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Compensatory gaze nystagmus: Visual, vestibular and somatosensory contributions to gaze stabilization during circular locomotion in the monkey

Solomon, David, Ph.D.

City University of New York, 1990

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COMPENSATORY GAZE NYSTAGMUS: VISUAL, VESTIBULAR AND SOMATOSENSORY CONTRIBUTIONS TO GAZE STABILIZATION DURING CIRCULAR LOCOMOTION IN THE MONKEY

by

David Solomon

A dissertation submitted to the Graduate Faculty in Biomedical Sciences in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1990

This manuscript has been read and accepted for the Graduate Faculty in Biomedical Sciences in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

October 9, 1990
Date

Bernard Cohen
Chairman of Examining Committee

October 9, 1990
Date

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The City University of New York

Abstract

COMPENSATORY GAZE NYSTAGMUS: VISUAL, VESTIBULAR AND SOMATOSENSORY CONTRIBUTIONS TO GAZE STABILIZATION DURING CIRCULAR LOCOMOTION IN THE MONKEY

by

David Solomon

Advisor: Professor Bernard Cohen

Head and eye movements of two monkeys were recorded during circular locomotion around the perimeter of a 1 meter platform. Only horizontal angular movements, i.e. rotation of the head on the body and the eye in the orbit about the vertical axis were considered. Angular body velocity relative to earth was also measured. The head and eye movements combined to generate what is here termed "compensatory gaze nystagmus," consisting of slow phases opposite in direction to body rotation (hence 'compensatory') and quick phases which direct gaze forward. In order to investigate the role of the visual, vestibular and somatosensory systems in the maintenance of stable gaze, the animals were observed running in light, in darkness and on a counter-rotating platform, respectively.

During running in light, the nature of the visual surround influenced the behavior both qualitatively and quantitatively. When fixating a presumed target of interest, an eye-head coordination strategy was utilized which preferentially utilized head movement, indicating strong visual control of neck muscles. Depending on the distance of the animal from the visual surround, the gain of the compensatory gaze nystagmus (eye + head slow phase velocity / body velocity) was altered to account for the rotational and translational components of the animal's trajectory.

In darkness, gaze compensation during constant velocity rotation was maintained for longer periods when the animals actively ran than when they were passively rotated around the same path. The duration of the response was associated with the time constant of the velocity storage integrator, an element in a model of the vestibular-ocular reflex (Raphan et al. 1979). This suggests that velocity storage may be generalizable to control of head movement via the vestibulo-collic reflex, and have physiological significance in maintaining an estimate of angular body velocity in space during locomotion. When running on a counter-rotating platform, body movement relative to the running surface (gait velocity) was faster than actual angular body velocity with reference to the earth. This increased afferent somatosensory activity resulted in higher compensatory gaze velocities. Signals associated with active limb movement enabled compensatory head movements and were important inputs into the velocity storage mechanism.

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My thanks to my Supervisory Committee, Drs. Bizzi, Goldfarb, Raphan and Wilson, who persevered through this document and provided cogent and helpful criticisms.

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Finally, my heartfelt thanks to my dear friends, whose experiences, continued love and understanding did inspire and encourage me to join them in the real world.

DEDICATION:

This dissertation is dedicated to my family:

My brother Dean, who taught me, and inspired my amazement, and eventual career in Neuroscience

My brother Jacob, who struggled and succeeding in understanding this alien material

My mother, whose practicality, ingenuity and varied abilities make her a paragon of creativity to which I aspire

My father, who taught by example to think clearly and to respect my patients, and whose confidence in me allowed me to reach for the goals I've achieved

My wife, Debra, whose love and patience were my soul and my salvation throughout it all.

ABBREVIATIONS IN THE TEXT AND FIGURES:

Note: All positions and velocities are in angular terms (degrees and deg/sec, respectively).

E_H-horizontal eye position in head, $\dot{E}_H$-horizontal eye velocity in head, $\dot{H}_S$-yaw head velocity in space, $\dot{H}_B$-yaw head velocity re body, H_B-yaw head position re body, $\dot{G}_B$-horizontal gaze velocity re body, $\dot{G}_S$-horizontal gaze velocity in space, G_S-horizontal gaze position in space, $\dot{B}_S$-yaw body velocity in space, $\dot{B}_P$-body velocity on platform, B_P-body position re platform, $\dot{P}_S$-platform velocity in space. VOR- vestibulo-ocular reflex, VCR- vestibulocollic reflex, COR-cervicocollic reflex, CCR- cervicocollic reflex, OKN- optokinetic nystagmus, OKAN- optokinetic after-nystagmus, OVAR- off vertical axis rotation.

Upward deflections represent movements or velocities to the right or clockwise (CW) as viewed from above, downward equals to the left or counterclockwise (CCW).

PREFACE:

This work was done in a laboratory mainly concerned with investigating and modeling the vestibulo-ocular reflex, utilizing eye position recordings in alert monkeys. Animals were typically seated with their head fixed to the primate chair and passively rotated or exposed to moving visual surrounds. A great deal of the physiology and anatomy of the vestibular and oculomotor systems has been elucidated using these techniques, however many of the discoveries, although robust and reproducible laboratory phenomena, were without obvious physiological significance to the animal in its native environment.

A "velocity storage integrator" was incorporated into the model of the vestibulo-ocular reflex proposed by Raphan et al. (1979) to account for the persistence of compensatory eye movements (slow phases of ocular nystagmus) for up to 30-60 s after the termination of the relevant stimulus. This integrator is "charged" by afferent activity in the VIIIth nerve (modulated by head acceleration) and maintains an estimate of head velocity in space which determines the velocity of the slow phases of nystagmus generated by the oculomotor system.

As discussed in the Introduction, Bles et al. (1983-6) demonstrated that somatosensory signals generated during locomotion also charged the velocity storage mechanism in humans, although relatively weakly. In patients with damaged vestibular systems, however, the influence of somatosensory inputs increased to compensate for the loss. We sought to reproducing these results in an animal model in which velocity storage was more apparent, and in which controlled lesion studies could be carried out. To that end, the apparatus described in the Methods section was constructed and two monkeys were trained to run around the perimeter of the circular platform. A major difference emerged, however, between our preliminary findings and Bles' work: while human subjects were instructed not to move their heads during experiments, the monkeys exhibited head movements qualitatively similar to the ocular nystagmus observed during passive rotation. It therefore remained to characterize the patterns of eye-head interaction during the combined gaze (eye + head) nystagmus.

The plethora of subscripts which appear throughout the text are indicative of the need for relating eye, head and body movement to various reference frames. While the term "gaze" is sometimes understood to mean position of the visual axis in space, we use the term to describe the combined angle of eye and head displacement relative to either the body or to space. We hope to demonstrate that body velocity in space is most likely the parameter which is estimated by the velocity storage integrator, using visual (retinotopic), vestibular (craniotopic) and somatosensory information. This estimate, we believe, is the source of command signals for the neck and extra-ocular muscles employed in maintaining stable gaze during body movement in space.

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INTRODUCTION:

Gaze compensation during locomotion is produced by a complex interaction of reflexes, individually testable in various laboratory paradigms, but potentially quite different in function and efficiency in the active state. Movement of the visual world relative to the subject is a sufficient stimulus for the production of compensatory movements of the eyes (Purkinje 1819) and head (Brecher 1936; Wilson et al. 1983). However, there are also vestibular and somatosensory inputs during locomotion and when voluntarily turning the head, which when they occur together under natural conditions, result in better reflex performance (Collewijn et al. 1983; Takahashi et al. 1980; Tomlinson et al. 1980). This emphasizes the need to study the various reflexes working together in the active state in the intact animal.

The vestibulo-ocular reflex (VOR) has been extensively studied with subjects being passively rotated. However, there is considerable evidence that the VOR is quite different in active and passive conditions. The head may move in space due to whole body movement, which may be active, as during locomotion, or passive, as when riding in a vehicle. The head can also rotate around the neck on a stationary or moving body. Thus, activity from the limbs and neck as well as vestibular information may influence or initiate gaze reflexes to compensate for body movement in space.

There is a difference in VOR gain when eye movements are elicited by whole body rotation (vestibular only), by passive rotation of the head on body (vestibular plus neck proprioception) or by active, voluntary head movement. The VOR gain is higher with head on body movement than with passive whole body rotation, reflecting the addition of cervical activity to vestibular signals (de Jong et al. 1981). In addition, the eyes acquire targets more accurately during active head movements (Pelisson et al. 1988).

Optokinetic and opto-collic (Fuller 1987; Kubo et al. 1981) reflexes are initiated by the slip of images on the retina which induce eye and head motion, respectively, to minimize the slip. This sensory information is initially coded in a retinocentric frame. The visual surround usually remains fixed with regard to earth during locomotion, but other reference frames shift with regard to one another and to the earth. Semicircular canal stimulation results from both the angular movement of the head as it accompanies the body through space, as well as from compensatory (slow phase) and gaze reorienting (fast phase) head on body movements. Within the frequency limits of the semicircular canal receptors, this provides an estimate of head velocity in space (Goldberg and Fernandez 1971).

When the head moves relative to the body, additional reflex loops could affect gaze compensation. These include the vestibulo-collic reflex (VCR), the cervico-collic reflex (CCR), and the cervico-ocular reflex (COR) (see Wilson and Melvill Jones 1979, for review). The vestibulo-collic and cervico-collic reflexes excite neck muscles which cause the head to compensate for motion in space and motion relative to the body, respectively. The cervico-ocular reflex drives the eyes to compensate for head movement on the body (Fuller,1980; Meiry 1971). (For a review of reflexes with cervical proprioceptive origin, see de Jong and Bles 1986). The cervico-collic reflex is basically a stretch reflex acting to reduce head rotation, and has been shown to have similar dynamics to the vestibulo-collic reflex in the decerebrate cat, despite the different transducers involved (Peterson et al. 1985). Both the cervico-collic and cervico-ocular reflexes have consistently been relegated to minor role in gaze stabilization in intact subjects (Jurgens et al. 1982; Bohmer and Henn 1983; Fuller 1980; Dichgans et al. 1974), largely leaving the vestibulo-ocular and vestibulo-collic reflexes to provide this function.

There is a fundamental difference between the vestibulo-ocular and the vestibulo-collic and cervico-collic reflexes: unlike the open loop VOR in darkness, the motor output of the VCR and CCR reduces the afferent sensory signal (Melvill Jones and

Milsum 1965). When the head participates in gaze compensation during body rotation in space, the head-based semicircular canal signal underestimates angular body velocity in space by the amount of the compensatory head rotation on the body. To maintain an accurate estimate of body velocity in space, therefore, the canal signal must be combined with information concerning relative rotation of the head on the body. The sensory arms of the CCR and COR, or efference copy, are potential sources for this information.

Factors such as attention to imagined targets (Barr et al. 1976; Melvill Jones et al. 1984), and linear acceleration due to eccentric angular rotation, sensed by the otolith organs (Gresty 1987), can also substantially affect the gain of compensatory eye movement during head movement. Since the VOR functions primarily during active movement, it seems appropriate to study it under this condition.

As an animal moves through its environment, compensatory movements of the head and eyes combine to hold gaze stable on objects of interest. Traditional distinctions between types of eye movements become difficult in the freely moving animal (Collewijn 1977a, b). Head and eye nystagmus, consisting of both slow and quick phases, combine as gaze nystagmus relative to the body. This takes place while the animal is engaged in circular locomotion (Solomon and Cohen 1986-1988, 1991, submitted). The net result is that gaze is saccadic in space. Compensatory vestibular and optokinetic eye movements and fast recentering movements, all considered 'reflex' phenomena, when viewed from the earth fixed reference in a moving animal become saccades, thought to be 'voluntary' shifts of gaze to desired targets. In freely moving, but not circling rabbits and cats, movements in space were found to be exclusively saccadic. So called 'smooth pursuit' movements were not observed in the head free rabbit or cat, with ocular movements being saccadic (Collewijn 1977a, b).

There is relatively little information about how the head and eyes interact to produce compensatory gaze movements during locomotion. Gaze stabilization during locomotion requires eye movements to offset translation (McDonald et al. 1983) as well as angular rotation of the head (Grossman et al. 1988, 1989). Additional demands are made during angular locomotion or when gaze is directed to the side during linear motion; gaze movements must have an angular component relative to the body to fixate earth-fixed targets which the animal passes. While gaze compensation during locomotion is automatic, rapid and accurate, it nevertheless involves complex transformations between multiple frames of reference: retinocentric, craniocentric, bodycentric and earthcentric (Howard and Templeton 1966). Many of these transformations have not been thoroughly studied, particularly in the freely moving animal.

The vestibular system initiates three-dimensional head and eye compensatory movements via the vestibulo-ocular and vestibulo-collic reflexes (VOR and VCR), as well as by postural movements of the trunk and limbs (Wilson and Melvill Jones 1979). Proprioceptive and other somatosensory cues are generated by the limbs which propel the animal along its trajectory, and mechanoreceptors are activated at the points of contact with the platform surface and restraining harness. These signals are delivered to the brain in a bodycentric reference, in which all targets must be localized (Jeannerod 1983). In the presence of gravity, however, an underlying earthcentric reference frame is assumed.

Somatosensory input and motor activity are known to influence compensatory oculomotor behavior and motion perception (see Young 1984 for review). Movement of the arms about the perimeter of an optokinetic drum moving in darkness causes compensatory 'arthrokinetic nystagmus' (Brandt et al. 1977). The peak slow phase eye velocity and time constant of decay of per-rotatory nystagmus is greater when subjects use their arms to rotate themselves actively than when they are being passively rotated (Guedry and Benson 1983). The sensation of after-rotation (somatogyral illusion) is also different after active than passive rotation. Subjects sense that they continue to move in the same direction (antisomatogyral illusion) after active motion, rather than being moved in the opposite direction, as after passive rotation (Darwin 1794; Correia et al. 1977; Grusser 1984). Sensation and compensatory nystagmus are not tightly coupled in many instances, however (Guedry and Benson 1983; de Jong and Bles 1986).

Comprehensive studies of the influence of body movement on the eyes under natural conditions have been done by Bles and collaborators (1983-1986). They demonstrated that during active walking in a circle in darkness, i.e., during 'stepping around', compensatory eye velocity is increased at the onset of walking, and there is continuous nystagmus of the eyes for as long as walking continues. When the subjects come to a halt after active stepping around, there is a reduction in the velocity of the after-nystagmus. Since walking around at a constant velocity would not continuously excite the semicircular canals, activity responsible for the increase in slow phase velocity at the onset of walking and for the increase in the duration of per-rotatory nystagmus must have arisen elsewhere, probably in somatosensory inputs. Bles concluded that this information was activating the velocity storage mechanism in the vestibular system (Cohen et al. 1977; Raphan et al. 1979; see Raphan and Cohen 1985 for review) to produce the continuous nystagmus and reduce the intensity of the post-rotatory response.

Bles also had its subjects perform 'apparent stepping around'. The subjects walked in a circle in darkness, but the platform beneath them counter-rotated, so that they were stationary in space. As before, there was continuous nystagmus for the duration of stepping around, but the velocity of the slow phases was lower than when there was actual forward motion. In addition, there was an OKAN-like response in the same direction after stopping, supporting the idea that somatosensory inputs or efference copy related to walking around were activating velocity storage.

The implication of Bles's studies is that velocity storage might support compensatory ocular nystagmus during locomotion and minimize inappropriate after-nystagmus at the cessation of movement. The current studies grew from an interest in this problem, particularly since velocity storage is considerably stronger in the monkey than in the human (Raphan et al. 1979; Cohen et al. 1981; Jell et al. 1985). We reasoned that there might be evidence for its action on the VOR during locomotion in the monkey. In the course of the experiments, the importance of head movements in maintenance of compensatory gaze movements became apparent, as well as the importance of vision and velocity storage in driving the vestibulo-collic reflex (VCR).

We therefore investigated the effects of the visual environment on the gain and pattern of compensatory eye and head movements while running in light. We then eliminated visual information, and contributions of the VOR, VCR, somatosensory signals, and velocity storage were determined while running in darkness. The immediate goal was to characterize gaze compensation while animals ran under various conditions which differentially affected the visual, vestibular and proprioceptive systems. The larger aim of the research was to understand how signals utilized in active spatial orientation are integrated during locomotion.

METHODS:

SUBJECTS: Two docile juvenile male macaque monkeys (4-6 years old) were used in this study. One was a rhesus monkey (Macaca mulatta; "rh", Fig. 1) who ran spontaneously in his cage, moving exclusively in the counterclockwise direction. The second was a cynomolgus monkey (Macaca fascicularis; "c") who did not circle spontaneously. Both animals were naive to vestibular testing.

After being conditioned to handling and to wearing a harness, the animals were trained to walk around the edge of a circular platform by baiting their path with fruit. They moved predominantly in one direction in any session. The direction of movement was alternated between sessions. Gradually, they were rewarded only for successive full revolutions until after several months, they spontaneously circled on the platform in light or darkness without an experimenter being present. We have called this behavior "circular locomotion" since it entailed forward movement with an angular component.

Only positive reinforcement was used to encourage running. The monkeys ran intermittently for as long as they were interested in the task, generally for about an hour. (Initially, a liquid reward was presented through a tube fixed near the animal's mouth in an attempt to reinforce running, but it proved to be an impediment and was discarded).

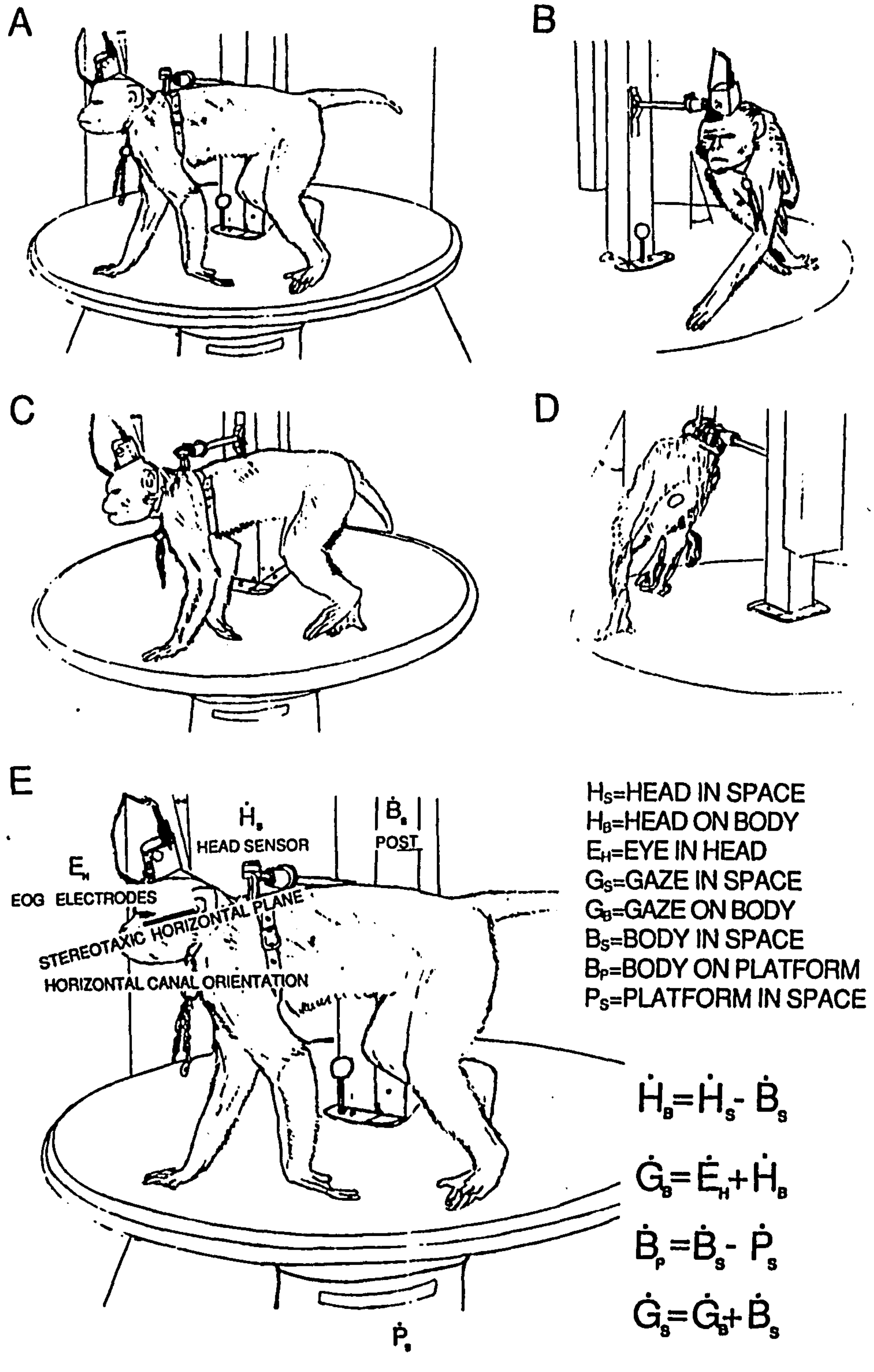
After an initial period of training, silver/silver chloride electrodes were implanted in the bone around the eye under anesthesia to record eye movements with electro-oculography (EOG) (Bond and Ho 1970). Stainless steel screws were fixed to the skull with dental acrylic cement to allow fixation of the animal's head in the horizontal stereotaxic plane during passive testing and to attach head movement measurement devices during locomotion. Antibiotics were given before and after surgery. The monkeys resumed running about a week after surgery.

Figure 1

A-D, Line drawings of monkey rh running in CW direction with a diagonal gait on a stationary circular platform. An angular rate sensor, inserted into a plastic block fixed to the animal's head in a vertical stereotaxic plane, sensed yaw head movement. A separate cable and plug connected the EOG electrodes to slip rings. The animal was tethered to a post that rotated independently. The post carried a separate velocity sensor that registered body velocity in space. The enclosure was covered on three sides by a textured visual surround. A light-tight curtain on the fourth side could be opened or closed.

In A the right forepaw and the left hindpaw were on the platform, thrusting the animal forward, and the left forepaw and right hindpaw were lifted as they were being advanced. C shows the reverse. The forward tilt of the animal's head during running is shown in A and C by the small angles drawn behind the plastic block holding the head velocity sensor. These were approximately 15 deg. The inward tilt of the animal to account for its centripetal acceleration is drawn in B and D, next to the animal. Note the angle of tilt of the chain attached to the animal's collar in B, reflecting the centripetal acceleration at that moment. There was a similar tilt of the tail in D.

E, Abbreviations used in the text and equations for derived signals are shown on the right. The dotted variables indicate the first derivative with respect to time (velocity). All measurements are angular, with dimensions of degrees or deg/s. Note that the head is pitched nose down approximately 15 deg from the horizontal stereotaxic plane in an optimum position to maintain gaze (Berthoz and Pozzo, 1988).


A
B
C
D
E
$\dot{H}_s$
HEAD SENSOR
$\dot{B}_s$
POST
E_H
EOG ELECTRODES
STEREOTAXIC HORIZONTAL PLANE
HORIZONTAL CANAL ORIENTATION
$\dot{P}_s$
H_S=HEAD IN SPACE
H_B=HEAD ON BODY
E_H=EYE IN HEAD
G_S=GAZE IN SPACE
G_B=GAZE ON BODY
B_S=BODY IN SPACE
B_P=BODY ON PLATFORM
P_S=PLATFORM IN SPACE
$\dot{H}_B=\dot{H}_S-\dot{B}_S$
$\dot{G}_B=\dot{E}_H+\dot{H}_B$
$\dot{B}_P=\dot{B}_S-\dot{P}_S$
$\dot{G}_S=\dot{G}_B+\dot{B}_S$

APPARATUS: The paradigms used in this study originated in the work of Bles et al. (1983-1986) on human subjects. Our apparatus is shown in Fig. 1. The animals walked or ran around the perimeter of a 1.1 meter diameter circular platform. They wore a harness tethered to a 0.3 meter radial arm fixed to a freely rotating center post. A bearing and slip rings coupled the center post to the platform. An additional set of slip rings were interposed between the platform and earth. The top of the platform was padded with foam and covered with a rough rubber mat to provide a stable running surface. The room was illuminated either with standard fluorescent lighting or with a dim red bulb. The latter was used to reduce EOG gain changes when the animals also ran in darkness. A video camera with an extended red vidicon tube (RCA) was mounted above the animal. It was either attached to the ceiling, so that it was earth-stationary, or it was fixed to the post that rotated with the animal to provide a bodycentric view of the running animal. The running was highly overtrained, and there was no gross difference in performance in light or in darkness or from day to day.

Only horizontal head movements were recorded, and vertical movements will not be considered in this study. An angular velocity sensor (Watson Industries) measured angular head velocity in space about a yaw axis ($\dot{H}_S$, Fig. 1E). A similar device mounted on the center post measured the angular velocity of the animal's body in space ($\dot{B}_S$, Fig. 1E). These sensors had a gain of 10 mv/deg/s, less than 5 mV of noise (0.5 deg/s), and their output was linear from 0 to 300 deg/s. Horizontal eye movements were measured with EOG, (E_H, Fig. 1E) using amplifiers with a bandpass of DC to 30 Hz. Voltages related to eye position and to head and post velocity were passed with video signals through the slip rings between the post and the platform and the platform and earth.

The platform and post were mounted on a motorized rate table, controlled by a velocity servo (Neurokinetics Inc.). When rotated, the platform accelerated and decelerated at a constant rate (167 deg/s/s). Maximum velocities of platform rotation were limited to 400 deg/s. A voltage from the tachometer of the motor was used to monitor platform velocity in space ($\dot{p}_s$, Fig.1E). The entire apparatus was located in a 2.4 by 1.4 meter rectangular space bounded by 3 walls and a light-tight curtain (Fig. 6 A). The walls were covered with a high contrast pattern. A photocell sensed the state of illumination.

To separate effects of vestibular and somatosensory drive on head and eye movements during running in darkness, a circuit was devised to null or reduce running velocity in space by counter-rotating the platform when the animal moved forward. The gain of the feedback amplifiers could be varied to allow different degrees of reduction of the running velocity. The circuit only drove the platform backward with regard to the animal, i.e., in the direction opposite the animal's forward velocity. The latency between post movement and compensatory counter-rotation was about 3 ms. Platform accelerations and decelerations were constant at 167 deg/s/s up to a maximum velocity of 400 deg/s. A tachometer voltage from the motor was used to monitor platform velocity in space ($\dot{p}_s$, Fig.1E). For a more comprehensive description of this circuit and its operation, see Appendix A.

During passive optokinetic testing, the animal was seated with his head fixed to a primate chair that was mounted in the center of the platform. An internally illuminated optokinetic drum, 91 cm in diameter, with alternating 10 deg black and white bars, could be lowered and rotated around the animal to induce optokinetic nystagmus (OKN) and after-nystagmus (OKAN).

During passive vestibular testing, the animal was seated with its head fixed to a primate chair that was mounted to the platform. The animal was either centered over the axis of rotation or eccentrically positioned near the edge of the platform to add linear acceleration to the rotation. In this position it was facing forward during rotation, in a manner similar to that experienced while running.

SIGNAL PROCESSING:

Equations describing the method for obtaining the various signals are given in Figure 1E. All positions and velocities reported will be in angular terms (deg and deg/s). Voltages related to horizontal eye position (E_H) were electronically differentiated to yield eye velocity relative to the head ($\dot{E}_H$). Head on body velocity was determined by subtracting post velocity, which is equivalent to the animal's angular body velocity in space, from yaw head velocity in space using an analog mixer ($\dot{H}_B = \dot{H}_S - \dot{B}_S$). Gaze velocity relative to body velocity was obtained by summing eye in head velocity with head on body velocity ($\dot{G}_B = \dot{E}_H + \dot{H}_B$). Gaze velocity in space ($\dot{G}_S$) is alternatively the sum of gaze on body and body in space velocity, or eye in head and head in space velocity. The first equation ($\dot{G}_S = \dot{G}_B + \dot{B}_S$) describes the actual procedure used for deriving this signal. A potentiometer measured angular position of the animal relative to the platform (B_P). As the animals made a complete circle when running, it reset once every 360 deg. When the platform was stationary, body position on the platform (B_P) equalled body position in space (B_S). During platform rotation, $\dot{B}_P$ was obtained by subtracting platform angular velocity (rate table tachometer signal, $\dot{P}_S$, Fig. 1E) from the animal's angular velocity re earth ($\dot{B}_P = \dot{B}_S - \dot{P}_S$).

The various voltages were recorded on FM magnetic tape (bandwidth, DC to 625 Hz) and displayed on an oscillograph. Data were analyzed with a digital computer (PDP 8E). Signals were digitized at a rate of 625 samples/sec with 10 bit resolution. Head on body velocity and gaze in space velocity were digitally integrated to yield head on body position (H_B) and gaze position in space (G_S), respectively. The integration algorithm was susceptible to small errors in baseline determination and possibly underestimated position changes in the quick phase direction. For analysis, the time of the beginning and end of each gaze slow phase was determined by visual inspection of the gaze on body velocity trace ($\dot{G}_B$) on a video display. The transition from quick phase to slow phase was unambiguous. The end of the slow phase was denoted when gaze velocity began to decline rapidly toward zero. Digitized data were sampled (at 1.6-16 msec intervals), scaled or used to calculate derived values.

Rapid eye movements opposite in direction to the slow phase compensatory movements were analyzed using a computer algorithm that identified the beginning and end of each movement. The duration, amplitude, and maximum velocity were measured for each movement (Bahill et al. 1975b; Baloh et al. 1975). Quick phases made with the head fixed were compared to eye quick phases made during head and eye nystagmus.

Due to the shape of the experimental chamber, the distance from the running animal to the visual surround varied during the course of each revolution (Fig. 6A). In addition, the surround distance also varied if the curtain at the end of the enclosure was open. In one set of experiments, the gain of slow phase gaze velocity ($\dot{G}_B / \dot{B}_S$), eye velocity ($\dot{E}_H / \dot{B}_S$), head velocity ($\dot{H}_B / \dot{B}_S$) and the animal's body velocity in space were averaged over 30-40 revolutions. Data were averaged in 3.6 degree bins according to the animal's angular position relative to the fixed platform. Each angle corresponded to a particular surround distance and orientation with regard to the entrance to the chamber. Data were analyzed for running in both directions with the curtain open and closed.

CALIBRATIONS:

Eye movements were calibrated by assuming that the gain of slow phase velocity of ocular nystagmus was essentially unity when the head was fixed and the animal was rotated around a vertical axis in light at 30 deg/s (Raphan et al. 1979). All gains were calculated with respect to angular velocity of the body in space, with positive gains representing compensatory movements. Angular velocity sensors were calibrated using the rotating rate table. The head position trace was calibrated by integrating the signal derived from rotation of the sensors through a known excursion. In the figures upward deflections represent velocity or position to the right or clockwise as viewed from above. Downward deflections represent the reverse.

RESULTS:

First, the response of each animal to passive vestibular and optokinetic stimulation will be reported. Next, the general characteristics of both monkeys running in light will be presented, emphasizing the envelope of slow phase eye velocity relative to angular body velocity in space, and describing the pattern of eye-head interaction. The contribution of the optokinetic reflex, and the need to compensate for both rotational and translational components of locomotion will then be investigated by studies in which the animal ran in light with different visual surrounds, necessitating adjustment of gaze gains for various target distances.

With vision eliminated, the vestibular and somatosensory contributions to the generation of compensatory gaze movements will be demonstrated during running in darkness. The effect of active motion on head movement and the duration of nystagmus will be illustrated by contrasting running on a stationary platform with passive eccentric rotation. An asymmetry in the responses of monkey rh to CW and CCW rotation will be explored, followed by the results of running on a moving platform which isolate somatosensory signals. Finally, the characteristics of head-eye interaction will be considered in detail, with an analysis of the quick phases of ocular nystagmus with and without accompanying head movement in light and darkness.

BASELINE VESTIBULAR AND OPTOKINETIC TESTING

To provide a basis for evaluating data collected while running, animals were rotated around their vertical axis in light with a stationary visual surround at angular velocities from 30-150 deg/sec at 30 deg/sec intervals. Animals were also given velocity steps in darkness in the head fixed condition to elicit per and post rotatory nystagmus. Visual surround motion relative to their inertial frame was used to generate optokinetic nystagmus (OKN) and optokinetic after-nystagmus (OKAN) over the same range of stimulus velocities. When the visual surround was rotated around the head-fixed, stationary animal, slow phase eye velocity initially jumped to a given value and then rose more slowly to a steady state level. Slow phase eye velocity was in the direction of drum rotation.

Relevant measurements during passive testing included the peak slow phase eye velocity achieved following the start of rotation in light with a stationary surround. This represented the contribution of the vestibular and optokinetic reflexes. The peak slow phase eye velocity following rotation in darkness (initial jump) occurred within 1-2 seconds following the velocity step and represented the contribution of the vestibular system alone. OKN steady state velocity was obtained during visual stimulation alone, and consequently reflected the gain of the optokinetic reflex. Initial OKAN velocity was the slow phase eye velocity 1 s after the animal was put into darkness following 30 s of visual stimulation. This measure reflected the amount of activity present in the velocity storage integrator.

Figure 2

Passive vestibular and optokinetic testing of monkeys in this study. All values are in deg/s. Crosses represent leftward slow phase eye velocity, filled circles are rightward velocities. Dashed lines indicate unity gain.

Rotation in light: Animals were seated in a primate chair and rotated around their vertical (head centered) axis in an illuminated optokinetic drum.

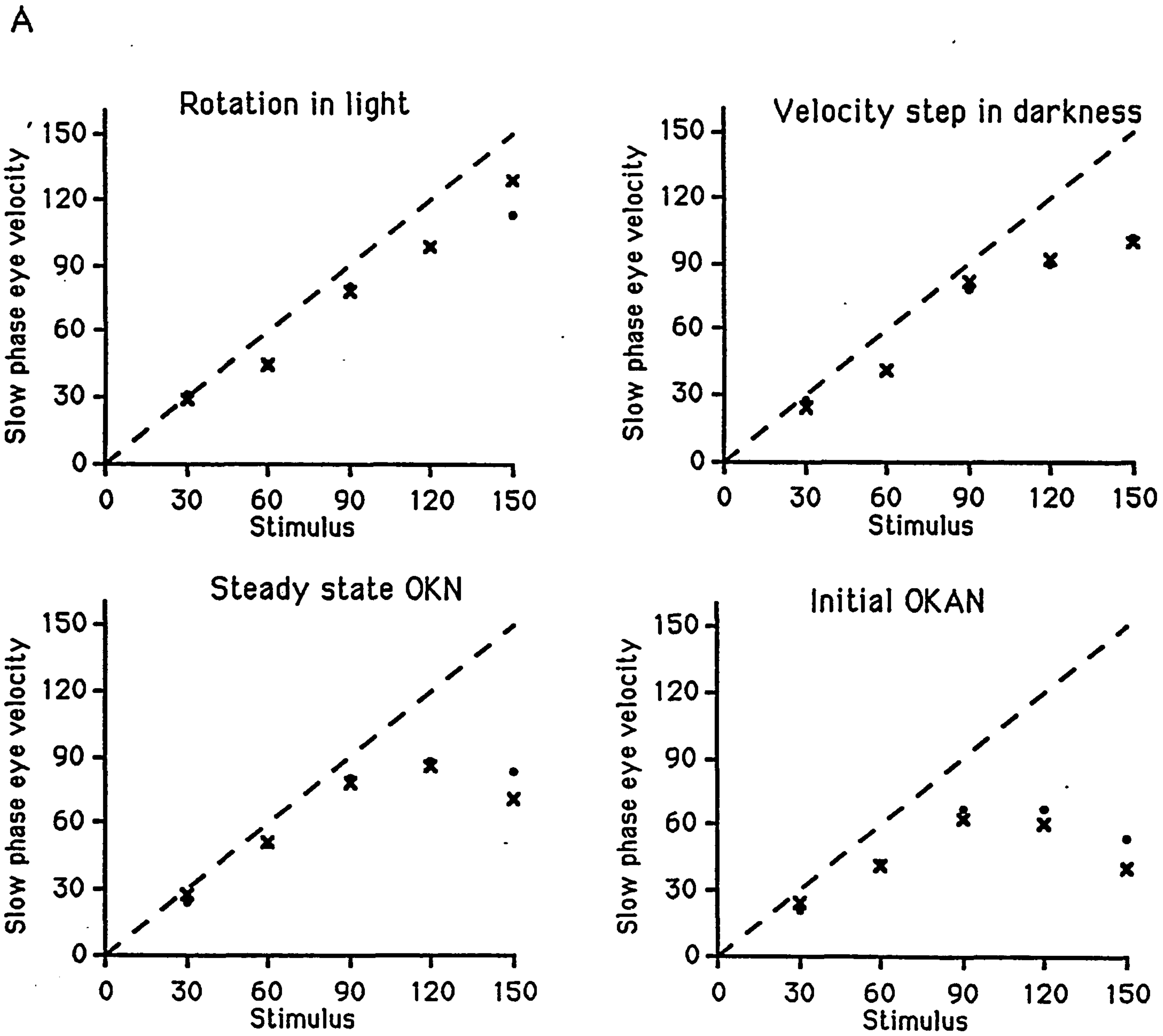
Velocity step in darkness: Passive vertical axis rotation with 1000 deg/s/s accelerations. Measurements are initial jumps in slow phase velocity immediately following stimulus.

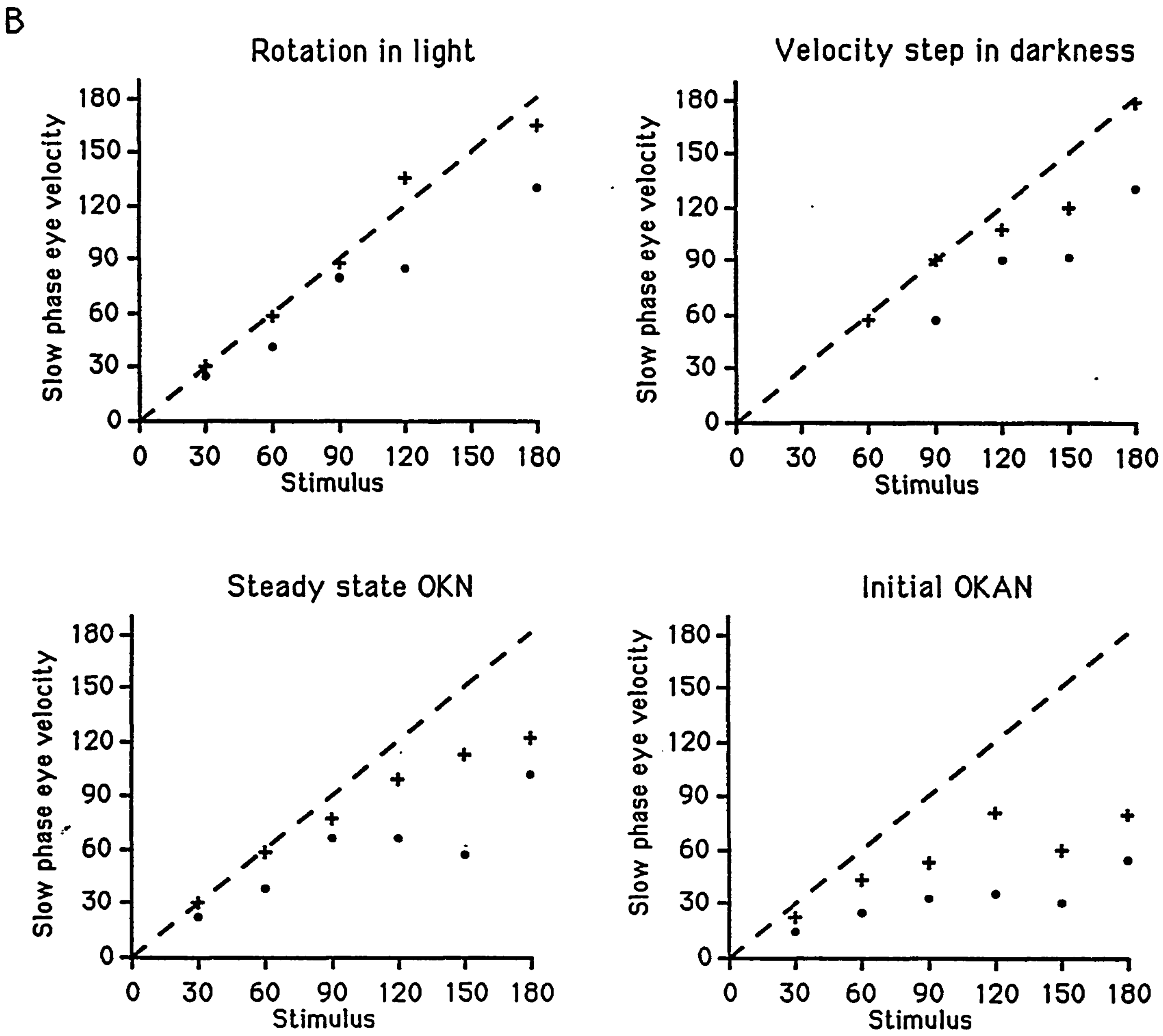
Steady state OKN (Optokinetic nystagmus): Animals stationary with a moving visual surround.

Initial OKAN (Optokinetic after-nystagmus): Value of slow phase eye velocity 1 s after lights were extinguished after steady state OKN was achieved.

A, Monkey c had symmetrical responses in both directions, with decreases in gain at higher velocities.

B, Monkey rh consistently generated better compensatory leftward eye velocities, which were comparable to monkey c. Rightward slow phase velocities, resulted from CW visual motion or CCW (leftward) angular rotation, which was the monkey's preferred circling direction in its cage.


A
Rotation in light
Velocity step in darkness
Steady state OKN
Initial OKAN
Slow phase eye velocity
Stimulus
0
30
60
90
120
150


B
Rotation in light
Velocity step in darkness
Steady state OKN
Initial OKAN
Slow phase eye velocity
0
30
60
90
120
150
180
Stimulus
0
30
60
90
120
150
180

Monkey c (Fig. 2 A) had roughly symmetrical responses to the left and right. During rotation in light, vestibular and OKN gains were nearly unity up to 90 deg/sec, with the gain of OKAN saturating between 70-80 deg/sec. Monkey rh (Fig. 2 B) was more asymmetric, with higher gains and longer time constants for nystagmus with leftward slow phase velocity. Both animals underwent cold water (20° C.) caloric stimulation of each ear.indispensible Peak eye velocities were obtained within 30 s of irrigation. Stimulation to either side resulted in nearly identical amplitude peak slow phase velocities for each animal, indicating that the peripheral vestibular sense organs, or at least the lateral semicircular canals, were roughly equal on each side. This suggests that the asymmetry observed in monkey rh is due to a difference in central organization.

Figures 8 B and 13 B are raw data from passive eccentric vertical axis rotation with the head fixed. Monkey rh was rotated around the same circumference about which he runs in the active paradigm. A step in angular velocity of 200 deg/sec was given so that the animal experienced similar angular velocities and linear accelerations (approximately .5 g directed centrifugally) as during running. The gain (slow phase eye velocity/stimulus angular velocity, Fig. 15 C,G) rose quickly following the velocity step to a peak value, then began to decay, eventually reaching zero, despite the continued angular velocity. An alternate presentation of the same data is shown in Figure 15 D,H. Instead of gain vs. time, here the slow phase eye velocity is plotted against the stimulus velocity.

GENERAL CHARACTERISTICS OF BODY, LIMB AND GAZE MOVEMENTS DURING LOCOMOTION:

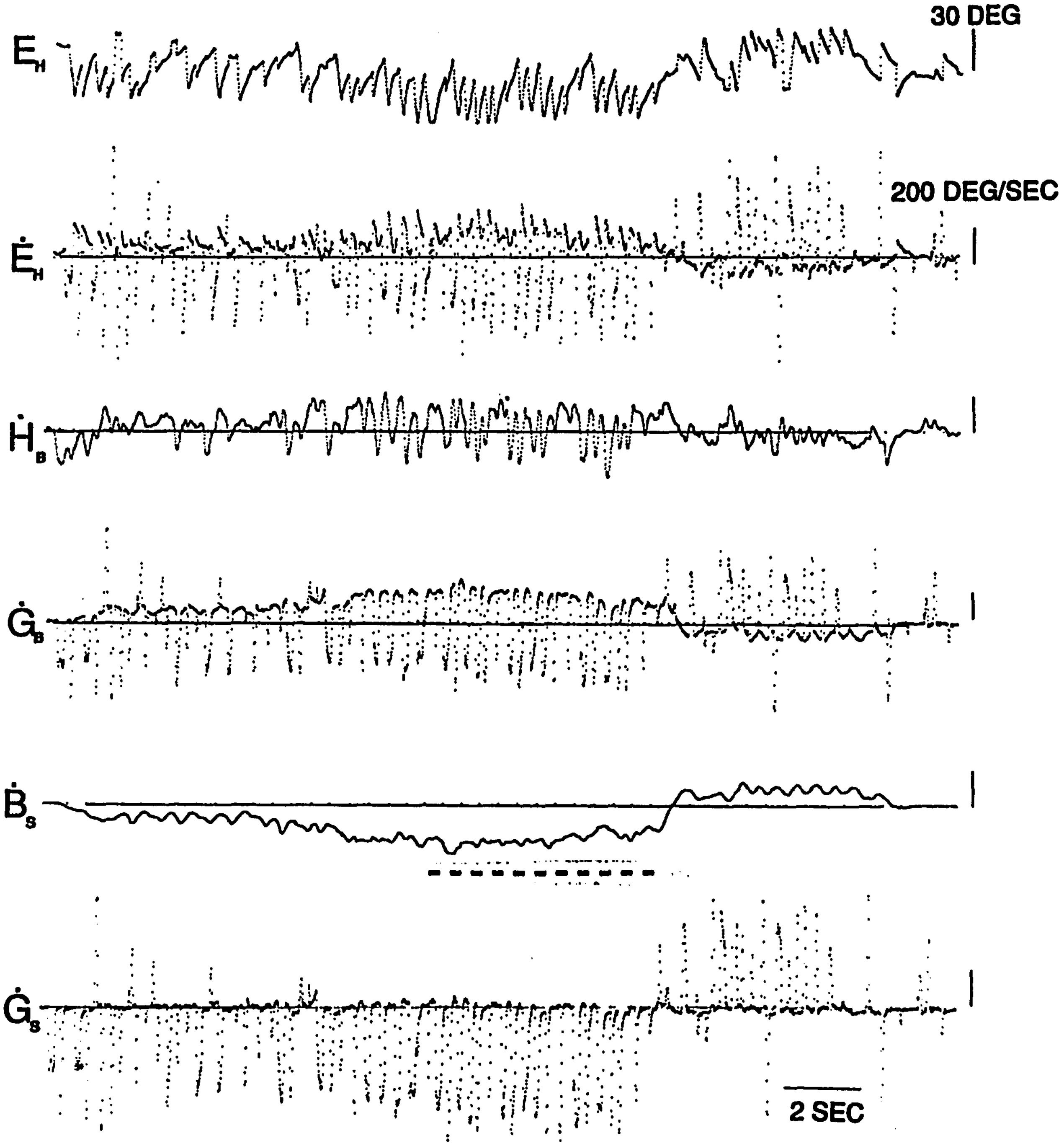
With minor differences the pattern of running was similar in both monkeys. Both animals circled intermittently and spontaneously in the direction in which they were pointed when attached to the apparatus. Line drawings taken from photographs of rh circling in the clockwise direction are shown in Fig. 1A-D. The animals both employed a diagonal, symmetrical gait (Hildebrand 1967) and at high velocities tilted in toward the center to compensate for the substantial linear acceleration generated by the eccentric angular motion (0.6 g at 200 deg/s). (The centripetal acceleration is reflected in the lateral swing of the animal's chain in Fig. 1B.) Both animals held their heads tilted slightly forward from the stereotaxic horizontal when running, as shown in Fig. 1 A, C, bringing the plane of the lateral canals and the utricles approximately parallel to the spatial horizontal. As recently noted (Berthoz and Pozzo 1988), this position is frequently utilized during active movement and is optimal for vestibular control of gaze.

Representative recordings from monkey c and rh are shown in Figs. 3 and 4, respectively. In both instances the platform was fixed and the room was illuminated. The monkeys' angular running velocity is shown by the body in space trace ($\dot{B}_s$). Monkey rh's circling velocity tended to be relatively constant at around 200 deg/s, and he frequently ran for periods of from 10 (Fig. 5) to 200 sec. Monkey c's running velocities were somewhat lower, except at times when he grabbed the knob on the center post, shown in Figs. 1 A, B, with his inside front paw and swung himself around at velocities in excess of 200 deg/s (dashed line under $\dot{B}_s$, Fig. 3). At these times he kept his head and upper body low to the platform. Monkey c generally ran for 10 to 60 s, and almost always ended by taking several backward steps without reversing his orientation. For example, in Fig. 3 he ran to the left (counter-clockwise) for 17 seconds, reaching peak angular velocities of 285 deg/s. He then stopped and moved backward at 140 deg/s for 6 seconds, giving himself a velocity step of 245 deg/s in the opposite (clockwise) direction.

Fluctuations in $\dot{B}_s$ at frequencies up to 7 Hz were superimposed on the envelope of angular velocity in association with the various phases of locomotion (Bernstein 1967). Peak to peak fluctuations in $\dot{B}_s$ were between 25-40% for c (Fig. 3) and between 10-20% for rh (Figs. 4,5).

Figure 3

Monkey c running CCW in light. During the animal's forward rotation to the left, there was head and eye nystagmus with rightward compensatory slow phases. Eye quick phases were always accompanied either by head quick phases or by decreases in head velocity. Eye slow phases, with high initial velocity, combined with head slow phases with rounded profiles to produce a relatively flat gaze on body velocity ($\dot{G}_B$). Note that gaze movements compensated for fluctuations in body velocity in space ($\dot{B}_S$) due to locomotion, so that gaze in space remained close to zero in between quick phases. When the animal reversed its direction by walking backwards, at right side of $\dot{B}_S$ trace, compensatory leftward movements stabilized gaze in space ($\dot{G}_S$). The vertical bars at the right of the traces are position or velocity calibrations. In this and subsequent figures unless otherwise noted the velocity traces are all 200 deg/s. The dashed line indicates time when the monkey's inside (left) forepaw was grabbing the center post.


30 DEG
E_H
200 DEG/SEC
$\dot{E}_H$
$\dot{H}_B$
$\dot{G}_B$
$\dot{B}_S$
$\dot{G}_S$
2 SEC

COMPENSATORY GAZE NYSTAGMUS:

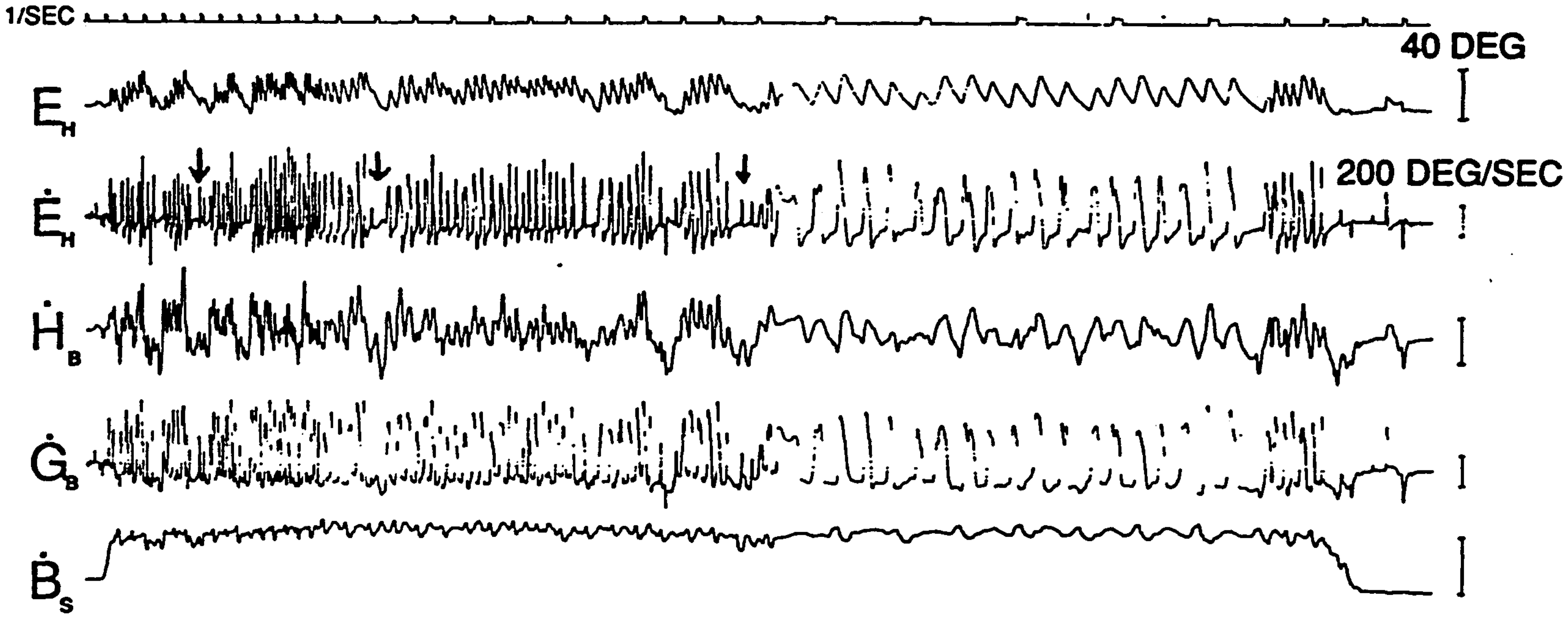
A typical example during clockwise running in light is shown in Fig. 4. Monkey Rh ran to his right in the lighted enclosure at close to 200 deg/s (bottom trace, $\dot{B}_S$) for about 30 s. The continuous ocular nystagmus (E_H) consisted of slow phases to the left that compensated for the animal's movement to the right, and quick phases to the right that reset the eyes. The shape of the slow phases was not linear, as during OKN or vestibular nystagmus with the head fixed. In concert with the eye nystagmus, there was head nystagmus ($\dot{H}_B$). A comparison of the eye in head ($\dot{E}_H$) and head on body velocity traces ($\dot{H}_B$) showed that during each eye quick phase the head either made a rapid movement in the same direction or decreased its velocity. The eye and head slow phase velocities ($\dot{E}_H$ and $\dot{H}_B$) combined to form gaze on body velocity ($\dot{G}_B$). The envelope of $\dot{G}_B$ generally followed the inverse of the velocity of the body in space ($\dot{B}_S$). At the end of the run, the animal came to a halt without either eye or head nystagmus. On top of the steady state gaze velocity there were small high frequency perturbations. These fluctuations were due to changes in forward motion associated with different phases of the locomotion cycle as the animal ran rapidly around the perimeter of the platform. Compensatory movements against these high frequency perturbations were present in both the $\dot{E}_H$ and $\dot{H}_B$ traces.

In both monkeys, circling in light was invariably accompanied by head and eye nystagmus which combined to compensate for body velocity in space. We have called these movements 'gaze compensatory nystagmus', since the slow phases were opposite in direction to body velocity in space ($\dot{B}_S$), bringing gaze velocity in space ($\dot{G}_S$, Fig. 3) close to zero between quick phases. As a consequence of this nystagmus, gaze position in space was approximately stationary during the slow phases, jumping in saccadic fashion during the quick phases.

Figure 4

Data from monkey rh circling in the clockwise direction. Note the changes in the time base (top trace). Leftward compensatory slow phase eye movements alternate with quick phases in the direction of running. Arrows indicate intervals during which slow phase head velocities provided most of the gaze compensation. There is no post-rotatory response when the animal stops in light.

RUNNING IN LIGHT



During gaze compensatory nystagmus the eye quick phases were large and could reach amplitudes of 60 deg or more (Fig. 5, E_H). This was considerably larger than quick phases of eye nystagmus recorded with the animals sitting at the edge of the platform while it was being rotated in light (Fig. 23 C). The shape of the slow phases was not linear; rather there were generally periods of relatively high velocity (up to 300 deg/s) at the beginning and usually toward the end of the movement, frequently giving the eye velocity profiles a 'J' or 'U' shape ($\dot{E}_H$, Figs. 3-5). In contrast, the velocity profiles of compensatory head on body movements ($\dot{H}_B$) were more rounded and bell-shaped.

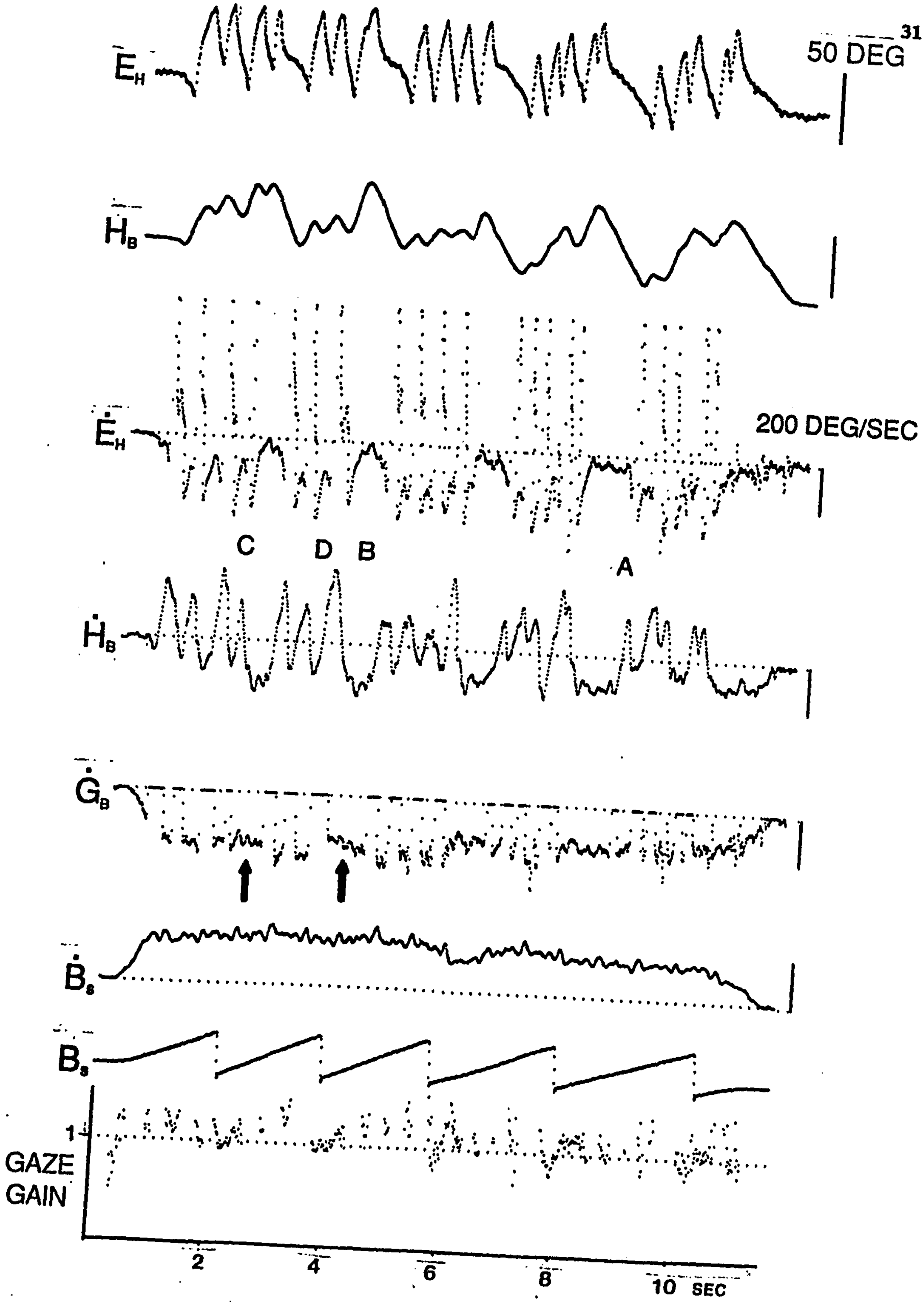
The initial peak in slow phase eye velocity ($\dot{E}_H$) occurred during the end of the head quick phase, just before the head slow phase began. As will be shown in greater detail below, this brought gaze velocity on the body ($\dot{G}_B$) quickly back to compensatory levels. Similarly, the rise in velocity of the eyes at the end of the eye slow phase counteracted the decrease in head slow phase velocity as the head began to accelerate in the quick phase direction. The consequence was that the gaze on body velocity trace tended to be flat and rather squared between the quick phases. Two examples are marked by upward arrows in the $\dot{G}_B$ trace in Fig. 5.

Superimposed on the steady-state gaze on body velocity ($\dot{G}_B$) were high frequency fluctuations that compensated for the oppositely-directed fluctuations of body velocity in space ($\dot{B}_S$, Figs. 3-5). As a result the slow phase envelopes of gaze on body velocity ($\dot{G}_B$) and body in space velocity ($\dot{B}_S$) were mirror symmetrical, and, as shown in Fig. 3, their sum, gaze velocity in space ($\dot{G}_S$), was close to zero during the intersaccadic intervals. Intersaccadic periods with non-zero $\dot{G}_S$ could have been due to the animal's choice of visual targets. If he were watching the surface of the platform while running, the gain of the compensatory movements would increase relative to Bs, and cause deviations from zero $\dot{G}_S$ in the $\dot{G}_B$ direction. Deviations in the $\dot{B}_S$ direction could indicate some tolerance of retinal slip, with the animal making compensatory movements which might be sufficient to extract whatever information from the visual environment was necessary for the safe negotiation of the platform, but might not require perfect compensation.

In contrast to eye nystagmus, during which anticompensatory quick phases in the running direction were much faster than the slow phases ($\dot{E}_H$, Figs. 3-5), head movements in the compensatory or 'slow phase' direction often had velocities as large as those in the 'quick phase' direction ($\dot{H}_B$, Figs. 3-5). We have called these periodic movements 'head nystagmus'. However, it should be emphasized that head velocity alternated and contributed not only to the maintenance of stable gaze in the backward or compensatory direction, but also to saccadic shifts in gaze in the forward or running direction. Accordingly, as in Fig. 3 the maximum velocity of the $\dot{G}_S$ saccades was larger and the profiles were broader than the $\dot{E}_H$ quick phases, reflecting the contribution of the head to gaze shifts (Note that $\dot{G}_S$ and $\dot{E}_H$ gains in Fig. 3 are the same).

Figure 5

Monkey rh running in the CW direction with the curtain open and an experimenter present. Body position in space (B_S) was measured with a potentiometer that reset just as the animal began to turn toward the open curtain. The $\dot{G}_B$ trace was rectified to demonstrate only slow phase velocity. The pattern of compensatory head and eye slow phases changed as a function of the animal's position on the circular platform with regard to the enclosure (B_S). When approaching the target of interest, the head and eyes were on the quick phase side. After the initial peak in slow phase eye velocity, head velocity increased, and the eyes slowed near midposition in the orbit. Eye velocity rose again at the end of the head slow phase. This allowed for stabilization of gaze on a single target for up to 140 deg of body rotation. Large amplitude smooth eye slow phases and small head movements prevailed while running around the remainder of the circumference. Gaze gain ($\dot{G}_B / \dot{B}_S$) also varied according to position with regard to the surround. Gain was unity when the animal faced the target and increased as the translation component added to the rotation. A-D indicate gaze movements which are shown in expanded form in Fig. 21.


E_H
50 DEG
H_B
Ė_H
200 DEG/SEC
C
D
B
A
Ḣ_B
Ġ_B
Ḃ_s
B_s
1
GAZE GAIN
2
4
6
8
10
SEC

GAZE WHILE WATCHING TARGETS OF INTEREST:

The characteristics of gaze compensation varied somewhat, according to the nature of the targets in the visual surround. In Fig. 5 monkey rh ran with a specific target of high interest in one portion of the visual field: the curtain was left open at the end of the enclosure, and an experimenter stood quietly with a fruit reward. The animal circled to his right (clockwise), watching the experimenter. The animal's position on the circular platform, i.e., its angular body position in space, is shown in the next to bottom trace of Fig. 5 (B_S). The potentiometer registering B_S reset each 360 deg, giving the trace a saw-tooth appearance. The reset occurred just before the point when the animal began to turn toward the experimenter.

While the animal ran, the frequency of the eye and head nystagmus averaged about 2 beats/s, with leftward slow phases and rightward quick phases. Gaze on body velocity ($\dot{G}_B$) during the slow phases generally mirrored and opposed the animal's body velocity in space ($\dot{B}_S$). There were periodic alterations in the nystagmus, with large slow phases of head and eye nystagmus that combined to hold gaze on target over a range of about 90-140 deg of body rotation each time the animal approached the open end of the enclosure. The occurrence of two such periods of fixation is shown in Fig. 5 by the upward arrows under $\dot{G}_B$. During these prolonged periods of fixation the eyes slowed when they were approximately centered in the orbit (E_H, Fig. 5). At that point the head was moving at a relatively constant velocity with regard to the body ($\dot{H}_B$), and was primarily responsible for compensating for the animal's angular motion and for holding the target image stationary on the retina.

Gaze gain relative to body velocity in space ($\dot{G}_B / \dot{B}_S$) during slow phases is plotted on the bottom of Fig. 5. The overall gain was maintained for the duration of the run, but there were changes related to the animal's position with regard to the open end of the enclosure. When the animal was moving toward the experimenter (corresponding to the point where the potentiometer reset), gaze was in the quick phase direction, and gaze gain dropped to below unity. As the animal approached the opening head on, gaze gain rose to unity and continued to increase as the monkey passed in front of the experimenter. During this time the eyes were relatively stationary in the head, and $\dot{H}_B$ was at its maximum. As the animal continued around, gaze gains remained high, reaching values as large as 1.3. These high gains were maintained by a mixture of head and eye velocities. The individual contributions of the head and eyes to gaze velocity is considered in the following.

HEAD AND EYE CONTRIBUTION TO GAZE VELOCITY AS A FUNCTION OF ANGULAR POSITION AND DISTANCE FROM THE VISUAL SURROUND:

Monkey rh usually ran at a relatively constant velocity (e.g., Fig. 4) for prolonged periods, making it possible to determine the average contributions of eye and head velocity to gaze compensation under different conditions. The characteristics of the experimental chamber were such that the distance to the visual surround varied as the monkey circled around the platform. This varied from 12.5-45 cm during each revolution with the curtain closed, and from 12.5 cm to 3 m with the curtain open. The open curtain allowed for the possibility of an investigator appearing with a fruit reward, thereby establishing a gaze direction of particular interest.

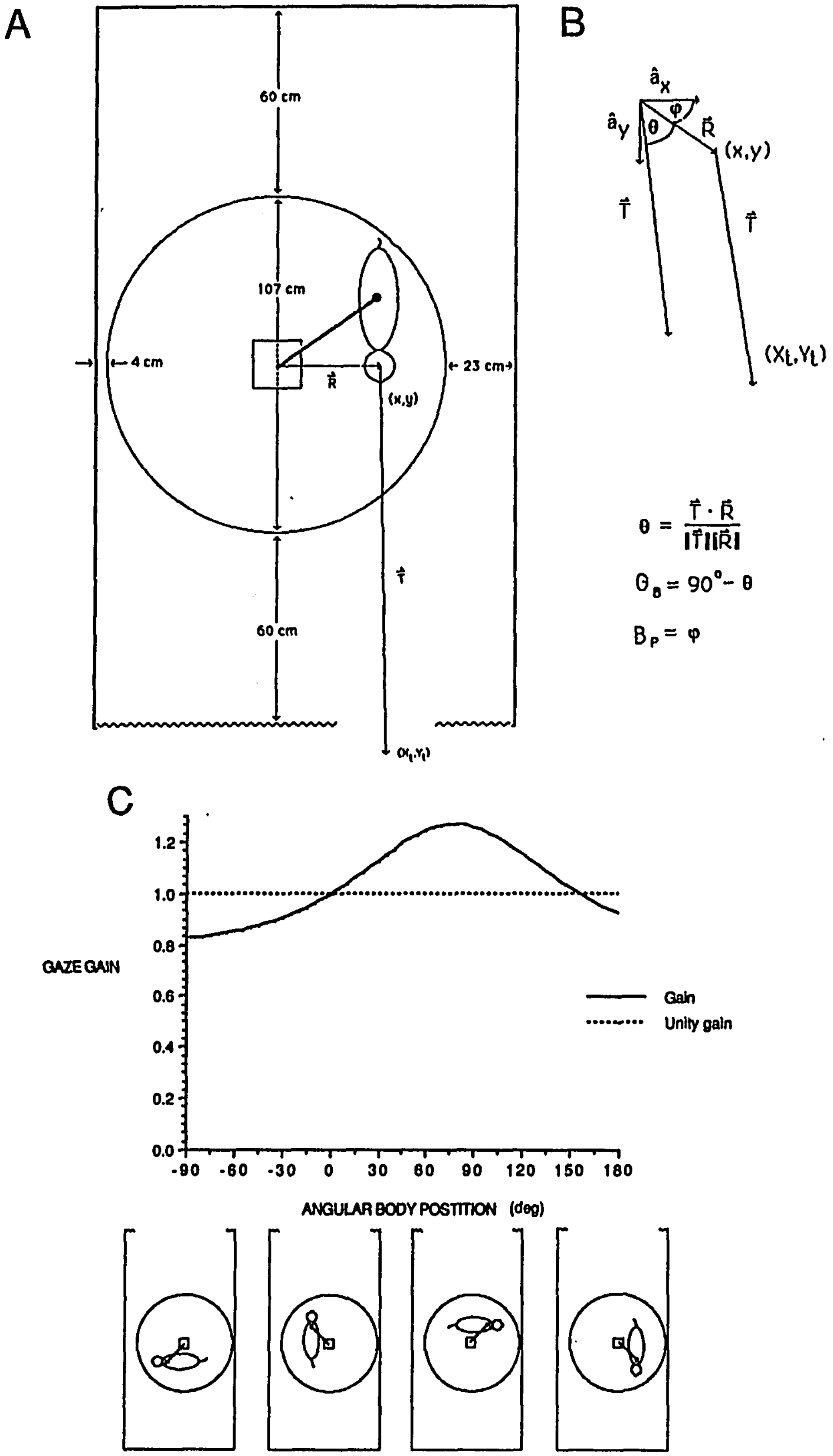
If the animals were attempting to fixate various portions of the chamber or a stable target in the external visual surround, there would have to be changes in gaze gain ($\dot{G}_B / \dot{B}_S$) as a function of body position in space (B_S) for reasons discussed below. Periodic variations in gaze gain in Fig. 5 suggest that this occurred.

The dimensions of the experimental chamber are shown in Fig. 6 A. The animal is depicted facing directly outward (the zero degree position), with the long axis of its body aligned with gaze. The target was assumed to be the experimenter, standing directly in front of the animal as in Fig. 5. We further assumed that the axis of rotation of the head relative to the body and the axes of rotation of each eye relative to the head were small compared to the axis of rotation of the body, and, therefore, only considered the latter. This problem has been dealt with for the simpler case of a uniform visual surround and for axes of rotation other than that of the cyclopean eye (Collewijn et al. 1982b; Blakemore and Donaghy 1980; Biguer and Prablanc 1981; Viirre et al. 1986). Measurements were made of the radius of cyclopean eye rotation ($|\vec{R}|=33$ cm), i.e., from center of the platform to the center of the head (x,y) and the position of the target relative to the platform (X_t, Y_t). In Fig. 6 A, the animal is pictured at zero deg, with the gaze vector ($\vec{T}$ pointing at the experimenter directly ahead ($|\vec{T}|=152$ cm).

Figure 6

A, Schematic representation of apparatus and experimental chamber. The walls, covered by high contrast media, are represented by the solid line and the curtain by the wavy line. $\vec{R}$, radial vector to cyclopean eye at (x,y); $\vec{T}$, gaze vector from eye to stationary target at (X_t, Y_t). B, Gain at any given angular position φ during fixation of a single target is determined by dividing change in gaze angle θ by change in φ.

C, Predicted gaze gains while circling the platform and watching an eccentric target. The target is 152 cm ahead of the animal along the body axis at zero deg. Icons on the bottom represent body position at -90, 0, 90 and 180 deg. They are centered beneath the corresponding angular body positions in degrees in the graph above.


A
60 cm
107 cm
4 cm
23 cm
$\vec{R}$
(x,y)
$\vec{T}$
60 cm
(x_t, y_t)
B
$\hat{a}_x$
$\hat{a}_y$
θ
φ
$\vec{R}$
(x,y)
$\vec{T}$
$\vec{T}$
(X_t, Y_t)
$\theta = \frac{\vec{T} \cdot \vec{R}}{|\vec{T}||\vec{R}|}$
$\Theta_B = 90° - \theta$
$B_P = \varphi$
C
GAZE GAIN
0.0
0.2
0.4
0.6
0.8
1.0
1.2
-90
-60
-30
0
30
60
90
120
150
180
ANGULAR BODY POSTITION (deg)
Gain
Unity gain

To predict gaze gain, the deviation of gaze required to hold fixation on a given target through a given body in space angular deviation was calculated as follows:

1) Fig. 6B shows the orientation of gaze after the animal has moved φ deg from A. The angular position of the animal's cyclopean eye at any time is given by the vector

$$\vec{R} = x\,\hat{a}_x + y\,\hat{a}_y \qquad (1)$$

2) A second vector is defined which is the animal's gaze

$$\vec{T} = (Xt-x)\hat{a}_x + (Yt-y)\hat{a}_y \qquad (2)$$

3) The dot product of the two vectors, $\vec{T}\cdot\vec{R}$ equals the cosine of the angle between the two vectors (θ) multiplied by their amplitudes.

$$\cos\theta = \frac{\vec{T}\cdot\vec{R}}{|\vec{T}|\,|\vec{R}|} \qquad (3)$$

4) Since G_B is with respect to the long axis of the body, which is perpendicular to $\vec{R}$, θ is the complement of the gaze on body angle. The position of the animal at any time is given by the radius and the angle (φ) relative to the platform (B_P).

$$G_B = 90° - \theta \qquad (4)$$

5) For each angle φ of the body from -90 deg to +180 deg, x and y were determined in one deg increments

$$x = r\cos\varphi,\ y = r\sin\varphi \qquad (5)$$

and were used to determine the instantaneous gain required at each position.

6) This was approximated iteratively by finding the change in gaze angle (G_B) for each successive one deg change in body angular position (φ). This analysis assumes the animal fixated a single target at -90 deg and kept its gaze on that target until +180 deg.

$$\text{Gain}_{(\varphi)} = \frac{G_B(\varphi) - G_B(\varphi\text{-1 deg})}{1 \text{ deg}} \qquad (6)$$

In fact, the animal usually only fixated a single target for up to half this range. (We assume the animal was fixating during the large slow phases, as in Fig. 5, since these slow phases were uninterrupted by saccadic movements).

We calculated the instantaneous gaze gain required for fixation at each position of the animal on the platform (Fig. 6 C), and compared the predicted gains to experimental data (Fig. 7 A-E). The icons below the graph show the position of the animal at 90 deg increments around the platform, starting at -90 deg, and indicate the direction of running (CW). In the quadrant between -90 deg and 0 deg, the target is in the animal's quick phase direction, and the gains are below unity since compensation for the translational component opposes and subtracts from the compensation for angular motion. (The forward, linear component of the animal's trajectory results in motion of the target to the right relative to the animal's body, necessitating leftward compensatory deviations of gaze. The angular component of body movement, however, is to the right, causing a leftward relative motion of the target relative to the body.) With the animal at zero deg (second icon) the target is straight ahead and the gain is unity, since instantaneously there is no translation, only rotation with respect to the target. With the target on the slow phase side, compensation for translational and rotational movement are additive, resulting in greater than unity gains. The gain reaches a maximum at +78 deg in this example, when the gaze on body angle equals 90 deg. Beyond

90 deg, the gain decreases toward unity. Table 1 shows the required gains predicted for perfect compensation at various target distances from the closest target (45 cm) to infinity. In each case, calculations are based on the target being straight ahead at zero deg.

TABLE 1: Predicted gaze gains relative to target distance and animal's orientation.

PREDICTED GAZE GAINS ($\dot{G}_B / \dot{B}_S$) AT:

Target Distance	-90 Deg	0 Deg	+90 Deg	Max.	Angle at Max. Gain
45 cm (closest wall)	.64	1.0	1.39	2.44	54 deg
64 cm (opposite wall)	.69	1.0	1.55	1.84	63 deg
94 cm (closed curtain and rear wall)	.75	1.0	1.44	1.49	71 deg
152 cm (position of investigator in Fig. 5)	.83	1.0	1.26	1.27	78 deg
Infinity	1.0	1.0	1.0	1.0	- -

Averages recorded in light over 30-40 consecutive revolutions are shown in Fig. 7 A-E. The velocity of running ($\dot{B}_S$, top trace) was about 200 deg/s in each of these panels without consistent large variations according to angular position (B_P) except for perhaps a slight decrease at the time of maximal gaze gain. From analysis of video images taken of the running animal from above, it was determined that the angle between the radial arm of the apparatus and the long axis of the body was approximately 45 deg (See also Fig. 1D). The icons below each panel indicate the direction of rotation, the animal's position with regard to the chamber, and status of the curtain. The dotted lines in the $\dot{E}_H / \dot{B}_S$, $\dot{H}_B / \dot{B}_S$, and $\dot{G}_B / \dot{B}_S$ traces show unity gain, and the short horizontal bars above and below the unity gain line represent gains of 1.1 and 0.9, respectively.

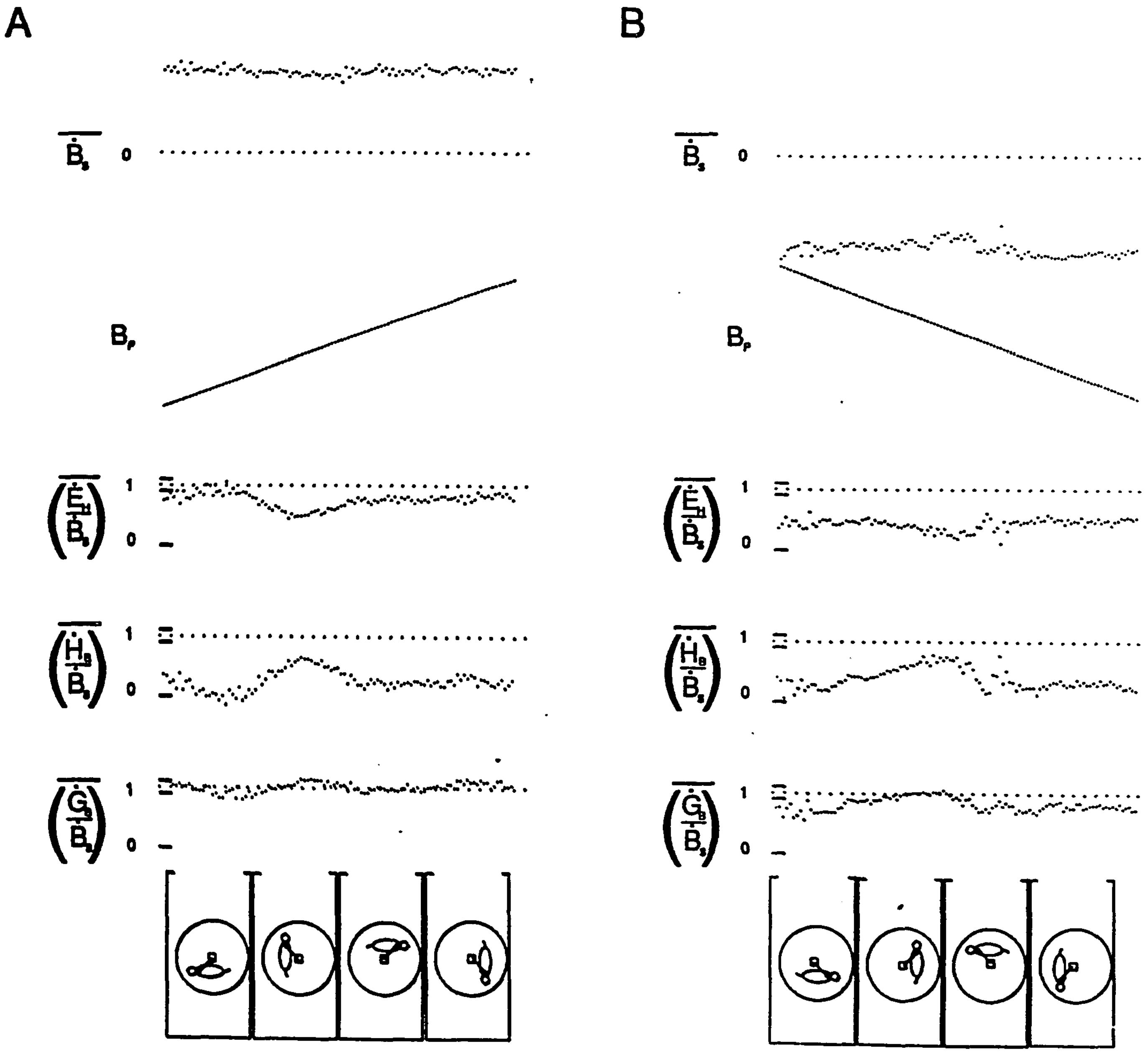
In Fig. 7 A, monkey rh was running in the clockwise direction with the curtain open. In the orientation represented on the left (first icon) the animal's gaze was probably in the quick phase direction, i.e., to his right, enabling him to view the laboratory through the opening of the experimental chamber. His gaze gain ($\dot{G}_B / \dot{B}_S$) was below unity, around 0.9, and was maintained almost exclusively by the gain of eye in head velocity ($\dot{E}_H / \dot{B}_S$). As the animal directly faced the opening (second icon), gaze gain rose to unity, as predicted in Fig. 6 C, and crossed into the supra-unity gain region. In this quadrant the gain of head on body velocity ($\dot{H}_B / \dot{B}_S$) became increasingly more responsible for the gain of gaze, with a corresponding decrease in the ocular component. As the animal continued around the remainder of the platform, gaze gain stayed between 1.0 and 1.1, with the eyes contributing around 80% and the head 20% of the compensatory velocity.

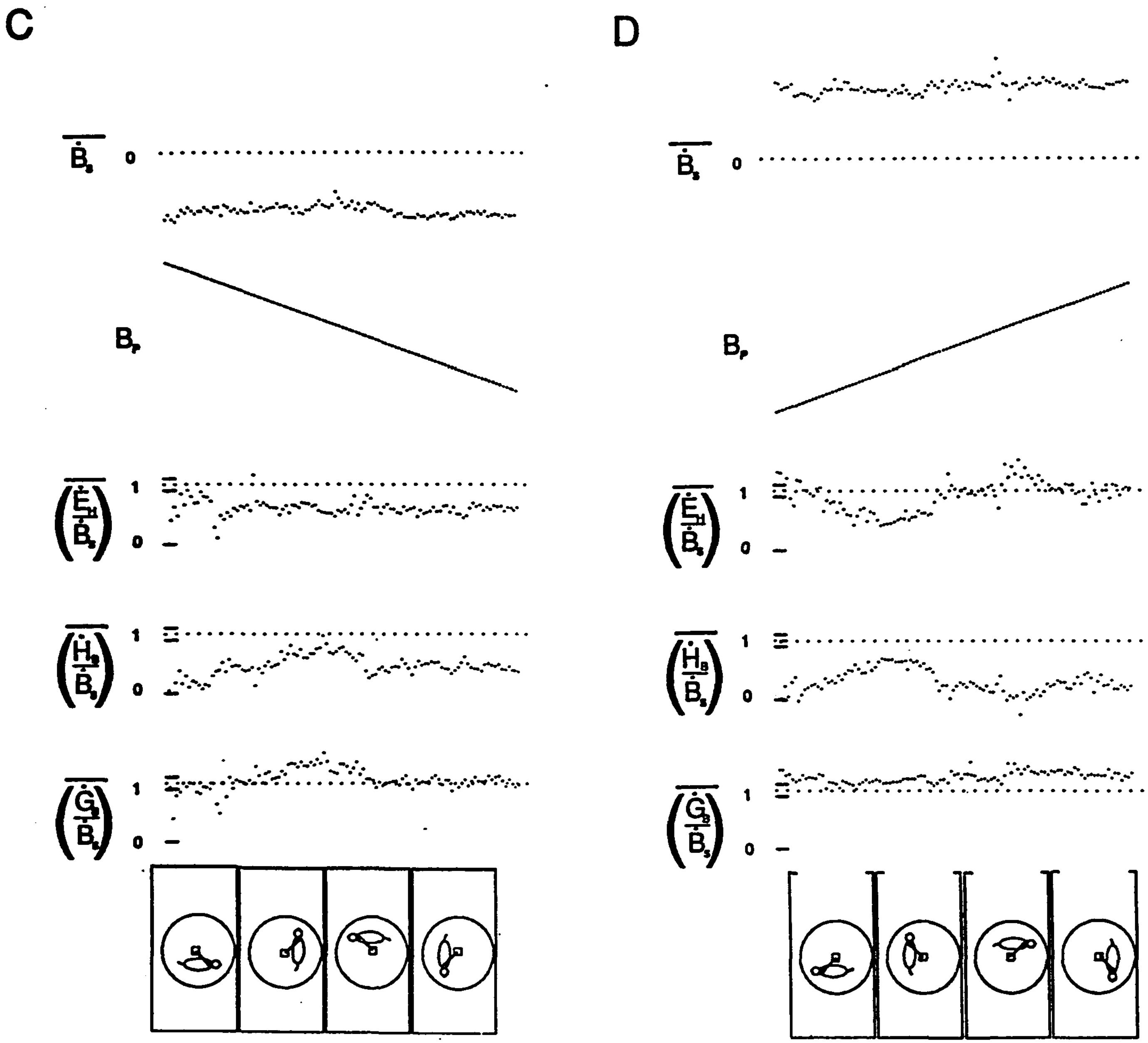
When the animal ran in the CCW direction with the curtain open (Fig. 7 B), with the target on the quick phase side (first icon), his gaze gain ($\dot{G}_B / \dot{B}_S$) was initially well below unity. It rose to unity as the animal moved to face the opening

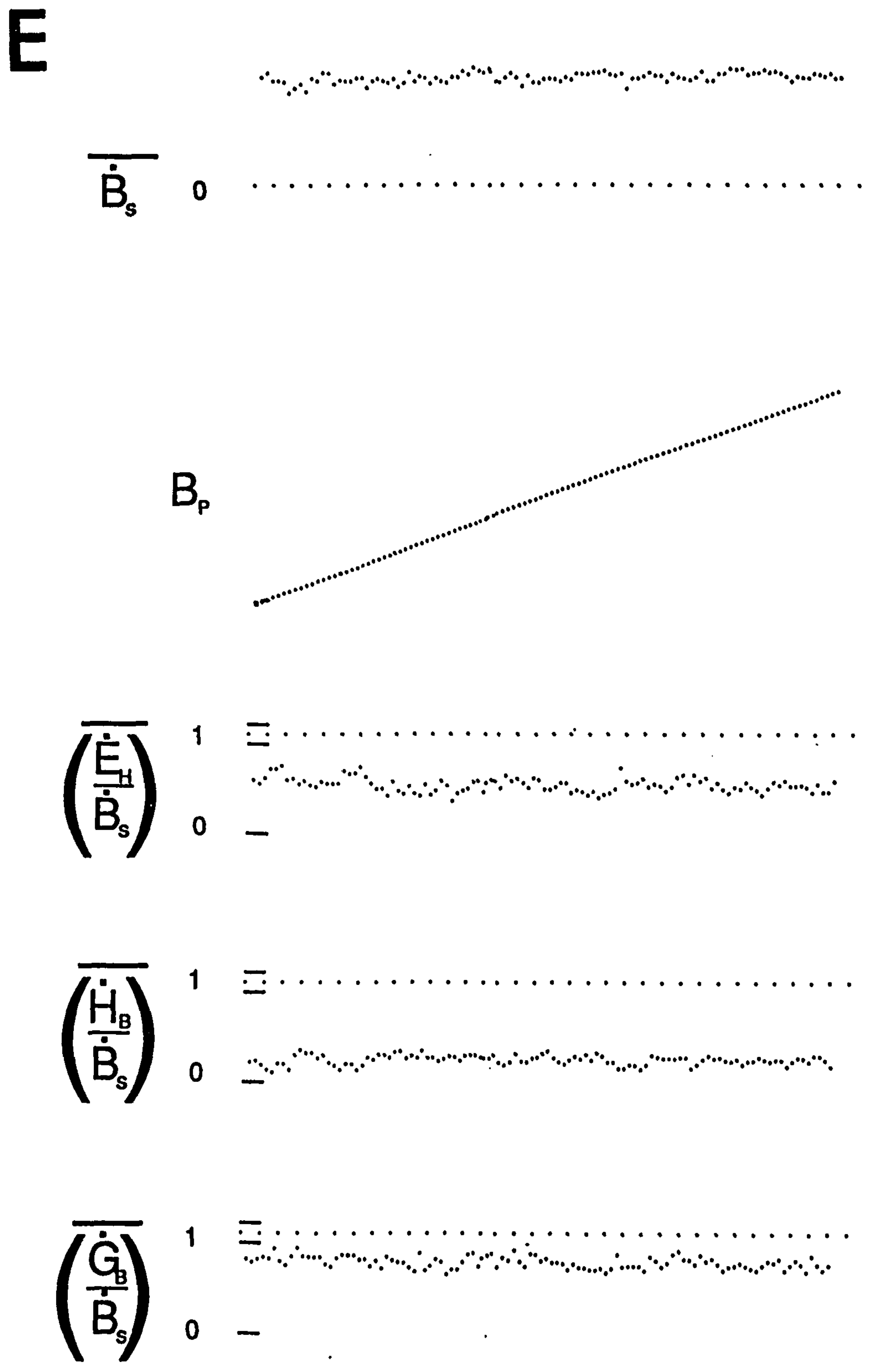
Figure 7

Gains of eye velocity ($\dot{E}_H / \dot{B}_S$), head velocity ($\dot{H}_B / \dot{B}_S$) and gaze velocity ($\dot{G}_B / \dot{B}_S$) relative to body position on the stationary platform. Averaged data from 30-40 revolutions in 3.6 degree bins for CW running (A,D,E) and CCW (B,C) running. Icons represent angular position (B_P) of the animal (rh) with regard to the visual surround, as defined in Fig. 6. The animal's angular body velocity in space was relatively constant as a function of position (mean $\dot{B}_S$, top traces). In all cases, head gain increased as the animal ran toward the opening of the chamber or the curtain (second quadrant) with a corresponding decrease in eye gain. Gaze gain reached unity when the animal faced the opening or the curtain, and was greater or less than unity at other positions due to translational components and or interest in the surround.

E, Running in darkness- body velocity in space ($\dot{B}_S$) did not vary systematically according to position, and there were no consistent changes in the relative contribution of eye and head movement to gaze compensation dependent on platform position. The average head gain is low because data included in the averages were from gaze slow phases. (At the beginning of each slow phase the head was still moving in the anti-compensatory direction).


A
B
$\overline{\dot{B}_s}$
0
B_p
$\left(\frac{\overline{\dot{E}_H}}{\dot{B}_s}\right)$
1
0
$\left(\frac{\overline{\dot{H}_B}}{\dot{B}_s}\right)$
1
0
$\left(\frac{\overline{\dot{G}_B}}{\dot{B}_s}\right)$
1
0


C
D
Ḃs
0
Bp
(ĖH/Ḃs)
(ḢB/Ḃs)
(ĠB/Ḃs)
1
0


E
$\overline{\dot{B}_s}$
0
B_p
$\overline{\left(\frac{\dot{E}_H}{\dot{B}_s}\right)}$
1
0
$\overline{\left(\frac{\dot{H}_B}{\dot{B}_s}\right)}$
1
0
$\overline{\left(\frac{\dot{G}_B}{\dot{B}_s}\right)}$
1
0

directly (second icon). The eye gain was initially about 0.5 but fell slightly as the head gain rose from 0.2 to 0.8. The animal's gaze gain around the rest of the circumference was around .8, with eye gain at 0.6 and head gainat 0.2. There were differences in the field of view during clockwise and counterclockwise running that may have accounted for the continued rise in head gain between the second and third quadrants and for the lower gains in the third and fourth quadrants.

The chamber in which the animal ran was located at one corner of the laboratory. During clockwise running, in the third quadrant the animal ran toward the center of the room, offering additional targets beyond the experimental enclosure. Running in the counterclockwise direction it had to 'look over its shoulder' to see the same field. This would be done more easily with the head than the eyes.

In Fig. 7 C the animal was circling CCW with the curtain closed. Presumably, it watched the curtain as it passed, in anticipation of a reward. As in A & B, gaze gain was below unity in the first quadrant. It rose through unity at the point when the curtain was straight ahead, to 1.3 as the animal passed the curtain. The higher gain was probably related to watching the curtain, a close target. The increase in gain was largely due to an increase in the head on body (H_B) contribution.

In the condition of highest visual interest, with the experimenter present (Fig. 7 D), gaze gain was above unity throughout the run except for a brief period when the animal was directly facing the experimenter and curtain. At this time gaze gain fell approximately to unity. As in the preceding three panels, head on body gain rose substantially as the animal moved through the second quadrant and then fell in the third quadrant.

To insure that there was no vision in the experimental enclosure and to control for possible cues that the animals might have gotten from the visual surround that would influence compensatory gaze movements, the gains of gaze and eye and head movements were averaged as a function of body position in space (B_p) while an animal circled in darkness (Fig. 7 E). There was no change in body velocity or in the relative contributions of the head and eyes as a function of angular body position. This, along with the presence of anti-compensatory nystagmus while the animal ran in the direction of its shorter VOR time constant (Fig. 14 B), indicated that the animal was not receiving visual input to produce gaze compensation during running.

As shown in Fig. 16 A, the gain of the compensatory gaze nystagmus fell somewhat with time, making the average dependent on the duration of running. The relative contributions of head and eye gains, however, were independent of duration. On average the head was responsible for about a third of the compensatory slow phase gaze velocity, while the eyes produced the remaining two thirds during continuous running in darkness (Fig 7 E).

Thus, the characteristics of the visual scene relative to the position of the animal on the platform and its direction of motion considerably affected its gaze strategy, as reflected in the gain of the head and eye slow phase velocities. As suggested in Fig. 5, the gain of the head on body velocity rose as the monkey passed targets of interest, presumably allowing for longer periods of fixation. In addition, there was a predictable change in gain, depending on whether the animal was travelling toward or away from a visual target. This is in contrast to averages of the same parameters taken while the monkeys were running in darkness. In this condition there were no variations in any of these parameters.

COMPENSATORY GAZE NYSTAGMUS DURING RUNNING IN DARKNESS; MONKEY RH:

The major finding of this study was that sustained compensatory gaze nystagmus of the head and eyes was elicited by circular locomotion when animals ran in complete darkness. Typical examples from rh and c are shown in Figs. 8, A and 9, respectively. There were individual differences in the characteristics of the eye and head movements according to the animal and the direction of running. Rh will be considered first. Its gait had a normal appearance, and its posture was similar to that during running in light (Fig. 1A-D). It leaned in toward the center of the platform to account for the linear accelerations generated during circling, and it held its head upright and tilted slightly forward. Paw placements were along a narrow base close to the edge of the platform, lateral to the sagittal plane of the animal's body.

A typical run of rh in the clockwise direction in darkness, i.e., to the right is shown in Fig. 8 A. It ran for nearly 50 s at about 200 deg/s, completing 28 revolutions. The striking finding was that there was continuous head and eye nystagmus for as long as it ran. The slow phases were compensatory movements to the left, and the quick phases were to the right in the direction of running. The frequency of nystagmus remained relatively constant throughout at about 1.4 beats/s with the slow and quick phases occurring synchronously in the head and eyes. The amplitude of eye quick phases were typically greater than 60 deg, and they were larger than the head quick phases, which were usually under 20 deg (Fig. 8 A, E_H and H_B; note difference in scale of E_H and H_B). The head movements began and ended more slowly giving them a rounded appearance. This is probably a reflection of the more sluggish dynamics of the head due to its greater mass. Neither the eye nor the head slow phases were linear. The slope of the eye slow phase was greatest at the beginning and end of each movement, and lowest in the middle when head slow phase velocity peaked (see below).

The result of the head and eye movements was that there was continuous gaze velocity on the body ($\dot{G}_B$) that compensated for the animals body velocity in space ($\dot{B}_S$). Superimposed on this gaze velocity were small fluctuations that compensated for similar fluctuations in body velocity. These were due to changes in forward motion associated with different phases of the locomotion cycle, and were also present during running in light.

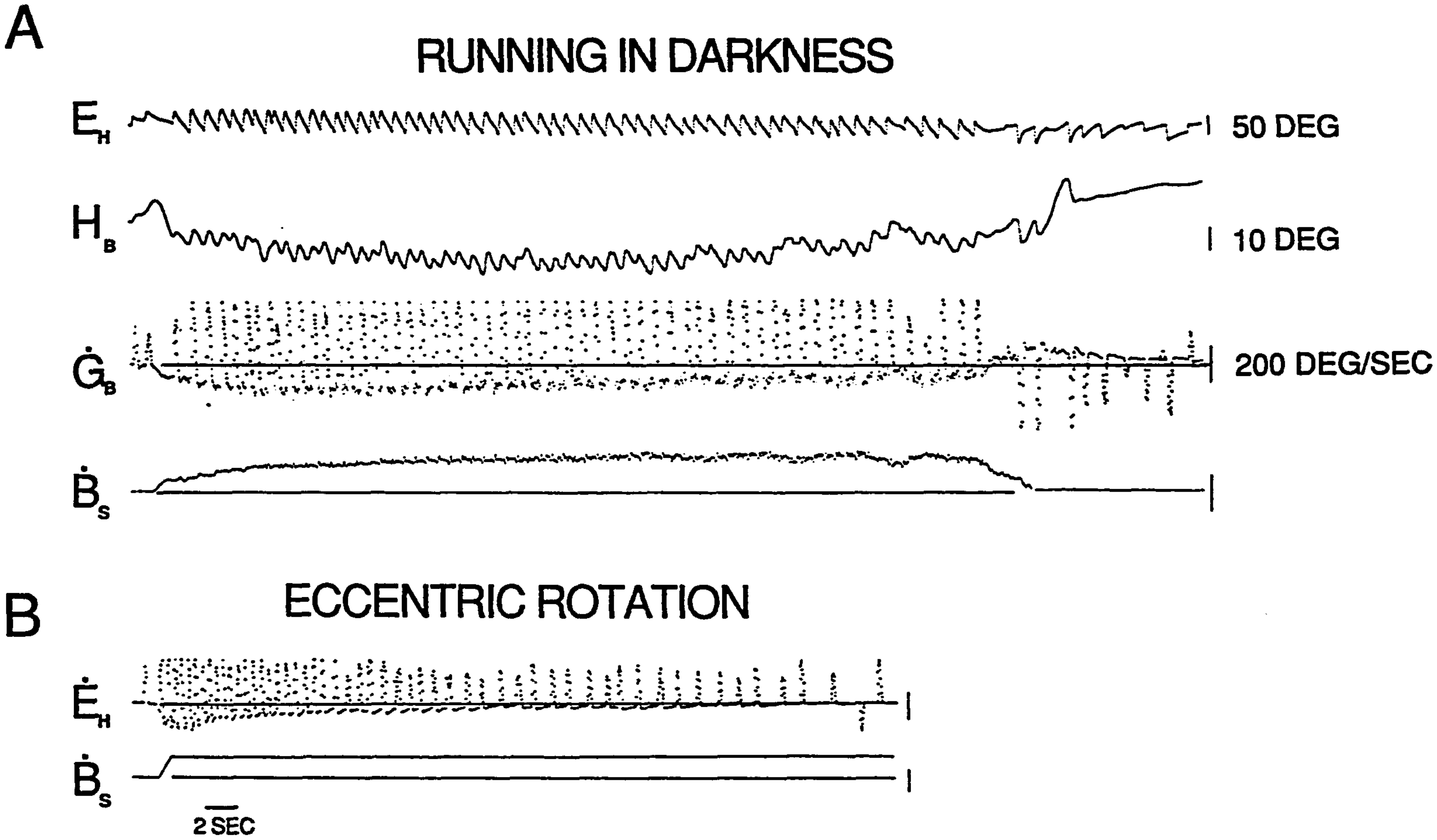
When the animal decelerated (Fig. 8 A, right and Fig. 10, arrow), the reduction in its angular velocity induced a brief post-locomotory response, seen as rightward slow phase velocity in the eye position and gaze on body velocity traces. The post-locomotory or post-rotatory response was weak, considering that the animal had been circling in darkness at 200 deg/s for close to a minute. The first three beats of nystagmus were synchronous in the head and eyes in Fig. 8 A. Following this, the head was stationary and only the eyes moved. This was typical; except for the first few beats, the post-locomotory response was generated almost solely by the eyes. It should be noted that as soon as the head stopped moving, horizontal eye position changed linearly with time during the slow phases, accounting for the more typical appearance of the nystagmus at the end of the response.

The weak post-locomotory (or post-rotatory) nystagmus after running in the clockwise direction, in which compensatory gaze velocities were maintained (Fig. 8 A), suggests that velocity storage was responsible for the maintenance of gaze during running and for the reduction in the post-locomotory nystagmus after running. This is similar to findings during passive rotation in light with a stop in darkness. The per-rotatory nystagmus is sustained during rotation and the post-rotatory nystagmus is canceled or attenuated by stored activity induced by optokinetic stimulation (Mowrer 1937; Ter Braak 1936; Raphan et al. 1979). The difference in the present situation was that the animal was running for prolonged periods in complete darkness, so that velocity storage must have been elicited by activity associated with the act of circular locomotion, itself. Consistent with this hypothesis, when the animal ran in the counterclockwise direction in which there was no continuous compensatory gaze velocity (Figs. 13 A, 14 & 15), i.e., in which velocity storage was weak, the leftward post-locomotory response was not attenuated, and was similar to the post-rotatory response after passive rotation in darkness (see below, ASYMMETRY).

Figure 8

Data from monkey rh in darkness, under active (A) and passive (B) conditions. A, During head-free, circular locomotion in darkness there is continuous and synchronous nystagmus of both the eyes in head (E_H) and head on body (H_B) for the duration of the 50 s run. These summed to generate compensatory gaze on body ($\dot{G}_B$) velocity. The $\dot{G}_B$ slow phase envelope mirrored the $\dot{B}_S$ trace. There was a weak post-locomotory response.

B, Eye velocity ($\dot{E}_H$) recorded during passive rotation at 200 deg/s with the head fixed. The animal was sitting at the edge of the platform, travelling through the same eccentric trajectory as during active running. It therefore experienced comparable linear accelerations. Note that the slow phase velocity decayed to zero in B despite the continued angular velocity and linear acceleration.


A
RUNNING IN DARKNESS
E_H
50 DEG
H_B
10 DEG
$\dot{G}_B$
200 DEG/SEC
$\dot{B}_S$
B
ECCENTRIC ROTATION
$\dot{E}_H$
$\dot{B}_S$
2 SEC

MONKEY C:

Monkey c differed from rh in two ways: First, during locomotion its body velocity ($\dot{B}_S$) was generally more irregular than rh, due to a slower, more lurching type of gait. Second, its pattern of response was symmetrical, and there was head and eye nystagmus with slow phases in the opposite direction to the animal's running direction. The compensatory gaze nystagmus was continuous, similar to that in rh when it circled in the clockwise direction (Fig. 8 A), and it persisted for the duration of the circling. Monkey c usually ended each run with several backward steps.

A typical example is shown in Fig. 9. The magnitude of the slow phase velocities varied directly with the steady state angular body velocity as well as with fluctuations in body velocity. The functional result was that the animal's gaze on body velocity ($\dot{G}_B$) summed with its body in space velocity ($\dot{B}_S$) to generate a gaze in space velocity ($\dot{G}_S$) that was close to zero during the slow phases (Fig. 9, third trace). The integral of the gaze velocity in space, gaze position in space (G_S ; fourth trace), was stable for periods up to 2 s. Thus, even though it was in complete darkness, the animal had periods of 'fixation', separated by head and eye quick phases that shifted gaze ahead to new positions in space. Had the animal been in light, this would have permitted stabilization of gaze on targets in the visual surround while it was running.

At one point in the run shown in Fig. 9, the animal abruptly reduced its running velocity, giving itself a velocity step of approximately 50 deg/s in the direction opposite to its rotation (arrow). There was no post-rotatory nystagmus. Rather, the animal maintained its slow phase gaze movements in the compensatory direction with a gain of close to 1. Moreover, when the animal came to a halt at the end of the run, there was no post-rotatory nystagmus. Both suggest that activity responsible for gaze compensation had been stored to sustain gaze on body velocity during running and to counteract the input from the semicircular canals to reduce or block post-rotatory, anticompensatory gaze nystagmus when the rotational velocity was reduced or when the animal halted.

Monkey c had a long dominant time constant for its VOR to both sides (about 25 s). As noted above, it maintained compensatory gaze velocities whenever it ran in darkness, although these periods of running were not as prolonged as in rh. Continuous nystagmus was also not produced by passive eccentric rotation of monkey c in darkness. The durations of its per- and post-rotatory nystagmus were similar whether the axis of rotation was head centered or eccentric. This substantiates the finding that linear acceleration during passive rotation by itself was not capable of producing continuous gaze compensation. This suggests that somatosensory activity or efference copy related to the circular running, or both, acting through velocity storage, had maintained the gaze compensatory nystagmus.

Figure 9

Monkey c circling to the right in darkness. Compensatory gaze nystagmus with leftward slow phases persisted for the duration of the run. Gaze in space velocity was close to zero during the slow phases, corresponding to a gaze gain of near unity. The integral of $\dot{G}_S$, i.e., gaze position (G_S) shows that gaze was saccadic in space. At the arrow the animal spontaneously slowed, experiencing a velocity step of 100 deg/s to the left. Despite this, it maintained leftward compensatory slow phase movements for its net rightward body velocity in space. There was no after-nystagmus at the end of the run. Calibrations of the $\dot{G}_B$, $\dot{B}_S$ and $\dot{G}_S$ traces are the same, i.e., 200 deg/s.

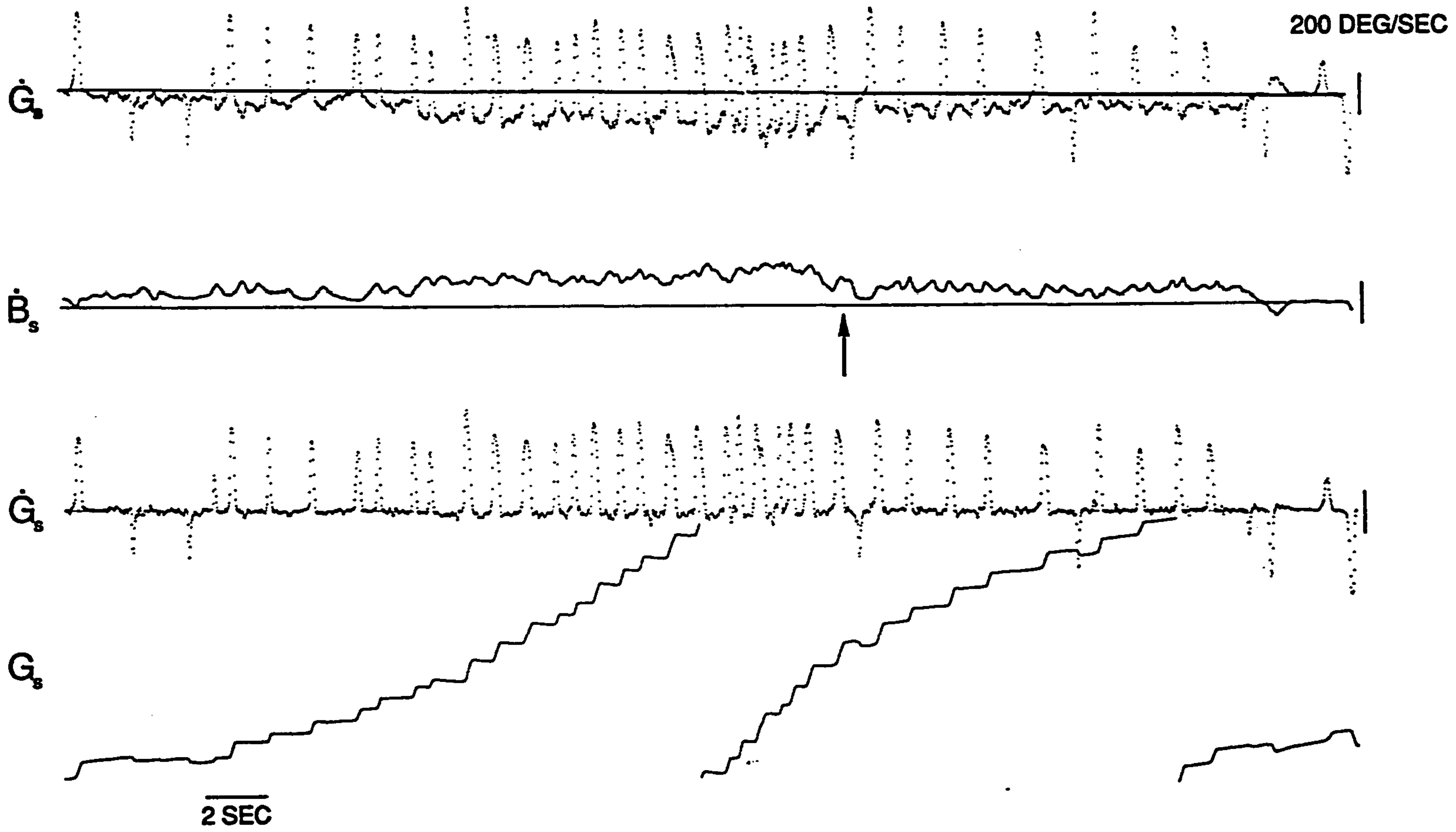
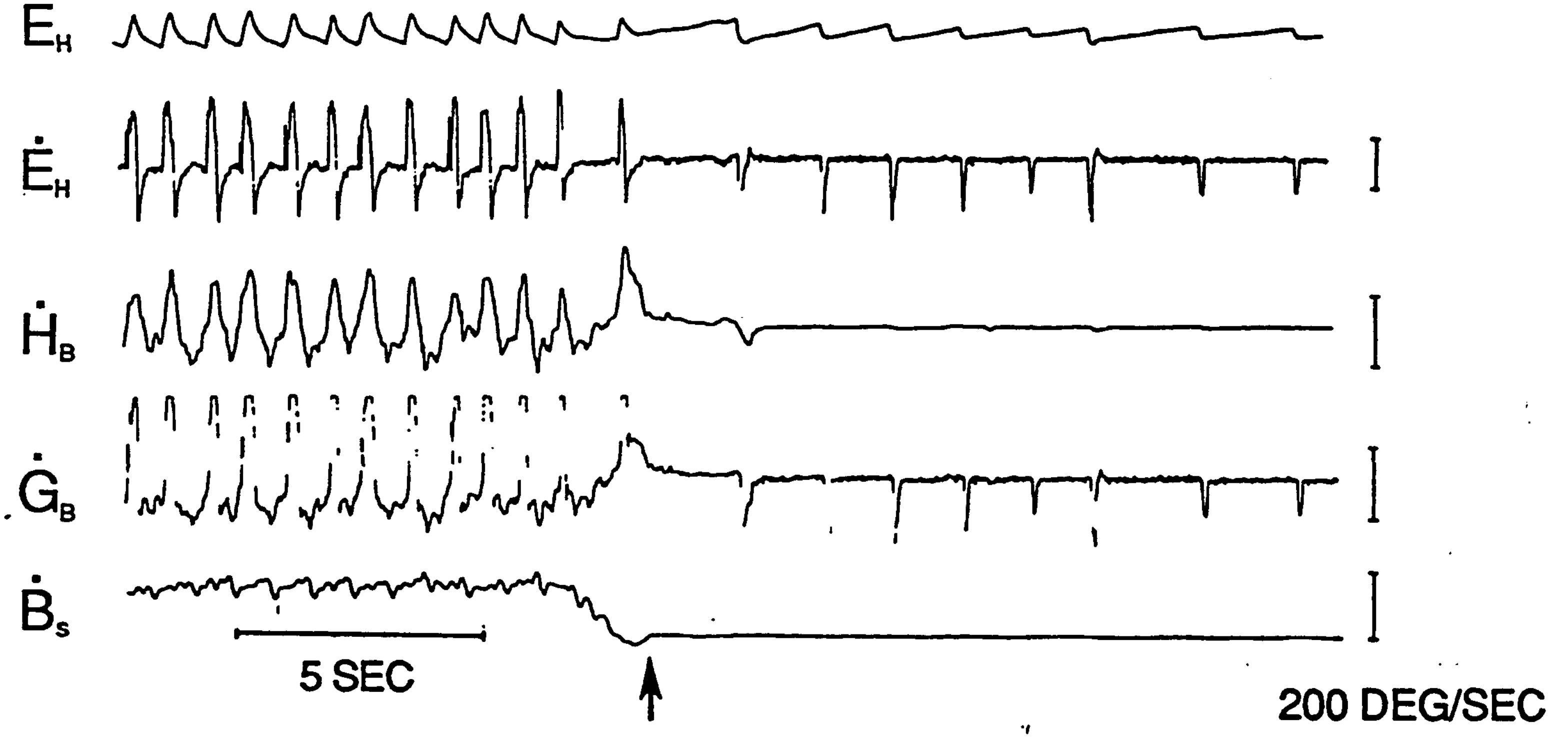

200 DEG/SEC
$\dot{G}_s$
$\dot{B}_s$
$\dot{G}_s$
G_s
2 SEC

Figure 10

End of a period of Monkey rh running in darkness in the CW direction. Scalloped slow phase eye velocity profiles and rounded head velocity profiles add to yield gaze velocity which compensates well for both high and low frequency components of angular velocity in space. After stopping (arrow), the post-locomotory response was present only in the eye movement traces, while the head was still. Ocular slow phases were linear, and quick phases were smaller in the absence of head and active body movement.


E_H
$\dot{E}_H$
$\dot{H}_B$
$\dot{G}_B$
$\dot{B}_s$
5 SEC
200 DEG/SEC

NYSTAGMUS DURING PASSIVE ECCENTRIC ROTATION WITH THE HEAD FREE

It was important to determine whether the linear acceleration associated with the eccentric position of the animal during running on the circular platform in darkness could have been responsible for its maintenance of gaze. A recording taken with rh's head free but its body stationary while being passively rotated in darkness at 100 deg/s at the same eccentricity as during running is shown in Fig. 11. The animal was facing forward during passive rotation, in the same orientation as when it ran. There was synchronous head and eye nystagmus with rightward quick phases for 6 s, and an isolated beat of head nystagmus at 10 s, after which the head did not move appreciably. The eyes continued to beat for 60s. Eye in head slow phase velocities ($\dot{E}_H$) changed from scallop-shaped to linear when the head stopped moving.

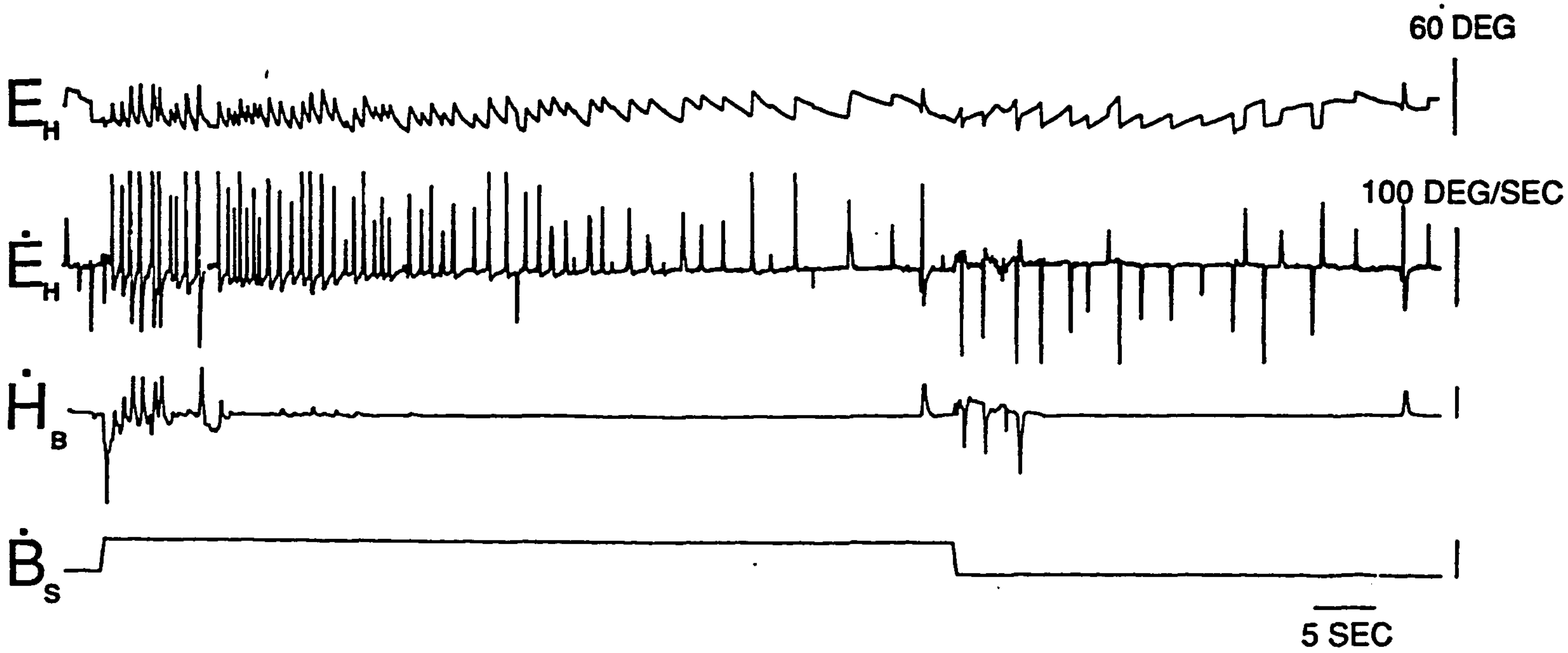
There were a few beats of head nystagmus following the post-rotatory step, but, as during the per-rotatory response, the head nystagmus decayed faster that the eye nystagmus. (Small head velocities were recorded for up to 20 s, indicating that sub-threshold motor control signals for head nystagmus were present, however). A comparison of Fig. 11 with Fig. 8 shows that head free passive rotation with a component of linear acceleration did not sustain continuous nystagmus, such as was present during running in dark in the same direction.

The characteristics of the per- and post-rotatory response to passive eccentric rotation with the head free (Fig. 11) were similar to the post-locomotory response in Fig. 13: head nystagmus was elicited only during the initial portions of the response, and the eye nystagmus persisted much longer. This is different from the nystagmus during running. Even when the duration of the per-locomotory response was short, as during the sequence recorded during CCW running in Fig. 13, both the head and eyes participated in producing whatever compensatory gaze velocity was generated. This indicates that head movements are an integral part of gaze compensation during running.

It also suggests that head movements are enabled by some aspect of running, such as body and limb movements or the intent to run (efference copy).

Figure 11

Passive eccentric rotation in darkness with a step of 100 deg/s. Monkey rh was seated in a primate chair mounted to the periphery of the platform approximately 30 cm from the axis of rotation. The head was unrestrained. Compensatory nystagmus was present in both the head and eyes only for the first 5-10 s of the rotation. After this there was only eye nystagmus. Note the asymmetry of the per- and post-rotatory responses, similar to that observed during passive vestibular and optokinetic testing (Fig. 1,B).


60 DEG
E_H
100 DEG/SEC
$\dot{E}_H$
$\dot{H}_B$
$\dot{B}_S$
5 SEC

COMPARISON OF RUNNING IN LIGHT AND DARK:

To provide a comparison of the relative characteristics of head and eye nystagmus during running, monkey rh was recorded while running in the CW direction while the lights were turned on or off each 5-8 s. Its running velocity was not altered by the presence of light, but as shown in Fig. 12, it had a very different strategy of eye-head coordination under the two conditions. During running in light, the gaze nystagmus had a relatively high frequency. The beats were of small amplitude in both the head and eyes, except, as described in the previous paper, when there was prolonged gaze compensation. Head on body velocity tended to be low and somewhat erratic, but was synchronized with eye nystagmus during both the slow and quick phases. The summed eye velocity in the head and head velocity on the body produced a gaze velocity on body that compensated for body velocity in space ($\dot{B}_S$). As a result, gaze velocity in space ($\dot{G}_S$) remained close to zero, implying gaze gains close to unity, except during the quick phases.

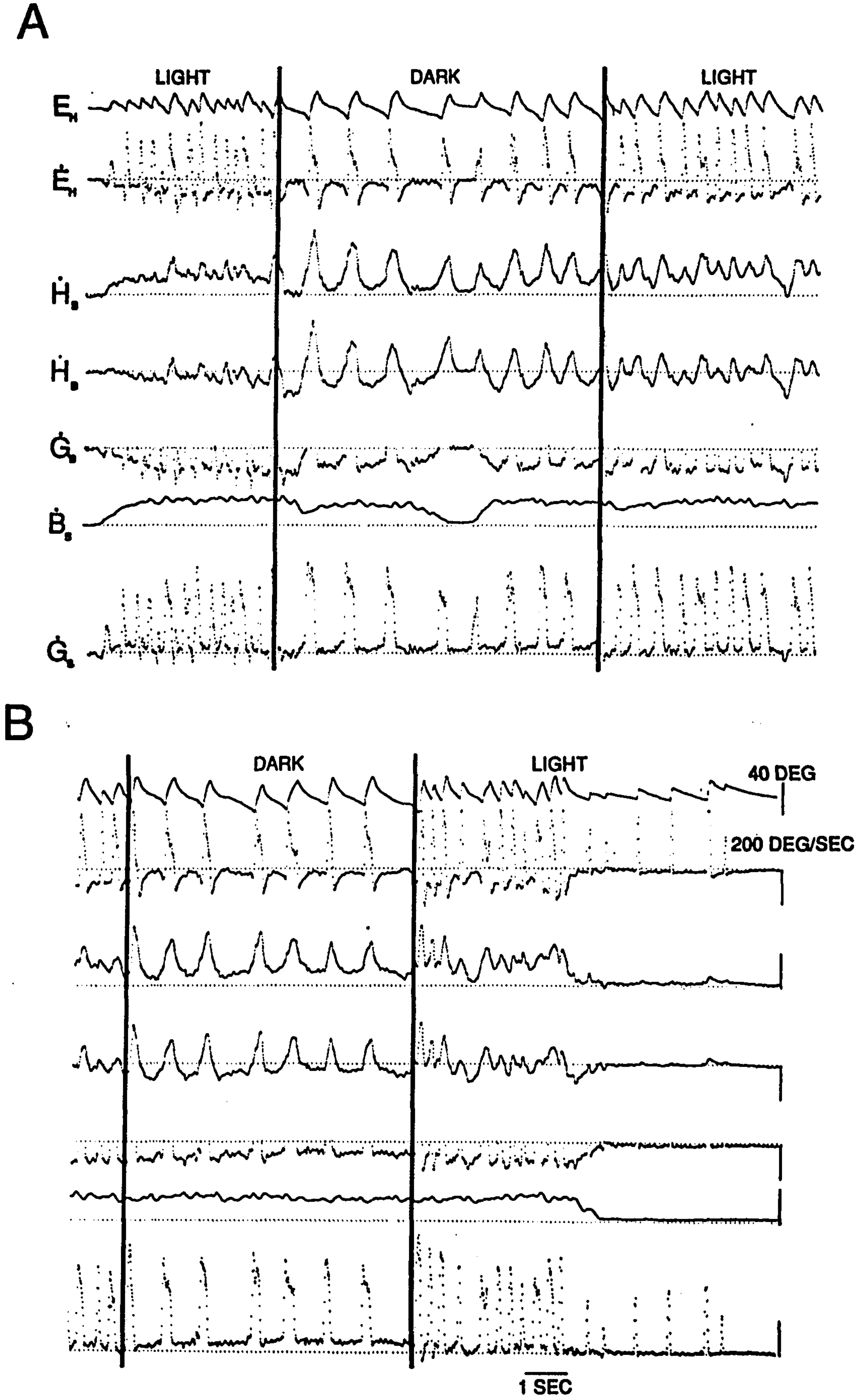
By contrast, during running in dark the beats of head and eye nystagmus were large, regular and of low frequency. The initial peak of eye slow phase velocity ($\dot{E}_H$) and the later rise of head slow phase velocity ($\dot{H}_B$) combined to produce gaze velocity profiles ($\dot{G}_B$) that were "squared off" and relatively flat. Head slow phase velocities were higher than in light. Consequently, head in space velocity ($\dot{H}_S$), the driving signal on the VOR, was lower. While gaze gains were slightly lower than in light, resulting in some slip of gaze velocity in space ($\dot{G}_S$) in the quick phase direction, compensation was, nevertheless, fairly well maintained.

Given the high $\dot{H}_B$ seen during running in darkness (Fig. 12, $\dot{H}_B$ in dark portions), it might seem contradictory that in the average presented in Fig. 7 E, the eyes accounted for roughly 70% of the slow phase gaze velocity, and the head only 30%. The lower overall contribution of $\dot{H}_B$ reflected in the average was because

Figure 12

A, Monkey rh running in light and darkness on a slowly rotating platform (20 deg/s). B, Continuation of traces from A. The illumination was changed four times with the animal going from light to dark and back. Eye and head movements were tightly coupled throughout, and gaze gains were high. In light $\dot{E}_H$ provided most of the compensation. The nystagmus was of high frequency, and the velocity of the head on body fast and slow phases was low, except during prolonged fixations (Note large head slow phase near end of second light interval).

In darkness, the head slow phase velocity was primarily responsible for gaze stability, except during the initial portion of each slow phase, when eye movement brought gaze in space to zero while the head quick phase was still in progress. Note the instantaneous nature of the transition between each mode of gaze nystagmus. Calibrations for the traces are shown in B and show 200 deg/s for all velocity traces.


A
LIGHT
DARK
LIGHT
E_H
$\dot{E}_H$
$\dot{H}_S$
$\dot{H}_B$
$\dot{G}_S$
$\dot{B}_S$
$\dot{G}_B$
B
DARK
LIGHT
40 DEG
200 DEG/SEC
1 SEC

$\dot{H}_B$ was still in the quick phase direction at the beginning of each gaze slow phase. This anticompensatory head velocity was offset by the high eye slow phase velocity, increasing the overall ocular component.

The transition in nystagmus from one form to another was practically instantaneous. (The platform was moving at 20 deg/s throughout to encourage running, and accounts for the appearance of ocular nystagmus at the end of the run.) Thus, differences between running in light and darkness included the frequency of nystagmus, relative contributions of the head and eyes and a difference in amplitude of the eye quick phases.

ASYMMETRY IN PASSIVE AND ACTIVE PARADIGMS IN MONKEY RH

Note that the same asymmetry present in compensatory gaze nystagmus during running, was also present during passive rotation. That is, there was a long dominant time constant when the slow phases were to the left and a short time constant when the slow phases were to the right. Since the dominant time constant of the VOR is heavily dependent on the velocity storage mechanism (Raphan et al. 1979), it suggests that gaze compensatory nystagmus was being manifest, at least in part, through velocity storage.

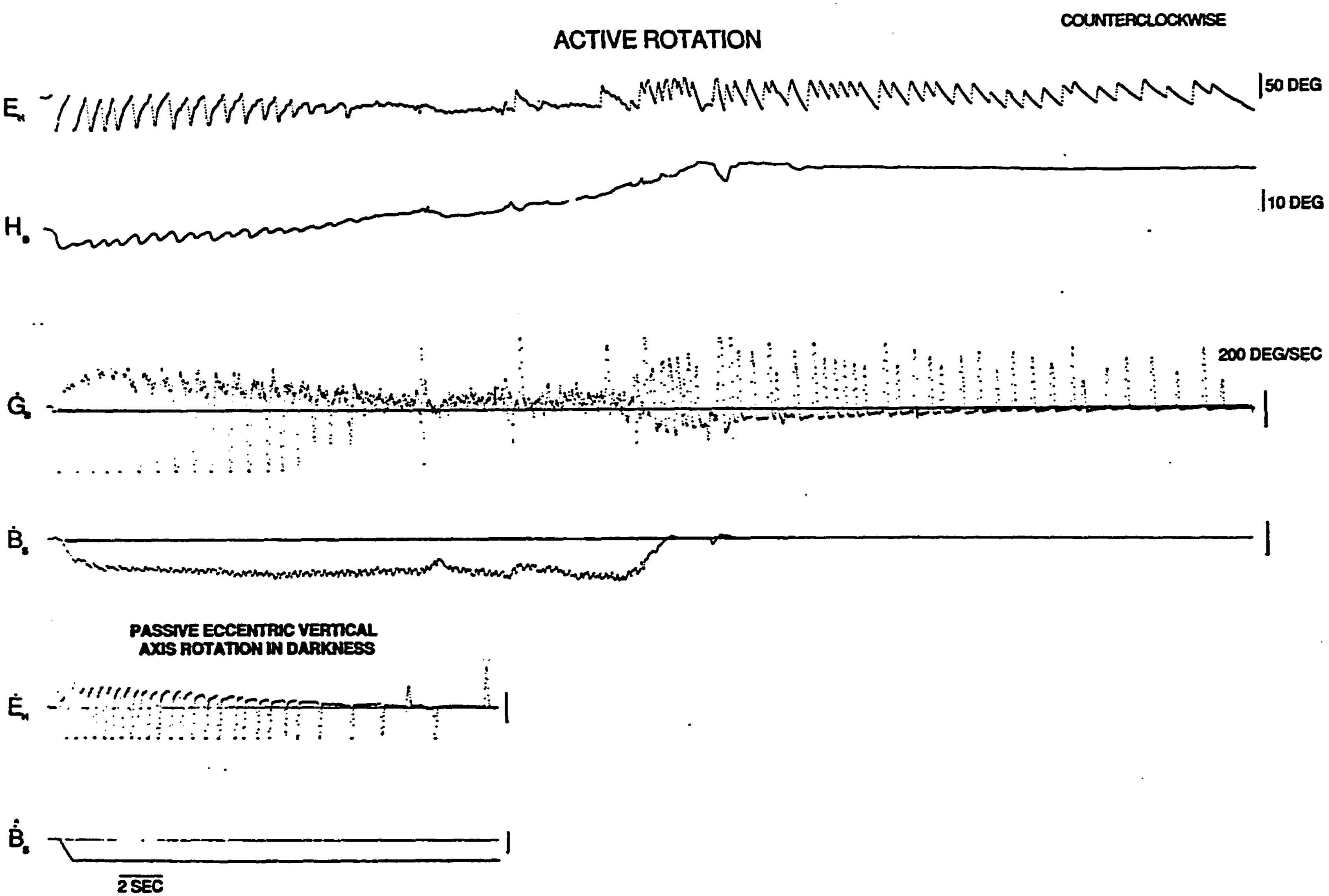
When this animal ran in the counterclockwise direction (Fig. 13), the pattern of induced head and eye movements was quite different. Initially, there was gaze compensatory nystagmus in both the head and eyes, but the nystagmus disappeared in 20-25 s, after which the monkey ran with its head and eyes almost stationary. The post-locomotory nystagmus upon deceleration was much stronger than after running in the clockwise direction. Striking was the lack of head movements during the post-locomotory response, and the relatively linear eye slow phases when the animal was stationary. It was rare for rh to allow a post-locomotory response to go to completion. Rather, it would soon resume running, terminating the nystagmus (Fig. 14).

It was not as common for rh to run for a prolonged period in the CCW direction in darkness, although this was its preferred direction of running in light. During one such run, as it ran to its left (Fig. 15, $\dot{B}_S$), following the decay of the initial per-locomotory response (rightward slow phases) there was anti-compensatory nystagmus with slow phases to the left. This nystagmus was present both in the head and eyes and persisted for the duration of the run. At the end of running, when it stopped, it gave itself a step of velocity to the right. The post-locomotory response added to the previous anti-compensatory nystagmus, and the initial beats of head nystagmus with leftward slow phase velocities were considerably stronger (arrow).

Figure 13

Top, While running continuously in darkness in the CCW direction, in which the animal had poor velocity storage, compensatory head and eye movements decayed to near zero velocity in 15 s. Note that the post-locomotory response was stronger than after running in the CW direction (Fig. 9), and that it was mainly in the eyes. Note also that the ocular slow phases where linear when the head was still and scalloped when the head was in motion.

Bottom, Passive eccentric rotation in darkness resulted in a similar decay in the compensatory response. The animal's head was fixed relative to the body.

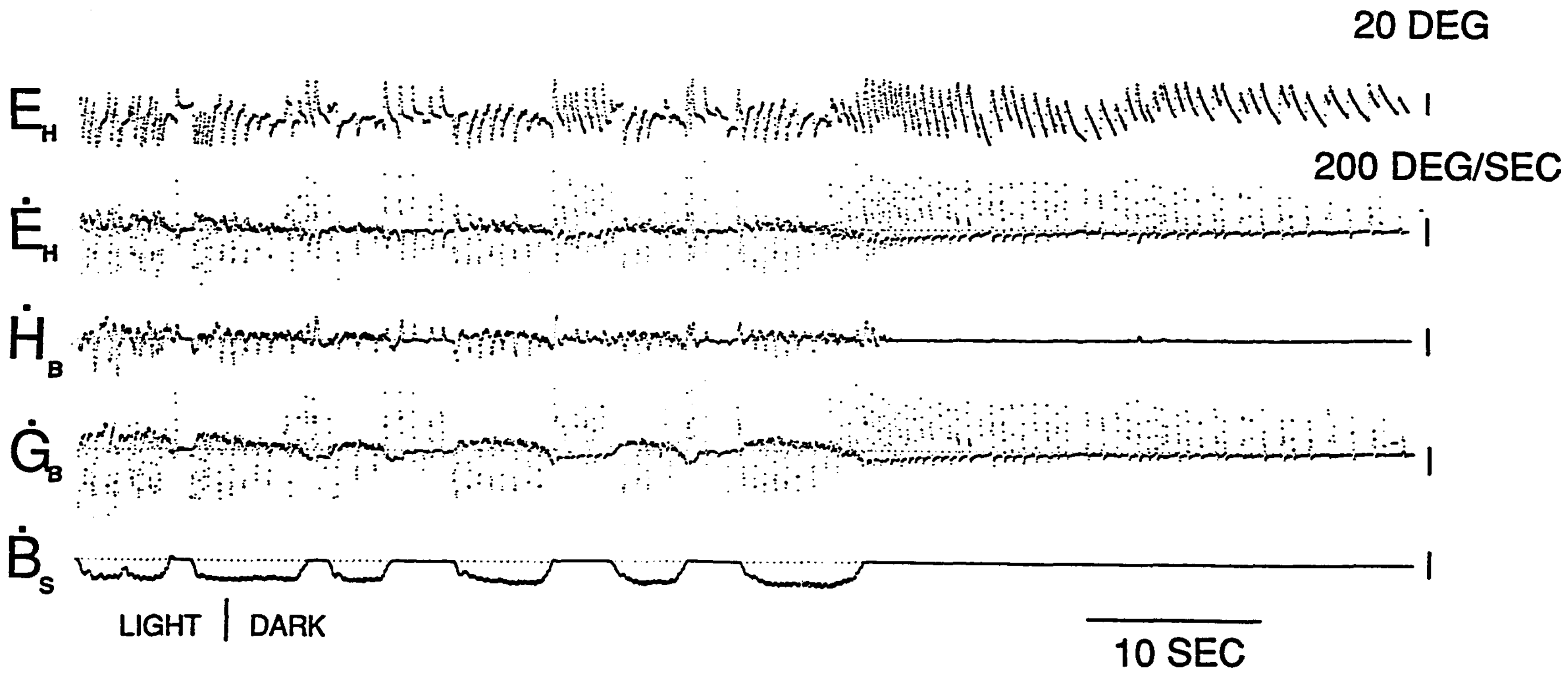

ACTIVE ROTATION

COUNTERCLOCKWISE

PASSIVE ECCENTRIC VERTICAL AXIS ROTATION IN DARKNESS

Figure 14

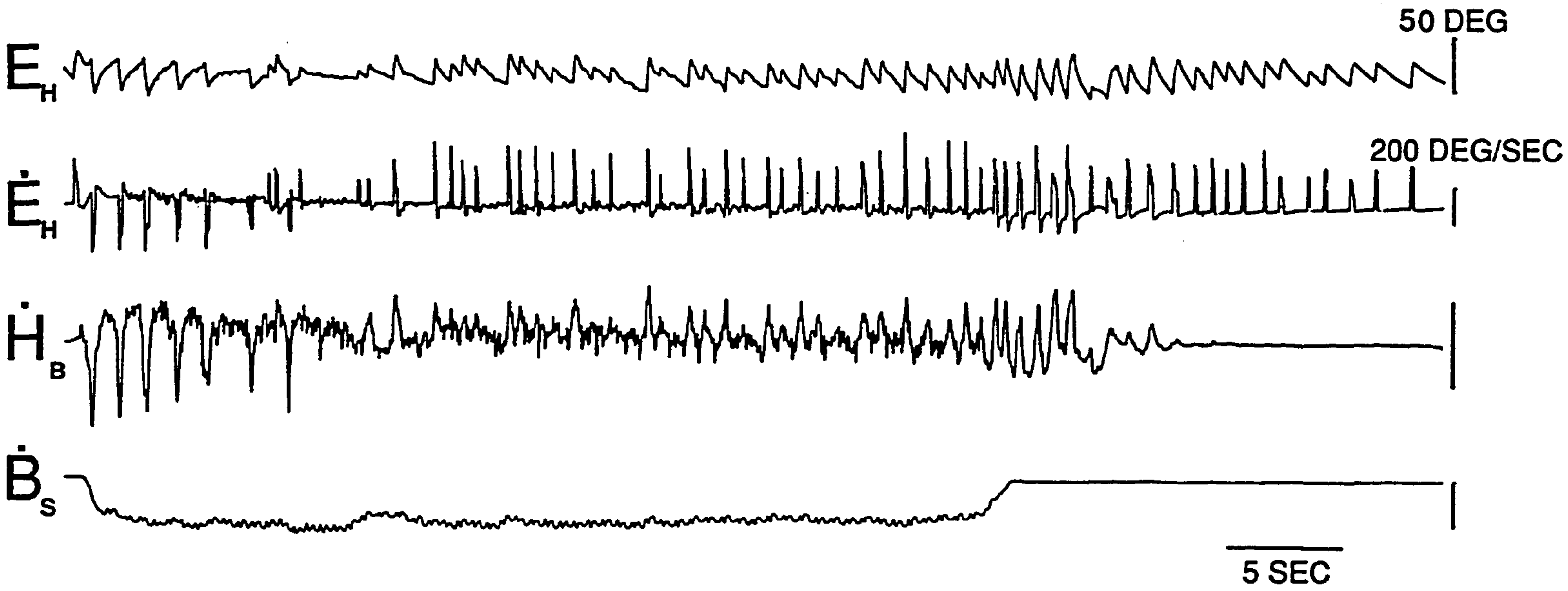
Typical sequence of short intervals of running followed by periods of the animal remaining stationary but experiencing strong post-rotatory responses, which were usually eliminated by active rotation. All velocity calibrations are 200 deg/s.


20 DEG
E_H
200 DEG/SEC
$\dot{E}_H$
$\dot{H}_B$
$\dot{G}_B$
$\dot{B}_S$
LIGHT | DARK
10 SEC

The anti-compensatory head and eye nystagmus during running in Fig. 15 could have been either secondary after-nystagmus or spontaneous nystagmus, but the interesting feature is that such nystagmus was expressed through both the head and eyes for as long as the animal was actively moving. This provides evidence that a central storage or integration mechanism influences head slow phase velocity, since no peripheral sensory transducer could have been responsible for such movements. It also shows that compensatory head movements were not merely a function of head torque due to linear acceleration, but were linked to a central representation of body velocity in space, even when this was in error. As in the other post-locomotory recordings, prolonged post-rotatory nystagmus was present only in the eyes in Fig. 15 after the initial 6-8 beats of concurrent head nystagmus.

Figure 15

Compensatory and anticompensatory nystagmus recorded during prolonged CCW running by monkey rh. After the initial compensatory gaze nystagmus had decayed to zero, anticompensatory gaze nystagmus followed with leftward slow phases. When the animal stopped, the slow phase velocity of the anticompensatory eye movements intensified. Initially, the post-locomotory response consisted of brisk head and eye nystagmus. The head nystagmus decayed rapidly and the eye nystagmus continued.


50 DEG
E_H
200 DEG/SEC
$\dot{E}_H$
$\dot{H}_B$
$\dot{B}_S$
5 SEC

QUANTITATIVE ANALYSIS OF SLOW PHASE VELOCITIES DURING ACTIVE AND PASSIVE ECCENTRIC ROTATION:

The gains of compensatory slow phase gaze velocity during active running at approximately 200 deg/s and passive eccentric rotation at 200 deg/s with the head fixed were compared (Fig. 16). The angular acceleration was greater than 2 radian/s during both active and passive rotation. Thus, both would cause maximal deflection of the cupula (Goldberg and Fernandez 1971). The linear accelerations were equal, being approximately 0.5 g. Gaze gains were normalized to the animal's body velocity in space ($\dot{B}_S$) so that they could be compared directly. During active rotation, i.e., during running, gaze gains were composed of contributions of the head and eyes, whereas during passive eccentric rotation, only eye velocities contributed to changes to gaze velocity. While actively running in the clockwise direction (Fig. 15 A), rh's gaze compensation was close to 1 for about 12 s (Points A1-A4). This is also shown in the plot of $\dot{G}_B$ versus $\dot{B}_S$ on the right (Fig. 15 B), in which the corresponding points 1-4 lay along the unity gain line. Thereafter, gaze gain fell slowly to about a gain of .4 after 48 seconds (Fig. 15 A & B, point 8). The average gain value for the entire run was .59.

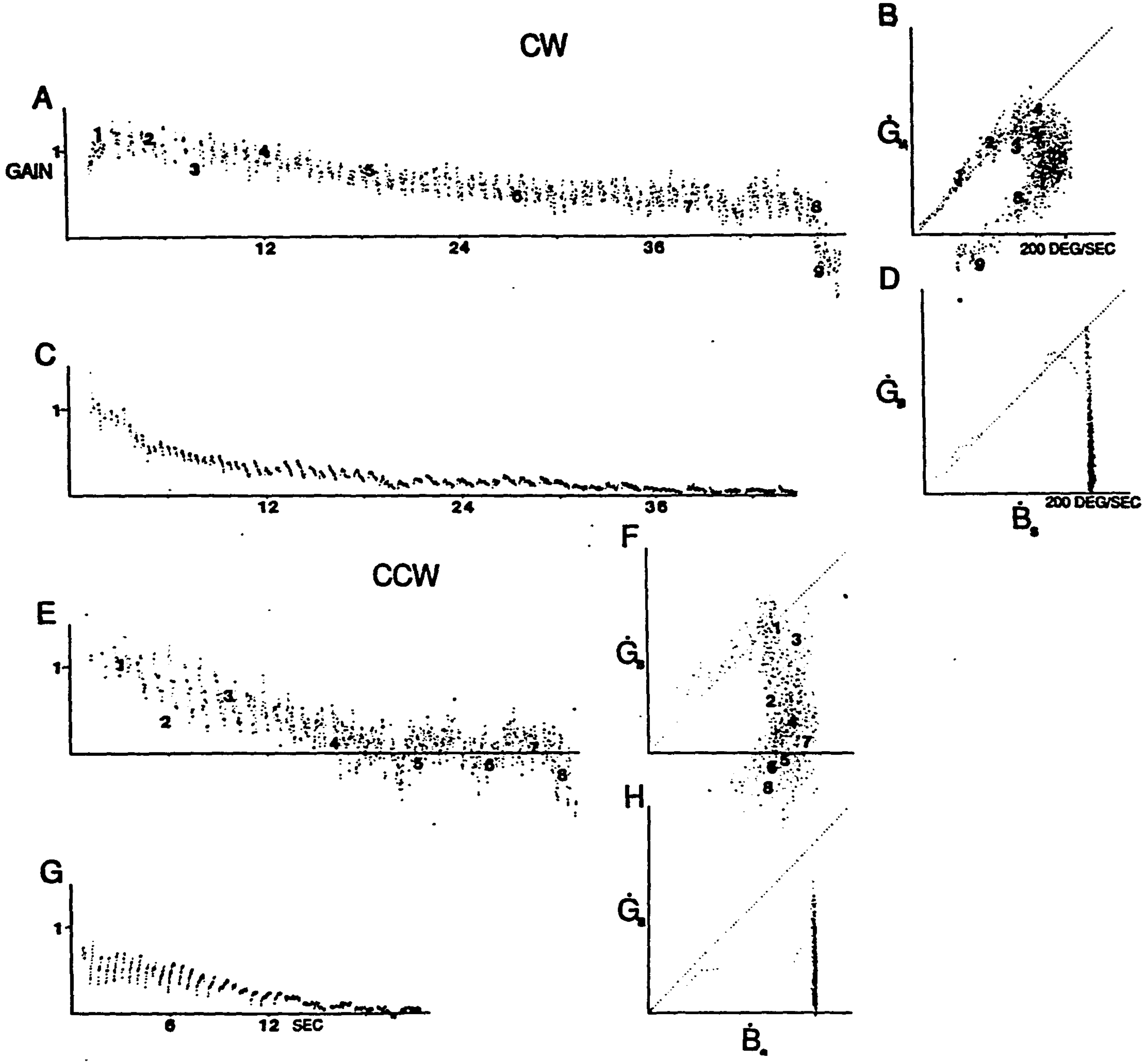
During passive eccentric rotation, on the other hand, gaze velocity was initially close to unity, but fell more rapidly, so that by 12 seconds the gain was approximately .33, and by 48 seconds it had fallen to zero (Fig. 15 C). The average value for the rotation was .22. The predominance of the low gain values is emphasized in the $\dot{G}_B$ vs $\dot{B}_S$ plot (Fig. 15 D). Findings were similar during counterclockwise rotation (Fig. 15 E-H). In this instance, the initial gaze gain was higher during active rotation (Fig. 15 E & F) than during passive eccentric rotation (Fig. 15 G & H), and gaze compensation was maintained somewhat longer during active than passive rotation, although at a low level. The average gain of the slow phase gaze velocity during counterclockwise running was .31, slightly above the values for passive counterclockwise rotation (.28). The comparison of active and passive responses during comparable rotations documents that the initial gain of the compensatory movements was higher when the animal was in active motion, and that gain compensation lasted longer and was stronger when the animal was running than when it was stationary. The data also show that when an asymmetry was present in the dominant time constant of the VOR, as in rh, the gain of gaze compensation was better in the direction of the longer dominant time constant, i.e., toward the side of the greater velocity storage. This provides additional support for the hypothesis that velocity storage supports gaze compensation during active running.

Figure 16

Characterization of monkey rh's asymmetry and comparison of active and passive gains. A, Gaze gain ($\dot{G}_B / \dot{B}_S$) plotted against time for the CW run pictured in Fig. 1A. B, slow phase gaze velocity plotted against body velocity in space. Numbers in A and E indicate the same data points in B and F, respectively. The dotted line in B indicates unity gain. A higher density of points indicates more time spent around at various velocities. Points below the abscissa (i.e. 9) were anticompensatory due to deceleration, when the monkey stopped running and had post-rotatory nystagmus.

C, D, Same format as in A and B except the monkey was passively rotated eccentrically at 200 deg/s around the same radius with the head fixed. Note the decay of slow phase velocity to zero despite continued rotation.

E, F, Active rotation, taken from the data shown in Fig. 1B. Note the more rapid decay and lack of continuous compensatory nystagmus during running. G,H, Passive eccentric rotation in the CW rotation direction with the head fixed. Note the similarly short time constant in G as in E.


CW
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GAIN
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9
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36
B
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GAZE COMPENSATION WHILE CIRCLING ON A MOVING PLATFORM:

Numerous cues could potentially be used by the animals to generate an estimate of body velocity in space which could be used to drive gaze compensatory nystagmus during prolonged running in darkness. In addition to excitation of the semicircular canals by angular acceleration and the otolith organs by linear acceleration, circular running resulted in shear forces between the paws and platform, torque on the head, pressure of the harness against the body and tension of the muscles of the limbs and axial skeleton. These extravestibular cues would be transduced by mechanoreceptors in the skin, muscle spindles, tendon organs and joint capsule receptors. We will consider all extravestibular, nonvisual input, including proprioception, as being subsumed under the term, 'somatosensory'. In order to investigate the contribution of motor activity and somatosensory input to the generation of compensatory gaze nystagmus, vestibular input was uncoupled from signals resulting from active body movement by counter-rotating the platform under the animal during locomotion.

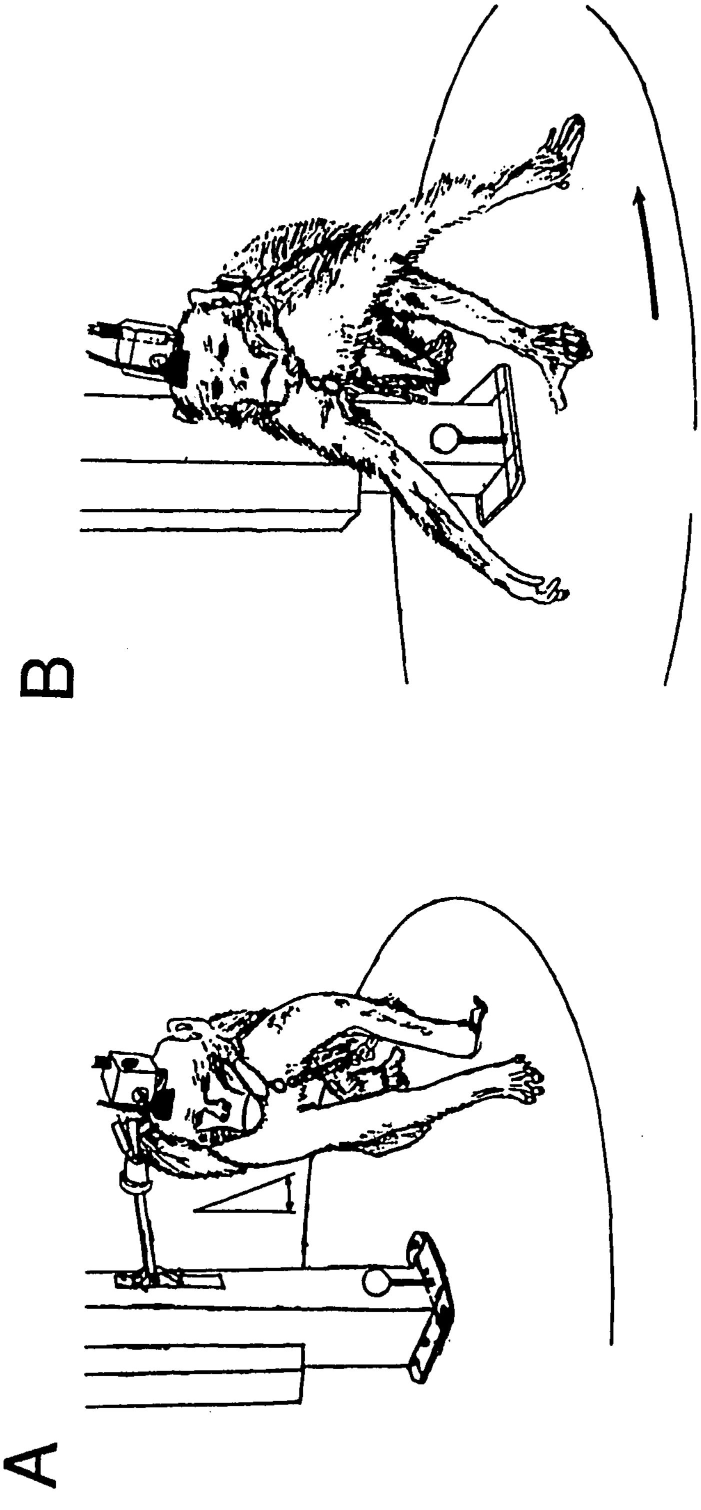
Both animals ran against the counter-rotating platform in darkness. Although the frequency and sequence of the locomotor activity was similar to that under normal conditions, there were distinct differences between the two, particularly in the posture and radius of circling. This was probably largely due to the absence of the linear acceleration when the animal's angular velocity in space was reduced. This is apparent in Fig. 17 which shows comparable postures of rh running in light on a stationary (A) and counter-rotating (B) platform. As determined by infrared imaging, the postures were similar in darkness.

The effects of linear acceleration when the animal was actively circling (Fig. 17 A) can be seen in the inward angle of the body with regard to the limbs and the lateral swing of the chain on the animal's collar. The head was held slightly

Figure 17

A, Drawings of rh running on a stationary platform. Its gait was narrow based, and the radius of rotation was large. The angle next to the animal shows the lateral displacement of its limbs and the collar chain due to centripetal acceleration.

B, Rh running on a counter-rotating platform. Its gait was wide based, and the center of gravity was closer to the axis of rotation. Its forelimbs were moved back and forth in a shuffling movement as it moved forward. Note the vertical position of the chain, denoting a lack of linear acceleration.


A
B

tilted forward, looking into the direction of motion. When the animal was running on the counter-rotating platform (Fig. 17 B), instead of the long axis of the body being roughly perpendicular to the radius of rotation, its hind quarters were tucked in closer to the post, and the forelimbs were moved laterally, almost in the animal's coronal plane. The body was closer to the upright, and the head was held nose up. Considering all of the postural differences, we would not imply that the animal was unaware of the change in experimental conditions.

A recording of rh running in the clockwise direction in darkness on a counter-rotating platform is shown in Fig. 18. Platform compensation gain was held constant at .2, so that the animal's actual velocity in space was 20% less than the velocity re platform (angular velocity - platform velocity = gait velocity). Continuous head and eye nystagmus was present for the duration of the 60 s run. The quick phases of the compensatory gaze nystagmus were removed from the gaze velocity trace.

In Fig. 19, the gain of the negative feedback amplifier was increased as monkey rh ran, causing the running surface to turn faster in the opposite (CCW) direction. The animal responded by increasing its motor activity to overcome the progressively greater platform velocity in space ($\dot{P}_S$), thus maintaining a relatively constant velocity in space ($\dot{B}_S$) of about 100 deg/s for 30 s. This change in locomotor frequency is reflected in the body re platform velocity ($\dot{B}_P$, gait velocity), which climbed to nearly 400 deg/sec.

Over this considerable range of motor activity, rh continued to have head and eye nystagmus ($\dot{E}_H$ and $\dot{H}_B$). The frequency and slow phase velocity of the compensatory gaze nystagmus ($\dot{G}_B$) remained fairly constant throughout the run. Eye velocity in the head ($\dot{E}_H$) was equal and opposite to head in space velocity ($\dot{H}_S$), except for the concurrent quick phases. When slow phase head on body velocity was

Figure 18

Recordings from rh running in darkness on a counter-rotating platform. Head and eye nystagmus persist for as long as the animal continues to run in darkness. The nystagmus lasts longer than that observed during passive rotation around the same path at a similar velocity. Quick phases of compensatory gaze nystagmus have been removed from the gaze velocity trace for clarity. The platform was counter-rotating at a low compensation gain. When the animal stopped, post-rotatory nystagmus occurred only in the eyes.

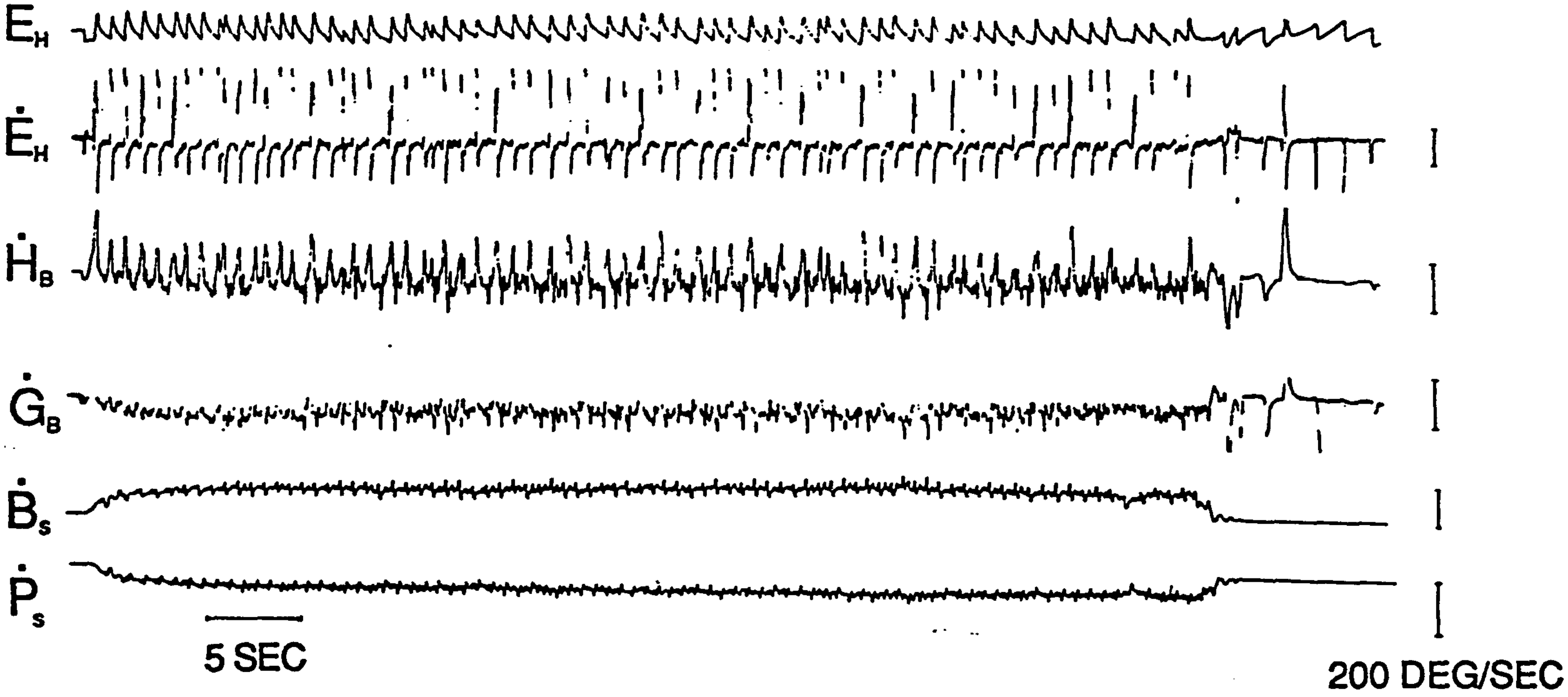
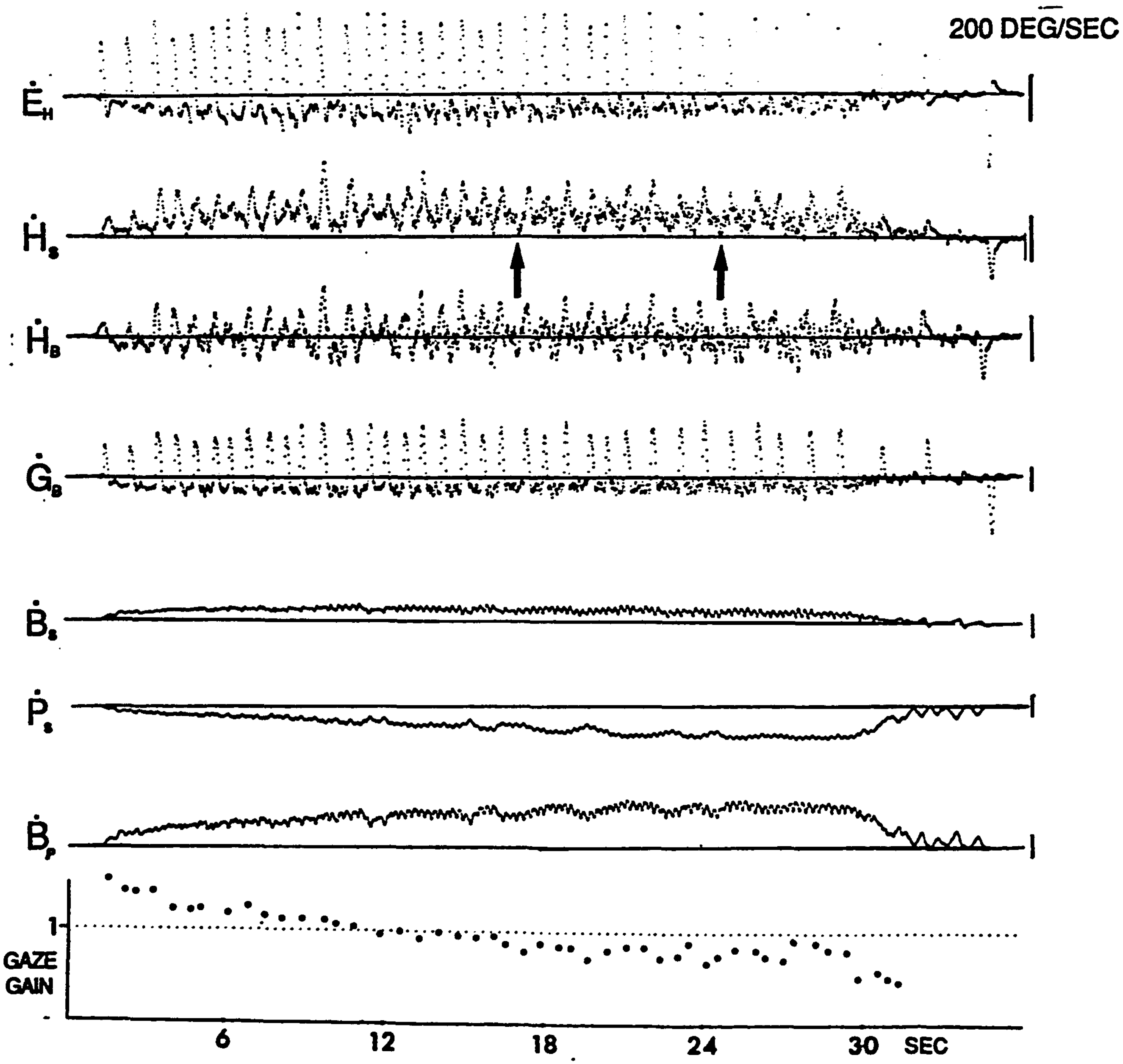

E_H
$\dot{E}_H$
$\dot{H}_B$
$\dot{G}_B$
$\dot{B}_s$
$\dot{P}_s$
5 SEC
200 DEG/SEC

Figure 19

Platform velocity in space ($\dot{P}_S$) increased linearly during the run, so that in order for the animal to maintain a desired body velocity in space ($\dot{B}_S$), it had to increase gait velocity ($\dot{B}_P$), as well. Gaze on body velocity was proportional to actual body velocity in space, but gains were greater than unity, reflecting increased somatosensory input. Gaze gain was smoothed by averaging over 640 ms intervals. Nystagmus frequency was constant despite great changes in locomotor activity. Head in space velocity ($\dot{H}_S$) frequently reached zero deg/s, indicating perfect head stabilization. Calibrations are 200 deg/s for each trace.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SEC

maximal, the head was momentarily stabilized in space ($\dot{H}_S$ = zero deg/s, arrows in Fig. 19). At those instances, eye velocity in the head also was at zero.

Of note was that the gaze nystagmus was primarily compensatory only for the animal's inertial velocity, and was not proportional to gait velocity over most of the duration of the running. This is shown in the calculation of gaze gain below. Over the first 12 seconds the gain was higher than unity, when canal output combined with somatosensory signals and velocity storage. Thereafter, the gaze gain hovered at unity for about 6 s and then was maintained at about .8 for the duration of the run. CW running against a counter-rotating (Fig. 19) and on a stationary (Fig. 16 A) platform resulted in similar gaze gain vs. time envelopes, except that gains were higher with additional locomotor activity.

In the experiment represented in Fig. 20, the platform compensation circuit was activated 10 s into the animal's run. This resulted in a velocity step of approximately 100 deg/s to the left. The gain of the feedback amplifier was high (.85), so that body velocity in space was only 15% of the animal's gait velocity. Gaze velocity was clearly maintained at a level well above that necessary to compensate for inertial movement. Again, the frequency of nystagmus was related to actual gaze velocity, and not influenced by the increased locomotor activity. At the end of the run, there was an OKAN-like after response seen in the eye position trace, even though there was a small velocity step which should have elicited rightward slow phase eye velocity, as seen in Fig. 18. The increased somatosensory activity during the latter part of the run in Fig. 20 presumably charged velocity storage which counteracted the velocity step and was responsible for the continued leftward slow phase eye velocity after stopping.

Figure 20

Sudden activation of platform compensation circuit during CW running in darkness (rh). The animal's angular velocity re earth was reduced, while the gait velocity increased. The animal experienced a velocity step when the platform began moving, but no post-rotatory response occurred. Slow phase gaze velocities were maintained even in the absence of significant linear acceleration or earth reference rotation. No post-rotatory response occurred when the animal and platform stopped.


E_H
$\dot{E}_H$
$\dot{H}_B$
$\dot{G}_B$
$\dot{B}_s$
$\dot{P}_s$
5 SEC
200 DEG/SEC

HEAD-EYE CONTRIBUTIONS TO GAZE ON BODY VELOCITY DURING INDIVIDUAL BEATS OF NYSTAGMUS:

Noteworthy features of the nystagmus of Fig. 5 are demonstrated in the expanded records and phase plots of Fig. 21. Two additional parameters are shown in this figure, head velocity in space ($\dot{H}_S$) and gaze velocity in space ($\dot{G}_S$). $\dot{H}_S$ is the driving force on the VOR, while $\dot{G}_S$ indicates how well gaze velocity compensates for movement relative to the visual surround. Thus, it demonstrates the functional consequences of the eye and head nystagmus.

A typical slow phase terminating in a quick phase is shown in Fig. 21 A. The trace began in the middle of the slow phase occurring at position 'A' in the $\dot{E}_H$ trace of Fig. 5. The animal's running velocity in space (Fig. 21 A, $\dot{B}_S$, bottom trace) was relatively constant. Head velocity in space ($\dot{H}_S$, top trace) was initially close to zero. This was due to head on body movement ($\dot{H}_B$), which largely compensated for body velocity in space. Since $\dot{H}_S$ is the driving force on the VOR, at that moment the VOR would not have caused eye movement. Eye in head velocity was low, with $\dot{E}_H$ and $\dot{H}_B$ combining to form a relatively constant gaze on body velocity ($\dot{G}_B$) which compensated for body velocity in space ($\dot{B}_S$). Adding $\dot{G}_B$ and $\dot{B}_S$ yielded gaze velocity in space ($\dot{G}_S$), the gain of which was slightly higher than unity.

Toward the end of the slow phase, $\dot{H}_B$ decreased as the head began to accelerate in the quick phase direction. This resulted in an increased head in space velocity ($\dot{H}_S$). Eye in head velocity ($\dot{E}_H$, a) increased correspondingly, due to activation of the VOR and possibly the visual system by retinal slip. This maintained gaze velocity in space ($\dot{G}_S$) constant and close to zero. The eyes then reversed direction and began a quick phase (b) which reached a peak (c), had an inflection on the falling portion (d) and terminated abruptly (e). The termination occurred well before the head quick phase ended. Thus, at e the head was moving in the forward or running direction, and the eyes were moving in the backward or compensatory direction (f). The eye movement raised slow phase gaze on body velocity rapidly so that it compensated for body in space velocity, bringing gaze on body velocity to approximately 200 deg/s, despite the head velocity in the opposite direction. Note that the head on body velocity ($\dot{H}_B$) was considerably larger than the eye in head velocity ($\dot{E}_H$) during much of the slow phase, and that gaze in space velocity ($\dot{G}_S$) was brought close to zero at the beginning and end of the head quick phases by the eyes which compensated for the changes in head velocity.

A phase plot of eye in head velocity ($\dot{E}_H$, Y axis) versus head on body velocity ($\dot{H}_B$, X axis) during this movement demonstrates the relationship between the head and eyes more precisely (Fig. 21 A, left). Each dot represents a sample every 1.6 msec, and the tick marks represent 200 deg/sec on each axis. The angular position of the animal during the movement is indicated by the darkened portion of the B_S trace, corresponding to the same trace in Fig. 5. The trace started on the left (arrow) at a time when the head was providing most of the compensatory gaze velocity. The density of dots at the onset of the trace indicates that considerable time was spent with that combination of head and eye velocity. As the slow phase terminated, head velocity fell and eye velocity rose in the compensatory direction (a). The slope of the line was approximately -1. This indicates that the head on body ($\dot{H}_B$) and eye in head ($\dot{E}_H$) velocities covaried linearly and reciprocally in compensating for the animal's constant velocity in space. At the onset of the quick phase at b, eye in head ($\dot{E}_H$) and head on body ($\dot{H}_B$) velocity fell rapidly, crossing zero at the same time. This indicates that eye and head quick phases began at the same moment. Eye velocity peaked first (c) and then fell rapidly as head velocity was maintained (d-e).

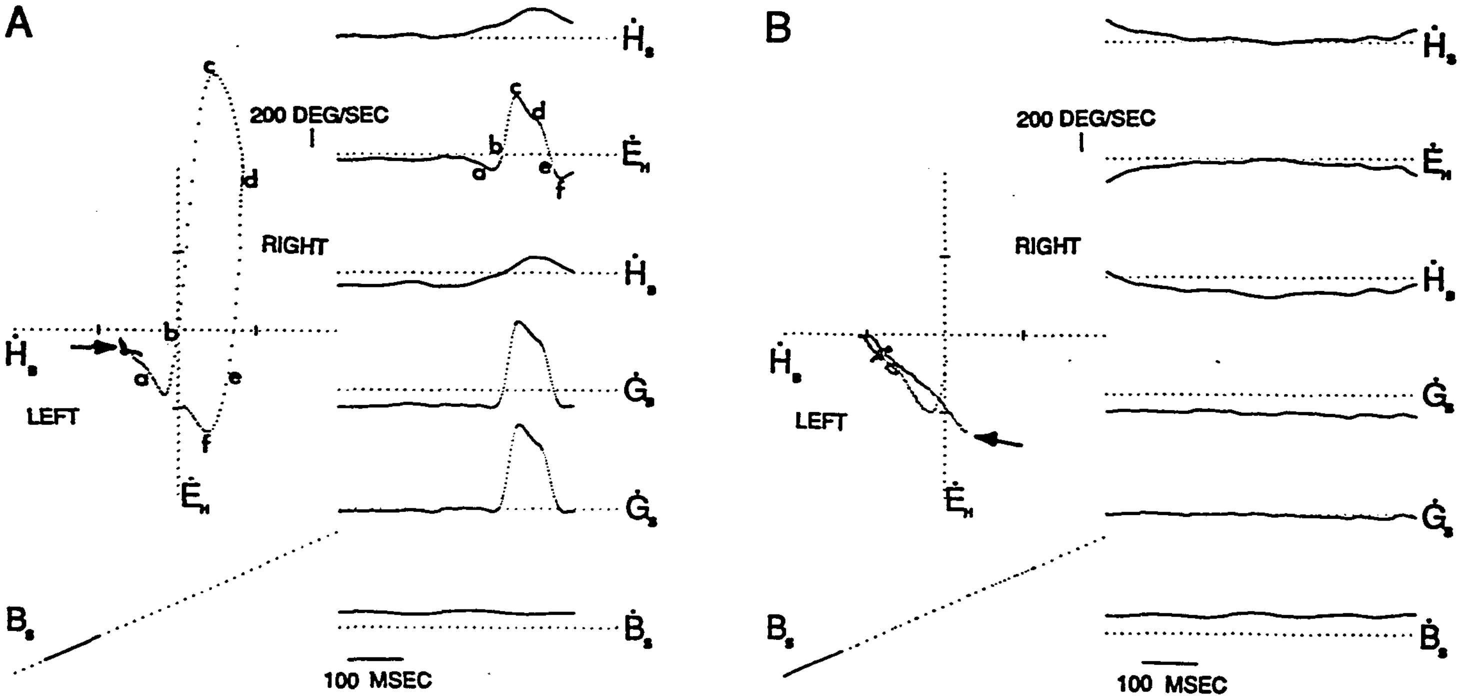
Figure 21

Phase plots and expanded view of four segments of data from Figure 5. A, End of long eye-head slow phase and subsequent quick phase. On the left, head on body velocity is plotted against eye in head velocity, with time as the implicit variable. Below is the potentiometer recording of the animal's body position in space. The solid segment of the B_S line indicates the animal's position in space at the time of the eye and head movements shown above. The arrows on the eye/head velocity phase plot in A and B indicates the earliest point in time. This corresponds to the leftmost point on the $\dot{E}_H$ and $\dot{H}_B$ traces on the right.

B, Slow phase taken during extended fixation. Note that the $\dot{H}_B$ slow phase brought $\dot{H}_S$ close to zero. Consequently $\dot{E}_H$ also remained very low. Gaze in space ($\dot{G}_S$) was stable throughout.

C, Slow phase that achieved zero $\dot{G}_S$ with lower $\dot{H}_B$ and higher $\dot{E}_H$ than in B. The head movement (Fig. 3, C) was small.

D, Large head and eye saccade with many inflections. The eye quick phase lasted for 320 ms, and the head quick phase was longer.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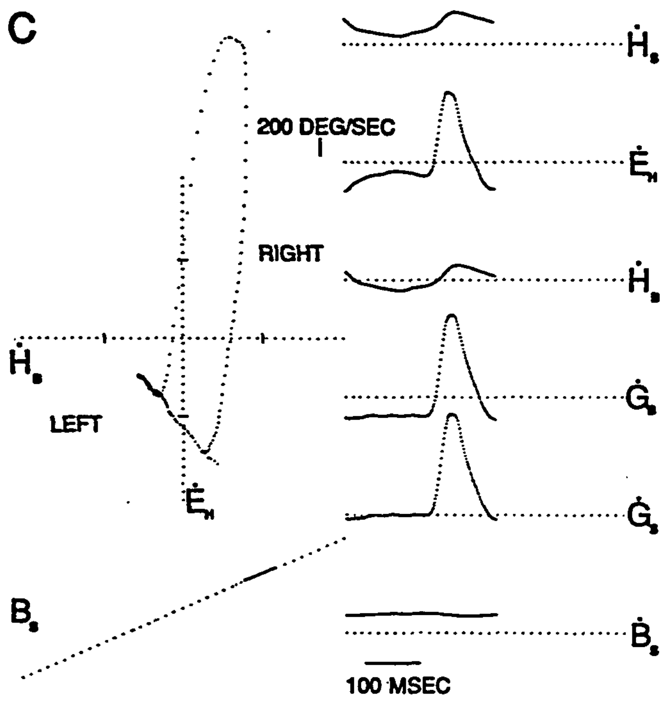
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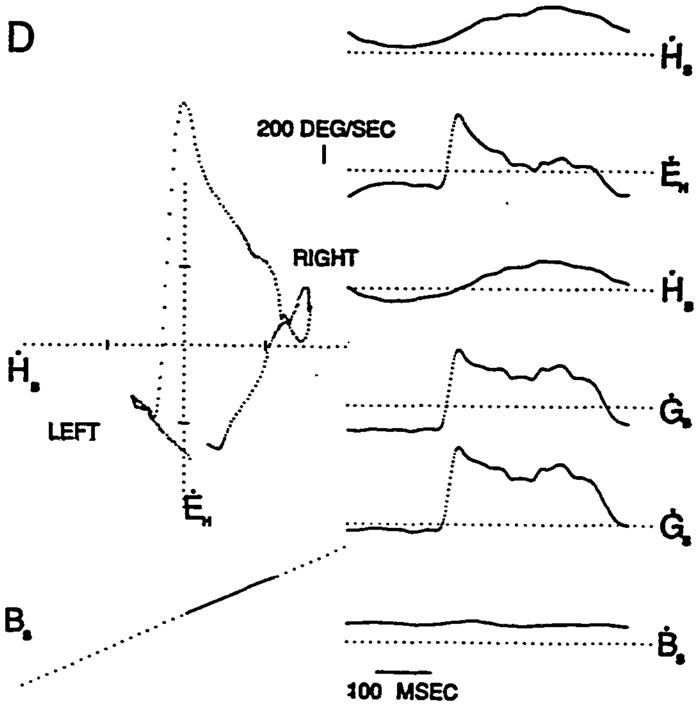
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A typical feature of gaze quick phases was a slight pause in eye deceleration which occurred frequently, as at d. This was associated with a similar deflection or peak in head velocity ($\dot{H}_B$). The eyes then moved rapidly in the compensatory direction (e) with little change in head on body velocity. When the head finally began to accelerate into the slow phase direction (f), eye in head velocity fell, and the phase plot moved along the same slope as the previous compensatory velocity. The interaction between the head and eyes in stabilizing gaze during slow phases is emphasized in Fig. 21 B, a record of the slow phase marked B in ($\dot{E}_H$) of Fig. 5. It occurred as the animal ran toward the experimenter. The trace in Fig. 21 B began as head on body velocity ($\dot{H}_B$) crossed zero into the compensatory direction initiating a head slow phase. Eye velocity ($\dot{E}_H$) fell toward zero where it remained as the head performed most of the gaze compensation. Small high frequency variations in head velocity in space were reflected in the eye in head velocity ($\dot{E}_H$) trace. The phase plot of eye in head ($\dot{E}_H$) against head in body ($\dot{H}_B$) velocity began with eye velocity at a maximum and head on body velocity still in the quick phase direction (arrow). It fell along a slope that was approximately unity as head velocity ($\dot{H}_B$) increased. Considerable time was spent in the middle of the slow phase with head on body velocity ($\dot{H}_B$) high and eye in head velocity ($\dot{E}_H$) low or nearly zero. At the end of the slow phase when the head velocity fell back toward zero, eye in head velocity ($\dot{E}_H$) rose to maintain unity gain, before initiating its own quick phase.

In this instance, head and eye velocities combined to provide gaze compensation during different parts of the slow phase. The eyes moved in the orbit primarily at the beginning and end of the slow phase to stabilize gaze at the end and onset of the head quick phase, respectively. The increases in leftward $\dot{E}_H$ was presumably in response to increased rightward head in space velocity (top trace), activating the VOR or optokinetic reflexes.

An example in which the eyes performed a larger portion of gaze compensation during the slow phase is shown in Fig. 21 C, taken from the portion marked, C, in Fig. 5. The recording started just before the head slow phase began. Eye in head velocity ($\dot{E}_H$) was high at the origin of the trace to overcome the anti-compensatory head quick phase still in progress. Eye velocity ($\dot{E}_H$) covaried reciprocally with head velocity ($\dot{H}_B$) to hold gaze on body velocity ($\dot{G}_B$) constant and gaze in space velocity ($\dot{G}_S$) close to zero. As head slow phase velocity ($\dot{H}_B$) decreased at the end of the slow phase, eye velocity ($\dot{E}_H$) transiently rose before the quick phase started. The phase plot on the left of Fig. 21 C demonstrates that in this instance the eye quick phase began before the head quick phase. Peak head quick phase velocity occurred 10-20 msec after peak eye velocity, so the pause in eye acceleration (d in A) caused a broadening of the eye velocity profile rather than an inflection. This is similar to gaze velocity profiles observed by Guitton et al. (1984) and Tomlinson and Bahra (1986a) in cat and monkey, respectively.

Eye quick phases could be considerably longer than shown in either Fig. 21 A or C. The example shown in Fig. 21 D, from the segment marked D in Fig. 5, was one of the longest. The eye quick phase lasted for 320 ms, and the head quick phase was even longer. Inflections were present on both the eye ($\dot{E}_H$) and head ($\dot{H}_B$) velocity traces during the quick phases, and appeared to be coincident. As in Figs. 21 A & C, the eyes compensated for the head on body ($\dot{H}_B$) velocity at the onset and end of the head quick phase to hold gaze on body ($\dot{G}_B$) velocity constant in between gaze quick phases. In this instance gaze in space ($\dot{G}_S$) velocity was higher than unity in the preceding slow phase. The phase plot, shown on the left, demonstrates that eye quick phase velocity varied irregularly as the head quick phase velocity rose, with the eyes reversing their velocity first to achieve compensatory gaze velocity.

In summary, when running in light, gaze in space was stationary during the slow phases, and it moved forward in rapid saccadic shifts in the running direction during the quick phases. Gaze compensation was accomplished by coordinated movements of both the head and eyes. While the head accelerated more slowly than the eyes, it began to accelerate in the quick phase direction prior to eye acceleration. The eyes, driven by the VOR, compensated for this lead in head deceleration at the end of slow phases, as well as for the lag in head velocity at the beginning of slow phases. This shortened the total time taken for the gaze quick phase, allowing the animal to maximize periods of fixation.

COMPOSITE BEAT OF COMPENSATORY GAZE NYSTAGMUS IN DARKNESS:

Since the beats of head and eye nystagmus were relatively regular while rh was running in the clockwise direction, it was possible to average them to obtain their typical characteristics. The zero crossing marking the onset of quick phase gaze velocity ($\dot{G}_B$) was used as a trigger. An average constructed from 20 consecutive beats taken during clockwise running in rh is shown in Fig. 22 B, with its associated $\dot{E}_H$ and $\dot{H}_B$ phase plot (Fig. 22 A). Two of the individual beats of head and eye nystagmus included in this average are displayed in Figs. 22 C & D. The number of beats that were averaged in each 16 ms interval after the initial trigger is shown in Table 2.

As indicated by the zero crossing of velocity (Fig. 22 A), both the head and the eyes reversed direction at approximately the same moment, although as shown in the phase plots of Fig. 22 C & D, the eyes could slightly lead the head. The velocity of the eyes peaked first, leading the peak head velocity by approximately 130 ms. This is similar to the data in the phase plots of quick phases during running in light (Fig. 21).

TABLE 2: Number and duration of eye and head movements contributing to average shown in Figures 22 A & B.

NUMBER OF MOVEMENTS IN AVERAGE	DURATION (ms)
20	0-464
19	480
18	496-592
16	608-656
15	672
13	688
11	704
10	720
8	736-768
6	784
5	800-832
2	848
1	864-896

Table 2: Number of movements contributing to the averaged gaze movements shown in Fig. 22 A and B. Time after the onset of recording is shown in the "Duration" column.

Slow phase gaze on body velocity ($\dot{G}_B$) was maintained on average for 528 ms with 675 ms being the longest slow phase. At the termination of the slow phase, head on body velocity ($\dot{H}_B$) fell first. This was accompanied by an increase in compensatory eye in head velocity ($\dot{E}_H$) which maintained gaze velocity on the body ($\dot{G}_B$) at a relatively constant level until the onset of the eye and head quick phases. Together they moved gaze forward in a saccadic fashion in the running direction. The irregularities in the $\dot{G}_B$ trace toward the end of Fig. 22 B are due to the termination of the individual beats.

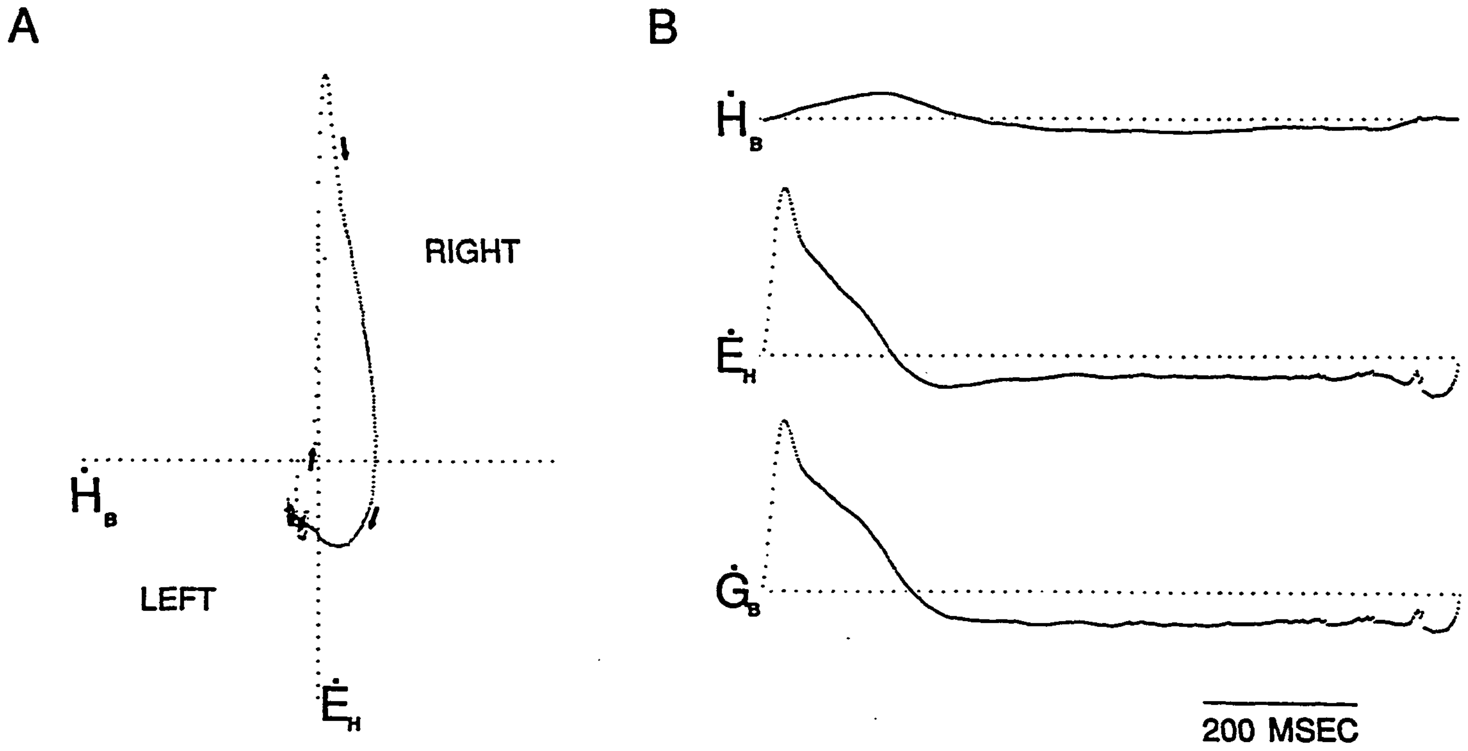
The average duration of the eye quick phases was 160 ms as against an average duration of the head quick phases of 250 ms. The eye quick phases often had prominent inflections that were also present in the head quick phases (Fig. 22 C & D). As during running in light, the velocity of the eyes reversed direction shortly after the head quick phase velocity ($\dot{H}_B$) had reached its peak. Rising rapidly in the compensatory direction, eye velocity ($\dot{E}_H$) quickly brought gaze on body velocity ($\dot{G}_B$) up to its steady state level, marking the beginning of the slow phase. As head on body velocity climbed toward a steady state level, $\dot{E}_H$ fell, probably due to a decrease in VOR activity as the head became more stable in space.This data demonstrates that the head and eyes were synchronized and tightly coupled during the head and eye nystagmus, and that they acted synergistically to hold compensatory gaze velocity constant during running in darkness. Thus, gaze compensation during circular locomotion in the absence of vision was essentially similar to that during running in light. Since the phases of locomotion and quick phases were not time-locked, high frequency perturbations in body velocity due to limb movement, and therefore in gaze velocity, were not present in the average.

Figure 22

A, Phase plot generated by averaging 20 beats of compensatory gaze nystagmus in darkness.

B, Averaged movements in time. Eye quick phases began slightly before head quick phases and reached peak velocity within 30 ms. Eye velocity paused during head accelerations. Gaze on body velocity became compensatory while head was still moving in the quick phase direction, due to slow phase eye velocity which decreased as head on body movement began to compensate for body velocity in space.

C,D, Individual beats included in average. The tick marks in C & D show 200 deg/s. A 200 deg/s calibration is shown for the $\dot{E}_H$ trace in C & D. The calibrations were the same for each of the velocity traces on all parts of the figure.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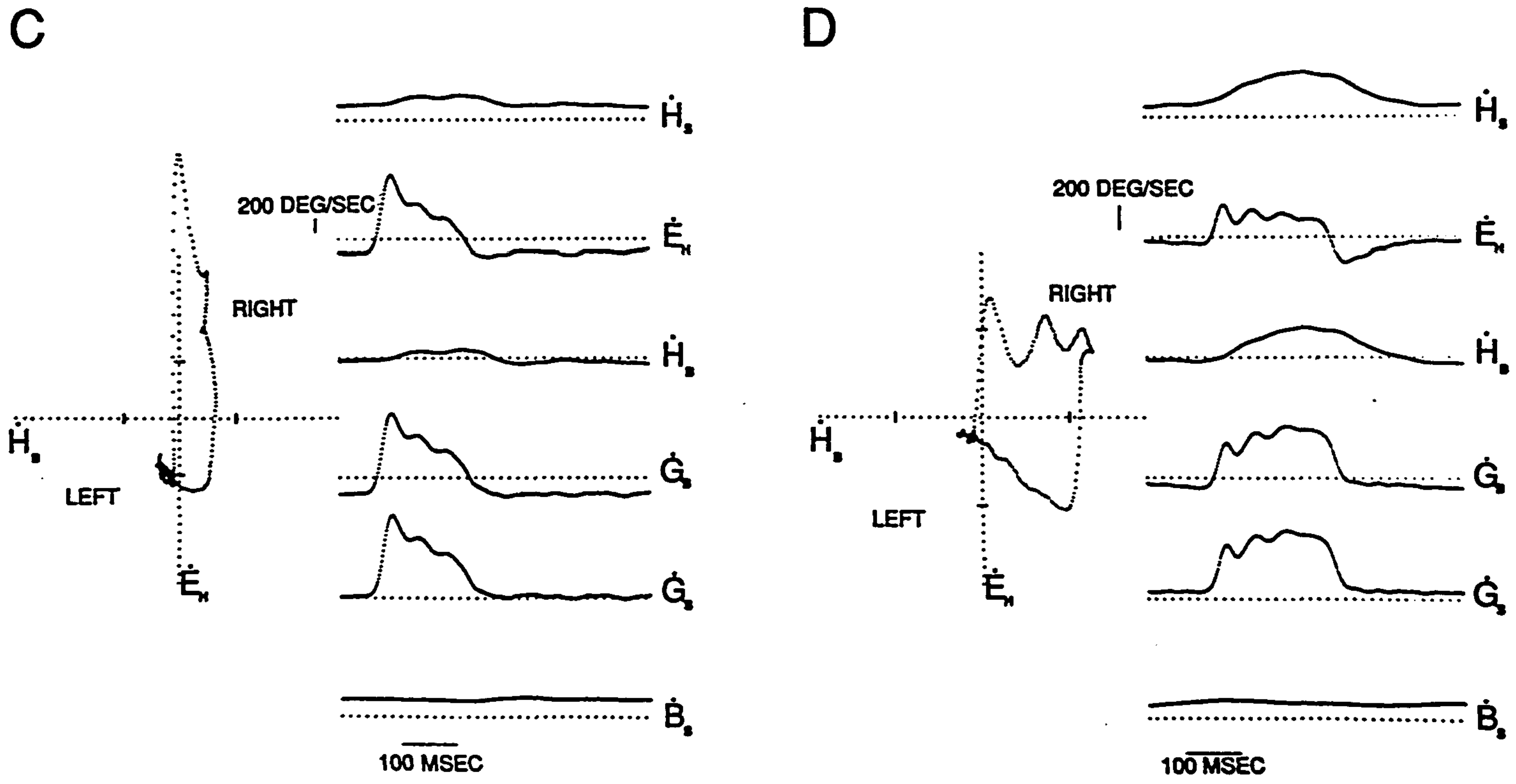
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100 MSEC

QUICK PHASES OF HEAD AND EYE NYSTAGMUS

During quick phases of compensatory gaze nystagmus, head in space velocity is due to the addition of body velocity in space and head on body rotation. If the VOR were active, ocular quick phases made during running would be slower than equal amplitude movements made only with passive whole body rotation. This was not observed however. Our findings were that quick phases had greater maximum velocities and shorter durations when the animal was running than when it was passively rotated, consistent with findings in the cat (Blakemore and Donaghy, 1980; Douglas, et al., 1982). Since the majority of eye movement amplitudes during running in light were greater than 20 deg, it seems likely that there was suppression of the VOR during the movement (Tomlinson and Bahra, 1986b).

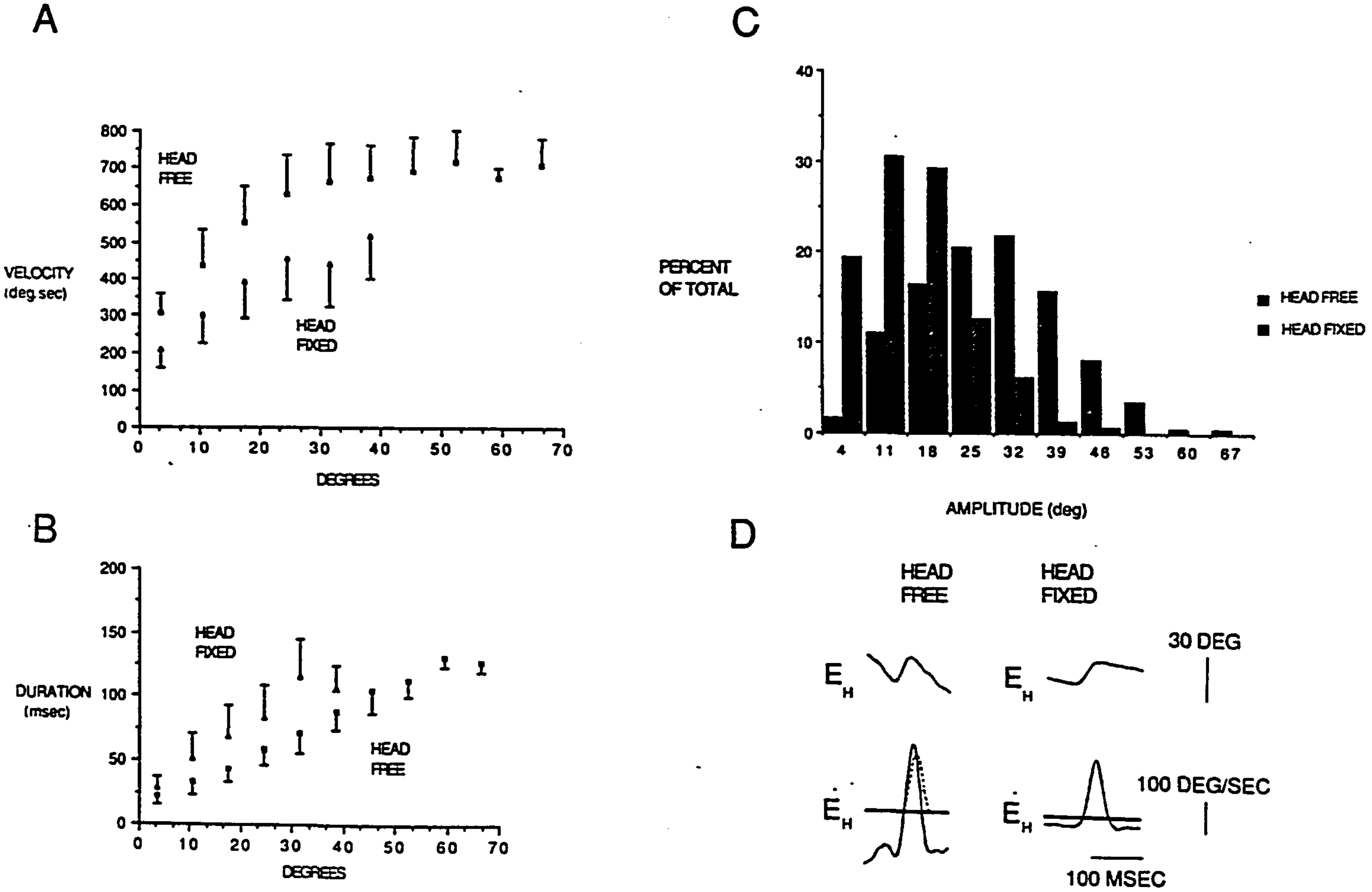
Horizontal eye quick phases of monkey rh in light were compared in head free and head fixed conditions. Head free quick phases were taken during running and head fixed movements during passive vestibular and optokinetic testing. Movements to the right and left were combined. The most significant finding was that the eye quick phases were substantially larger when the head was free to move than when it was fixed (Fig. 23 C). The mean amplitude of 595 head-free quick phases was 29 deg vs 16 deg for 470 head-fixed movements. These values were significantly different ($p>0.001$). Eye movements were averaged in 7 deg bins, and the maximum velocity and duration of equal amplitude movements were compared (Fig. 23 A & B). Quick phases of ocular nystagmus consistently had higher peak velocities (A) and were shorter (B) when they were associated with beats of head nystagmus than when the head was fixed. Examples demonstrating these differences for two equal amplitude quick phases are shown in Fig. 23 D. The head-fixed quick phase velocity is dotted onto the head-free velocity on the left.

Figure 23

Analysis of the horizontal component of ocular quick phases recorded during running (head free) or passive rotation (head fixed) in light in monkey rh. Eye movements during running were faster (A) and shorter (B) than equal amplitude movements made with the head fixed relative to the body. Error bars represent SEM.

C, Histogram of sizes of head free (black bars) and head fixed (cross hatched bars) movements. The head free eye movements had a larger median amplitude.

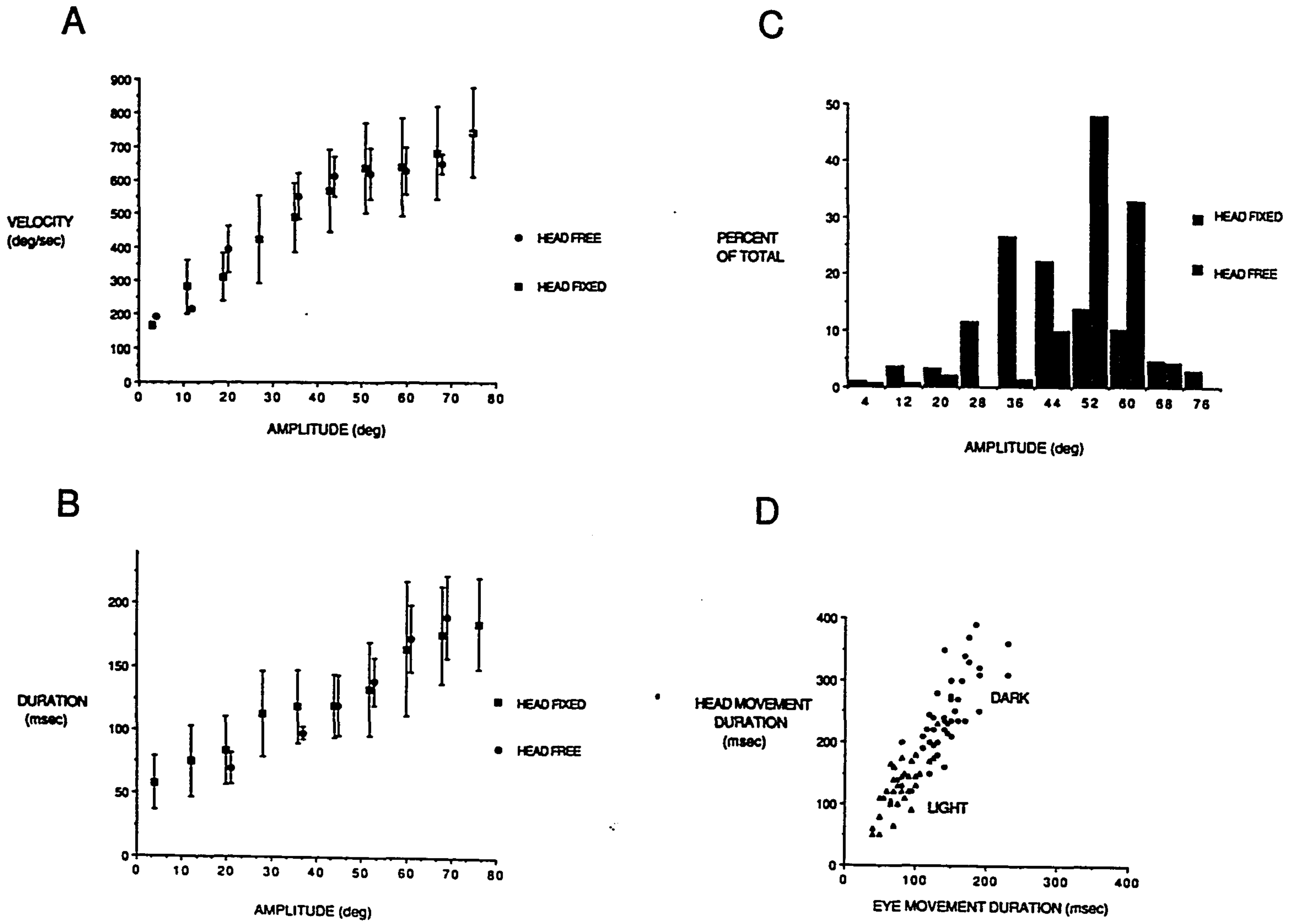
D, Typical head free and head fixed eye velocity profiles for quick phases of roughly equal amplitude. The dotted line behind the head free $\dot{E}_H$ trace is redrawn from head fixed data. It shows the tail in velocity at the end of the movement that accounts for its longer duration.


A
VELOCITY (deg sec)
800
700
600
500
400
300
200
100
0
HEAD FREE
HEAD FIXED
0
10
20
30
40
50
60
70
DEGREES
B
DURATION (msec)
200
150
100
50
0
HEAD FIXED
HEAD FREE
0
10
20
30
40
50
60
70
DEGREES
C
PERCENT OF TOTAL
40
30
20
10
0
4
11
18
25
32
39
46
53
60
67
AMPLITUDE (deg)
■ HEAD FREE
■ HEAD FIXED
D
HEAD FREE
HEAD FIXED
E_H
E_H
30 DEG
$\dot{E}_H$
$\dot{E}_H$
100 DEG/SEC
100 MSEC

Individual eye quick phases were compared in head free (running in dark) and head fixed (passive vestibular stimulation) conditions for monkey rh (Fig. 24). Only the horizontal component of movement was analyzed, and movements to the right and left were combined. Mean values for head free and head fixed quick phase amplitudes were 53 deg (n=140) and 42 deg (n=277), respectively (Fig. 24 C). This is similar to the findings for quick phases in light. Eye movements were averaged in 8 deg bins, and the maximum velocity and duration of equal amplitude movements were compared (Fig. 24 A & B). There were no differences in the amplitude-velocity or amplitude duration relationships in darkness when the head was free to move or was fixed. This is different from the findings during running in light, in which the saccades were faster and shorter when the animals were running. Durations of head and eye quick phases were plotted against each other in Fig. 24 D. (The assignment of eye movement duration to the abscissa and head duration to the ordinate does not imply that they are independent and dependent variables, respectively.) The durations covaried linearly, with movements made in darkness (circles) being significantly longer in duration than movements made in light (triangles), reflecting their greater amplitudes.

Figure 24

Amplitude-peak velocity (A) and amplitude-duration (B) relationships eye quick phases during head fixed passive rotation in darkness (squares) and during head and eye nystagmus while running (circles). Error bars represent the SEM. C, The amplitudes of ocular quick phases during running were significantly larger than those during head fixed nystagmus. D, The durations of eye and head quick phases in light (triangles) and darkness (circles) covaried.



A
VELOCITY (deg/sec)
900
800
700
600
500
400
300
200
100
0
0 10 20 30 40 50 60 70 80
AMPLITUDE (deg)
● HEAD FREE
■ HEAD FIXED
B
DURATION (msec)
200
150
100
50
0
0 10 20 30 40 50 60 70 80
AMPLITUDE (deg)
■ HEAD FIXED
● HEAD FREE
C
PERCENT OF TOTAL
50
40
30
20
10
0
4 12 20 28 36 44 52 60 68 76
AMPLITUDE (deg)
■ HEAD FIXED
■ HEAD FREE
D
HEAD MOVEMENT DURATION (msec)
400
300
200
100
0
0 100 200 300 400
EYE MOVEMENT DURATION (msec)
DARK
LIGHT

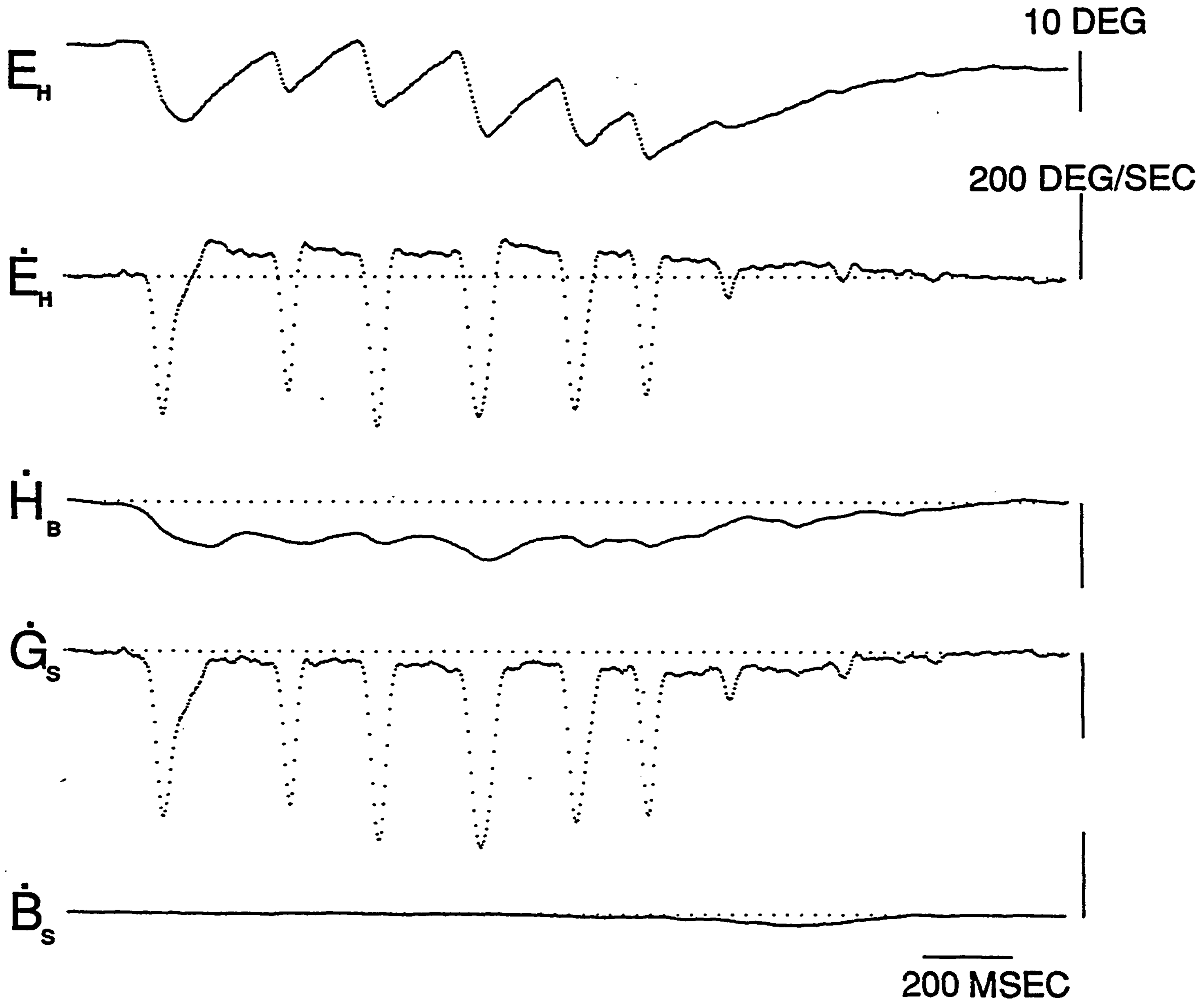
COMPENSATION DURING A LARGE GAZE SHIFT WITH THE ANIMAL STATIONARY

Gaze shifts made by trained animals to targets outside the oculomotor range are often done in multiple steps (Fuller 1983; Guitton et al. 1984). This was also commonly observed in both monkeys used in this study when they made large gaze shifts with the body stationary. In Fig. 25 monkey *rh* spontaneously made a gaze shift of about 130 deg. The animal was stationary throughout all but the final part of the movement. The eyes made the gaze shift in seven beats of nystagmus (E_H), moving on the side of the quick phases. The eyes were originally centered in the orbit and came to the same position at the end of the gaze shift. The frequency of the eye nystagmus was about 5 beats/s, and the shortest intersaccadic interval was under 80 msec. Eye velocity was slightly higher at the onset than the end of each of the slow phases, although gaze in space velocity ($\dot{G}_S$) was relatively constant. The velocity profiles of the rapid eye movements were smooth, without the inflections noted during eye and head nystagmus.

A single, continuous head movement was used to change gaze ($\dot{H}_B$). Upon close inspection, however, it can be seen that $\dot{H}_B$ increased transiently whenever there was a rapid eye movement. Moreover, although the animal did not perfectly stabilize the visual surround during the course of the gaze shift, retinal slip was relatively constant at under 40 deg/sec throughout the slow phases. Thus, gaze in space shifted in saccadic fashion in a series of steps to accomplish the 130 deg gaze change, similar to the saccadic shifts in gaze during circular locomotion (Figs. 3 & 9), with the head and eyes both contributing to the shift.

Figure 25

Record of a 130 deg gaze shift made by a stationary monkey (c). Eye nystagmus accompanied a continuous, but not smooth head movement. Beats of eye nystagmus occurred synchronously with accelerations of the head. While gaze in space was stabilized somewhat, retinal slip between quick phases remained around 40 deg/sec.


E_H
10 DEG
$\dot{E}_H$
200 DEG/SEC
$\dot{H}_B$
$\dot{G}_S$
$\dot{B}_S$
200 MSEC

DISCUSSION:

We have demonstrated that when monkeys run in light in a curved trajectory, head and eye nystagmus is elicited which compensates for the movement of the body in space, stabilizing gaze on targets of interest in the visual surround. Head nystagmus is generally considered to be pathological in humans (Gresty et al. 1976; Dell'Osso and Daroff 1986), and it occurs inconsistently in normal monkeys (Kubo et al. 1981), rabbits (Fuller 1981, 1987) and man (Mygind 1921; Outerbridge and Melvill Jones 1971) when the body and limbs are not actively in motion. On the other hand, combined nystagmus of the head and eyes invariably occurred when monkeys ran in light over hundreds of trials. In fact, we never observed an instance when it was not present. We suggest that head and eye nystagmus is a natural phenomenon that underlies the ability of monkeys to switch gaze in a saccadic fashion from one target to the next while actively running with an angular component. We propose that it be called "gaze compensatory nystagmus" to differentiate it from various types of physiological or pathological eye nystagmus. Gaze compensatory nystagmus may also evoked while viewing lateral targets when travelling in a linear trajectory. Ocular nystagmus induced by rotation with the head fixed is probably a subset of the pattern of head and eye movement that occurs during gaze compensatory nystagmus.

SIGNALS PRODUCING GAZE COMPENSATION DURING ACTIVE RUNNING:

Critical variables that determine the requirements of gaze movements during locomotion include body velocity in space, made up of both rotational and translational components, and the characteristics of the visual surround. Several sensory systems might contribute to the transduction of the relevant information required to stabilize gaze. The visual system provides identification of features targeted for fixation, retinal slip information about movement of the surround relative to the eyes, vergence information useful for ranging (determining target distance) (Barlow et al. 1967; Krotkov 1989; Paige 1989) and velocity field computation (Hildreth 1990). The vestibular system senses angular and linear acceleration of the head accompanying circular running (Benson 1974), while the somatosensory system also generates signals from which body velocity in space could be derived (Brandt et al. 1977; Bles et al. 1983; Guedry and Benson 1983). In addition, there is efference copy and experience in performing the behavior (prediction) that could contribute to the estimation of body velocity in space. All of these sources are presumably integrated into a single percept of self motion (Borah et al. 1989) which is used to drive the compensatory movements of the head and eyes.

With a stationary subject and a stationary surround, head movements are used to shift gaze and are never compensatory. In this instance, movements of the head on body are the same as head movement in space, and gaze stability is achieved by the VOR which causes ocular compensation for head movement. During circular locomotion, however, the body carries both the head and eyes in the running direction, and gaze stabilization is achieved by both compensatory head and eye movements. The goal of these slow phase movements is to change gaze velocity with regard to the body so that it compensates for body velocity in space. The observation that compensatory head and eye movements were synchronized indicates that the combination, i.e., gaze on body velocity, was the final output of gaze stabilization mechanisms. From this, it would follow that the nervous system must have a continuous and accurate estimate of body velocity in space during locomotion. Visual information in retinotopic coordinates and vestibular information in head-based coordinates could provide a stable estimate of body velocity in space while running only in the absence of head on body movement. Since the animal was always making either compensatory or reorienting head on body movements, signals related to head on body position from the neck would be required to transform head and eye in space information into a body in space coordinate frame.

SLOW PHASES OF COMPENSATORY GAZE NYSTAGMUS:

The animals exhibited a number of ways of coordinating compensatory movements of the head and eyes to stabilize gaze. At times head velocities were low during the slow phases, with most of the compensation provided by the eyes (Fig. 21 C). Higher eye velocities were often associated with shorter slow phases. This strategy would result in an increased number of gaze positions in space, and therefore a high rate of sampling of the visual surround. At other times the head movements were faster, and both the head and eyes were utilized to hold gaze on target (Fig. 12). Finally, when there were targets of high interest the animal utilized large head movements to maximize time of gaze on target. Under these circumstances fixation could extend for up to a second while the animals travelled at high velocities through angles as large as 140 deg (Fig. 5).

Two aspects of the head-eye interaction were consistently maintained, however. These were the high initial eye velocities that brought gaze onto target quickly during the initial portions of the eye slow phases, usually while the head quick phases were still in progress (Fig. 21 A-D), and the high eye velocities that maintained gaze on target at the end of slow phases when the head had begun to accelerate in the quick phase direction. This accounted for the nonlinear appearance of the eye position traces during slow phases (E_H, Fig. 10), which is different from the constant slow phase velocities characteristically recorded during ocular nystagmus with the head fixed, or during post locomotory responses with the head still (Fig. 13). The nature of the synergy between the head and eyes is undoubtedly related to the greater mass of the head than the eyes and its poorer high frequency characteristics. That is, during circular locomotion at high velocities the eyes supplied the high frequency components necessary to bring gaze rapidly onto target at the onset of the slow phase and to hold gaze stable for as long as possible at the end of the movement. At these times the drive from the VOR would be maximal, since head velocities were in the quick phase or anti-compensatory direction. During other portions of the slow phases, compensatory head movements were primarily responsible for stabilization of gaze, permitting maintenance of fixation over prolonged intervals of locomotion. Head pursuit mechanisms (Lanman et al. 1978; Dieringer and Precht 1982; Dieringer 1987) may have been used to visually track targets in the surround at these times. In head-free pursuit, subjects relied almost exclusively on head movements to track the target, while eye movements were able to correct for head perturbations with short latency and keep the image stable on the retina (Lanman et al. 1978; Collewijn, 1982b).

ALTERATION IN GAZE GAIN BY TRANSLATIONAL COMPONENTS:

The eccentric trajectory of the animals resulted in both angular and linear components of movement relative to the axis of rotation and elements of the visual surround, respectively. The nature of the surround also varied. Although uniformly of high contrast, there was a range of surround distances and features that were of interest to the animal. This prompted the animals to shift gaze from near to far targets, requiring changes in gaze gain to compensate for the varying distances. Although the animals were not trained to fixate on specific targets, they nevertheless behaved in a predictable way according to geometrical concerns (Figs. 6 & 7). As a result there was a substantial variation in the gain of gaze, varying from 0.8 when targets were in the same visual field as the direction of motion, to 1.3 or higher when the target region was to the slow phase side. This is due to the translational and angular components of movement causing target motion relative to the body in different or the same directions, respectively. Also, when they viewed targets closer than optical infinity, the gain of the translational component increased with decreasing surround distance. This emphasizes that gain of compensatory gaze is probably rarely unity when an animal is moving in an angular path through a structured environment. Similar increases in gain have been attributed to the effects of linear acceleration experienced during eccentric rotation of the head (Gresty et al. 1987; Viirre et al. 1986), while a role for vergence state in determining appropriate gains has been suggested (Paige 1989).

In summary, we have demonstrated that both the head and the eyes participate in gaze compensatory nystagmus during angular running in the monkey, and that their different dynamic characteristics complement each other in stabilizing gaze. The data indicate that the head is strongly enabled when animals are in motion, and that the head, driven by the visual system, makes an important contribution to fixation of visual targets during circular locomotion. The ability to determine head and eye movements while animals run in a relatively normal fashion in a limited area makes circular locomotion a useful tool for studying the contribution of the head and eyes to gaze stabilization.

GAZE COMPENSATION IN THE ABSENCE OF VISION:

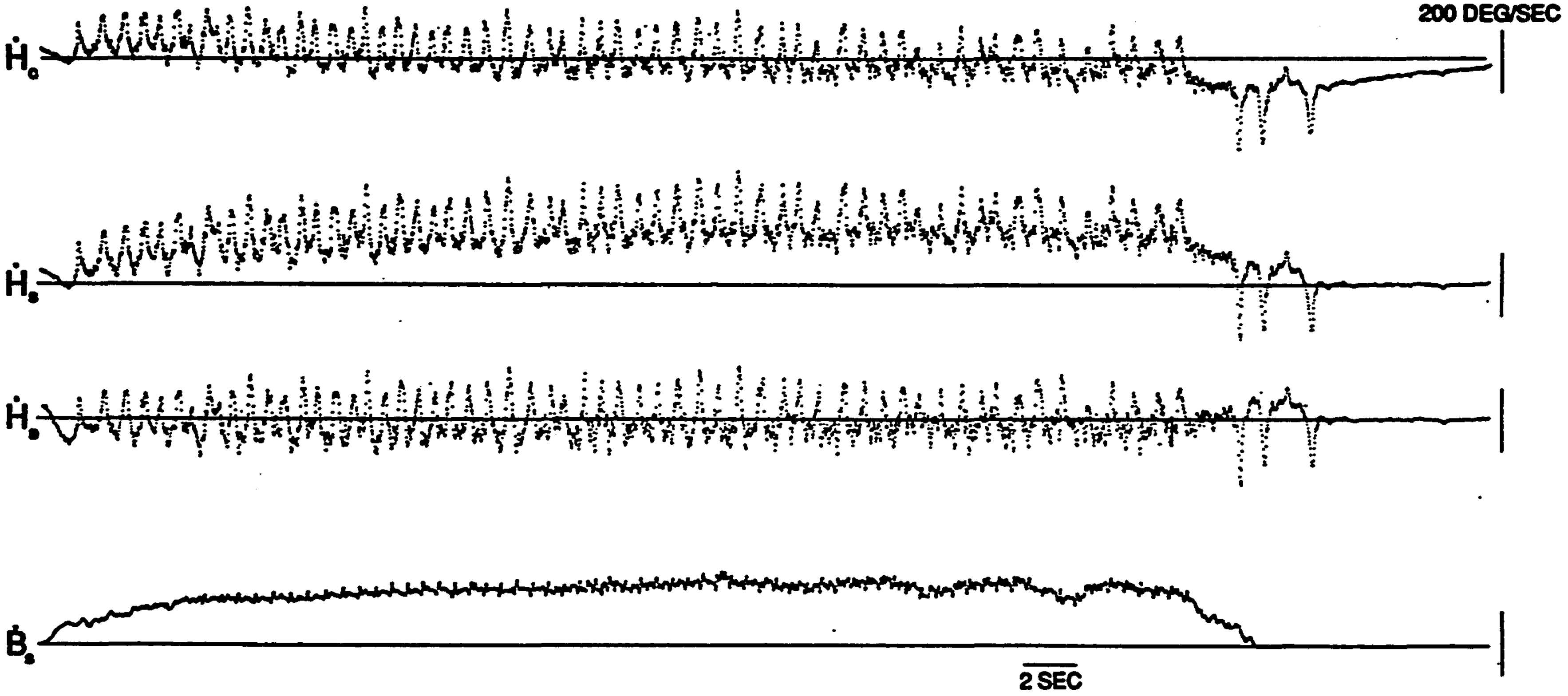
Presumably an important part of the activity that produced the head and eye nystagmus during running in light originated in the visual system. Here we studied the neural processing that produced compensatory gaze nystagmus, first by eliminating vision, then by reducing the animals' forward running velocity with a counter-rotating platform. Surprisingly, gaze compensation was maintained with high gain when animals ran in darkness in directions in which they had substantial velocity storage, despite the absence of visual input. The major finding of this study, therefore, was that the animals were able to estimate their body velocity in space continuously in the absence of vision, and generate a compensatory gaze on body signal to drive both the head and eyes. We will now consider how various inputs might be combined to form a central estimate of body velocity in space. Relevant sensory modalities that process information related to yaw angular motion are the horizontal semicircular canals, the visual system, somatosensory inputs from the limbs (Bles et al. 1983-1986), the otolith organs responding to off-axis rotation (Guedry 1965), the vertical semicircular canals during 'pitching while rotating' (Raphan et al. 1981, 1983) and efference copy.

Activity arising in the semicircular canals undoubtedly contributed importantly to sensing body velocity in space. However, it should be emphasized that activity that arose in the semicircular canals alone could not have been responsible for providing the continuous signal that drove gaze compensation during the slow phases. From the very beginning of any run, slow phase head movements compensated for the animal's angular movement in space, thereby reducing the angular acceleration of the semicircular canals relative to angular body movement. Thus, the canals alone could not have provided an estimate of body velocity even at the onset of running, nor could they have provided a continuous signal of body velocity in space when the animals ran at a constant velocity. This is illustrated in Fig. 26. The top trace, $\dot{H}_C$, was generated by high pass filtering head in space velocity ($\dot{H}_S$) with a 5 s time constant, approximating cupula dynamics (Steinhausen 1933; Goldberg and Fernandez 1971). $\dot{H}_C$ is therefore a reflection of the summed modulation of firing frequencies in the VIIIth nerve during head nystagmus while running.

A comparison of the $\dot{H}_C$ with the $\dot{H}_B$ trace indicates that after about 10 s, the two signals were grossly identical, alternating around zero during the slow and quick phases. As a result, input from the canals would transduce high frequency perturbations of the head associated with locomotion, as well as head on body velocity, making it useful for producing peak eye velocity at the beginning of slow phases. Since average cupula position would be centered around the null or resting position, head accelerations could be coded in the most linear and sensitive range of the receptor, thus optimizing the high frequency canal response. Canal output, however, could not supply the activity necessary to produce continuous compensatory nystagmus. As the animal continued to run, the average firing frequencies in the VIIIth nerve would soon vary around the baseline resting level and would not reflect the body velocity in space envelope. Instead, other input consistent with body angular velocity in space would be necessary to maintain compensatory gaze nystagmus during running. The velocity storage integrator would be particularly well suited for supplying this activity, and is likely to be the source of the compensatory gaze nystagmus during circular locomotion in darkness.

Figure 26

Comparison of head on body, head in space and afferent canal signal during the run pictured in Fig. 1A. The head velocity information that is relayed from the lateral semicircular canals ($\dot{H}_C$) was approximated by filtering the head in space signal ($\dot{H}_S$) with 5 s time constant. The canal signal ($\dot{H}_C$) reflects actual head velocity in space only transiently at the beginning of the run. After that, $\dot{H}_C$ approximates head on body velocity ($\dot{H}_B$).


200 DEG/SEC
$\dot{H}_o$
$\dot{H}_s$
$\dot{H}_s$
$\dot{B}_s$
2 SEC

CONTRIBUTION OF VELOCITY STORAGE TO GAZE STABILIZATION DURING RUNNING:

Velocity storage is a process in the vestibular system that prolongs or sustains slow phase velocity during rotation and counters post-rotatory nystagmus at the end of rotation. It has been modeled as an integrator that stores activity related to slow phase eye velocity during semicircular canal (Raphan et al. 1979) or optokinetic stimulation (Cohen et al. 1977). It is also activated when there is rotation with a continuous change in the attitude of the otoliths with regard to gravity (Raphan et al 1981; Cohen et al. 1983; Raphan et al 1983; See Raphan and Cohen 1985 for review). The time constant of the semicircular canal receptors is about 5 s (Goldberg and Fernandez 1971), whereas the time constant of the nystagmus induced by a step in velocity in the unhabituated monkey is generally about 30-40 s. The dominant time constant of the VOR, therefore, primarily reflects the time constant of the velocity storage integrator (Raphan et al. 1979). Virtually all cells receiving input from the semicircular canals in the vestibular nuclei show the dominant time constant of the VOR (Waespe and Henn 1977), suggesting that they receive an input from the velocity storage integrator. As yet, velocity storage has only been demonstrated in ocular nystagmus. Many second order neurons, however, project to sites other than the oculomotor nuclei (Wilson and Yoshida 1969; Isu and Yokota 1983; Highstein et al. 1987), implying that velocity storage may not be limited to eye movements, but may influence head movement as well.

Three lines of evidence suggest that the activity that drove both the head and eyes to maintain gaze while running in darkness was mediated through velocity storage:

1) Continuous compensatory gaze nystagmus (Figs. 8 A, 9, 16A) was present only in directions in which animals had a long dominant time constant of the VOR or of OKAN as tested under passive conditions (Figs. 1 & 16 C). Gaze compensation was poor (monkey rh, Figs. 13 A, 14, 15 & 16E) in the direction in which there was a short dominant VOR time constant (CCW, Fig.16 G). This suggests that there is an association between

velocity storage and the ability to maintain compensatory gaze velocity during locomotion in darkness.

2) When animals halted after running in darkness in directions in which they had continuous compensatory nystagmus, there was little post-locomotory nystagmus (Fig. 8 A). This demonstrates that activity stored centrally during circular locomotion was capable of counteracting activity coming from the semicircular canals at the end of rotation. A similar demonstration is given in Fig. 9 (arrow), when the animal decelerated from 200 to 100 deg/s, but continued to have gaze nystagmus in the compensatory direction. Conversely, strong post-locomotory, i.e. post-rotatory, nystagmus was observed following rotation in the direction with little velocity storage (Fig. 13 A). This shows that the canal response to the deceleration was unopposed by stored activity.The activity generated during running could not have arisen in the visual system because the animal was running in darkness. Neither could it have come directly from the semicircular canals, since the animals were circling at constant velocities for periods beyond the time constant of the peripheral labyrinth (See Fig. 26). Therefore, it must have come from alternate sources related to producing or sensing body velocity in space. This activity sustained gaze nystagmus during running and offset input from the canals at the end of rotation. These are important functions of velocity storage (Raphan et al. 1979).

3) Not only was rh unable to sustain compensatory gaze velocity when running in the CCW direction, but oppositely directed, anti-compensatory nystagmus in the direction of the animal's asymmetry in velocity storage was present. This added to the post-locomotory response, causing it to be intensified at the end of the run (Fig. 15). This nystagmus may have been related to secondary after-nystagmus, that appeared both in the head and eyes. In any case it must have been due to central processing, and could not have arisen from activity originating in the vestibular end organs or somatosensory

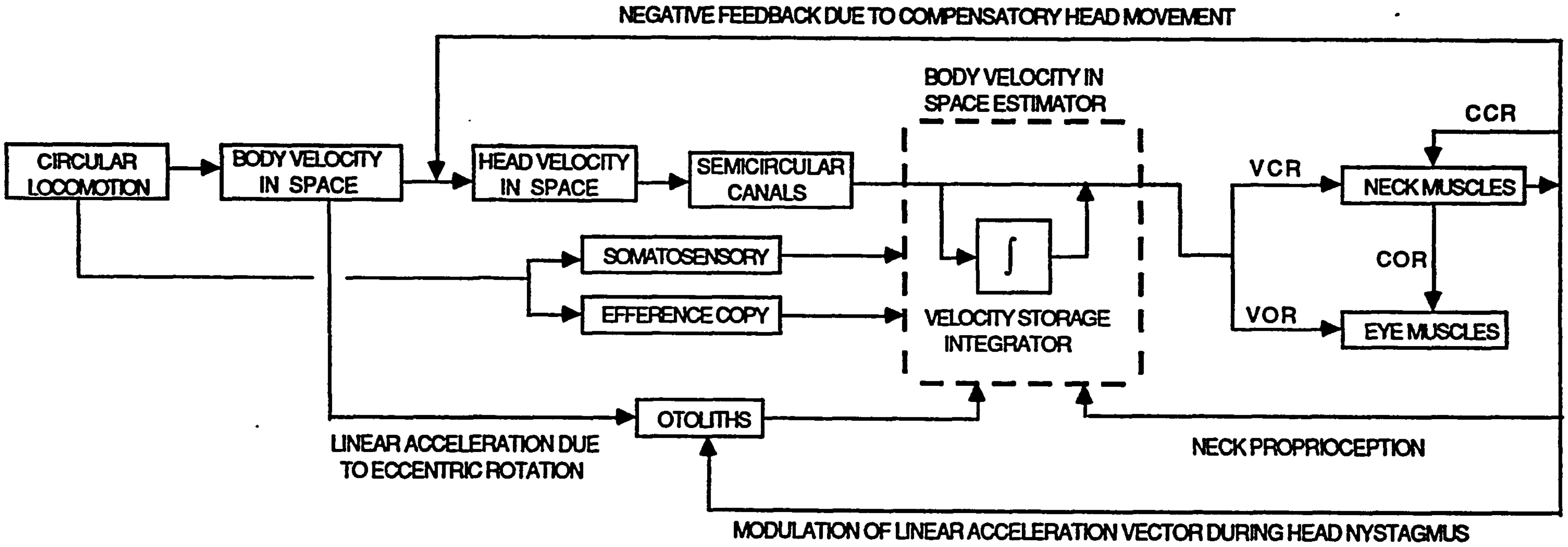
system. The fact that this activity, although inappropriate, drove head and eye movements, demonstrates that central activity had been added to the peripheral input to condition the response and add to the after-nystagmus. This is also consistent with the role of velocity storage.

Taken together, we postulate that velocity storage had been induced during running in darkness, and suggest that it was contributing to maintenance of gaze and to reduction of the post-rotatory response at the termination of running. The implication is that activity in the velocity storage mechanism can also be derived from the somatosensory system in a body reference frame, and that it can be utilized to drive both the head and eyes. It may also have more general functional consequences, such as in postural control. It is not unreasonable that velocity storage should be involved in maintenance of gaze during running since it has the appropriate frequency characteristics for this task. Normal head movements largely occur in a frequency range of 0.1 Hz and higher (Gresty et al. 1986), which is too fast to charge the velocity storage integrator (Raphan et al. 1979). As a result, it seems unlikely that velocity storage is substantially involved in gaze compensation when the head turns on the stationary body during normal gaze shifts. On the other hand, angular locomotion can occur over a time course that is considerably slower. For example, it would not be unusual during walking or running for there to be an angular component over a time course of tens or hundreds of seconds. In this circumstance velocity storage could provide the appropriate low frequency characteristics for maintenance of gaze. Recently it has been shown that velocity storage is organized in three dimensions with the longest dominant VOR time constants occurring during eye rotations around axes close to earth vertical, i.e., for eye movements in an earth horizontal plane (Raphan and Cohen 1988). This would be uniquely appropriate for locomotion which occurs most commonly in an earth horizontal plane. This is also the only plane where head rotations are not accompanied by changes in the orientation of the otolith organs with respect to gravity.

An important question that is raised by these results is whether the velocity storage integrator codes eye velocity in the head ($\dot{E}_H$), head velocity on the body ($\dot{H}_B$), gaze velocity on the body ($\dot{G}_B$) or body velocity in space ($\dot{B}_S$). Previous studies of velocity storage were done with the head stationary on the body (Cohen et al. 1977; Raphan et al. 1979; Waespe et al. 1983; Cohen et al. 1987). In this condition one could not determine whether eye velocity was compensating for head velocity or body velocity in space, since they were the same. In the running animal, however, neither $\dot{E}_H$ nor $\dot{H}_B$, but only their sum, gaze on body velocity, $\dot{G}_B$, accurately compensated for body velocity in space. In addition, head and eye nystagmus was always synchronous during running, indicating that both the head and eyes were coactivated by the same central mechanism. This strongly suggests that an estimate of body velocity in space signal is reconstructed in the velocity storage mechanism from the various inputs that signal angular motion during circular locomotion, and that this estimate is used to drive both the head and eyes to provide a gaze velocity on the body signal that compensates for the animal's body velocity in space. This is represented in Fig. 27, which summarizes the inputs and processing that we believe are involved in producing compensatory gaze nystagmus during circular locomotion. It is also possible that the velocity storage integrator becomes less 'leaky' under more physiological conditions such as locomotion. This could be modulated by activity in the nodulus, which has been shown to affect the dominant time constant of the VOR (Waespe et al. 1985; Solomon et al. 1985).

Figure 27

Flow diagram summary of sensory and motor processes underlying slow phase gaze compensation during running in darkness. During circular locomotion, somatosensory and vestibular signals are generated, which are used to estimate body velocity in space. The output of the velocity storage integrator drives both eye and head movement. Head on body movement causes the semicircular canal signal to underestimate body velocity in space, but it also results in continuous phasic otolith input. VOR, vestibulo-ocular reflex; VCR, vestibulo-collic reflex; CCR, cervico-collic reflex; COR, cervico-ocular reflex.


NEGATIVE FEEDBACK DUE TO COMPENSATORY HEAD MOVEMENT
BODY VELOCITY IN SPACE ESTIMATOR
CCR
CIRCULAR LOCOMOTION
BODY VELOCITY IN SPACE
HEAD VELOCITY IN SPACE
SEMICIRCULAR CANALS
VCR
NECK MUSCLES
∫
SOMATOSENSORY
COR
EFFERENCE COPY
VELOCITY STORAGE INTEGRATOR
VOR
EYE MUSCLES
OTOLITHS
LINEAR ACCELERATION DUE TO ECCENTRIC ROTATION
NECK PROPRIOCEPTION
MODULATION OF LINEAR ACCELERATION VECTOR DURING HEAD NYSTAGMUS

CONTRIBUTIONS OF OTHER INPUTS TO VELOCITY STORAGE TO MAINTAIN A SIGNAL RELATED TO BODY VELOCITY IN SPACE:

Compensatory gaze velocities, even in darkness and in the face of paradoxical somatosensory and vestibular inputs, were maintained for relatively long periods of active rotation. During circling on a moving platform, despite high gait velocities, the frequency and slow phase velocity of the compensatory gaze nystagmus were more a reflection of inertial body movement than locomotor activity. While the increased somatosensory activity generated by limb movement did augment the response over that observed during running on a stationary platform (Gaze Gain, Fig. 16 vs. Fig. 16 A), head and eye movements were clearly driven by a velocity estimate rather than being a component of the locomotor program. Information about head on body movement is needed in order to reconstitute a body velocity in space signal, since the canals relay only head in space velocity ($\dot{H}_s$). $\dot{H}_s$ underestimates $\dot{B}_s$ because of head slow phases (Negative feedback due to compensatory head movement, Fig. 27). This indicates that the vestibular system must employ other means than the semicircular canals to accurately sense angular body movement. Potential sources of this additional information include neck proprioception, linear acceleration, head pitching while rotating and efference copy.

Neck afferent signals (Neck proprioception, Fig. 27) could be combined with $\dot{H}_s$ to yield $\dot{B}_s$, accomplishing a coordinate transformation to a body reference. That neck receptors could provide an estimate of head on body velocity is not unreasonable, given the rich feedback that originates in the neck muscles and joints (McCouch et al. 1951; Richmond and Abrahams 1975). Bles and de Jong (1982) simultaneously activated the semicircular canals and neck proprioceptors at different phases, and showed that circular vection was dominated by cervical rather than vestibular input. Stimulation of cervical nerve roots by neck torsion elicited compensatory eye movements and even nystagmus in both intact rabbits and humans (Philipszoon 1963), and vibration of neck muscles affected motion perception (Biguer et al. 1988). Nuchal afferents influence vestibular nuclear cells which project to the abducens nucleus (Hikosaka and Maeda 1973) and to the spinal cord (Brink et al. 1980; Kasper and Thoden 1981). Convergence of labyrinthine and cervical inputs has been demonstrated in vestibular nucleus (Rubin et al. 1975, 1977; Anastasopoulus and Mergner 1982; Kasper et al. 1988; Fuller, 1988), cerebral cortex (Mergner et al. 1985) and spinal cord (Suzuki et al. 1985; Wilson 1988), and the dynamics of the VCR and CCR were matched at frequencies in the range of physiological head on body movement (Peterson et al. 1985). These connections are likely to mediate the interaction of the VCR, CCR, COR and VOR. Interruption of these pathways has a marked effect on equilibrium and ocular nystagmus (Cohen 1961; Biemond and de Jong 1969; de Jong et al. 1977; see de Jong and Bles 1986 for review).

Afferent information from the trunk and limbs related to locomotion (Somatosensory, Fig. 27) could be utilized in estimating $\dot{B}_S$. Somatosensory signals have been shown to drive compensatory eye movements (Bles et al. 1983-1986; Brandt et al. 1977; Lackner and Levine 1979; Guedry and Benson 1983). The powerful perception of forward angular motion during 'apparent stepping around' suggests that signals related to gait velocity are likely to play an important role in activating velocity storage during running in darkness. In the reduced, deafferented tadpole, during fictive swimming, compensatory eye movements were observed in the absence of any sensory inputs that could coordinate eye movements with locomotion (Stehouwer 1987), suggesting a role for corollary discharge from the spinal cord (Efference copy, Fig. 27) or a common generator. On the other hand, the counter-rotating paradigm was useful for establishing that gait velocity ($\dot{B}_P$) was not the only determinant of gaze compensatory nystagmus, since $\dot{G}_B$ slow phase velocity was more a reflection of $\dot{B}_S$ than $\dot{B}_P$ (Figs.

19 & 20). The frequency of the nystagmus was also independent of the locomotor frequency, suggesting that separate generators were involved, and that gaze compensation was determined by activity that arose either from somatosensory inputs or from vestibular information.

Linear acceleration alone does not elicit horizontal nystagmus (for review, see Barnes 1979), nor did we find that it significantly altered the response to passive rotation. Horizontal nystagmus was elicited, however, when the linear acceleration vector rotated in the transverse plane of the head during counter rotation at the end of a centrifuge arm (Benson 1974). In the active paradigm the animal clearly utilized information about linear acceleration for postural stability (see the animal's body tilt in Fig. 17 A). To make use of linear acceleration in determining angular body velocity in space the animal would have to know its radius of rotation. Since the paradigm was predictive, the radius of rotation was, in fact, well known, although how linear acceleration might be transduced into an estimate of angular velocity is less certain.

An interesting possibility is suggested by the model for off-vertical axis rotation (OVAR) by Raphan and Schnabolk (1988). They posit that during head angular rotation about an axis tilted from the vertical, a linear acceleration vector due to gravity sweeps across the otolith organs. This generates an estimate of head angular velocity that excites the velocity storage mechanism to produce the continuous horizontal nystagmus seen during OVAR (Raphan et al. 1981; Cohen et al. 1983). As noted, the animals experienced up to .6 g of centripetal acceleration during circling on a stationary platform (Linear acceleration due to eccentric rotation, Fig. 27). During compensatory head nystagmus, this acceleration vector would partially sweep across the utricle as the head moved in the plane of rotation (Modulation of linear acceleration vector during head nystagmus, Fig. 27). During OVAR, however, the linear acceleration vector rotation and the observed slow phase gaze movements are in the same direction, while during circular locomotion they were in opposite directions.

Alternatively, horizontal nystagmus and activation of velocity storage is produced by pitching the head while rotating, utilizing the vertical semicircular canals and the otoliths to sense the angular rotation of the head (Raphan et al. 1981, 1983). Vertical head movements were not recorded in this study, but pitching movements commonly occur during locomotion (Grossman et al. 1988, 1989). Such a mechanism could also be utilized in generating a signal related to angular velocity that would maintain gaze nystagmus while running. It should be emphasized that both of these methods of sensing head angular velocity, i.e. off-axis rotation and pitching while rotating, are processed through velocity storage (Cohen et al. 1983; Raphan et al 1983).

While gaze gains were higher during running in light than in darkness, good gaze compensation was nevertheless maintained when animals ran in darkness in directions with velocity storage, in the absence of vision. Mowrer (1937) and Ter Braak (1936) originally noted that optokinetic stimulation sustained responses during rotations in light and blocked after-responses. Functional meaning to these observations are suggested by the results in the paradigm used in Fig. 12, in which the animal ran in alternating periods of light and darkness. If canal input were the only signal used to generate compensatory gaze nystagmus during these dark intervals, the gain during the latter period would have been much lower, as the animal had been circling at a relatively constant velocity. Instead, the gaze gain at the start of the second dark period was as high or higher than the gain at the end of the first dark period. The optokinetic stimulation during the intervening periods of running in light presumably charged velocity storage, and helped maintain gaze stabilization during locomotion and counter post-locomotory responses when the animal halted.

Vision was also important in determining the strategy of eye-head coordination. As demonstrated in Fig. 12, the pattern of eye and head movements was different in light and darkness. The contribution of head movement to gaze velocity was greater in the dark, resulting in much better stabilization of the head in space ($\dot{H}_S$, Fig. 12) during slow phases. A higher VCR gain in darkness than in light could explain this finding, but it is more likely that different eye-head coordination strategies were involved. In light, eye movements dominated, providing most of the compensatory gaze velocity. Their are relative advantages to the two strategies which may be important in determining when each is utilized. The higher frequency, OKN driven pattern present in light consisted of smaller amplitude head quick phase movements, and therefore shorter duration gaze quick phases. This minimized the duration of intervals during which the animal was without vision, and maximized sampling of the visual surround. When the animal stabilized gaze for prolonged intervals in light, however, large head slow phase movements were utilized. During running in darkness, longer durations of gaze slow and quick phases were observed, due to greater participation of the head. Greater stability of the head in space might allow for better utilization of olfactory auditory cues in orientation.

How the relative contributions of $\dot{E}_H$ and $\dot{H}_B$ are determined remains to be investigated. A model for head and eye pursuit was proposed in which a central representation of target motion in space drives both the eye and head movement systems, with central oculomotor commands combining with the VOR signal to keep the eyes on target (Lanman et al. 1978). One possibility would be for the output of the velocity storage integrator (Body velocity in space estimator, Fig. 27) to be used as this command for both the head and eyes, with the VOR subtracting head velocity from eye velocity. However, as noted above, the animals used a variety of strategies of head-eye coordination to shift gaze and achieve gaze stabilization suggesting that additional mechanisms are involved in generating different control signals for the head and eye movers.

Two additional findings merit comment, the larger eye movements made when animals were in motion (Figs. 23 C & 24 C), and the powerful effect of locomotion in activating head movements. Eye movements were significantly larger either in darkness or in light when animals were in motion, and there was an invariant occurrence of synchronous head and eye movements when animals were running, and a lack of head movement during post-rotatory nystagmus when they were not. The implication is that the drive on the head and eyes is quite different during locomotion versus passive rotation of the animal, possibly due to increased gamma loop activation by cervical afferents (Ezure et al. 1987) participating in reflex head stabilization (Goldberg and Peterson 1986). This suggests that the vast literature on the characteristics of the vestibulo-ocular reflex and the oculomotor system must be considered in context: most of the data were obtained while human or animal subjects sat with the body fixed relative to the chair. This would tend to underestimate the amplitude of eye movement and to overlook the potentially powerful contribution of the head to gaze compensation, as in during locomotion. If correct, then testing paradigms which do not take the full potential of the system into account are unlikely to adequately describe deficits in function.

PATHWAYS RESPONSIBLE FOR HEAD AND EYE NYSTAGMUS:

The organization of the oculomotor system is striking for the separation of pathways that carry activity responsible for producing slow and rapid eye movements. These pathways are discrete at early levels of processing, and the separation is maintained until the activity is recombined at the level of the motoneurons (Raphan and Cohen 1978; Shimazu 1983). The same is likely to be true for head movements that subserve gaze. The colliculus and frontal eye fields are primarily involved in producing rapid eye and head movements that would generate saccadic shifts in gaze (Goldberg and Segraves 1990). With regard to compensatory gaze nystagmus, we would expect the tecto-reticulo-spinal system to generate rapid gaze movements in the running animal, i.e., quick phases of head and eye nystagmus (see Berthoz and Grantyn 1986 for review). Pontine reticular neurons may code for either eye saccade amplitude or eye and head gaze shift amplitude (Whittington et al. 1984). Tonic and phasic coupling of eye position and neck EMG signals have been described (Bizzi et al. 1971; Berthoz et al. 1982; Vidal et al. 1982; Grantyn and Berthoz 1985,1987; Andre-Deshays et al. 1988), but was not present in all cases during active head movement (Crommelinck et al. 1982). During prolonged intervals of gaze stabilization (Fig. 5), peak head on body velocity occurred with the eyes stationary near the midposition. This shows that there was strong activation of neck muscles while there was no horizontal movement of the eyes. From this we infer that there must be at least partly separate neuronal mechanisms for the slow component of eye and head movement.

Prablanc and Biguer (1982) studied eye-head-hand movements to targets under conditions which eliminated reafferent corrections of trajectories. While actual movements followed the sequence of eye (220 msec after target onset) head (40 msec later) then hand (100 msec after eye movement), the neck and biceps emg latencies were coincident with eye movement, or could even precede extraocular EMG activity for large displacements (Biguer et al. 1982), making the possibility of oculomotor commands being the source of the neck and arm signals unlikely. Additional evidence that the oculomotor signals are not the sole source of head motor control comes from Banovetz et al. (1988), who demonstrated eye-head coupling only for orientation responses to visible targets. When the animal was rotated in the absence of targets, neck muscle EMG and head torques were related to the vestibular signal, but free of influence of eye saccades. Further, when the VOR was adapted using orthogonal visual and vestibular experience, only the ocular response was altered in darkness, implying separate head and eye control at an early level, rather than using eye position signals to drive the neck. They suggest higher centers, like the tecto-reticular spinal pathway, as possible ways to coordinate eye-head movements, although slow compensatory movements are not likely to use this pathway, since these types of movements have not been observed following collicular stimulation.

Activity responsible for ocular pursuit movements and for slow phases of optokinetic nystagmus is processed in visual areas MT and MST (Newsome et al. 1985; Dursteler and Wurtz 1988), the nucleus of the optic tract (Schiff et al. 1988, 1990), the dorsolateral pontine nuclei (May et al. 1988) and the flocculus (Miles and Fuller 1975; Lisberger and Fuchs 1978; Zee et al. 1981; Waespe and Cohen 1983). Presumably, any or all of these structures could also participate in generating slow phases of head nystagmus during running. (That vision has a role in generating compensatory head movements is shown by the modulation of head velocity gain depending on the animal's orientation with regard to the visual surround.) On the other hand, eye velocities generated during ocular pursuit (Collewijn et al. 1982a; Lisberger et al. 1981) are considerably lower than either the peak compensatory eye or head velocities that were reached during circular locomotion, which could be as high as 20-0-300 deg/s (Fig. 5). Improved ocular pursuit has been demonstrated with concurrent efferent and/or proprioceptive skeletal motor signals (Leist et al. 1987). Alternatively, these high eye and head velocities could have been generated through the vestibular system, utilizing velocity storage acting on the vestibulo-ocular and vestibulo-collic reflexes. If the latter hypothesis is correct, then signals related to many of the parameters that were characterized in this study, such as body velocity in space, should be present in the vestibular nuclei of the running animal.

NEURAL ORGANIZATION OF GAZE MECHANISMS DURING CIRCULAR LOCOMOTION:

We would propose that the driving signal for gaze compensatory nystagmus is an internal representation of body velocity in space which is derived from vestibular, visual, somatosensory and/or efference copy signals in conjunction with the velocity storage mechanism. Given the variety of gaze movement strategies that we observed, it is difficult to explain our results as a simple combination of reflexes (VCR, OKN, OCR, etc.). Commands to the head and eye movers are probably dependent on the presence of vision, the amount of time the animal wishes to fixate any particular target in the field, and the retinal slip that the animal will tolerate. The VOR, however, has a specific role in mediating the interaction between head and eye movements before and after gaze quick phases and to compensate for high frequency jostling of the head during locomotion.

Gaze velocity necessary to stabilize the visual surround is achieved by activation of pathways to neck and eye movers. The question remains as to how the central nervous system decides how much to move the eyes versus the head under different conditions. The observation of several different head-eye coordination patterns argues against models in which identical control signals are used for both the eyes and head.

It is not clear that the visual drive on the neck during running is best conceptualized in terms of the optocollic reflex (OCR). The contribution of head movement to gaze stabilization, reflecting the gain of the OCR, varies depending on how long the animal fixes gaze on a target, i.e. the eye head coordination strategy being used at that time. Thus, there appears to be separate pathways for the generation of quick and slow movements, and at least for slow phases, the eye and head also appear to be activated by different mechanisms at an early level.

In summary, we have demonstrated that synergistic movement of the head and eyes provides gaze stability during circular locomotion, even in the absence of vision. We have shown that the slow phases of gaze nystagmus compensate well for angular body velocity in space, suggesting that the brain can generate an adequate estimate of $\dot{B}_s$ using somatosensory and/or vestibular cues. We postulate that the continuous nystagmus during circular locomotion is strongly dependent on velocity storage, which is activated by several sensory modalities, each coding movement in different reference frames. It seems likely that an important function of velocity storage is to stabilize gaze during locomotion by maintaining an estimate of angular body velocity in space.

QUICK PHASES OF HEAD AND EYE NYSTAGMUS:

There is an extensive literature characterizing gaze during active head and eye saccades that orient a stationary subject to targets (Bizzi et al. 1971, 1972; Morasso et al. 1973; Fuller 1983; Guitton et al. 1984; Laurutis and Robinson 1986; Guitton and Volle 1987; Tomlinson and Bahra 1986a,b; Zangemeister and Stark 1981). However, it was difficult to compare our results with other studies for several reasons. We measured only amplitudes of horizontal eye position changes, while many other reports used amplitudes of gaze shifts (eye + head position changes) to compare durations and velocities. For example, gaze shifts tended to have longer durations and lower peak velocities than equal amplitude head fixed eye saccades in monkeys (Tomlinson and Bahra 1986a), while we found that eye saccades made as part of gaze shifts had shorter durations and higher peak velocities than equal amplitude saccades with the head fixed. Also, it is unclear how to label the ocular quick phase component of compensatory gaze nystagmus. Differences in amplitude-duration relationships have been noted between saccades and quick phases, and between quick phases in light and dark (Ron et al. 1972). Others, however, have reported no differences between quick phases of OKN and vestibular nystagmus (Jurgens et al. 1981).

The addition hypothesis for describing the interaction of saccadic eye movements with head movements during gaze shifts (Bizzi et al. 1971) maintains that the VOR is continuously active. Gaze movements in which peak head velocity was reached near the end of the saccadic eye movement were observed by Atkin (1964). While eye in head velocity was reduced by concurrent head velocity, and inter-movement variability in eye velocity seen, eye in space (gaze) velocity remained relatively constant over the course of a large saccadic gaze movement, and was fairly invariant from movement to movement. Atkin concluded that vestibularly induced compensatory signals and saccadic gaze movements were additive under some circumstances, and that optokinetic and cervical joint motion had little contribution. Gaze shifts to visual targets were found to have the same accuracy whether or not the head moved (Morasso et al. 1973), suggesting that eye commands were combined with the VOR signal such that any movement of the head was subtracted from the originally programmed eye saccade.

This has been challenged, especially for larger amplitude movements (for summary and discussion, see Laurutis and Robinson 1986; Guitton and Volle 1987; Becker 1989). For example, Tomlinson and Bahra (1986b) reported that the VOR was suppressed during eye-head gaze shifts greater than 20 deg. During quick phases of compensatory gaze nystagmus observed during circular locomotion, head in space velocity was due not only to head on body rotation, but also to body velocity in space, both of which resulted in head velocity in the running direction. If the VOR were continuously active, ocular quick phases made during running would be expected to be slower than equal amplitude movements made only with passive whole body rotation. This was not observed, however. When animals were running, quick phases had greater maximum velocities and shorter durations with active head movement than when they were passively rotated. This is consistent with findings in the cat (Blakemore and Donaghy 1980; Douglas et al. 1982). It seems likely that there was suppression of the VOR, at least during the highest velocity components of the movement. Other conditions have been described in which the VOR signal is only partially summed with the oculomotor command or is functionally disconnected, such as during quick phases of nystagmus and when large gaze movements out of the oculomotor range are made (Chun and Robinson, 1978; Jurgens et al. 1981; Roucoux et al. 1981). Robinson (1982) has proposed a model for the cancellation of the VOR during smooth head and eye tracking, and has provided convincing evidence that the VOR is not active during rapid head movements (Laurutis and Robinson 1986). If linear summation of the VOR and ocular commands occurred, then one would expect perturbations in head velocity to cause opposite changes in eye velocity, thereby maintaining the same gaze velocity. However, for eye movements both within and greater than the oculomotor range, whether the head was voluntarily or passively rotated, gaze velocities were in fact affected by head velocity, with accuracy maintained by changes in duration (Laurutis and Robinson 1986).

Mackensen (1958, 1960) first demonstrated that eye velocity declined slowly during medium and large saccades made with the head fixed. During compensatory gaze nystagmus, peak head quick phase velocity occurred in the period just following peak eye quick phase velocity. Quick phase eye velocity was abruptly terminated, and the eyes moved quickly in the compensatory direction to cause gaze velocity to compensate for body velocity in space. This termination could be due to late activation of the VOR or because of zero gaze error (Laurutis and Robinson 1986; Guitton and Volle 1987). This foreshortening of the quick phase was most probably responsible for most of the difference in the amplitude/maximum velocity and amplitude/duration relationships for head-free and head-fixed eye movements. Considering that the maximum velocity occurs near the beginning of the quick phase (Mackensen 1958; Robinson 1964), if the terminal portions of the quick phases were truncated by the quick phase head movements, the maximum velocity curve should be shifted to left in the head-free condition, as amplitudes would be decreased. Similarly, it would be expected that amplitude-duration relationships of movements of comparable size would be shorter when the head moved. Both of these results were observed (Fig. 23). Why the peak velocity occurred earlier in the head-free saccade of Fig. 23 D is not explained by a truncation of the saccade. Possibilities include individual variation in peak velocity among saccades, which is considerable, or a heightened level of alertness while running.

CLASSIFICATION OF HEAD AND EYE INTERACTIONS

Zangemeister and Stark (1981) describe four types of coordinated eye and head gaze shifts, depending on the latency and sequence of the individual components. A type I movement is the classical gaze shift described by Bizzi et al. (1971), in which the eye saccade to target is completed before the head begins to move appreciably. The VOR then causes the eye to counter-rotate in the orbit as the head aligns with the target. Although the eye may move 45 msec before the head moves, the neck EMG burst precedes initial eye position changes by 10 msec, indicating that the neural control sequence for this gaze shift is synchronous to both the head and eye movers. Thus there is a 45 msec position delay due to viscoinertial load following the agonist EMG burst. In a predictive gaze tracking task, neck EMG actually preceded eye EMG by 40 msec. The neural control signal to the head rotators follows reciprocal inhibition, but both agonist and antagonist muscles are active in accelerating and decelerating the head. The agonist activity comes first, with the pulse height of the rectified EMG varying with the velocity of the head movement. About 70 msec following agonist activity begins, the antagonist EMG burst arrives, and the agonist activity falls. Finally, there is another burst of agonist EMG activity as the head approaches its final position. Latency to eye movement proves relatively invariant under various conditions which do, however, effect latencies to head movement. These include natural versus forced movements, and the amplitude of the movement. Natural and larger head movements tended to have longer latencies, as did movements into a blind hemifield (eye latency increased also). Predictive tasks decreased latencies for both the eye and head equally, as opposed to longer latencies for head movement in unpredictable tasks. Fatigue during the prediction task also increased latencies equally.

In the type II movement, the head movement is delayed, and there is an anticipatory corrective, compensatory eye slow phase which begins prior to any actual head movement, and is therefor not mediated by the VOR. The type III movement was likened to the quick phase of nystagmus, in which the eye saccade occurs well into the head movement, and thus the VOR has a potential effect on the velocity and duration of the rapid eye movement, tending to truncate the saccade. In a type IV movement, the head moves first, with the VOR keeping the eyes on the original target. After the head movement is over, the eyes make their saccade to the target without any influence of the VOR. This strategy is especially good at reducing retinal error during a predictive task, taking advantage of the head's relatively better performance in predictive tracking, a trait shared with the arm movement system, but not the eyes. Type II movements occur mostly with small, slower head trajectories, while types III and IV are associated more with larger amplitudes, and therefore faster accelerations. Zangemeister and Stark conclude that head movements are more intentionally governed, influencing gaze and eye movements at higher levels of the nervous system (prediction) and lower levels, as in VOR compensation for variant dynamic head trajectories.

In a study of the effects of added inertial mass to coordinated head and eye gaze shifts to horizontally placed targets (Gauthier et al. 1986), it was found that VOR-saccade interactions depended on the type of head movement, particularly the latency of head movement relative to eye movement. A slow, natural gaze shift within the oculomotor range is likely to be Type I, and therefore, the eye saccade is completed (maximum velocity reached, maximum amplitude achieved) before the head begins to move. With instructions to the subject to "time optimize" the gaze shift, however, head movement latency decreases. Relative to a Type I gaze movement, or a head fixed eye movement to a given target, the eye saccade during a Type III movement is truncated, and has a lower average velocity and smaller amplitude. This is due to the fact that there are significant head velocities present during the eye saccade. With increased inertial loads added to the head, the dynamic lag increases, head latency increases, and consequently the gaze pattern more resembles the Type I case in which there is no overlap, and therefore no truncation, resulting in a higher amplitude and velocity.

To relate this to quick phases of head and eye nystagmus, in light, we presume that the gaze quick phases are Type III. This would be indicated by a phase plot which had its y ($\dot{E}_H$) maximum well off the y axis in the first or third quadrant for right or left quick phases, respectively. In darkness, there was no difference in amplitude-duration relationships with head free or fixed, as opposed to decreases in duration and increased velocity for head free gaze shifts in light. This might be explained in terms of time optimization of quick phases made in light, and longer latencies to head movement in darkness, which would allow for the eye quick phase to be completed before the head quick phase began.

The finding that eye saccades were larger when animals were running than when stationary is of interest. Bahill et al. (1975a) demonstrated that 86% of human saccades fall under 15 deg of arc. The same is true in the monkey (Blumenfeld and Cohen, unpublished data). It has been rather puzzling why the oculomotor range of humans and many animals is limited since there is no such physical limitation to eye movement in the orbit. Data in this report do not explain why this occurs, but do demonstrate that this limitation was state-dependent: the full movement field was utilized primarily when animals actively ran in light, and even larger saccades were made when they ran in darkness (Figs. 23 & 24). The implication is that the central organization of eye and head movements is somewhat different when there is active body motion. That is, not only does circular locomotion enable head movements, it also enlarges the range of saccadic eye movements.

Large gaze shifts in head free cats (>30 deg) showed a flattening, with peak velocity held over relatively longer times (>200 msec for 50 deg movement) than the typical bell shaped gaze velocity profile for smaller movements (Guitton et al. 1984).

The associated rapid eye movement had a high velocity and lower velocity region. Most eye saccades lagged head movement by 40 msec, and started with a compensatory movement resulting from the vestibular signal. Most gaze movements began with the eye within 1 deg of center, and ended with the head aligned with the target. They describe complex gaze displacements, accounting for roughly 75% of movements over 30 deg. These involved numerous eye movements with head accelerations corresponding to the rapid movements of the eyes. These movements were also observed by Fuller (1983) and called multiple step gaze shifts. They noted 'closely spaced overlapping saccades' which were never observed in the absence of an ongoing head movement, as during a braking experiment. The gaze shift shown in Fig. 25 is similar to those described above.

LIMITATIONS OF THIS STUDY:

As we have demonstrated, circular locomotion is a powerful paradigm with which to study the vestibular and oculomotor systems. It is important, however, to consider the limitations both of the paradigm and of our techniques.

1. Although great pains were taken to insure accurate calibration of eye velocity, there was undoubtedly some error in scaling the eye in head ($\dot{E}_H$) and the head in body velocities ($\dot{H}_B$). EOG gain changes are produced by different levels of illumination, and could have contributed to this difficulty as well as noise, nonlinearity at large eye deviations and phase errors introduced by analog electronic differentiation of eye position. Such problems could be reduced by having an animal run in a large rotating coil field, while carrying head and eye coils. However, this would not answer the problem of how to measure vertical eye movements in a freely moving animal with a technique that is more sensitive and reliable than electro-oculography.

2. It is unlikely that an added inertial load to the head due to the implant and mount for the rate sensor had changed the characteristic of head movement to any substantial degree. Stark and colleagues have systematically investigated this problem by making head movements with increased inertial loads. The major effect of loading was to increase the tail of saccades during gaze shifts. Since it was specifically this tail which was truncated in the running monkeys, it seems unlikely that the head was encumbered by the apparatus used for measurement.

3. As yet we have only considered the 'stereotaxic' yaw component of head and eye movements. Pitch movements of the head were recorded during locomotion, and vertical EOG traces, although difficult to analyze due to blinks, indicated compensation for rotations around the interaural axis. Restricting the analysis to the horizontal

component of eye movement makes it impossible to rule out some change in the metrics of quick phases due to the nystagmus potentially being oblique (Bahill and Stark 1977).

4. As noted above, when in motion the animal's head was usually pitched so that the lateral semicircular canals lay in a plane parallel to the platform, whereas the head mounted angular rate sensor was oriented stereotaxically. Therefore, we have probably underestimated head on body velocity by the cosine of the angle of deviation of the rate sensor from the natural axis of head rotation. Vidal et al. (1986) reported that the head was on average pitched 5 deg nose up from the plane of the horizontal canals, which would decrease this error. The Horsely-Clark vertical is rotated on average 11.9 deg from the axis around which the lateral canals respond maximally in rhesus monkeys (Reisine et al. 1988). Therefore, we expect this to cause an error of at most 3%.

5. One problem the interpretations of observed gaze gains was that there was had no way of definitively establishing where the animal was actually looking. Unity gain at any instance might represent the animal 'imagining' far targets when looking laterally and passing a nearby wall, acceptance of some tolerable amount of retinal slip when a higher gain is required for perfect compensation, correct compensation for a target straight ahead, or a mixture of the above. Likewise, subunity gain might represent the animal looking at the running surface (and therefore compensating with more of a vertical component), a target in the quick phase direction or some amount of retinal slip depending on the distance to the target.

6. Only two animals were used in this study. Only very docile monkeys were eligible for consideration, and they had to not be interested in pulling or chewing on wires, peeling

wallpaper, tearing the rubber mat, etc. While the results from each animal were complementary, additional subjects might have added to both the validity of the conclusions as well as the diversity of behaviors observed.

POTENTIAL FUTURE STUDIES:

Since velocity storage appears to play a significant role in the generation of compensatory gaze nystagmus during locomotion, experimental interventions which are known to affect velocity storage could be tested. Baclofen has been shown to decrease the dominant time constant of the VOR without affecting the gain (Cohen et al. 1987). We would predict that monkeys would be unable to maintain compensatory gaze nystagmus during continuous circular locomotion in darkness after administration of baclofen.

We postulate a key role for proprioceptive afferent information from the neck in maintaining an estimate of body velocity in space. Dorsal rhizotomy has been performed on monkeys (Bizzi et al. 1976, 1978) to study the importance of these inputs in gaze changing behavior in the stationary monkey. Injections of local anesthetics has also been used to reversibly eliminate these afferents (de Jong et al. 1977). If animals were capable and willing to circle following such procedures, the contribution of sensory feedback could be gauged and distinguished from motor efference copy.

With the advent of the floating microwire technique for recording single unit activity in head free behaving animals (Munoz), it might be possible to record from cells in the vestibular nucleus during passive as well as active paradigms. We would predict that cell which have been shown to code for head velocity in space would actually carry a signal related to body velocity in space, and would provide a signal which would eventually command both extraocular as well as cervical muscles.

Analysis of EMG activity from neck muscles involved in the yaw head on body rotation would yield tremendously useful information. For rotation at 180 deg/s on the platform, the torque generated on the head in the slow phase direction is roughly equivalent to the peak torque generated during an active head movement of 30 deg (Bizzi et al. 1978). Questions could be asked to determine whether compensatory head on body rotation is accompanied by agonist muscle activity in the direction of rotation, or active stretching of antagonist muscles which would be involved in opposing the torque on the head caused by centripetal acceleration.

POSTURE AND DYNAMIC EQUILIBRIUM:

A wealth of information concerning dynamic postural reflexes is easily obtained from this paradigm. Linear accelerometers could be attached to the animal's head and trunk, and adjustments in body tilt in the sagittal and horizontal planes could be correlated with linear acceleration experience by the animal during circling. Video image analysis could be employed to quantify the orientation of the head and long body axis relative to the axis of rotation, the radii of circles which pass through the points of paw placement (Hildebrand 1976), as well as distance of the animal's center of gravity from the running surface under conditions of varying centripetal acceleration.

Changes in posture could be mediated by either descending vestibulospinal influences (see Wilson 1985 for review) or by local proprioceptive feedback loops involving the spinal cord and limb musculature (Nashner 1976). Optokinetic stimulation has been shown to influence walking in place, causing "stepping deviation" in the direction of stimulation (Tomura et al. 1985). To determine which mechanism might be responsible, an optokinetic stimulus could be used, since visual information would influence only the vestibular system's estimation of rotational velocity. The animal would run in light on a fixed platform with the optokinetic drum lowered and either stationary or in motion. Drum motion in the direction of running would provide a visual stimulus consistent with less linear acceleration than the animal would be experiencing, and drum motion opposite to body velocity in space might augment the compensatory response to linear acceleration, if central mechanisms were influencing postural stability in this paradigm.

A linear accelerometer on one of the limbs could serve as a signal to determine if head and eye movements were time locked to the locomotor cycle. Roberts (1976) has suggested that the head acts as an "inertial paddle" to store potential energy during bovine locomotion.

ADAPTATION:

Plasticity of the VOR by the central nervous system has been studied using reversing prisms (Gonshor and Melvill Jones 1976), and the ability of the VOR to rapidly recalibrate to adjust for moderate changes in magnification has been demonstrated (Miles and Fuller 1974; Collewijn et al. 1983). Helmholtz (1886) also experimented with prismatic displacement of the visual surround, and described the skeletal sensorimotor adaptation to this "dc shift." Is there a similar dynamic response by the skeletomotor system to changes in magnification? To investigate this question, experiments in which information conveyed by a single sensory channel (vision) would be altered by having the animal wear lenses which either reduce or enlarge the visual surround. Neutral lenses which do not alter surround size (and therefore do not affect retinal slip velocities) but narrow the visual field would also be required. All lenses restrict the amplitude of eye movements the animal can make to targets, making head movement more important in larger gaze shifts.

Long term changes in sensory input can be accomplished by having the animal wear the lenses for up to days prior to testing. This has been shown to drive the gain of the VOR in darkness up or down for enlarging and reducing lenses, respectively. Effects of adaptation on the slow phase gaze velocity of compensatory gaze nystagmus would be investigated by having the animal run in darkness and comparing the slow phase gaze velocity with control values. Changes in gaze velocities would suggest that like the vestibular system, somatosensory input and/or efference copy signals are subject to calibration and modification by visual feedback.

Also of interest would be the effect of changing the effective visual field of the animals. If gaze velocities are to be maintained at control levels with the neutral lenses, different eye-head coordination strategy would have to be implemented if the visual axis is to remain within the useful visual field of the animal. If the animal opts to keep the relative contributions of the eyes and head to gaze constant, then the frequency of compensatory gaze nystagmus must increase, and the amplitude of movements must decrease. Alternatively, the animal could decrease the velocity of the eyes relative to the head during the slow phases of nystagmus. The actual strategy used by the animal would be determined during running in light with the neutral lenses by comparing experimental and control values for average inter-fast-phase-intervals, amplitudes of eye movement and the range of eye and head slow phase velocities observed. Any long term effects would be investigated by having the animal run in darkness immediately after wearing the lenses in light and looking for similar changes from control values.

If the animal does change eye velocity relative to head velocity, this would be evidence against a model of eye-head coordination in which gaze accuracy is maintained during head movements solely by the addition of the peripheral VOR signal to the ocular command signal (Bizzi et al. 1971). Rather, for this strategy to be implemented, the individual head and eye components of gaze would have to be centrally co-determined according to some coding of surround velocity in gaze coordinates.

Adaptation following the loss of vestibular responses to angular acceleration around the vertical axis would be studied by surgically plugging the horizontal semicircular canals bilaterally after extensive testing. Following recovery, the animal would be tested with caloric stimulation and passive rotation to determine the success of the procedure. Changes in VOR gain and the slow phase gaze velocity gains with respect to gait velocity and linear acceleration would also be determined to determine if an increase in the gain of somatosensory inputs might have compensated for the vestibular loss.

The animal could be tested in an apparatus which allows for simultaneous recording of head and eye position using the search coil technique. Following plugging, it is expected the animal would initially make characteristic overshoots in gaze due to the lack of a vestibular signal which normally acts to decrease the amplitude of the saccade (Dichgans et al. 1973). Recovery due to increased neck receptor input, compensatory correction saccades and a recalibration of the saccadic system would be characterized and followed as it paralleled changes in compensatory movements while running.

APPENDIX A: PLATFORM RATE CONTROL FEEDBACK AMPLIFIER

General Description:

This circuit was designed to control the platform's angular velocity in space, so that the monkey's velocity in space is some fraction of his velocity relative to the platform (gait velocity). When enabled, it uses the post sensor signal (animal's velocity in space) as an error signal to rotate the platform in the direction opposite the animal's velocity in space (Figs. 17-20). For reasons of stability, the output of the device is rectified, so that only forward motion on the part of the animal results in compensatory platform rotation. The circuit has variable gain, such that at zero gain, the platform remains stationary regardless of the animals velocity in the inertial frame, and at full gain, the system seeks to maintain the animal stationary in space regardless of running velocity. The latency between post movement and compensatory counter-rotation was about 3 ms. Platform accelerations and decelerations were constant at 167 deg/s/s up to a maximum velocity of 400 deg/s. The maximum output of the device is limited by adjusting the + and - rails of the circuit. There is some nonlinearity near the upper limits, as the output nears saturation. There is a polarity switch which determines the direction to which the circuit will respond, and coarse and fine zero offset adjustments. Two additional variable potentiometers control the cut-in and cut-off thresholds, ie the minimum absolute velocity over which the circuit will generate an output, and the velocity at which the output will fall to zero.

Operation:

The circuit requires a +/- 15 VDC supply and ground. The input signal from the angular rate sensor has a gain of 1 VDC/100 deg/sec rotation. The output signal goes to the external reference input of the Contraves control unit. The gain of this input is such that .38 VDC commands 100 deg/sec rotation of the platform. Output rails should be adjusted so that the circuit cannot drive the controller past its rate trip settings. The controller's cutoff velocity is adjusted on card A10: R27 determines the CW maximum velocity, R26 the CCW velocity (CW rotation of the screw pot lowers the cutoff). These trips were set at around 400 deg/sec in both directions. Commanding a higher velocity results in the controller output being disabled, allowing the table to spin freely. In order to avoid this potentially dangerous condition, the + and - maximum outputs of the feedback amplifier must be set below the rate trips. This is done by putting a +4 VDC input into the circuit and adjusting the appropriate rail upward until the rate trip occurs, and then slightly lowering the setting just below the cutoff. The same procedure is followed to adjust the other rail after the polarity switch is changed.

In order to zero the offset of the system, first the polarity is set such that manual rotation of the center post in the direction in which the animal will run results in motion of the platform in the opposite direction when the circuit is enabled and the gain is non-zero. (Rotation of the post in the non-running direction should have no affect on platform velocity.) With maximal gain, the coarse, and then fine offset pots are moved so that there is spontaneous platform motion. The pots are then turned back until the platform stops moving. Continuing to turn the offset pot after the platform stops will affect the start and stop thresholds described above. At this point the gain of the amplifier may be set so that to achieve a given velocity in space, more (high gain) or less (low gain) gait velocity is required. In other words, body velocity in space will be some fraction of body velocity re platform, the higher the gain, the lower the fraction. In still other different words, the higher the gain, the faster the animal must run on the platform to achieve any given velocity re earth. Adjustment of the start and stop thresholds is done according to the animal's disposition. When the start threshold is very low, movements of the animal's body while sitting or resting may cause the platform to move. If this is disturbing to the animal, the threshold may be raised so that the circuit will begin driving the platform only after locomotion has begun. The circuit's logic dictates that the stop threshold must be closer to zero than the start threshold. In practice, this setting is usually set to zero, so that platform compensation occurs until the animal has come to a halt.

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