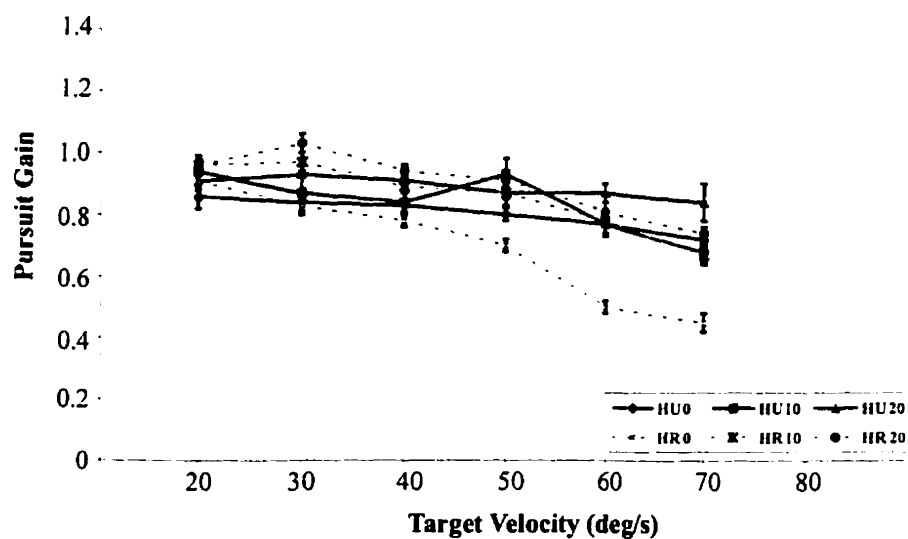


**Figure 2-4:** Comparison of gaze, eye, and head movement gains during *head-unrestrained* pursuit. Gains were defined as the average velocity over the 300-400ms interval following target onset divided by the target velocity over that interval. Note that the numbers in the insets represent the initial target eccentricity of the data from which the averages were calculated.

### Monkey C

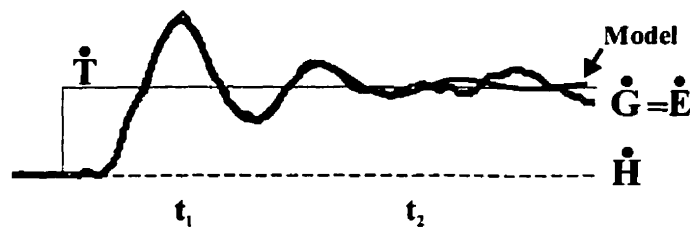


### Monkey J

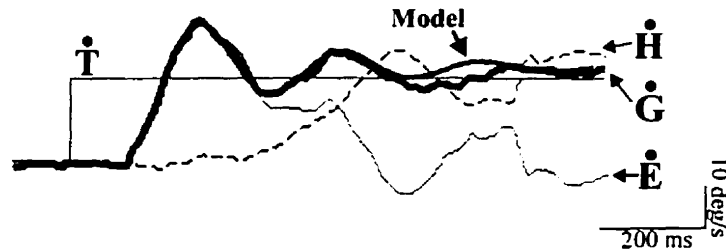


**Figure 2-5:** Comparison of steady-state pursuit gains in the *head-restrained* and *head-unrestrained* conditions. Note that pursuit gains are nearly identical in both the HR and HU conditions.

### A. HR Example



### B. HU Example



**Figure 2-6:** 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 deg/s. In both the HR and HU conditions, a damped oscillation model (dark lines) of gaze velocity provided a good estimate of the oscillation parameters. For instance, the frequency of the oscillation (i.e. the model frequency) was 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 as the difference in velocity between  $t_1$  (peak velocity) and  $t_2$  (steady state velocity). For the HR and HU example trials, the overshoot was 16.7 deg/s and 12.7 deg/s, respectively.

**Table 2-1****Monkey C**

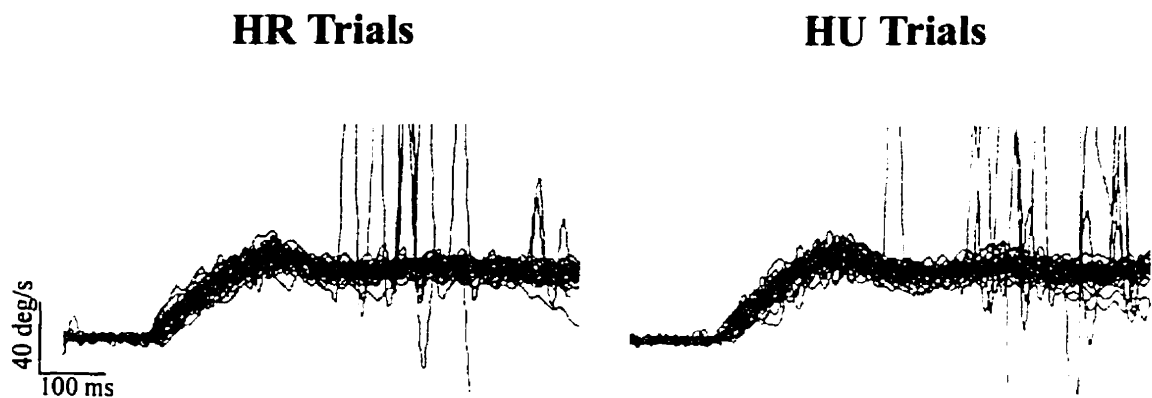
	HR 20°/s	HU 20°/s	p	HR 40°/s	HU 40°/s	p
<i>Calculated</i>						
<b>Overshoot</b>	8.2 (3.0)	7.9 (2.7)	ns	7.2 (3.6)	8.0 (3.6)	ns
<i>Model</i>						
<b>Frequency (f)</b>	4.1 (1.4)	3.4 (1.0)	*	4.3 (0.6)	4.2 (0.8)	ns
<b>Amplitude (A)</b>	12.6 (6.6)	14.4 (8.8)	ns	9.7 (6.2)	11.9 (7.4)	ns
<b>Time-constant (k)</b>	-5.1 (2.8)	-5.5 (4.0)	ns	-3.5 (4.3)	-4.1 (3.1)	ns

**Monkey J**

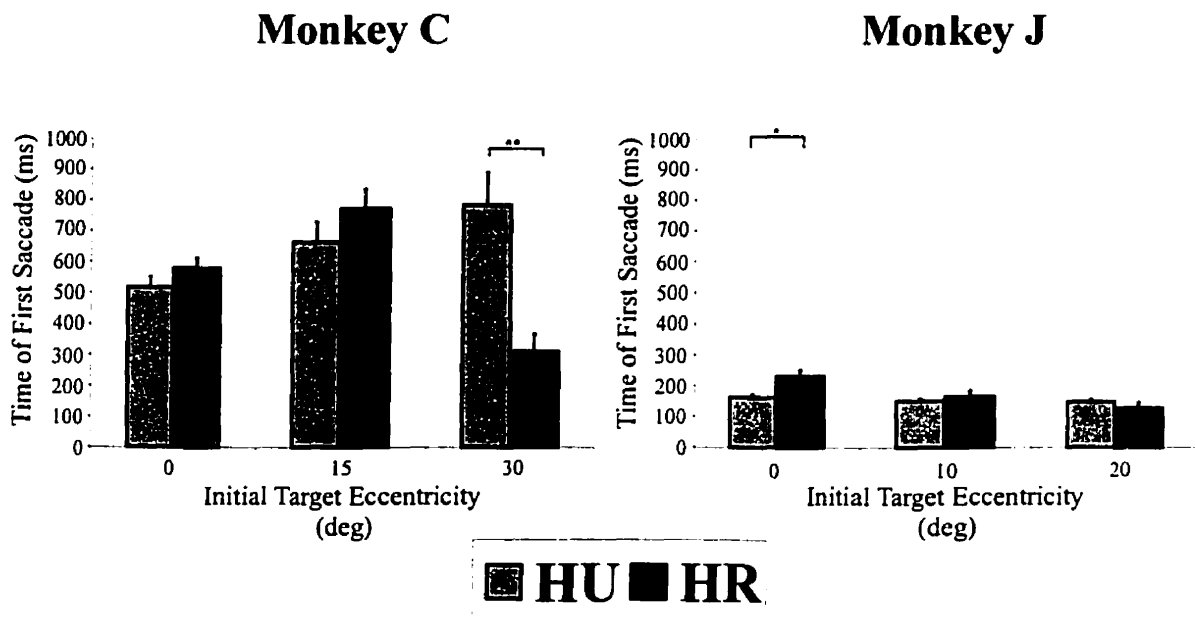
	HR 20°/s	HU 20°/s	p	HR 40°/s	HU 40°/s	p
<i>Calculated</i>						
<b>Overshoot</b>	9.9 (3.6)	7.9 (2.7)	ns	14.7 (2.0)	14.1 (8.6)	ns
<i>Model</i>						
<b>Frequency (f)</b>	4.7 (1.0)	3.8 (1.7)	ns	5.5 (2.1)	4.9 (1.3)	ns
<b>Amplitude (A)</b>	16.0 (8.3)	9.6 (3.3)	*	20.5 (10.2)	18.2 (12.9)	ns
<b>Time-constant (k)</b>	-7.6 (4.1)	-4.2 (2.4)	*	-6.7 (3.9)	-5.5 (4.0)	ns

**Table 2-1:** Comparison between head-restrained and head-unrestrained mean (std) oscillation characteristics. A Student's *t*-test was used to determine whether the means differed from each other. Symbols: 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.

A.



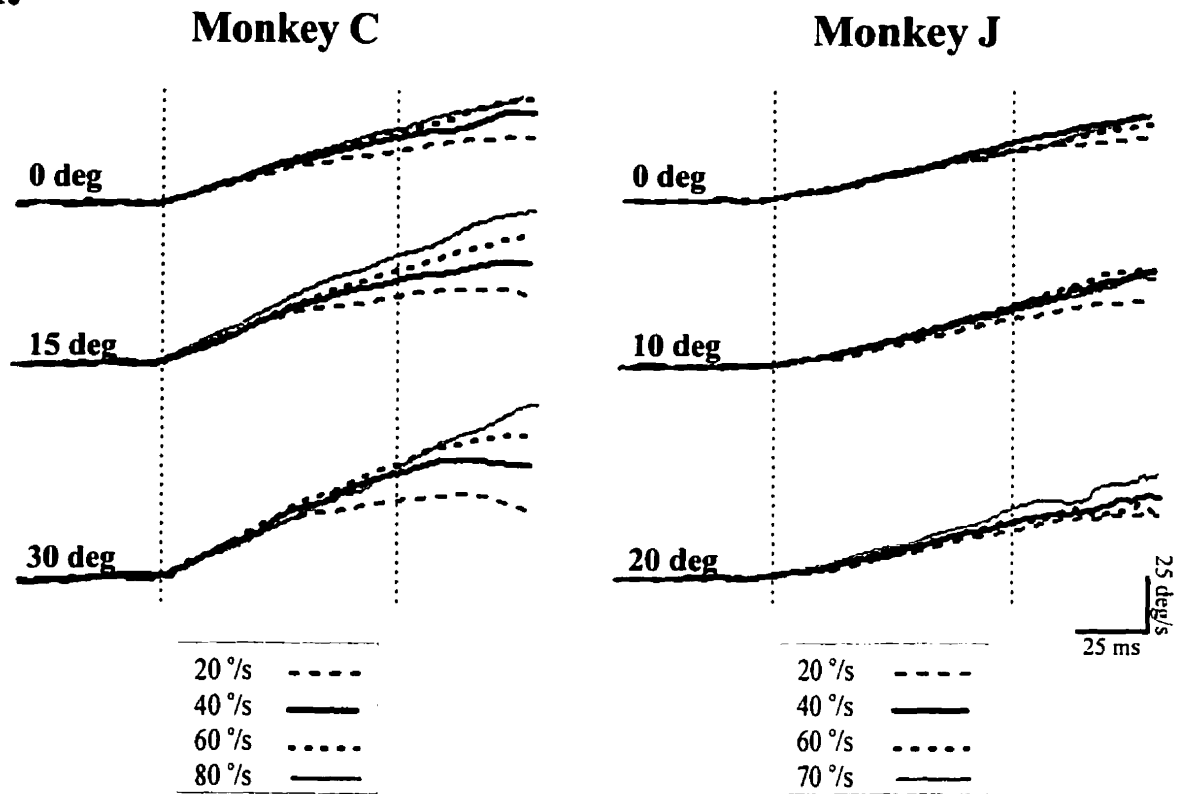
B.



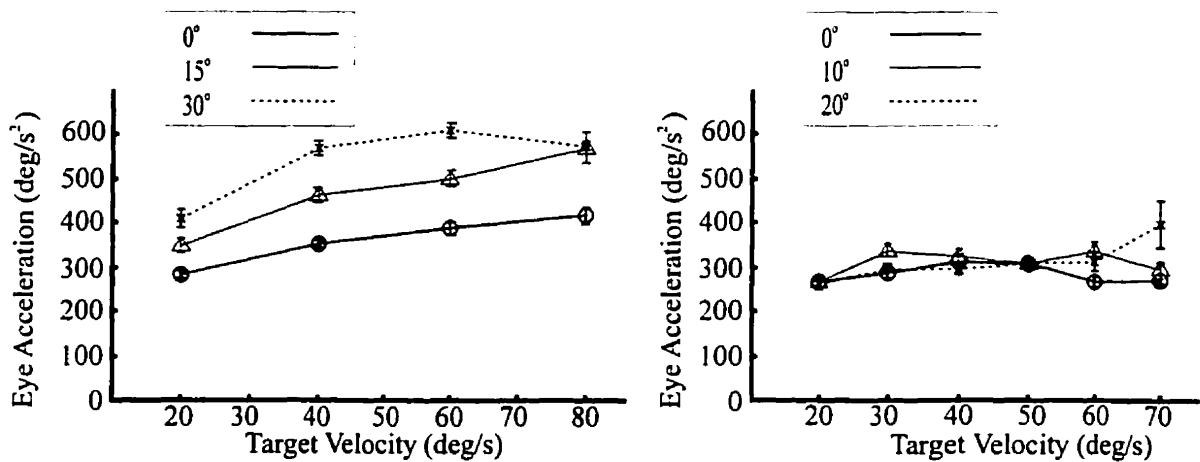
**Figure 2-7:** A. Superimposed head-restrained and head-unrestrained individual trials of monkey C's pursuit responses to 40 deg/s step-ramp target trajectories that were initially centered. B. Comparison of the time of the occurrence of the first corrective saccade, relative to pursuit onset, between head-restrained and head-unrestrained trials for 40 deg/s step-ramp target trajectories. Symbols as in Table 1.



**A.**

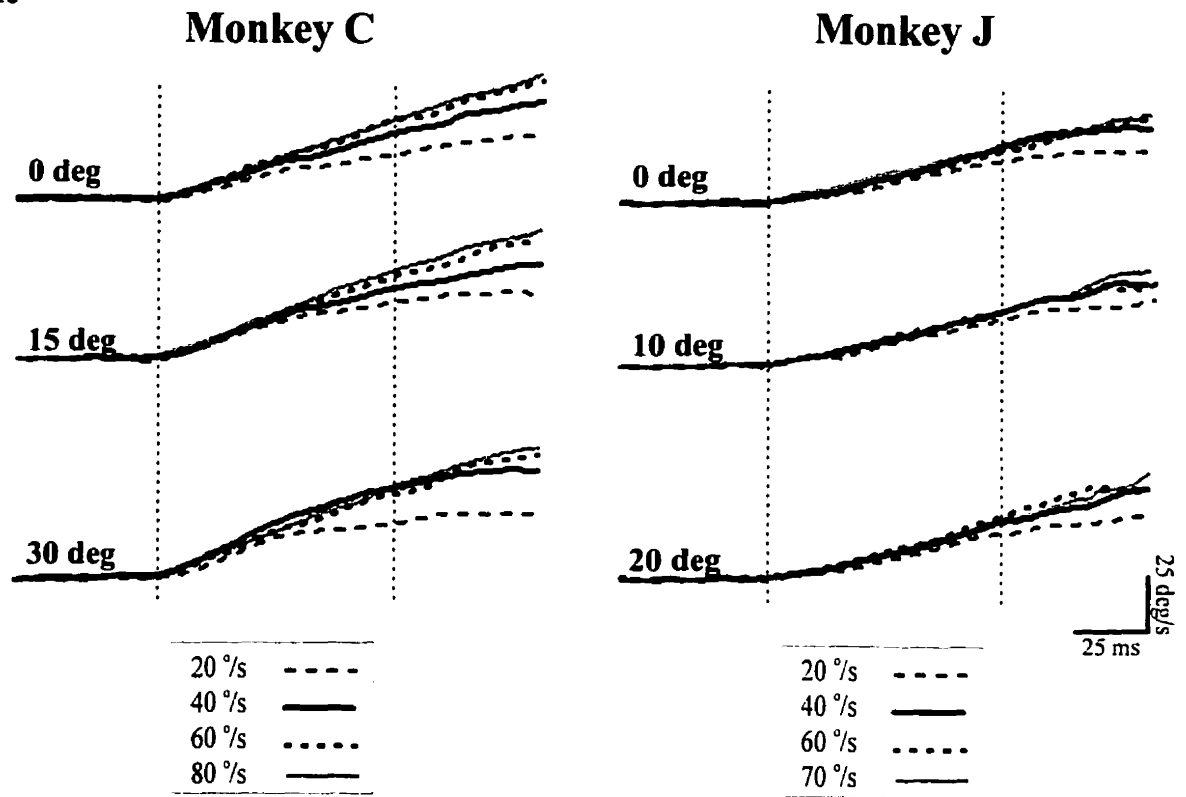


**B.**

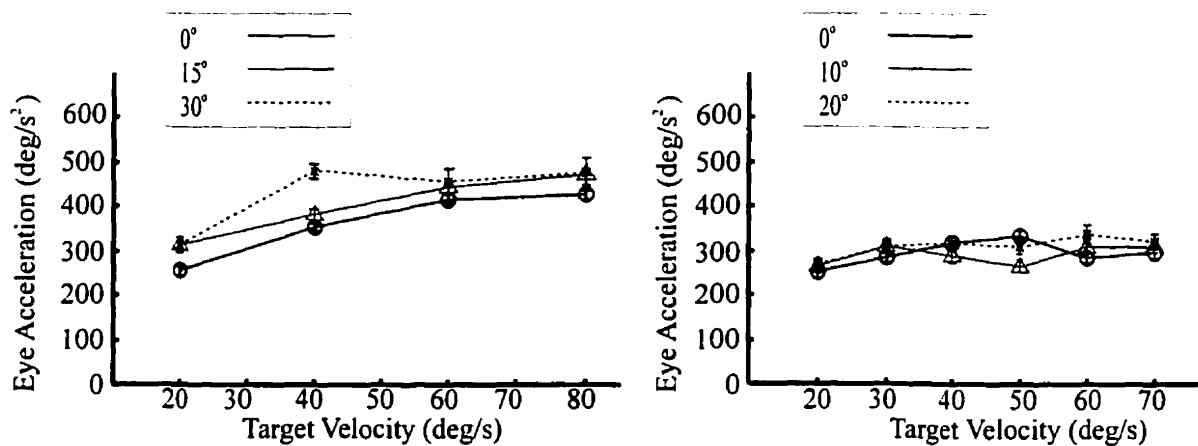


**Figure 2-8:** Effect of target velocity on initial *head-restrained* eye (=gaze) acceleration. **A.** Average eye velocity traces in response to target motion at different velocities in the HR condition aligned on eye movement onset. Dotted lines denote the 80ms interval over which acceleration was quantified. **B.** Effect of target velocity on initial HR eye acceleration for all eccentricities tested.

**A.**

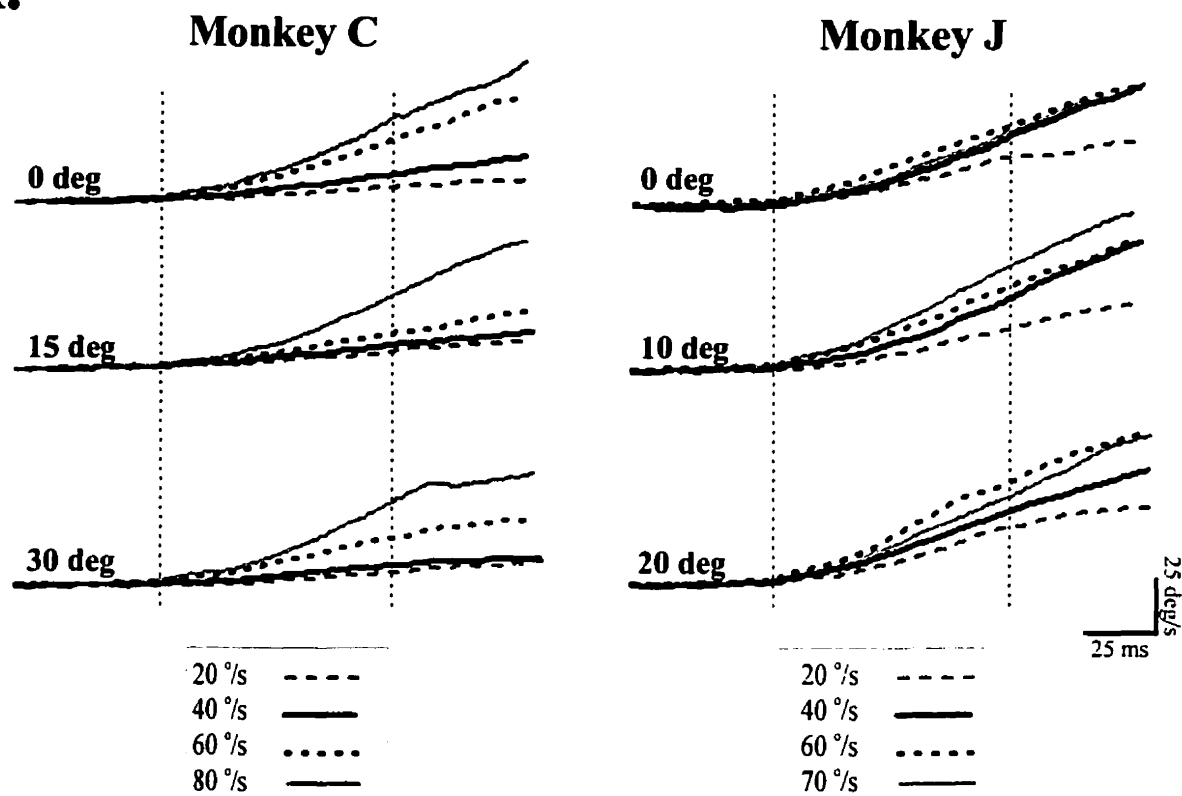


**B.**

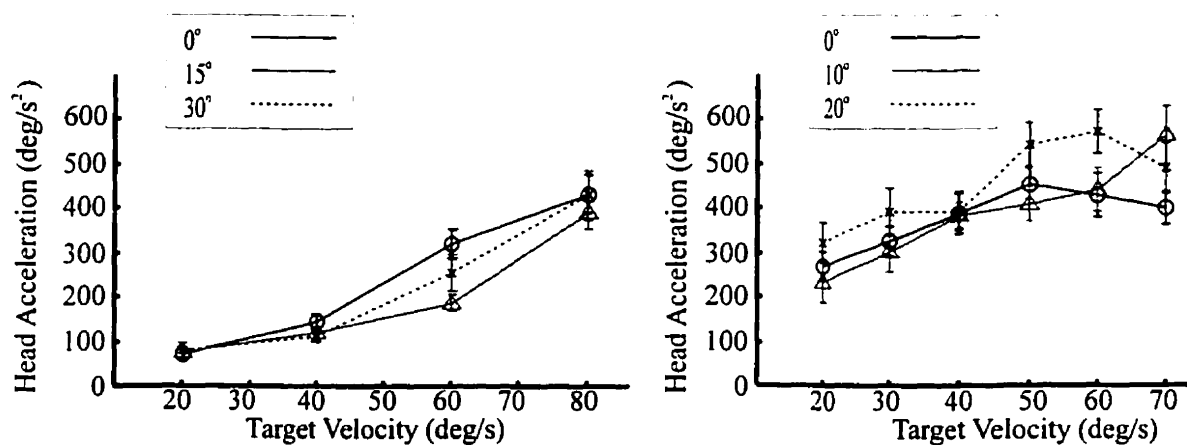


**Figure 2-9:** Effect of target velocity on initial *head-unrestrained* eye acceleration. **A.** Average eye velocity traces in response to target motion at different velocities in the HU condition aligned on eye movement onset. Dotted lines denote the 80ms interval over which acceleration was quantified. **B.** Effect of target velocity on initial HU eye acceleration for all eccentricities tested.

**A.**



**B.**



**Figure 2-10:** Effect of target velocity on initial head acceleration during *head-unrestrained* pursuit. **A.** Average head velocity traces in response to target motion at different velocities in the HR condition aligned on head movement onset. Dotted lines denote the 80ms interval over which acceleration was quantified. **B.** Effect of target velocity on initial head acceleration for all eccentricities tested.

**Table 2-2**

**Monkey C**

	<b>T</b>	<b>n</b>	<b>m</b>	<b>R</b>	<b>p</b>
<b>HR Gaze</b>	0	117	2.19	0.57	**
<b>HU Gaze</b>	0	160	2.77	0.65	**
<b>HU Head</b>	0	160	6.47	0.56	**
<b>HR Gaze</b>	15	110	3.56	0.66	**
<b>HU Gaze</b>	15	133	2.7	0.64	**
<b>HU Head</b>	15	133	5.12	0.64	**
<b>HR Gaze</b>	30	81	2.92	0.51	ns
<b>HU Gaze</b>	30	89	2.06	0.35	ns
<b>HU Head</b>	30	89	6.11	0.63	**

**Monkey J**

	<b>T</b>	<b>n</b>	<b>m</b>	<b>R</b>	<b>p</b>
<b>HR Gaze</b>	0	173	-0.21	0.05	ns
<b>HU Gaze</b>	0	131	0.69	0.16	ns
<b>HU Head</b>	0	131	2.98	0.26	*
<b>HR Gaze</b>	10	145	0.44	0.11	ns
<b>HU Gaze</b>	10	125	0.62	0.15	ns
<b>HU Head</b>	10	125	5.79	0.43	**
<b>HR Gaze</b>	20	149	2.08	0.29	**
<b>HU Gaze</b>	20	133	0.99	0.22	*
<b>HU Head</b>	20	133	4.52	0.31	**

**Table 2-2:** Repeated-measures linear regression through the initial gaze (=eye) and head acceleration data as a function of target velocity from both the head-restrained and head-unrestrained experiments. Symbols: T, initial target position; 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.

Table 2-3

**Monkey C**

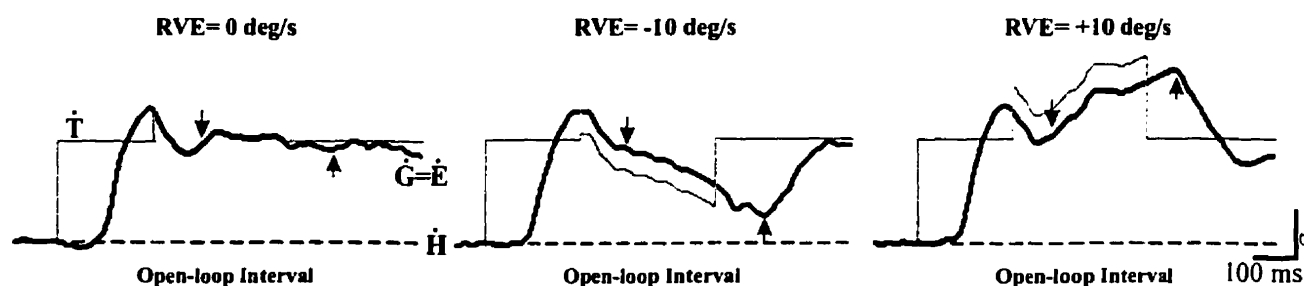
	T'	n	m	y-int	R	p
HR	60	78	6.97	399.42	0.66	**
HU	60	109	4.04	421.98	0.41	*

**Monkey J**

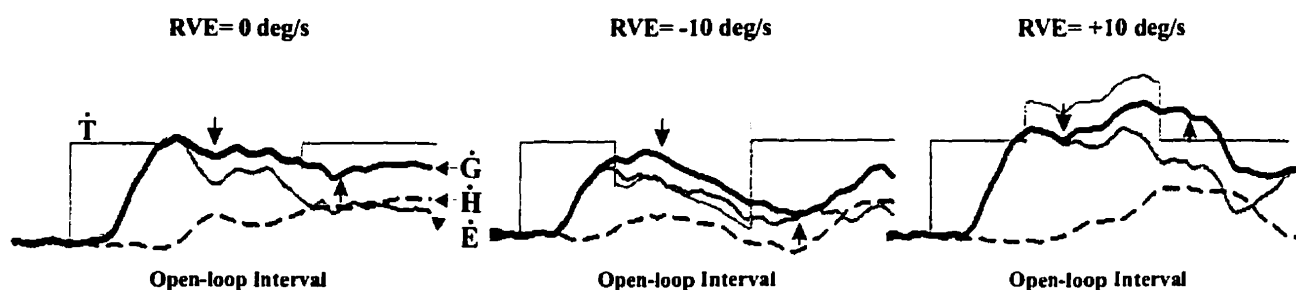
	T'	n	m	y-int	R	p
HR	60	67	3.95	274.59	0.41	**
HU	60	63	6.44	287.09	0.39	**

**Table 2-3:** Linear regression through the initial eye acceleration data as a function of initial eye position for all trials where target velocity was 60 deg/s. Symbols as in Table 2.

## A. HR Trials



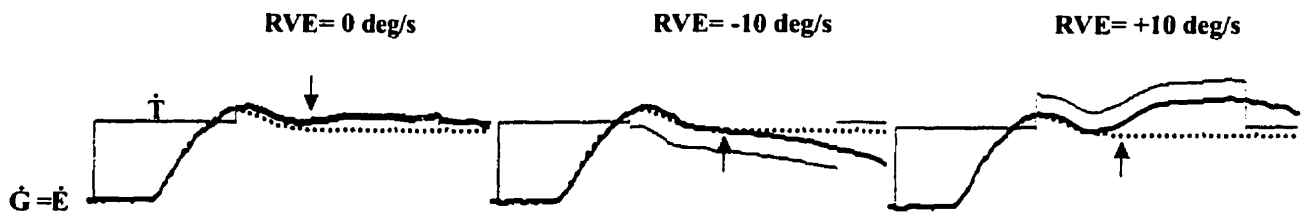
## B. HU Trials



**Figure 2-11:** Open-loop experiment. Head-restrained (A) and head-unrestrained (B) examples of monkey C's open-loop responses to step-ramp target trajectories during experiment 2. Dashed lines represent onset and offset of the open-loop interval, which was 300 ms in all open-loop experiments. During the open-loop interval in these examples, the target was either artificially stabilized with respect to the animal's fovea such that the retinal velocity error was equal to 0 deg/s (right panel), or a retinal velocity error of -10 or +10 deg/s was imposed (center and left panel, respectively). The *downward and upward arrows* indicate one visual feedback latency (~100 ms) from loop onset and offset, respectively.

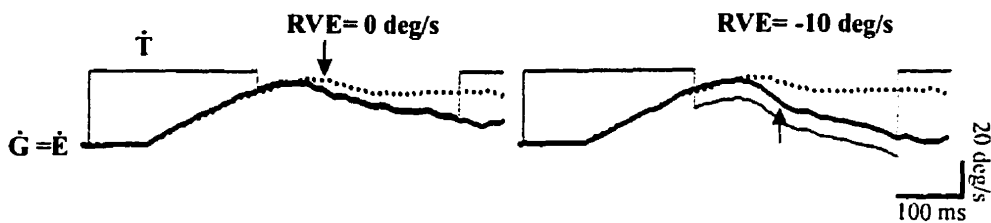
### A. Monkey C

( — ) Open-loop  
( ..... ) Control



### B. Monkey J

( — ) Open-loop  
( ..... ) Control

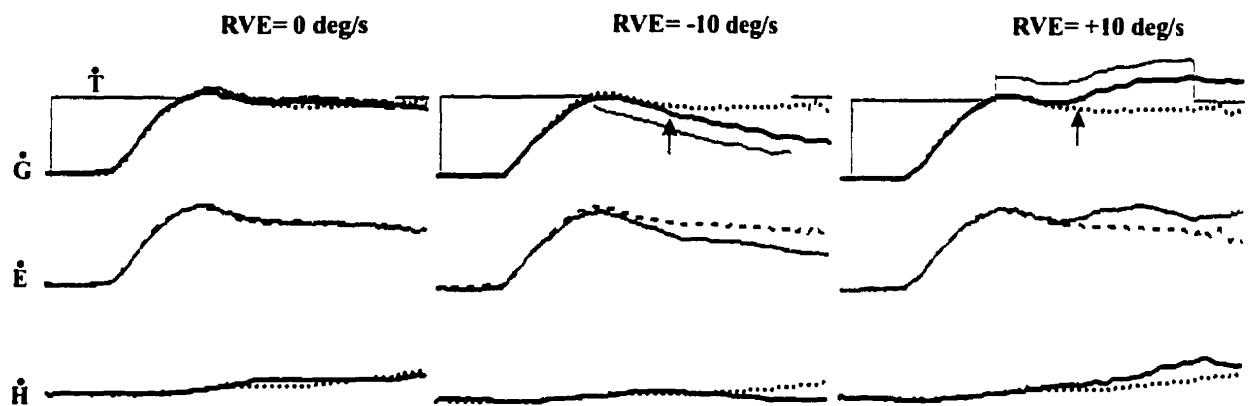


**Figure 2-12:** Comparison of open-loop and closed-loop control responses. Average *head-restrained* eye velocity trace during open-loop trials (solid line) superimposed on average *head-restrained* eye velocity during closed-loop control trials (dashed line) in monkey C (A) and J (B). Downward arrows indicate the time at which the standard error of the open-loop response diverged from that of the closed-loop control response (i.e.  $0 \text{ deg/s}$  vs control). Upward arrows indicate the time at which the standard error of the open-loop trace with an imposed error of  $10 \text{ deg/s}$  diverged from that of the response to a stabilized target (i.e.  $\pm 10 \text{ deg/s}$  vs  $0 \text{ deg/s}$ ).

### A. Monkey C

( $\equiv$ ) Open-loop

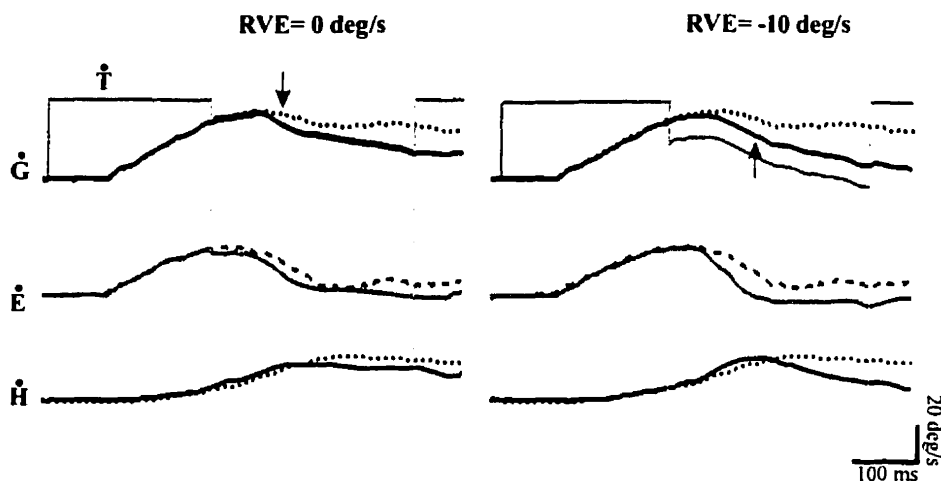
( $\cdots$ ) Control



### B. Monkey J

( $\equiv$ ) Open-loop

( $\cdots$ ) Control



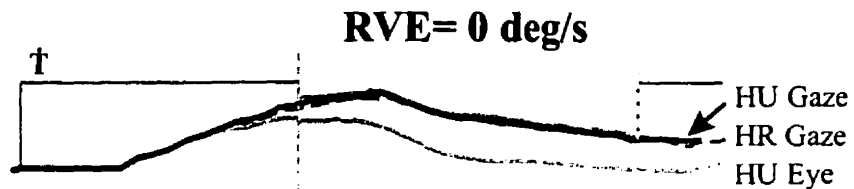
**Figure 2-13:** Comparison of open-loop and closed-loop control responses. Average *head-unrestrained* gaze, eye, and head velocity traces during open-loop trials (solid line) superimposed on average gaze, eye, and head velocity traces during *head-unrestrained* closed-loop control trials (dashed line) for monkey C (A) and J (B). Arrows as in figure 12.



### A. Closed-loop Control Responses



### B. Open-loop Responses



**Figure 2-14:** 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. 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.

Table 2-4

**Monkey C**

RVE =	Control	0°/s	p
<b>HR Gaze</b>	38.5	45.0	<b>**</b>
<b>HU Gaze</b>	37.9	35.7	ns
<b>HU Eye</b>	29.2	28.0	ns
<b>HU Head</b>	8.6	7.8	ns

**Monkey J**

RVE =	Control	0°/s	p
<b>HR Gaze</b>	30.5	18.8	<b>**</b>
<b>HU Gaze</b>	28.8	17.2	<b>**</b>
<b>HU Eye</b>	4.7	0.6	ns
<b>HU Head</b>	22.5	17.0	ns

**Table 2-4:** Comparison of average velocity in the 50ms interval following loop offset between open-loop trials in which the target was artificially stabilized with respect to the monkey's fovea (i.e. RVE= 0 deg/s) and closed-loop control trials. Symbols as in Table 1.

Table 2-5

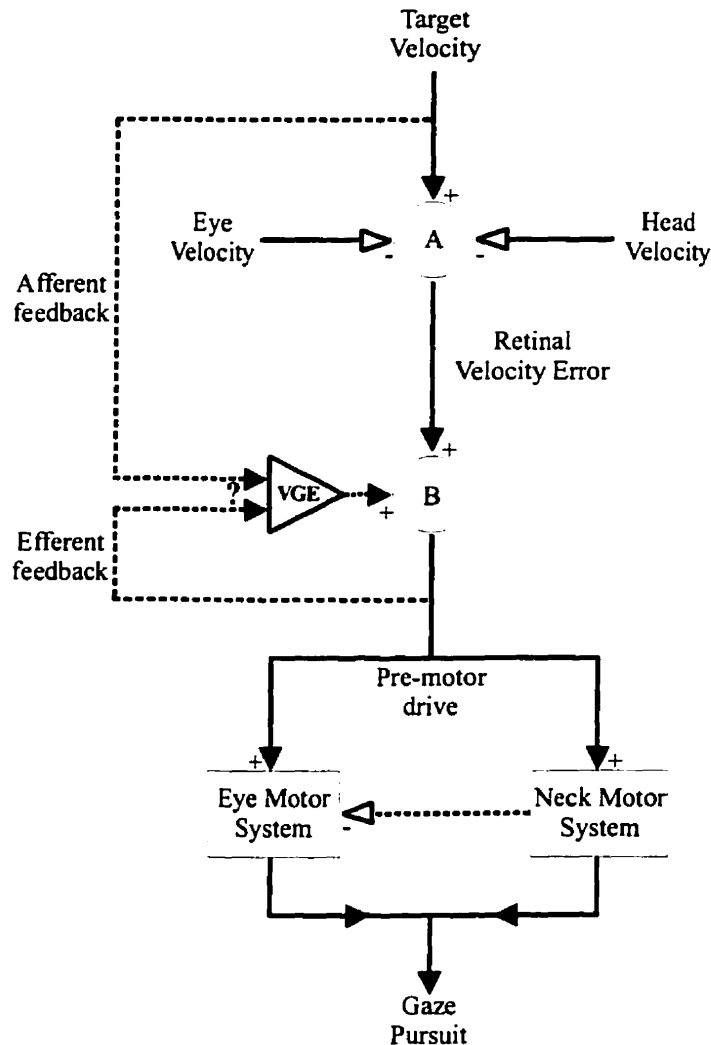
**Monkey C**

RVE =	0°/s	-10°/s	p	+10°/s	p
<b>HR Gaze</b>	45.0	26.7	**	55.5	**
<b>HU Gaze</b>	35.7	21.8	**	50.5	**
<b>HU Eye</b>	28.0	20.4	**	37.5	**
<b>HU Head</b>	7.8	2.3	**	15.7	**

**Monkey J**

RVE =	0°/s	-10°/s	p	+10°/s	p
<b>HR Gaze</b>	18.8	9.1	**	-	-
<b>HU Gaze</b>	17.2	12.8	**	-	-
<b>HU Eye</b>	0.6	-1.7	ns	-	-
<b>HU Head</b>	17.0	12.3	ns	-	-

**Table 2-5:** Comparison of average velocity in the 50ms interval following loop offset between open-loop trials in which the target was artificially stabilized with respect to the animal's fovea (i.e. RVE= 0 deg/s) and trials in which a fixed error was imposed to the target velocity (RVE=±10 deg/s). Symbols as in Table 1.



**Figure 2-15:** A model of the eye-head pursuit system. Retinal velocity error, which is derived at the retina (junction A), provides the principle signal from which the pre-motor command is formed. To account for the sustained velocity we observed in the absence of retinal error, we propose that at junction B, an afferent copy of the velocity of the target or an efferent copy of the pursuit command is fed forward, via a variable gain element (VGE), and added to the retinal velocity error signal to form a new pre-motor pursuit command, which then drives the motion of the eyes and of the head. The contribution of the head to the pursuit response is then subtracted, possibly via the vestibular system, from the pre-motor drive to the eye motor plant. The dark solid lines indicate the flow of neural signals, the dashed lines represent hypothesized flow of neural signals, and the gray solid lines represent actual physical events. The circles represent summing junctions, the rectangles represent motor systems, and the triangle represent the variable gain element in which the incoming signals are multiplied by a variable gain. The filled arrows indicate signals that are added while the open arrows indicate the signal that are subtracted at the summing junctions.

## **CHAPTER 3: General Discussion and Summary**

The motivation for this study was to examine the control of eye and head movements during head-unrestrained gaze pursuit. First, we characterized the eye-head strategies used by two rhesus monkeys to acquire and subsequently pursue different step-ramp target trajectories. Secondly, we compared their head-unrestrained and head-restrained pursuit performances. Thirdly, we compared the initial eye and head movement dynamics in response to the different step-ramp stimuli. Lastly, we examined the gaze, eye, and head movement responses when the target was artificially stabilized with respect to the monkey's fovea and when a constant retinal velocity error was imposed during ongoing pursuit.

### **I. Head-unrestrained pursuit strategy**

The characterization of eye-head pursuit responses revealed that rhesus monkeys naturally use their head as well as their eyes to pursue moving targets. In agreement with Wellenius and Cullen (2000), we demonstrated that the onset of head motion typically lags the onset of eye motion by ~80 ms and that pursuit initiation was mediated primarily by the eyes alone. Although different eye-head strategies were used to pursue a particular step-ramp target trajectory, the gaze responses were highly stereotyped in the HU condition. This machine-like nature of pursuit responses was also observed in the HR condition, as has been previously reported (Carl and Gellman 1987).

We subsequently compared HU and HR pursuit responses in order to determine whether there was any apparent advantage to using the eyes and the head to pursue a moving target as compared to using the eyes alone. We thus compared the following measures of pursuit accuracy between the HU and HR conditions: 1) pursuit gains (i.e.

gaze velocity/target velocity), 2) oscillation parameters, and 3) timing of the first corrective saccades. In agreement with previous investigations of pursuit responses to periodic target trajectories (Lanman et al. 1978; Barnes 1981; Leigh et al. 1987; Cullen and McCrea 1990), we failed to reveal a general advantage, in terms of pursuit accuracy, for the use of the head and the eyes to pursue moving stimuli. However, examination of the average eye and head position trajectories revealed that the eyes never deviated far from primary position. Thus, the use of the head to pursue a moving object appears to have a teleological advantage for the subject since it ensures that if a second object of interest reveals itself, the subject will be able to more rapidly align its line of sight in either direction with the object since only a small viscoelastic effort is required to rapidly rotate the eyes as compared to the head (Zangmeister et al. 1981, or see Peng et al. 1996).

## **II. Initial eye and head movement dynamics**

Our study, in agreement with previous studies (Lisberger et al. 1981; Lisberger and Westbrook 1985; Tychsen and Lisberger 1986; Morris and Lisberger 1987; Carl and Gellman 1987; Mann and Morrow 1997), found that in the HR condition, the eyes initially accelerate more rapidly in response to faster moving visual targets. A novel finding was that in the HU condition, initial eye and initial head accelerations increased with increasing target velocities. Thus, the signals that drove the initiation of pursuit were similar in nature during both eye-only and eye-head pursuit. Furthermore, the finding that both the initial eye and head movements accelerate more rapidly to faster moving targets suggests that smooth head movements are driven by the same visual signals that drive smooth eye movements. Such a notion follows the current gaze control

models that have been proposed for the control of gaze shifts (for review see Guitton 1992; Galiana and Guitton 1992).

### **III. Gaze, eye, and head response to retinal velocity errors**

By stabilizing the target relative to the monkey's fovea, we demonstrated that the non-visual signals that have been reported to play a role in maintaining ongoing eye velocity in the HR condition (Morris and Lisberger 1987; Becker and Fuchs 1985; Carl and Gellman 1987; Newsome et al. 1988), are also involved in maintaining gaze, eye, and head velocity in the HU condition. Furthermore, we also showed that similar to the HR gaze responses, HU gaze response are modified by imposed retinal velocity errors and that both the eyes and the head mediated the changes in gaze velocity that were attempting to correct for the imposed error in tracking. Therefore, it seems as though the pursuit system uses visual as well as non-visual signals to drive coordinated eye-head pursuit responses.

### **IV. Concluding remarks**

The findings of the present study suggest that the eye and the head movements generated in order to pursue moving objects are not independently controlled during head-unrestrained pursuit, but rather, are controlled by a shared upstream controller within the pursuit pathway. Additional behavioral studies will need to be carried out in order to completely characterize the signals used to drive eye and head motion during head-unrestrained pursuit, such as an investigation of whether retinal position and retinal acceleration errors are also effective stimuli for altering head velocity during eye-head pursuit. Also, neurophysiological experiments are needed in order to determine how the control of coordinated eye-head pursuit is encoded within the neural pathways that

mediate pursuit. For example, future lesion and unit-recording studies should utilize non-periodic targets in rhesus monkeys to determine whether the flocculus, and/or other pursuit-related areas, can be attributed the role of a shared-controller during gaze pursuit.



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