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Cortical and subcortical contributions to coordinated eye and head movements

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Abstract

This paper summarizes recent experiments conducted by the authors — experiments that studied the behavioral characteristics of large gaze shifts and the neural bases of coordinated movements of the eyes and head.

Keywords: Gaze; Superior colliculus; Frontal eye fields; Pontine reticular formation

1. Introduction

In primates, images of objects along the line of sight fall on parafoveal regions of the retina and are seen with fine detail; those that fall on more eccentric regions of the retina are viewed with less spatial resolution. The photoreceptors are mounted on a mobile platform and movements of the eyes and head are part of an active strategy for learning about what is present in the visual environment. The coordinated movements of the eyes and head that enable high spatial frequency samples of the visual environment by shifting the line-of-sight from one part of the visual scene to another are an essential aspect of the visual process. Understanding the strategies and mechanisms by which these gaze shifts are used to sample the visual environment is as critical to a complete understanding of visual perception as an understanding of events occurring at the retina.

In the natural world large changes in the direction of the line of sight are often produced by coordinated movements of the eyes and head. For the past several years, we have been studying the behavioral features of large gaze shifts produced by rhesus monkeys, the animals most commonly used in studies of the neural control of gaze. Also, we have been examining the neural bases of coordinated movements of the eyes and head generated when rhesus monkeys look to visual targets presented in unpredictable locations. This paper presents a summary of some of our findings.

2. Methods

The methods used to obtain the data reported in this paper, described in detail previously (Freedman, Stanford, & Sparks, 1996; Freedman & Sparks, 1997a,b), are briefly summarized here. Young, 3–5 kg rhesus monkeys (*Macaca mulatta*) served as subjects. During data collection sessions, animals were seated in a modified primate chair that prevented movements of the hips and restricted upper body rotations to approximately $\pm 20°$ but did not restrict movements of the head. The primate chair was placed within two alternating magnetic fields that were in phase and amplitude quadrature and position signals were obtained using the method of Robinson (1963). Later experiments used a phase-angle detection system (CNC Engineering, Seattle, WA). A scleral search coil implanted under the conjuctiva of one eye (Fuchs & Robinson, 1966; Judge, Richmond, & Chu, 1980) provided a signal of gaze position. A signal of head position was obtained from

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another coil attached to the head and the signal was subtracted from the gaze signal to also provide a signal of the position of the eye in the orbit.

All experimental protocols were reviewed and approved by the Institutional Animal Care and Use Committee of the University of Pennsylvania or the Baylor College of Medicine. Protocols conformed to all standards set forth in the National Institutes of Health's Guide for the Care and Use of Animals.

2.1. Recording and microstimulation

A hydraulic microdrive (Kopf) was used to lower stimulating and recording electrodes into the brain. Standard physiological techniques were used for amplification (Bak Electronics) of neural signals. Recordings were filtered to reduce contamination with the signal of the alternating magnetic fields. Neural spikes were converted into standard pulses and interspike intervals, timed with 100 μs resolution, and stored for off-line analysis.

Constant current stimulation trains were generated using a Grass S88 stimulator in combination with a Grass PSIU6 isolation unit. Stimulation trains consisted of monopolar, cathodal pulses 0.2 ms in duration. Current, pulse frequency and train duration were routinely varied in the range of 10–250 μA, 200–700 Hz and 40–600 ms, respectively.

2.2. Behavioral tasks

Visual targets were presented by either back projecting a laser beam (Uniphase) on a tangent screen located 75 cm from the subject using a pair of mirrors attached to galvanometers (General Scanning) or using an array of light-emitting diodes (Gandhi & Sparks, 2001). Data were obtained while animals were performing tasks in which reward was contingent on the completion of gaze shifts to spatial windows around the target within a temporal interval. The tasks are described in detail elsewhere (Freedman & Sparks, 1997a,b; Gandhi & Sparks, 2001).

The starting and ending positions of all movements considered in this report fell within $\pm 45^{\circ}$ of the midsagittal plane. To present secondary targets displaced by 90° from the initial target, it was necessary to present the initial target close to one edge of the tangent screen and the secondary target on the opposite side of the screen center. Thus large-amplitude movements crossed the body midline. It is not clear how the data in this report extrapolate to movements generated from different initial conditions. The general principles of eye–head coordination described below, for example, may or may not hold for 90° gaze shifts initiated with the eyes and head centered on the body midline, rather than 45° contralateral to the direction of the movement.

3. Results

3.1. Behavior: eye and head contributions to the change in gaze

During the natural viewing of visual scenes, most large gaze shifts are initiated when the eyes are near the centers of the orbits. Under these conditions, the pattern of eye and head movements is somewhat stereotyped. Fig. 1A illustrates a coordinated horizontal movement of the eyes and head that produced about a 65° change in the line of sight. The gaze shift was initiated by a movement of the eyes. After a delay, the head began to move toward the target and the eyes and head moved in the same direction until the gaze shift ended. The head usually continues to move for about 100 ms, but the eyes move in the opposite direction and gaze remains fairly stable.

The amplitude of the head movement generated during the active change in the line of sight is the head contribution to the gaze shift and is usually smaller than the total head movement, much of which occurs after the gaze shift has ended. Panels B–D plot the eye (B) and head (C) contributions to gaze and the amplitude of the total head movement (D) for a large number of horizontal gaze shifts with amplitudes between 10 and 80°. For horizontal gaze shifts initiated with the eyes near the center of the orbits, the eye component of the gaze shift increases as gaze amplitude increases, but for most animals this rarely exceeds 35°. The head contributes little or nothing to gaze shifts smaller than 25° in amplitude, but, thereafter, the head contribution increases linearly as a function of gaze amplitude. As illustrated in panel D, the head often moves during small gaze shifts to which there is no head contribution and, once recruited into action, the amplitude of the total head movement is linearly related to the amplitude of the gaze shift.

Two major factors influence the ratio of the eye and head contributions to changes in gaze angle. The effect of the initial position of the eyes in the orbit has been documented by a number of investigators using a variety of subjects (Tomlinson & Bahra, 1986; Tomlinson, 1990; Delreux, Abeele, Lefevre, & Roucoux, 1991; Becker & Jurgens, 1992; Fuller, 1992, 1996; Volle & Guitton, 1993; Freedman & Sparks, 1997a). In animals trained on a task that allows experimental control over the positions of the eyes in the orbits (Chen, Gandhi, & Sparks, 1999; Gandhi & Sparks, 2001) immediately before the initiation of combined eye–head movements, we have explored the effects of varying initial eye position over a greater range than previously studied. Fig. 2 plots the horizontal head contribution to horizontal gaze shifts ranging from 5 to 70° in amplitude. When the eyes are directed 22–35° in the direction opposite to the subsequent gaze shift, the head con-

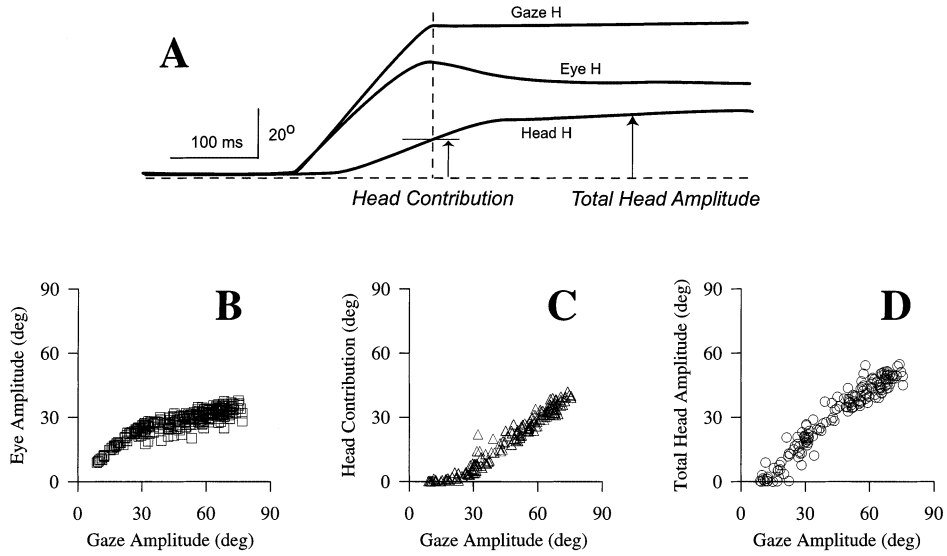

Fig. 1. Typical pattern of eye and head movement made when gaze is directed to a horizontal target presented in an unpredictable location. Gaze H: horizontal gaze position; Eye H: horizontal eye position; Head H: horizontal head position. Note the distinction between head contribution, the amplitude of the head movement during the active gaze shift, and the total amplitude of the head movement. The eye (B) and head (C) contributions to gaze and the amplitude of the total head movement (D) for a large number of horizontal gaze shifts with amplitudes between 10 and 80°. Modified plots of data reported by Freedman and Sparks (1997a).

tributes little to gaze shifts smaller than 40° and the latency of the head movement is increased (not illustrated). If the eyes are already displaced 22–35° in the direction of the impending gaze shift, the latency of the head movement is reduced (not illustrated) and the head makes significant contributions to gaze shifts smaller than 20° in amplitude.

Another factor that affects the ratio of eye–head contributions to gaze shifts is the direction of the gaze shift (Freedman & Sparks, 1997a), an effect that was not observable in early experiments in which the head was free to move only horizontally. The head contribution to gaze and the total vectorial amplitude of the head movement, is reduced systematically as the vertical component of the gaze shift increases. The eye component of the gaze shift increases to compensate.

3.2. Behavior: eye and head velocity

The eye velocity profiles recorded during coordinated eye–head movements may provide insight into the neural mechanisms involved. Panels A–C of Fig. 3 illustrate eye and head velocity profiles during three gaze shifts in which the amplitude of the eye component was the same (25°) but the amplitude of the associated total head movements was about 10° (A), 20° (B) or 40° (C). Notice that in these representative traces the peak eye velocity decreases as the amplitude of the gaze shift increases. Freedman and Sparks (2000) have shown that this decrease in eye velocity is correlated with the amplitude of the head movement. Note, too, the reacceleration of the eyes in panels B and C. The degree to which velocities are reduced, and the amplitude and timing of the reacceleration of the eyes depends upon the concurrent head movement. The converse is not true. Eye movements have little or no influence on the velocity profiles of head movements. Freedman and Sparks (2000) argue that this eye–head interaction must occur at a point in the control circuits where the eye and head control signals are separate. They also

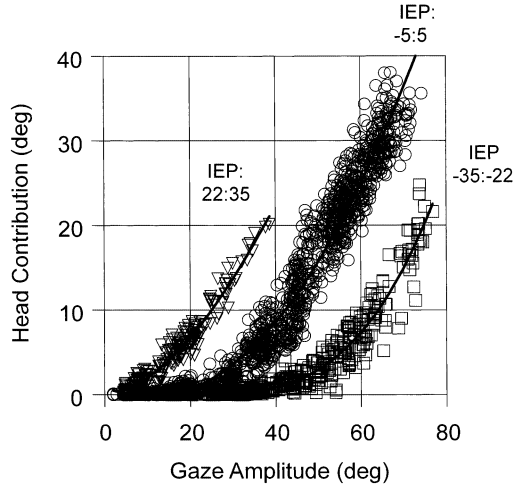

Fig. 2. The horizontal head contribution to horizontal gaze shifts ranging from 5 to 70° in amplitude depends upon initial eye position (IEP). For example, when the eyes are deviated 22–35° in the direction of the impending gaze shift (triangles) the head contributes significantly to gaze shifts smaller than 20°. When the eyes are deviated 22–35° in the direction opposite to the impending gaze shift (squares), significant head contributions are not associated with gaze shifts smaller than about 50°. See text for more details.

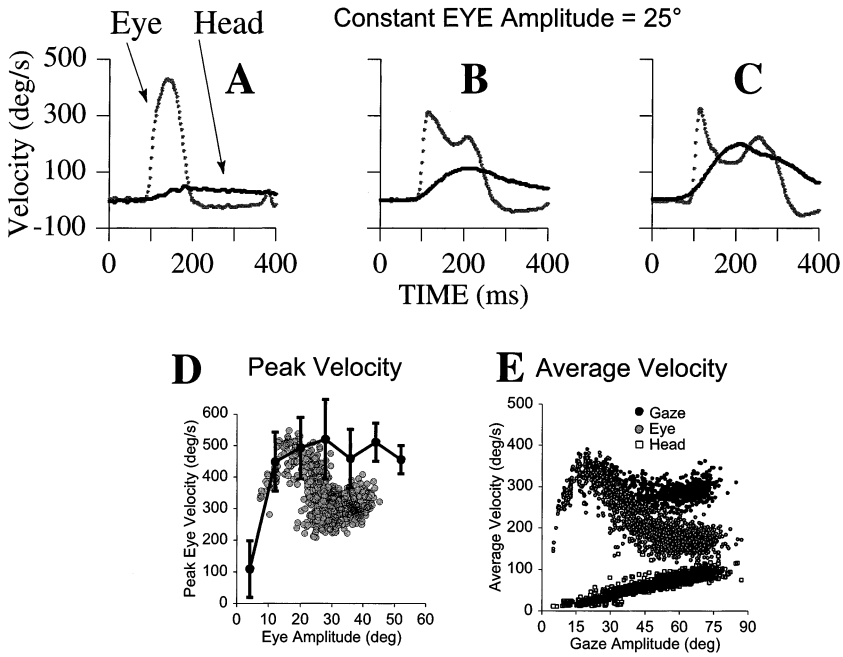

Fig. 3. Eye and head velocity profiles during three gaze shifts in which the amplitude of the eye component was the same (25°) but the amplitude of the associated total head movements was about 10° (A), 20° (B) or 40° (C). Notice that in these representative traces the peak eye velocity decreases as the amplitude of the gaze shift increases. From Freedman and Sparks (2000). D. The relationship between peak eye velocity and eye amplitude when the head is restrained (filled symbols, solid line) and the peak eye velocity measured during movements made when the head was not restrained (grey symbols). Modified from Fig. 7, Freedman and Sparks (1997a) E. Average gaze, eye, and head velocities during 318 gaze shifts ranging in amplitude from 5 to 90° (all directed along the horizontal meridian and initiated with the eyes near the centers of the orbits). Modified from Fig. 9, Freedman and Sparks (1997b).

note that during individual movements the decelerations in eye speed are often double, or even greater, the acceleration of concurrent head movements. Thus, if the dynamic changes in eye speed are to be attributed to the VOR, the gain of the VOR would need to be greater than one. Freedman (in press) developed a model that can account for the initial reduction in eye velocity as well as the occurrence of two velocity peaks. In his model, a copy of a head velocity command inhibits the gain of the saccadic burst generator.

Panel D of Fig. 3 plots the relationship between peak eye velocity and eye amplitude when the head is restrained (filled symbols, solid line) and the peak eye velocity measured during 596 movements made when the head was not restrained. Panel E compares average gaze, eye, and head velocities during 318 gaze shifts ranging in amplitude from 5 to 90° (all directed along the horizontal meridian and initiated with the eyes near the centers of the orbits). Both panels D and E reveal a decline in gaze velocity when gaze amplitude exceeds about 20°. The decrease in gaze velocity is associated with a decline in eye velocity.

3.3. Recordings from the superior colliculus

Many neurons in the primate superior colliculus discharge before and during large gaze shifts accomplished by coordinated movements of the eyes and head (Fig. 4). As discussed by Sparks (1999), because movements of the eyes and head are correlated and because of measurement issues, it is surprisingly difficult to determine what movement metrics are being coded by the activity of these cells.

Freedman and Sparks (1997b) used the general principles of eye–head coordination to develop a strategy for determining if the activity of individual cells in the SC was correlated with the overall change in gaze or

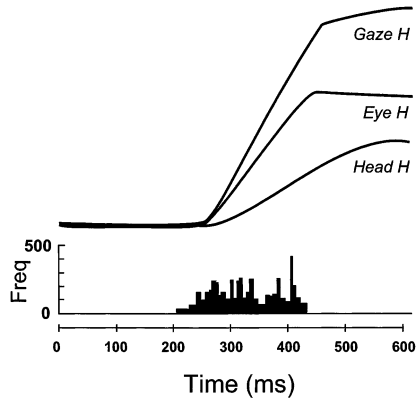

Fig. 4. Discharge of a neuron in the primate superior colliculus before and during a large horizontal gaze shift accomplished by coordinated movements of the eyes and head. Gaze H: horizontal gaze position. Eye H: horizontal eye position. Head H: horizontal head position.

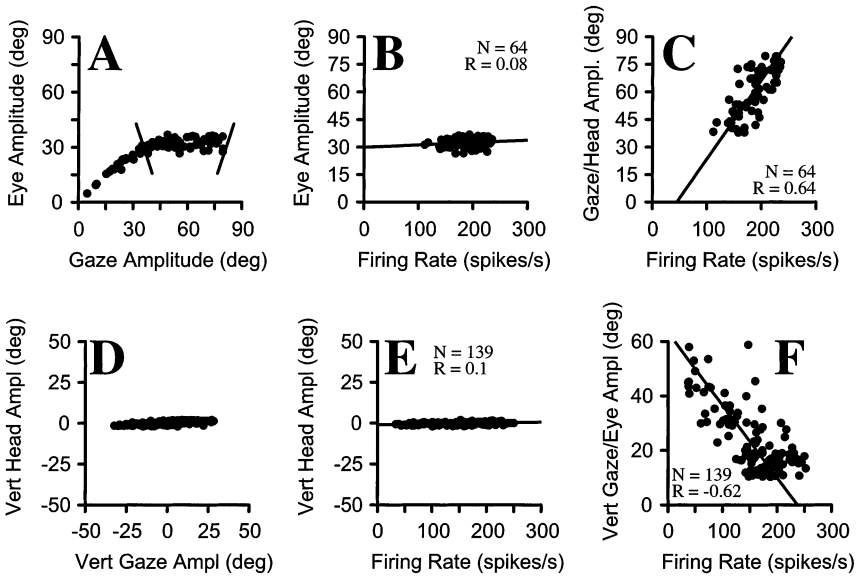

Fig. 5. During movements directed along the horizontal meridian with the eyes initially centered in the orbits, eye movement amplitude is about the same for horizontal gaze shifts between 40 and 80° in amplitude. B. During horizontal gaze shifts in the range of 40–80°, firing rate varied from 100 to 250 spikes per second, but was poorly correlated with eye amplitude. C. These variations in firing rate were related to changes in gaze amplitude and, since the eye contribution was constant, also related to changes in head amplitude. D. As the vertical amplitude of the gaze shift varied from 30° down to 25° up, the vertical amplitude of the head component was about the same. E. Firing rate varied from 40–250 spikes per second during the changes in gaze in which the head contribution was constant. F. These changes in firing rate were systematically related to vertical changes in gaze and, since the head contribution was constant, to changes in vertical eye position. Modified plot of data found in Freedman and Sparks, 1997b.

with the eye and/or head components of the gaze shift. They recorded the activity of single neurons in the intermediate and deep layers of the monkey SC during combined eye–head gaze shifts made to an array of visual targets that extended $\pm 45°$ horizontally and $\pm 40°$ vertically. The cells were studied in conditions in which: (a) the amplitude and direction of gaze movements was relatively constant, but the eye and head components varied over a wide range; and (b) either the eye or head contribution was fixed but the direction and amplitude of gaze changed over a large range. Thus, the activity of collicular neurons was studied under conditions in which gaze and the eye and head contributions to gaze were dissociable (see Fig. 5).

For all of the cells for which these analyses could be performed, motor-related activity was best correlated with the amplitude and direction of the gaze shift, and only weakly correlated with eye or head components of gaze. Gaze shifts having similar amplitudes and directions were associated with similar motor-related bursts. These cells generate activity that specifies the displacement of the line of sight but not the individual components (eye, head) of the orienting gaze shift.

3.4. Microstimulation of the superior colliculus

Freedman and colleagues (Freedman et al., 1996) stimulated the SC of rhesus monkeys with completely unrestrained heads while systematically varying the site and parameters of microstimulation. Their results confirmed and extended an earlier brief report (Segraves & Goldberg, 1992) that collicular stimulation produces high velocity, combined eye–head gaze shifts that are remarkably similar to naturally occurring visually-guided gaze shifts of comparable amplitude and direction (Fig. 6A).

The amplitude and velocity of stimulation-induced gaze shifts depend on the site of stimulation and on the parameters (frequency, current level, and duration of the stimulation train) of stimulation. Increases in the duration (varied from 5 to 400 ms) of the stimulation train systematically increases the amplitude of evoked gaze shifts until a site specific maximal amplitude is reached (Fig. 6B). The frequency of stimulation affects the velocity of evoked gaze shifts; higher frequencies result in higher peak velocities.

As is true for visually-guided gaze shifts, the head contribution to stimulation-induced gaze shifts depends on the position of the eyes relative to the head at the onset of stimulation. When the eyes are deviated in the direction of the ensuing gaze shift, the head contribution increases and the latency to head movement onset decreases. The head contribution to stimulation-induced gaze shifts also depends upon the direction of the gaze shift. The head contribution decreases as the gaze shift becomes more vertical.

Stimulation of a particular site using constant stimulation parameters produces gaze shifts with relatively

constant amplitudes and directions. This does not depend upon a particular eye movement always being coupled with a particular head movement. Rather, stimulation-induced gaze shifts of similar directions and amplitudes are accomplished with many combinations of eye and head components, depending on the initial positions of the eyes in the orbits and the direction of the gaze shift (Fig. 6C).

Based upon the results of the stimulation and recording experiments, our working hypothesis is that the superior colliculus generates a signal of the desired displacement of gaze — not separate signals for moving the eyes and head.

3.5. Microstimulation of frontal cortex

If the SC generates a signal of desired gaze displacement, do cortical areas such as the frontal eye fields (FEFs) that project to the SC also generate commands for coordinated eye–head movements? Bizzi and Schiller (1970) described FEF cells in the monkey that discharged in association with head turns in a specific direction and Guitton and Mandl (1978b) found cells in the cat frontal oculomotor area that discharged only in association with voluntary neck muscle activity. Also, stimulation of the frontal oculomotor area in alert cat often evoked neck muscle activity that could precede eye movements by 15–30 ms (Schlag & Schlag-Rey, 1970; Guitton & Mandl, 1978a). The FEF has a direct, topographically organized projection to the superior colliculus (Komatsu & Suzuki, 1985; Segraves & Goldberg, 1987; Stanton, Bruce, & Goldberg, 1988; Sommer & Wurtz, 1998, 2000) and it would not be surprising to find that the frontal eye field signal reaching the SC is organized in the same coordinate frame as the collicular signal. As was the case with microstimulation of the SC, coordinated movements of the eyes and head following FEF stimulation may not have been observed because in most experiments the head was restrained or brief stimulation trains were used.

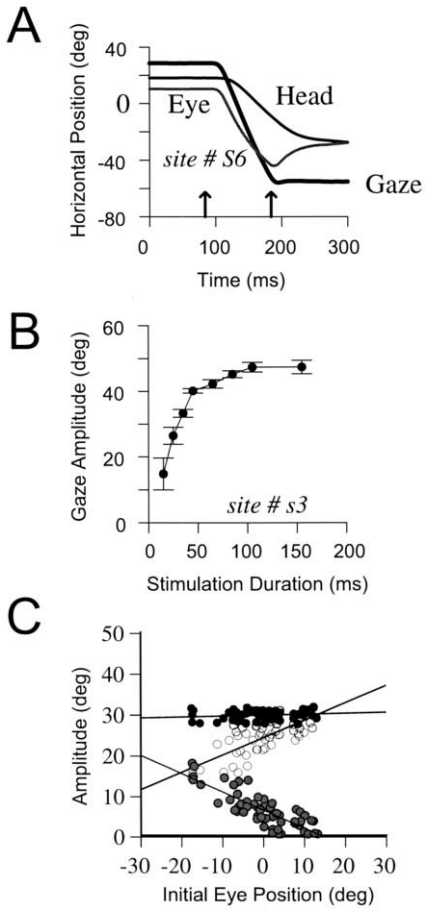

Fig. 6. (A) Gaze shift involving coordinated movements of the eyes and head evoked by stimulation of the superior colliculus of a rhesus monkey. (B) Effects of stimulation duration on gaze amplitude. Symbols represent means ± SD for each stimulation duration. (C) Effects of initial eye position on head contribution (grey symbols) and eye components (unfilled circles) of 57 constant amplitude stimulation-induced gaze shifts (black circles). Modified plots of data reported by Freedman et al. (1996).

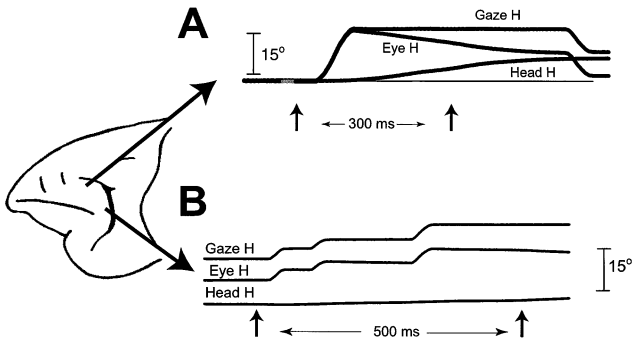

Fig. 7. (A) Stimulation of a medial site in FEF produced a 20° gaze shift with a latency of about 70 ms. The gaze shift was accomplished almost entirely by movements of the eyes. Stimulation also produced a longer latency movement of the head that began after the stimulation-evoked gaze shift ended. Because of the counter-rotation of the eyes, no change in the direction of gaze was observed during the stimulation-evoked head movement; (B) Long stimulation trains delivered to the low threshold region of FEF produced staircases of small eye movements, but did not evoke significant changes in the position of the head.

However, as illustrated in Fig. 7B, when long trains of suprathreshold stimulation comparable to those that were effective in producing large coordinated eye–head movements with stimulation of the SC were delivered to the low threshold region of FEF (Bruce, Goldberg, Bushnell, & Stanton, 1985), we observed staircases of gaze and eye movements, but no or very small movements of the head (Chen & Sparks, 2000). Note that long stimulation trains of stimulation are being used because that may be a necessary condition for observing coordinated eye and head movements.

Stimulation, with similar stimulation parameters at more medial sites did produce eye and head move

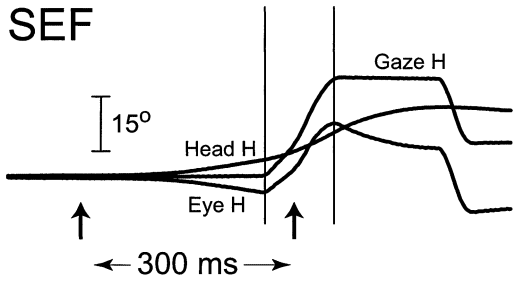

Fig. 8. Changes in eye, head, and gaze position produced by microstimulation pulses delivered in the supplementary eye fields (SEF). See text for more details.

ments, as illustrated in Fig. 7A. At the site illustrated, stimulation evoked a 20° gaze shift with a latency of about 70 ms. This gaze shift was accomplished almost entirely by movements of the eyes. After an additional interval, stimulation also evoked a head movement of about 10°. The head movement began after the stimulation-evoked gaze shift ended and did not produce a change in gaze because of the counter rotation of the eyes.

In contrast to FEF stimulation, stimulation of SEF usually produced changes in gaze that involved movements of both the eyes and the head (Fig. 8). Unlike movements produced by stimulation of SC, the head movement usually occurred first. Initially, gaze did not change because the VOR was active. Later, a gaze shift was initiated (left vertical line) and the eyes and head moved in the same direction until gaze reached a particular amplitude. At that point (right vertical line), the head continued to move but the eyes moved at an equal speed in the opposite direction and gaze remained stable.

At a few stimulation sites in frontal cortex, between FEF and SEF, a different stimulation effect was observed. Stimulation did not evoke a change in gaze, but if the direction of gaze and the direction to which the head was pointed were different, stimulation evoked a head movement that moved the head toward the current direction of gaze (see Fig. 9).

In panel A, the head was pointed toward the direction of gaze, and stimulation did not affect the position of the eyes, head, or gaze. In panel B, the head was pointed about 15° to the left of the direction of gaze and microstimulation produced a rightward movement of the head. In panel C, the head was pointed about 15° to the right of the direction of gaze and microstimulation produced a leftward movement of the head. Referring to panel D, when gaze was directed in eight different directions, stimulation evoked head movements of eight different directions, but in each case the direction of the head movement was appropriate to move the head toward the current direction of gaze. These head movements did not change the direction of gaze because the eyes moved in opposite directions.

3.6. Microstimulation in the pontine reticular formation

If the activity of collicular neurons specifies desired changes in gaze, rather than desired changes in eye or head position, how and where is the collicular gaze command converted into signals appropriate for moving the eyes and head? What is known about the structural and functional properties of collicular neurons and neurons in the pontomedullary reticular formation that send axons along the pathways that reach spinal cord has been summarized in several recent review papers (Berthoz & Grantyn, 1986; Grantyn & Berthoz, 1988; Guitton, 1988; Roucoux & Crommelinck, 1988; Sparks, 1991). These studies establish a physiological and morphological basis for synergistic movements of eyes and head during orienting responses. Signals carried by reticulospinal neurons are related to both neck muscle activity and eye position (e.g. Grantyn & Berthoz, 1985). Accordingly, these signals distribute not only to the spinal cord, but also to the abducens nucleus and other structures closely concerned with the control of eye movements.

The fact that single pontine neurons send axons to the spinal cord and to the motor nuclei of extraocular muscles allows the same signals to be sent to neck and eye muscles. In the Galiana and Guitton (1992) model, a reference signal of desired gaze displacement, derived from the SC, serves as the input to a single gaze motor error comparator that controls both eye and head movements. Feedback signals of eye and head displacements are subtracted from the desired gaze displacement until the reference signal is nulled. Related experiments show that the activity of inhibitory burst neurons in the brainstem, previously thought to be related to eye velocity, is also highly correlated with gaze velocity (Cullen, Guitton, Rey, & Jiang, 1993; Cullen & Guitton, 1997). In contrast, Phillips and colleagues (Phillips, Ling, Siebold, & Fuchs, 1995) argue that the eye and head components of gaze shifts are controlled independently.

We are extending our studies of the neural control of gaze to brainstem regions receiving relatively direct inputs from the superior colliculus using both recording and microstimulation methods. Results of ongoing microstimulation experiments are briefly described below.

Excitatory burst neurons (EBNs) in the pontine reticular formation generate a burst of activity during saccadic eye movements. EBNS have monosynaptic connections with motoneurons innervating extraocular muscles. It has been suggested (see above) that the output of the EBNs is really a gaze command reaching not only the motoneurons innervating extraocular muscles but also motoneurons innervating neck muscles. If EBNs send commands only to extraocular muscles, then microstimulation would be expected to produce only movements of the eyes and if this result were

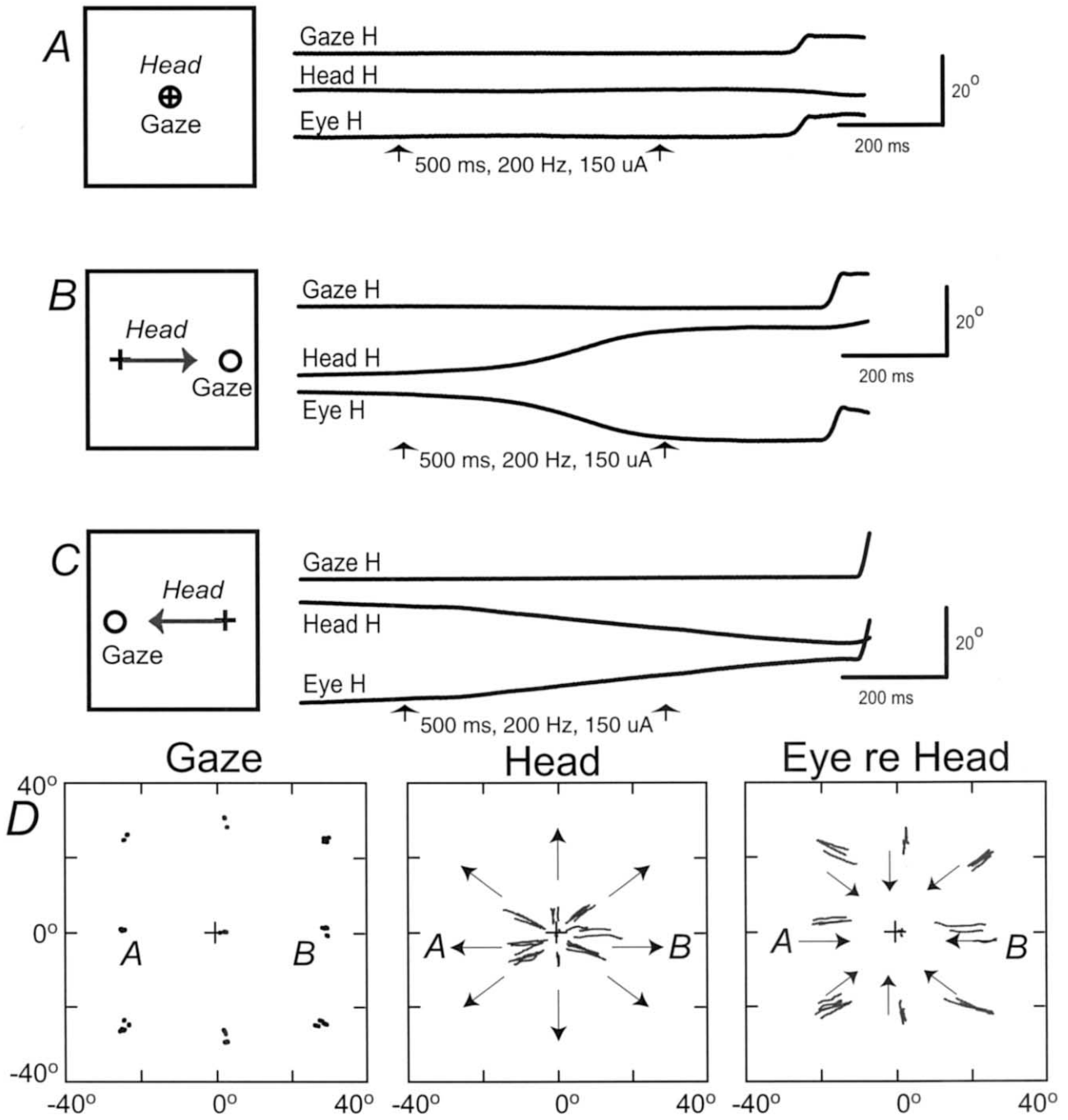

Fig. 9. Effects of microstimulation at a site in frontal cortex between FEF and SEF. (A) When the head was pointed toward the direction of gaze, stimulation had no effect upon the positions of the eyes, head, or gaze. (B) When the head was pointed 15° to the left of the direction of gaze, microstimulation produced a rightward movement of the head. (C) When the head was pointed 15° to the right of the direction of gaze, microstimulation produced a leftward movement of the head. (D) When gaze was directed in eight different directions while the head was pointed straight ahead, stimulation evoked head movements with eight different directions. In each case, stimulation produced movements that moved the head toward the current direction of gaze. These head movements did not affect direction of gaze because the eyes moved in the opposite direction.

obtained, predictions of the 'eye-only' hypothesis would be confirmed.

We found (Gandhi & Sparks, 2000) that stimulation at the site of putative EBNs produced slow, constant velocity changes in gaze that were initially due to movements of the eyes, but later primarily due to a movement of the head. The ratio of eye–head contribution to slow changes in gaze direction was influenced by the positions of the eyes in the orbits. This finding is difficult to interpret because EBNs are intermingled with long-lead burst neurons and reticulo-spinal cells. Thus, we also manipulated EBN activity by stimulation

of omnipause neurons (OPNs), cells that provide a strong, tonic inhibition of EBNs. Stimulation of OPNs during an ongoing gaze shift halts the gaze shift without modifying the ongoing head movement (Gandhi & Sparks, 2000). During the stimulation-evoked plateau in gaze position, the VOR compensates for the ongoing head movement. Gaze shifts resume when OPN stimulation ended. The OPN-induced perturbation does not affect the accuracy of the gaze shift. Stimulation pulses delivered to the OPN region before the onset of a visually-guided gaze shift produce significant delays in the onset of the gaze shift. Only occasional, small delays in the onset of the head movement are observed.

4. Discussion

4.1. Behavioral data

The relationships between saccade amplitude and duration and velocity, the interactions between horizontal and vertical components of saccadic movements, and other properties of the kinematics and kinetics of saccades have placed important constraints upon models of the saccadic system. Similarly, the behavioral characteristics of coordinated eye and head movements provide important constraints upon models of gaze. It is important to continue studying the behavioral characteristics of coordinated eye and head movements in a variety of conditions, for it is the behavioral data that place the most important constraints on models of the neural control of gaze (e.g. Misslisch, Tweed, & Vilis, 1998; Crawford, Ceylan, Klier, & Guitton, 1999).

4.2. The role of the superior colliculus in the control of gaze

Sparks (1999) has recently reviewed the literature related to the role of the superior colliculus in the control of coordinated movements of the eyes and head. He notes that the question of whether neurons throughout the rostral-caudal extent of the SC generate a single unitary signal of desired gaze displacement or generate eye movement commands in one region and commands for movements of the eyes and head in other regions has not been resolved. Additional microstimulation and recording experiments are needed to provide an accurate motor map of the superior colliculus and to enhance our understanding of how coordinated eye and head movements are represented by neurons in the superior colliculus.

4.3. The role of the frontal cortex in the control of gaze

Relatively little is known about the role of various cortical areas in the control of large changes in gaze. We are currently engaged in experiments examining the effects of microstimulation of the frontal eye fields (FEFs) in animals with unrestrained heads. In these experiments we identified the smooth pursuit sites and small saccade sites in the fundus of the arcuate sulcus (Bruce et al., 1985), the SEF located medially from the small saccade sites of the FEF (Schlag & Schlag-Rey, 1970; Chen & Wise, 1995a; Chen and Wise, 1995b), the PMd located caudally from the small saccade sites of the FEF (Wise, Boussaoud, Johnson, & Caminiti, 1997), and the large saccade sites located rostrally from the small saccade zone (Bruce, 1990). Then we studied the effects of microstimulation throughout the rostro-caudal extent of the dorsal FEF. To date, we have seen no evidence that FEF stimulation produces gaze shifts with significant head contributions—a finding that is consistent with the results of lesion experiments (Van Der Steen, Russell, & James, 1986).

A recent brief report by Tu and Keating (2000) suggests that FEF stimulation can produce large gaze shifts that have significant head contributions. We are puzzled by this report because we have not been able to replicate their findings. It should be noted that Tu and Keating use the terms head contribution and total head movement interchangeably and that their paper does not illustrate any gaze shifts with large head contributions. Some of their results are similar to the effects we observe when stimulating SEF.

4.4. The role of neurons in the pontine reticular formation in the control of gaze

Much remains to be learned about the contribution of pontine and medullary neurons to the control of combined eye–head movements. As discussed by Sparks (1999), it is difficult to interpret electrophysiological recordings of neurons in these areas when more than one oculomotor subsystem (e.g. saccadic, pursuit, vergence, vestibular) is active. These neurons may be shared by various oculomotor subsystems and models perform differently depending upon whether these interactions occur before or after feedback signals are formed. For example, because of interactions occurring at the level of motoneurons and possible intereactions between eye and head commands (Freedman & Sparks, 2000), the activity of brainstem cells sending commands for a movement of the eye to oculomotor motoneurons would not be expected to be highly correlated with the executed eye movement — a movement that reflects the interaction of gaze commands, vergence commands, and vestibular inputs.

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