Head Movement Evoked by Electrical Stimulation in the
Supplementary Eye Field of the Rhesus Monkey

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ABSTRACT

Although the supplementary eye field (SEF) has been implicated in the control of head movements associated with gaze shifts, there is no direct evidence that SEF plays a role in the generation of head movements independent of gaze. If the SEF does, varying the duration of stimulation should selectively alter the head movement kinematics during the post-gaze-shift period. The duration of the stimulation was manipulated while head-unrestrained monkeys maintained stable head forward postures. The initial positions of the eyes in the orbits were systematically varied. Although combined movements of the eyes and head were produced in the majority of the trials, head movements were sometimes evoked in the absence of gaze shifts. These head-alone movements were most frequent when the initial eye position was contralateral to the stimulated side. When the stimulation produced eye and head movements, gaze onset was sometimes preceded by a relatively low-velocity phase of the head movement. Evoked head movements were primarily horizontal, unlike the gaze shifts, which typically had vertical components that varied according to the initial positions of the eyes in the orbits. The post-gaze-shift head movements tended to be of low velocity and in many cases persisted until stimulation offset. In general, prolonging the stimulation resulted in improved centering of the eyes in the orbits. These findings suggest that, in addition to its previously described role in the generation of coordinated eye-head gaze shifts, the SEF is also involved in the control of head movements in the absence of a change of gaze.
INTRODUCTION

The supplementary eye field (SEF) occupies a small region in the dorsomedial frontal cortex. The SEF extends from the caudal end of the arcuate sulcus to the rostral end of the superior arm of the arcuate sulcus and is approximately 2-5 mm from the midline (Huerta and Kaas, 1990; Matelli et al., 1991; Schall, 1991; Schlag and Schlag-Rey, 1987; Wise et al., 1997). Early observations have suggested that this region is associated with the initiation of both eye and head movements (Ferrier and Yeo, 1884; Penfield and Welch, 1951; Smith, 1949). Due to the lack of techniques for adequate assessment, these anecdotal observations have received little attention until recently. It is of interest that Levinsohn (1909, described in Smith, 1949) noted that stimulating the dorsomedial frontal cortex, i.e. the SEF, evoked head movements that preceded eye movements. He also reported that the electric current needed to evoke such movements was relatively higher for the dorsomedial frontal cortex compared to that of the lateral oculomotor cortex, i.e. the frontal eye field (FEF). These unique characteristics were reported by these investigators as the major differences between the two regions, later identified as the SEF and the FEF.

Schlag and Schlag-Rey (1987) redefined the SEF based on the stimulation-evoked eye movements in head-fixed preparations. Since then, the role of the SEF in saccadic eye movement has been extensively studied (Amador et al., 2000; Bon and Lucchetti, 1997; Chen and Wise, 1995, 1996; Fujii et al., 1997; Missal and Heinen, 2004; Russo and Bruce, 1993, 2000; Schall, 1991; Schiller and Chou, 2000; Schlag and Schlag-Rey, 1987; Stuphorn et al., 2000; Tehovnik and Lee, 1993). All of these studies were conducted in head-restrained conditions. There were four anecdotal examples provided by Schlag and Schlag-Rey (1987), suggesting that SEF stimulation evoked not only eye movements but also head movements.
Several findings emerge in the studies involving SEF stimulation. Like the other oculomotor regions in the cortex, the evoked saccades in the SEF were directed toward the side contralateral to the stimulated hemisphere. In the large-amplitude sites, the stimulation-evoked saccades often converged toward a region located on the contralateral side (Russo and Bruce, 1993; Schlag and Schlag-Rey, 1987; Tehovnik and Lee, 1993). When the horizontal initial eye positions (IEPh) were deviated toward the ends of the converging saccades, the probability of stimulation-evoked saccades decreased and the threshold current (i.e. the stimulation current which evoked eye movements 50% of the time) increased up to 100 µA or higher. In some cases, eye movements were not elicited even at the highest current levels tested (Schlag and Schlag-Rey, 1987; Tehovnik and Lee, 1993; Tehovnik and Sommer, 1997). When saccades did occur, their onset latencies increased. It was also reported that, when the eyes were deviated in the unresponsive initial eye positions (IEPs) at target onset, stimulating the SEF prevented the saccadic execution (Tehovnik and Lee, 1993). This unresponsive oculomotor space often covered a large contralateral field or occasionally up to the entire contralateral hemisphere. Whether head movements could be evoked within this relatively unresponsive oculomotor region remains unknown.

Recent developments in movement control techniques have made it possible to adequately assess the stimulation-evoked movements in head-unrestrained monkeys (Corneil et al., 2002a, b; Freedman and Sparks, 1997; Phillips et al., 1995; Sparks et al, 2001). A recent microstimulation study investigated the SEF in head-unrestrained monkeys (Martinez–Trujillo et al., 2003). This study observed that SEF stimulation evoked coordinated movements of the eyes and head. This study also noted no sign of site-specific clustering for particular movements, e.g. segregation of eye movement sites and head movement sites. Instead the SEF stimulation evoked both eye and head movements that were kinematically similar to the visually guided eye-head movements.
If the SEF plays a role in controlling movements of the eyes and head, the following issues can be raised. First, are the stimulation-evoked head movements in the SEF necessarily accompanied by gaze shifts? It has been shown that subthreshold stimulation in the superior colliculus, which is interconnected with the SEF, can evoke slow head movements in the absence of gaze (monkey: Corneil et al., 2002a, b; cat: Galiana and Guitton, 1992; Pelisson et al., 2001). It is not known whether, under similar or different circumstances, the SEF stimulation evokes similar types of head movements. Second, do the stimulation-evoked head movements in the SEF follow the rules established under the visually guided conditions, i.e. is the relative contribution of the eyes and head to the gaze shift affected by the initial positions of the eyes in the orbits (Delreux et al., 1991; Fuller, 1992; Volle and Guitton, 1993; Freedman and Sparks, 1997; Gandhi and Sparks, 2001; Goossens and van Opstal, 1999; Guitton et al., 1990; Sparks et al., 2001; Tomlinson and Bahra, 1986)? Third, does SEF stimulation affect a process that is unique to head movement control following gaze shifts, i.e. centering the eyes in the orbits (Sparks et al., 2001)? Previous research has shown that a short duration of microstimulation truncates movements prematurely (review see Graziano et al., 2002; Freedman et al., 1996; Stanford et al., 1996). When the stimulation duration is extended to permit movement completion, complex movement sequences rather than muscle twitches or movement segments could be observed. Previous SEF stimulation studies in head-unrestrained conditions had used relatively short stimulation trains (160-200 ms; Schlag and Schlag-Rey, 1987; Martinez–Trujillo et al., 2003); the stimulation was terminated before the head movement was completed. Whether extending the stimulation in the SEF affects the post-gaze-shift head movements which in turn facilitate centering the eyes in the orbits is not known.
The present study was designed to address our questions by employing stimulation of the SEF in head-unrestrained monkeys. Stimulation duration and the initial eye positions were varied systematically. The present data showed that stimulation in the SEF evoked head movements in the absence of gaze on some trials, particularly when the eyes were deviated in the contralateral direction at stimulation onset. Increases in stimulation duration resulted in increases in the duration of the head movements during the post-gaze-shift periods. This portion of the head movements contributed significantly to centering the eyes in the orbits. The present results suggest the SEF plays a role in head movement control independent of gaze.

**METHODS**

Subject and experimental procedures. Two juvenile rhesus monkeys (*Macaca mulatta*, 5-7 kg) served as subjects. In each monkey, a scleral coil was implanted over one eye to monitor eye movements (Fuchs and Robinson, 1966; Judge et al., 1980). A different search coil, serving to monitor head movements, was cemented above the parietal bone near the midline. A stainless steel head-post was implanted over the occipital bone in order to restrict the animal’s head movements during part of the experiments. A separate stainless steel post was implanted on the anterior ridge of the frontal bone; this post served to secure a lightweight microlaser (Edmund Scientific Inc., #M52263) fixture and juice-delivering tubing. A rectangular recording chamber (36 X 28 X 6 mm) was implanted and cemented over the left side of the frontal bone (17 mm A-P and 12 mm M-L). During recording, a cylindrical adaptor (18 mm in diameter) was used to fix the microdrive and the micro-positioner to the recording chamber at the known coordinates in order to facilitate access to the SEF.

The monkeys were seated in a primate chair for daily training and experiments. The
monkeys’ heads were placed in a position near the center of the magnetic field. Upon head-restrained conditions, the head-post was clamped to a fixture that was secured to a rigid bar attached to the frame of the primate chair. Upon head unrestrained conditions, the head post and the clamping bar were removed. A primate chair designed for conducting the head-unrestrained monkey experiment was used. The typical, horizontal neck plate that prevented the animals from moving their heads vertically was removed. Instead, the monkeys’ collar (Primate Products, Inc) was secured between two pieces of paralleled Plexiglas plates, one against the animals’ chests and the other against the animals’ backs. When the monkeys’ heads were free to move, the fore-aft displacements of their upper torsos and shoulders were limited to less than 2 cm between the two plates. Given these constraints, the head rotations were likely accounted for by neck rotations in the cervical segments of the spine. Contribution of the rest of the body to head rotations was minimal. The range of the head rotations was approximately ± 50° along the horizontal meridian and ± 30° along the vertical meridian. All surgical and experimental procedures conformed to the guidelines for the Care and Use of Animals of National Institutes of Health and the Institutional Animal Care and Use Committee.

**Data acquisition.** A 42” cubic coil and a phase-angle detection system (CNC Engineering Inc.) were used to measure the horizontal and vertical position signals of the gaze (eye re space) and head, sampled at 500 Hz. This system, in the horizontal dimension, was linear within 2% error over the entire range. Signals of the gaze coil were calibrated in the head-fixed condition by rewarding the monkeys for aligning their line of sight with the visual targets. In head-unrestrained conditions, the signal of the eye coil would reflect the line of sight with respect to the space (i.e. gaze), not with respect to the head. Signals of the head coil were calibrated in a head-fixed condition in which the overhead microlaser was turned on and the microlaser beam (with the head)
was aligned with the visual targets of known angles. The position of the eyes (re head) was computed off line by mathematically converting the horizontal and vertical coil signals to unit vectors, and the vectors were rotated with respect to the head in Fick coordinate. All of the displacement measurement was carried out following vector rotations by assuming zero torsion (Haslwanter, 1995; Straumann et al., 1991).

A hydraulic microdrive (Kopf instruments, Inc.) was used to advance the epoxylite-insulated tungsten electrodes (Frederic Haer, Inc.) through the dura surface, which was pre-punctured by a sharpened needle (details see Chen et al., 2001). Neural signals were band-pass (50 Hz – 5 kHz) filtered using a differential amplifier (Bak Electronics, Inc.). Microstimulation was carried out using a stimulator (S88, Grass Instruments, Inc.) and an optical isolation unit (PSIU6, Grass Instruments, Inc.). The stimulation pulses were discriminated using a BAK window discriminator. The stimulation trains consisted of 0.2-ms, monopolar, cathodal pulses. Stimulation duration ranged from 300 to 600 ms. Because there was no previous report regarding the current threshold of the stimulation-evoked head movements in the SEF, we typically explored with a 2-3X suprathreshold current identified for evoking gaze shifts. Typical current intensity and stimulation frequency were 100 µA (range: 80-150 µA) and 200 Hz (range: 100-200 Hz), respectively. We found that the current of 100 µA was, in general, effective in evoking eye-head combined gaze shifts. When it was necessary during exploring the effectiveness of other stimulation parameters, current intensity of 100 µA was commonly used. It was difficult to monitor the actual current delivered through the high-impedance electrodes; all of the current intensity reported in the present report was taken from the face value of the stimulator.

Data were acquired using a Pentium microcomputer running an in-house data acquisition software originally developed by P. Glimcher and D. Sparks. This data acquisition program
allowed a laboratory computer to control the location and duration of visual targets and to monitor horizontal and vertical positions of gaze and head. In addition, the software allowed for controlling the delivery of the stimulation trains and the juice reward.

**Behavioral paradigms and microstimulation.** Visual targets were presented on a tangent screen with a rectangular array of tri-state (red, green, yellow) light-emitting diodes (LEDs), which consisted of 41 rows of 49 lights equally spaced by 2 inches in either horizontal or vertical dimension. Throughout the experiments, the LED board was placed at a distance of 72 cm (28.5 inches) from the monkeys. The spacing between the adjacent horizontal or vertical LEDs near the center of the board was approximately two degrees with respect to the monkeys.

The monkeys were trained in a visually guided gaze shift task that permitted independent control of the gaze and head. Figure 1A illustrates the onset and offset sequence of the targets in the task. The task began with the monkeys sitting straight ahead, aligning a head-mounted microlaser beam with a visual (red) target via visual feedback. Later, a second (green) target was illuminated, and the monkeys deviated their eyes to the target while maintaining a stable head posture. The green target was usually displayed in 27° steps (i.e. approximately 15 LED in spacing) horizontally or vertically with respective to the horizontal or vertical meridian of the initial red target. Some 600-800 ms following the onset of the green target, all targets and the microlaser were extinguished for 400-500 ms. The same red and green targets and the microlaser were re-illuminated (500-700 ms) and then re-extinguished. Some 400-600 ms later, a third (yellow) target was illuminated at a randomly chosen location, and the monkeys made a gaze shift to acquire the target. A drop of juice reward was delivered in contingency upon the successful execution of the gaze shift. To achieve eye-head postural constraints, gaze and head “windows,” typically ranging 5° and 10° in radius, respectively, were set up in a close-loop real-time control. Reward was
contingent upon the monkeys keeping their gaze and head positions within these windows. If either
gaze or head stepped outside of the windows during the designated period of postural constraints,
the trial was aborted.

It is worthwhile to point out that the (red and green) targets used to manipulate the gaze and
head positions were spatially (up-down and left-right) balanced. The location of the targets was
also randomly chosen in order to minimize the directional bias of the animals’ movements.
Likewise, the gaze (yellow) targets upon which the rewards were contingent were spatially
balanced and selected at random.

Electrical microstimulation trials (Fig. 1B), interleaved with control trials, were carried out
in approximately 50% of the trials for each block. The stimulation trials were similar to the control
trials except that the electrical stimulation was always delivered 200 ms following the first
extinction of both the red and green targets. From that point on, the red and green visual targets and
the microlaser remained extinguished. Approximately 800-1400 ms later, a visual (yellow) target
was illuminated, just like that in the control trials, and the monkeys were rewarded for making a
gaze shift to the target. A major difference between the stimulation and the control trials was that
the former imposed postural constraints up to the point before stimulation was delivered, whereas
the latter imposed postural constraints throughout the task.

The control trials were designed to mimic the stimulation trials. Both trial types imposed
that the monkeys maintained stable eye and head postures in darkness following the extinction of
the red and green targets and the microlaser (Fig. 2E). Two critical features in these designs are
worth of pointing out. The red and green targets were re-illuminated 500-700 ms after the
beginning of the gap period (in the control trials), and the stimulation was always applied 200 ms
after the beginning of the gap period (in the stimulation trials). Therefore, at the time of
stimulation, there was no way for the monkeys to know whether the trial was a stimulation trial or a control trial. The monkey could only anticipate the re-appearance of the red and green targets at locations corresponding to their current eye and head positions. In other words, re-illuminating the visual targets in the control trials ensured that the animals were motivated to maintain their current eye and head positions rather than anticipating and executing volitional or anticipatory movements.

In some stimulation sites, we carried out the “non-task mode” stimulation, in which the stimulation train was delivered during the inter-trial interval (duration: 500-1500 ms; see Results). Like the “task mode” stimulation, there was no visual target and no postural constraints prior to, during, or after the delivery of the stimulation. However, a visual (yellow) target was illuminated following a similar time course as the task-mode stimulation, and the monkeys were rewarded for making a gaze shift to the target. There were two important aspects of this trial type. First, the stimulation was delivered without warning, i.e. there were no visual or auditory stimuli that cued the animals as to when the trial started. Even if the animals wanted to, they could not time the upcoming stimulation. Second, there was no postural restriction for the positions of the eyes or head. The animals were presumably as relaxed as they could be in any natural upright postures. It was unlikely for the animals to generate volitional movements on a consistent basis within tens of msec following the stimulation.

Due to the fact that it was impossible to know whether a given electrode penetration was made parallel, orthogonal, or oblique with respect to the cortical surface, we considered the stimulation depth separated by 500 µm as different sites. Concerning the fact that SEF was located on top of the dorsomedial frontal cortex and was relatively shallow, in general, a successful electrode penetration yielded one stimulation site with usable data. Occasionally, 2 sites with distinctive characteristics were obtained in the same penetration. The evoked movements in
different sites were analyzed separately. In addition, care was taken to avoid stimulating the white matter beneath the cortex. The electrodes were always advanced sufficiently deep, and the border between gray and white matter was identified based on the diminishing unit discharge in the background. Once the electrode was confirmed to have reached the white matter, the electrodes were then slowly withdrawn. The stimulation was carried out at least 100 µm away from the border of the white and gray matter. Data obtained in the white matter, if any, were excluded from the analyses.

Data analyses. Data analyses were performed using an in-house program on a Windows platform. Movement onsets and offsets were determined based on a set of velocity criteria (gaze: 80 °/s for the horizontal onset and 60 °/s for the vertical offset; head: 6 °/s for both horizontal and vertical onset and offset). Movements were displayed 100 ms prior to and 800 ms following the stimulation onset, and measurements were taken strictly based on velocity criteria. Any movement detected prior to stimulation onset was removed from further analysis. Due to the inherent noise in the low-velocity head movement data, the head movement velocity was filtered separately from the gaze data. A digital Taylor-series filter and a sliding probabilistic threshold-window were implemented. The latter, probabilistic threshold-filter computation was designed to circumvent the situation in which the head velocity fluctuated around the velocity threshold (Chen and Walton, 2004). For the head movement onset velocity cutoff, a 36/50 ratio (i.e. 72 ms vs. 100 ms) was used. For head movement offset velocity cutoff, a 11/16 ratio (i.e. 22 ms vs. 32 ms) was used. In our experience, there were only a few cases, if any, where the onset of the head movements was ambiguous. These head movements often had an inconsistent velocity profile near or below the detection threshold, such that no human intervention would make much difference. These trials were abandoned.
Staircase gaze shifts were occasionally encountered in the SEF stimulation data. These gaze trials could be accompanied by multiple head movements that were not within the scope of the present study. These trials were excluded from the analyses. Statistical analyses were performed using Statistica (Statsoft Co.). Throughout this paper, the averages of the data are presented as mean ± S.D. unless otherwise indicated.

At the end of experiments, the monkeys were sacrificed with an overdose of pentobarbital and the brains were removed for histological examination. Stainless-steel pins were inserted through the known coordinates and left in the brain during perfusion for the facilitation of coordinate reconstruction.

RESULTS

A total of 78 stimulation sites were studied in the left SEF of two head-unrestrained monkeys (72 in M1 and 6 in M2). The SEF was identified based on the existence of low current threshold for evoking gaze shifts and staircase saccades (Russo and Bruce, 1993; Schall, 1991; Schlag and Schlag-Rey, 1987; Tehovnik and Lee, 1993). Large-amplitude sites (at least 10° when the eyes deviated in the direction ipsilateral to the stimulated side) were selected for conducting the stimulation experiment, as large-amplitude gaze shifts would recruit significant head movements (Guitton et al., 1990; Sparks et al., 2001; Tomlinson and Bahra, 1986). Data shown in the present study included the conditions in which the monkeys’ initial head positions were maintained in head forward positions (see Methods). That is, the initial head position was controlled within a limited and consistent range. The initial eye position (re head, IEP) was systematically varied. Due to the fact that the observations in the SEF stimulation of both monkeys were comparable, the data from both monkeys were pooled in all analyses.
Figure 2 illustrates the horizontal position (Fig. 2A) and velocity traces (Fig. 2B) of the stimulation-evoked (gaze, eye [re head], and head) movements in a given SEF site. Since the head velocities were typically lower than those of the gaze and eye movements, the peaks of gaze and eye velocity traces were truncated in order to facilitate the display of head velocity profiles (Figs. 2B-D). As shown in the velocity traces in Figure 2B, the gaze, eye, and head velocity traces initially overlapped one another. About 70 ms following the onset of stimulation, the head velocity increased to approximately 20 °/sec. At the same time, the eye velocity increased in synchrony with the head by approximately the same magnitude but opposite in direction (i.e. VOR gain equals one). Some 100 ms later, the gaze shift was initiated; head velocity increased to approximately 40-50 °/sec. Head velocity peaked after the offset of gaze shift and eventually declined to approximately zero. As in the examples shown in Figure 2, the entire movement was accomplished within 300-400 ms. The gaze shifts, which occurred with the head movements, were as brief as 50-100 ms. Furthermore, the onset latency of the head movements could vary relative to either the onset of stimulation or the onset of gaze shifts. Head onset preceded gaze onset by 60-100 ms, as was the case in Figures 2B and D. By contrast, head onset lagged gaze onset by approximately 35 ms in Figure 2C.

Figure 2E shows that the horizontal velocities of gaze, eye, and head were near the baselines during the comparable epochs in the control trials (interleaved with the stimulation trials in the same block), indicating that the animals could voluntarily maintain consistent eye and head postures in the absence of stimulation. The velocity traces often remained stable throughout the periods in which the visual target and laser were turned on (gray box shown in E) or off. The absence of such movements in the control trials indicated that the movements observed in the stimulation trials were indeed evoked by the electrical stimulation as opposed to the animals’ self initiation.
We often observed “eye and head,” “head alone,” and “eye alone” trials in the same site. There was no indication of any site-specific clustering for the movements evoked by electrical stimulation. However, depending upon the context of movement execution (e.g. stimulation duration and eye positions in the orbits), the characteristics of the stimulation-evoked movements would vary. These points will be elaborated in later sections.

**Kinematics of the stimulation-evoked head movements**

The trials in which the initial head position was centered with respect to the body (see Methods) and the head displacements were at least 2° (n= 1163) were selected for the kinematics analysis. Figure 3A plots the relationship between the horizontal and vertical components of these head movements, in which two features can be noted. First, the overwhelming majority (99.1%, 1153/1163; M1= 1074/1084; M2= 79/79) of these head movements were directed away from (i.e. contralateral with respect to) the stimulated side. The rest of the head movements had very small displacements (-2.6 ± 1.2°) in the ipsilateral direction.

Second, the vertical component (Hv; 0.9 ± 2.1°) of these head movements was very small compared to its horizontal component (Hh; 7.9 ± 6.4°; Fig. 3A). The Hv/Hh ratio was 0.13. The slightly upward bias of head movement persisted across all IEP conditions, in that all slope values remained positive (ipsiversive IEP [IEPi]: slope= 0.19, n = 294; IEP centered in the orbit [IEPo]: slope= 0.11, n= 493; contraversive IEP [IEPc]): slope= 0.04, n= 233). The ranges of the IEPh were -28°: -15° (IEPi), -6°: 6° (IEPo), and 15°: 28° (IEPc), unless otherwise indicated. This unique but small vertical head component is best appreciated by viewing the box plots. The middle 98% (between 1% and 99% whiskers in the box plots) of the evoked vertical head displacements ranged from –0.01° to 1.5°. In sharp contrast, the vertical components of the fast eye displacements with
respect to the head (Ev; re head) ranged widely from \(-30.6^\circ\) to \(29.8^\circ\) \((n= 1393; \text{Fig. 3C})\).

Figure 3B plots the main sequence characteristics, i.e. peak velocity versus displacement, of these head movements. The slope of the linear regression of the data was 3.86 (Pearson Correlation \(r = 0.90; p < 0.01\)), which closely resembled the main sequence of the visually guided head movements. When the data were separated for IEP\(\text{Ph}\) conditions, the slope in the IEP\(\text{o}\) condition (slope= 3.5, \(r= 0.89\)) was slightly lower than that in IEP\(\text{i}\) (slope= 4.2, \(r= 0.95\)) or IEP\(\text{c}\) (slope= 4.7, \(r= 0.89\)) conditions (ANCOVA for homogeneity of slope model, \(F= 7.8, p < 0.01\)).

The horizontal peak head velocity (Fig. 3B) was dwarfed when compared to the horizontal peak eye (re head) velocity (Fig. 3D). In general, the horizontal peak head velocity was highly limited, e.g. approximately 1/6 of the magnitude of the horizontal peak eye velocity for a 20° horizontal eye displacement. These data were consistent with those of visually guided head movements (Corneil et al., 2002a, b; Freedman and Sparks, 1997; Guitton et al., 1990; Martinez-Trujillo et al., 2003; Phillips et al., 1995).

**Effects of stimulation duration**

To gain insights into the detailed characteristics and timing of the stimulation-evoked movements, Figure 4 plots individual traces of the horizontal head and gaze velocities for a given SEF site. The top panels illustrate the example head velocity traces evoked by 300-ms stimulation, and the bottom panels illustrate the traces evoked by 600-ms stimulation. The plots are grouped by IEP\(\text{Ph}\) conditions. Five traces (two of high peak velocities, two of low peak velocities, and one of medium peak velocity) were selected to represent the typical head and gaze velocity profiles for a given stimulation condition. Several features can be noted in the plots. First, similar to those observed in the visually guided eye-head combined movements, the stimulation-evoked head
velocity typically rose to peak near or following the end of gaze shifts (i.e. when the gaze velocity declined to near baseline). The peak velocities of the head movements varied from ~20 to ~120 °/sec. However, for a given IEP condition, there was no consistent trend that could predict the peak head velocity on a particular trial.

Second, the head velocities typically dropped from their peaks to baselines within 100-200 ms following gaze completion. This observation is best appreciated in the traces of 300-ms stimulation (top panels). By contrast, in the case of 600-ms stimulation (bottom panels), the head velocities typically dropped to approximately 20-30 °/sec within 100-200 ms after gaze offset. The head velocities were maintained at this low velocity until near or beyond the end of the stimulation train. In many cases, the head movements continued as long as the stimulation continued. This observation was consistent across all IEP conditions.

Third, head onset varied significantly with respect to stimulation onset. Also, head onset varied significantly with respect to gaze onset. The variability of head onset persisted from trial to trial in all IEP conditions. A close examination of this figure suggests that the stimulation often produced a low-velocity phase of head movement that remained below threshold for up to several tens of milliseconds. Unfortunately, this early phase of the movement was sometimes of such a low velocity that it was impossible to reliably detect. Nonetheless, it is clear that the stimulation did not consistently produce a robust head movement beginning at a particular latency.

Fourth, significant head movements were sometimes evoked in the absence of gaze shifts. These head-alone movements were fairly common in the IEPc condition (93%, 1000/1074). Head-alone movements were also sometimes observed in the IEPo condition (114/212). In sharp contrast, the majority (97%, 289/297) of the trials obtained in the IEPi condition contained eye-and-head movements. In general, the peak head velocities of the head-alone trials were comparable to
those of the eye-and-head trials. The biased occurrence of the head-alone trials in the IEPc condition was consistent with the notion that the majority of SEF sites contained unresponsive IEP regions in the direction contralateral to the stimulated sides (Schlag and Schlag-Rey, 1987; Tehovnik and Lee, 1993). Also, the existence of the head-alone trials suggests that gaze shifts were not a pre-requisite for the stimulation-evoked head movements.

**Onset and offset latencies of head movements**

To quantify the effects of stimulation duration on the onset and offset latencies of head movements, the data obtained in two SEF sites were selected for plots in Figure 5. It can be noted that the distributions of the head onset latencies for 300-ms (117 ± 44 ms [n= 50] and 120 ± 52 ms [n= 48] for sites A and B, respectively) and 600-ms (107 ± 39 ms [n= 30] and 134 ± 54 ms [n= 41] for sites A and B, respectively) trials overlapped each other. No significant differences were found between the two trial types (F = 1.5, p= 0.22 for Fig. 5A1; F = 1.1 p= 0.29 for Fig. 5B1).

There was a significant difference in the distributions of the head offset latencies between the 300-ms (448 ± 37 ms, n= 506) and 600-ms (653 ± 98 ms, n= 30) stimulation trials in site A (Fig. 5A2; F= 71, p< 0.01). There was also a significant difference between the 300-ms (493 ± 94 ms, n= 48) and 600-ms (660 ± 92 ms, n= 41) stimulation trials in site B (Fig. 5B2; F= 177, p< 0.01). In other words, head movements were greatly prolonged when the stimulation duration was 600 ms, compared to 300 ms. There was no significant difference in head offset latency across IEPc conditions in site A (ANOVA, F= 0.8, p = 0.43). But there was a tendency for the IEPc to have larger offset latency when compared to the IEPo and IEpi conditions in site B (ANOVA, F= 7.1, p < 0.05; Scheffe test, p< 0.02).

Figure 6 quantifies the latencies of head onset as a function of IEPc across all of the
stimulated sites in the SEF. When head movements with onset latencies within 50-300 ms were selected for this analysis, there was a significant correlation between the head onset latencies and the IEPH (slope= -1.13 [M1= -1.11; M2= -1.14]; r= 0.32, F= 178, p< 0.01; Fig. 6). When the IEPH was deviated in the direction opposite of the movements (i.e. IEPi; negative IEPH values), the latency of head onset was increased as compared to the other conditions. Post-hoc analyses revealed that the head onset latency in the IEPi condition (mean latency: 155 ± 63 ms, n= 297) was significantly longer than those in IEPo (mean latency: 123 ± 68 ms, n= 326) and IEPc (mean latency: 111 ± 46 ms, n= 493) conditions (ANOVA, Scheffe test, p< 0.01 for both). There was no significant difference in the latencies of head onset between IEPo and IEPc conditions (Scheffe test, p= 0.31).

Figure 7 illustrates the distributions of head offset latencies for different stimulation durations. The mean offset latencies were 481 ± 88 ms (n= 1031), 519 ± 109 ms (n= 386), and 585 ± 105 ms (n= 368) for the 300-ms, 500-ms, and 600-ms stimulation trials, respectively. When all stimulation trials of all sites were pooled together for comparison, the effect of stimulation duration was highly significant (ANOVA, F= 112, p < 0.001), and all pair-wise post-hoc comparisons were highly significant (Scheffe test, p< 0.01). These results suggest a high and positive correlation between the duration of electrical stimulation and the duration of horizontal head displacements. Note that the head did not always continue to move till the termination of the stimulation train. The variability in the head offsets with respect to the stimulation offsets suggests that, in addition to the stimulation duration, other variable(s) may be involved.

**Head contribution to eye counter-roll**

As the stimulation-evoked gaze shifts often drive the eyes to the eccentric positions in
which the visual and oculomotor performances were limited, one may wonder whether the eye positions in the orbits are correlated with the displacements of the post-gaze-shift head movements. Figure 8 illustrates the examples of the effect of eye positions at gaze offset on the displacement of the post-gaze-shift head movement. The displacement of the post-gaze-shift head movement, measured as the head displacement between gaze offset and head offset during which the gaze was stabilized (Fig. 8A), will be referred to as “head contribution to eye counter-roll (HcEc) during the post-gaze-shift period” in the remainder of the text. Several observations are described below.

There was a consistent and positive correlation between horizontal head contribution to eye counter-roll (HcEch) and horizontal eye position (EPh) at gaze offset in two SEF sites (Fig. 8; r= 0.58, p< 0.01 in site B, n= 15; r= 0.37, p< 0.01 in site C, n= 28). When stimulation duration was considered as a covariant of the EPh, stimulation duration exerted a significant interactive effect on the horizontal head contribution to eye counter-roll (ANCOVA, separate slopes model; F= 9.7, p< 0.01 in site B; F= 4.7, p< 0.02 in site C).

Figure 9 quantifies this effect across all SEF sites tested. The analysis was carried out on the eye-and-head trials among those analyzed in Figure 7. For the sake of comparison, the trials in which gaze shifts were most consistently observed across three different stimulation durations (i.e. IEPi and IEPo conditions) were pooled together for analysis. Overall, the horizontal head contribution to eye counter-roll was strongly correlated with the horizontal eye position at gaze offset (Fig. 9A; r= 0.59, p< 0.01, n= 560). Note that in Figure 9A, when EPh was equal to or less than 0° (i.e. ipsilateral to the stimulated side), the head contribution to eye counter-roll was negligible (0.5 ± 0.8°, n= 27). In other words, when the eyes were already near the center of the orbits, stimulation failed to drive the head to continue moving. But, as the horizontal eye positions were deviated further contralaterally, the head contribution to eye counter-roll was increased
systematically as a function of the horizontal eye positions at gaze offset.

When stimulation duration was considered as a covariant of EPh, a highly significant interactive effect was found (ANCOVA, separate slopes model; F= 103, p < 0.001). Except for the conditions when EPh was 0° or less, 300-ms stimulation consistently evoked relatively less head contribution to eye counter-roll, compared to either 500-ms or 600-ms stimulation trials (Scheffe test, p< 0.02). That is, extended stimulation prolonged the head movements and thus improved the head contribution to eye counter-roll.

As pointed out earlier (Fig. 3), the stimulation-evoked head movements in the SEF were primarily horizontal. The vertical head contribution to eye counter-roll in these trials was negligible (average: 0.2 ± 0.7°) regardless of stimulation durations (r= 0.01, p> 0.80; Fig. 9B).

**Head-alone trials.** In these trials, the correlation between horizontal head contribution to eye counter-roll and eye position at *head onset* was relatively weak but remained significant. Figure 10A illustrates the example of a positive correlation between the horizontal head displacement and the horizontal eye positions (r= 0.60, p< 0.01, n= 53 for site B; r= 0.58, p= 0.001, n= 28 for site C) in two SEF sites. The stimulation duration had a significant interactive effect in these trials (F= 17.5, p< 0.01 in Fig. 10B; F= 8.9, p< 0.01 in Fig. 10C), indicating that extended stimulation indeed improved the horizontal head contribution to centering the eyes in the orbits.

When all of these trial types were combined, the same positive correlation between horizontal head contribution to eye counter-roll and EPh was significant (Fig. 11A; r= 0.29, p< 0.01, n= 642). When the stimulation duration was considered as a covariant of EPh, a significant difference was found (ANCOVA, separate slopes model, F= 19.5, p < 0.001). Post-hoc analysis indicated that, when EPh was between 15° and 30° in the contralateral direction, stimulation of a short duration (i.e. 300-ms trials) evoked smaller head displacements compared to stimulation of
longer durations (i.e. 500-ms or 600-ms trials; Scheffe test, $p<0.01$ for each $5^\circ$ bin). By contrast, when EPh was $5^\circ$ or less, there was no significant difference between these trials (Scheffe test, $p>0.23$).

The average vertical head displacements of these trials were small (300-ms trials: $0.7 \pm 1.5^\circ$; 500-ms: $0.1 \pm 1.6^\circ$; 600-ms: $1.1 \pm 2.7^\circ$; Fig. 11B). However, there was a tendency for vertical head displacement to increase slightly as a function of eye position in the direction of movements (slopes= 0.07, 0.06, and 0.13 for 300-ms, 500-ms, and 600-ms trials, respectively; pooled $r=0.42$; $p<0.01$).

Several unique differences could be noted in the comparison between the eye-and-head trials (Fig. 9A) and the head-alone trials (Fig. 11A). First, the former contained a negligible horizontal head contribution to eye counter-roll when EPh was $0^\circ$ or less. The latter contained a small but consistent horizontal head displacement ($4.1^\circ \pm 2.2^\circ$, $n=76$) even when EPh was centered in the orbit (range: $0^\circ$; $5^\circ$) or biased ipsilaterally (range: $-5^\circ$; $0^\circ$) (indicated by a downward arrow in Fig. 11A). The difference between the two trial types was highly significant (t test, $p<0.01$). This unique feature was reminiscent of the stimulation-evoked head-alone movements in the superior colliculus and had not been reported in the SEF in the past (Corneil et al., 2002a, b; Pelisson et al., 2001). Second, the head-alone trials (Fig. 11A) did exhibit a general tendency for the horizontal head displacement to increase as a function of the horizontal eye positions. However, detailed inspection indicated that this effect was not significant between when the eyes were deviated 20-25$^\circ$ in the orbits and when the eyes were deviated 25-30$^\circ$ in the orbits ($F=0.02$, $p>0.86$ for 600-ms trials; $F=0.03$, $p>0.87$ for 500-ms trials; $F=3.6$, $p>0.06$ for 300-ms trials; Fig. 11A). It appears that the differences occurred depending upon whether or not gaze shifts took place.
Head contribution to gaze shift

Figure 12 illustrates the effect of IEPh on the relationship between head contribution to gaze shift and gaze amplitude. The horizontal head contribution to gaze shift (HcGh; defined as the horizontal head displacement between gaze onset and gaze offset; Fig. 12A) was positively correlated with horizontal gaze (Gh) amplitudes (Fig. 12B). This relationship shifted when the IEPh was systematically varied. The vertical head contribution to gaze shift (HcGv, defined as the vertical head displacement between gaze onset and gaze offset) was negligible (0.32 ± 0.77°; slope= 0.00-0.01; Fig. 12C). These results were reminiscent of those observed in the visually guided gaze shifts (Guitton et al., 1990; Phillips et al., 1999; Sparks et al., 2001; Tomlinson and Bahra, 1986).

We further analyzed the eye-and-head trials in order to assess whether the “early head” and the “late head” trials differed in the horizontal head contribution to gaze shifts. The histograms in Figure 13 (top) illustrate the distributions of the timing difference between head onset and gaze onset, separated by IEPh conditions. These distributions were significantly different across IEPh conditions (average of IEPi: 42 ± 62 ms, n= 419; average of IEPo: -28 ± 90 ms, n= 173; average of IEPc: -31 ± 92 ms, n= 98; ANOVA, F= 74, p< 0.01). The differences in the distributions are best appreciated in the box plots below the histograms. For IEPi condition, the middle 50% of the data ranged from 8 to 58 ms. For IEPo and IEPc conditions, the middle 50% of the data ranged from -84 to 30 ms and from -114 to 38 ms, respectively. That is, when the IEPh was ipsilateral to the stimulated side, the temporal association between head and gaze onset was much tighter than when the IEPh was centered or contralateral at stimulation onset (e.g. Fig. 4).

The bottom scatter plots of Figure 13 show the horizontal head contribution to gaze shifts as a function of the timing difference between head onset and gaze onset. When only the trials in
which the horizontal head contributions were at least $1^\circ$ were considered, a trend becomes clear and can be best appreciated in the box plots. In IEPi condition, the middle 50% of the data was centered about zero (range: from -14 to 18 ms, n= 165). That is, as long as the head and gaze movements took place within 20 ms of each other, significant head contribution would be recruited. However, in IEPo and IEPc conditions, the middle 50% of the data ranged between -139 and -44 ms (n= 56) and between -188 to -130 ms (n= 15), respectively. In other words, if the head was already moving when gaze shifts began, the head often made a significant contribution to gaze shifts.

We further contrasted the timing difference between the head onset and gaze onset of the stimulation trials with that of the visually guided gaze shift trials. The latter trials took place following the illumination of the yellow target in the task (see Fig. 1 and Methods). This timing difference in the visually guided gaze shifts ranged from -204 to 196 ms, with an average of $-5.1 \pm 43.4$ ms (n= 1370; $-5.2 \pm 39.6$ ms for M1, n= 638; $-4.9 \pm 46.6$ ms for M2, n= 732). Similar to the finding illustrated in Figure 13, when the horizontal head contributions to gaze shifts of at least one deg were considered, the values leaned toward the negative end, i.e., the difference between head onset and gaze onset became $-20.8 \pm 29.2$ ms ($-19.1 \pm 24.9$ ms for M1; $-22.2 \pm 32.4$ ms for M2). In essence, consistent with previous studies, the significant head contributions to gaze shifts in these visually guided trials came primarily from those in which head onset led gaze onset (Gandhi and Sparks, 2001; Galiana and Guitton, 1992; Goossens and Van Opstal, 1997; Guitton et al., 1990).

**Eye-alone trials.** As pointed out earlier, SEF stimulation sometimes evoked gaze shifts in the absence of head movements. The head movements in these eye-alone trials (n= 543) were simply nonexistent or below the velocity criteria (see Methods). The majority (81%; n= 438; M1= 419/522; M2= 19/21) of the eye-alone trials were obtained in the IEPi condition while the minority
was obtained in the IEPo condition. In the IEPi condition (average IEPh: -23.0 ± 2.7°), the average horizontal gaze displacement was 22.5 ± 7.4°, and the average EPh at horizontal gaze offset was −0.2 ± 6.6°. In the IEPo condition (average IEPh: -0.2 ± 1.5°), the average horizontal gaze displacement was 7.7 ± 5.0°, and the average horizontal eye position (EPh) at gaze offset was 7.2 ± 4.6°. Only one eye-alone trial was found in the IEPc condition; this trial had a horizontal gaze displacement of 3.4°. In essence, the movement metrics exhibited in the eye-alone trials had two main features: the horizontal gaze displacements remained comfortably within the oculomotor range and the eye deviations at the end of the gaze shifts remained close to the center of the orbits. In such a case, head movements were not recruited, as shown in visually guided gaze shifts (Freedman and Sparks, 1997; Guitton et al., 1990; Sparks et al., 2001).

**Non-task mode stimulation.** One may wonder whether the visual stimuli or the postural control in the task had biased the outcome of SEF stimulation. Specifically, one may wonder whether the observed early head movements had been voluntary movements initiated by the animals. To rule out these possibilities, we conducted the non-task mode stimulation in 18 SEF sites (16 in M1 and 2 in M2) during the intertrial interval in the dark (see Methods).

Figure 14A illustrates the stimulation-evoked movement traces under this trial type in a SEF site. Based on the comparison between the traces of Figure 14A and those of Figure 4, one can note that these trials were alike in many aspects. Head onset could lag or lead gaze onset (Fig. 14A, 300-ms stimulation). The head-alone trial could be evoked occasionally (Fig. 14A, middle traces in 600-ms stimulation). Also, the early-head trials were prevalent. These trial types were present in both monkeys.

To further quantify these movements under the non-task mode stimulation, the stimulation
trials of all sites were pooled together for analysis. The major findings can be summarized as follows. First, like the movements observed in the task-mode conditions, the SEF stimulation evoked eye-alone, head-alone, and eye-and-head trials. Second, the ranges of these head displacements were comparable to those of the task-mode stimulation. For the eye-alone trials (n=59), the average horizontal eye displacement was 12.6 ± 5.9°, and the average Ev displacement was 4.5 ± 5.5°. For head-alone trials (n=115), the average horizontal head displacement was 6.3 ± 3.8°, and the average Hv displacement was 0.8 ± 1.0°. For the eye-and-head trials (n=263), the average horizontal head displacement was 13.8 ± 9.0°, the average vertical head displacement was 2.0 ± 2.2°, the average horizontal gaze displacement was 22.5 ± 10.2°, and the average vertical gaze displacement was 4.3 ± 6.2°. The data from the two monkeys fell within similar ranges. Third, the average latency difference between head onset and gaze onset was –44.9 ± 67.4 ms (maximal range: -236: 198 ms; n=263). Fourth, head contribution to gaze shifts ranged from –0.3 to 19.6° (4.5 ± 4.6°; n=85) when the IHPh ranged from –5° to 5° (i.e. centered with respect to the body as in the task-mode condition). Similar to Fig. 12B and the observations in the visually guided gaze shifts, head contribution to gaze shift in this case could be appreciated as a function of horizontal gaze displacement. Fifth, head contribution to eye counter-roll in these trials (Fig. 14B; 300-ms trials: triangles; 600-ms trials: open squares) were comparable to that illustrated in Figure 9. The stimulation duration had a significant interactive effect over the head contribution to eye counter-roll (ANCOVA, separate slope model; F= 42.8, p< 0.001).

We further compared the stimulation-evoked head movements to the visually guided head movements. Figure 14B illustrates the average (circles) and the range (shaded region) of head contribution to eye counter-roll for the visually guided gaze shift trials (n= 1370; n= 638 for M1 and n= 732 for M2). Two major points can be noted. First, the data points of both 300-ms and
600-ms stimulation trials fell within the range of the visually guided gaze shift trials. Second, consistent with the fact that 300-ms stimulation prematurely truncated the head movements, the 300-ms stimulation trials exhibited smaller head contribution to eye counter-roll as compared to the average of the visually guided gaze shift trials. On the other hand, 600-ms stimulation exceeded the completion of typical head movements, and thus these trials exhibited higher than average head contribution to eye counter-roll.

**SEF map.** Figure 15 summarizes the distributions of eye-alone, head-alone, and eye-and-head trials in the SEF of one monkey in which the SEF was thoroughly mapped. Only movements of at least 2° were included in this analysis. It can be noted that the eye-alone trials were relatively evenly distributed (Fig. 15B). The center of gravity for these sites was approximately 7 mm rostral from the caudal end of the arcuate sulcus and about 4 mm from the midline. This SEF map appears consistent with previous studies which suggest that the saccadic sites are located rostrally whereas the smooth pursuit sites are located caudally (Chen and Wise, 1995; Fujii et al., 2002; Fukushima et al., 2004; Schall et al., 1993).

Figures 15B and C further indicate that there was a tendency for eye-alone, head-alone, and eye-and-head trials to intermix in the majority of these sites (e.g. Fig. 4). Nonetheless, there exists a biased aggregation of the head-alone trials in the rostral end of the SEF (Fig. 15C). To quantify the possible bias in the distribution along the AP (anterior-posterior) and ML (medial-lateral) axes, these data were divided into rostral versus caudal groups based on an AP cutoff at the chamber coordinate (corrected to parallel the staterotexic coordinate) of 8.2. The same data were divided into medial versus lateral groups based on a ML cutoff at the chamber coordinate of 4.2. The results indicated that there was no significant bias in the distribution of eye-alone trials either along the AP axis (Mann-Whitney U, U= 143, p> 0.21) or the ML axis (U= 165, p> 0.53). Neither was
there a significant bias in the distribution of the eye-and-head trials along the AP axis (U= 95, p> 0.89) or the ML axis (U= 93, p> 0.82). However, there was a significant bias in the distribution of head-alone trials along the AP axis (U= 79, p< 0.003) with higher occurrences of head-alone movements in the rostral sites than the caudal sites. There was no such biased distribution along the ML axis (U= 189, p> 0.96).

**DISCUSSION**

The present study has provided several lines of evidence supporting the hypothesis that the SEF is directly involved in the control of head movements independent of gaze. First, when the eyes were deviated in the contralateral direction (or near the unresponsive IEP region) at stimulation onset, head movements were often evoked in the absence of gaze shifts. Second, when the stimulation duration was increased, the post-gaze-shift portion of the head movements was prolonged, and the head contribution to centering the eyes in the orbits was greater. Finally, stimulation sometimes evoked low-velocity head movements that preceded the onset of gaze shifts. When this happened, the head contribution to gaze shifts often increased. Some alternative interpretations of these findings are discussed below.

**Head contribution to eye centering and SEF**

Two hypotheses have been postulated to account for the fact that the head often continues to move following large-amplitude gaze shifts. The *head displacement command* hypothesis states that the entire head movement is preprogrammed, and the head amplitude is determined by the desired displacement (Bizzi et al., 1971; Morasso et al., 1973; Laurutis and Robinson, 1986). Data supporting this hypothesis come from studies showing that the total head displacement is positively
correlated with target and gaze amplitudes (Freedman and Sparks, 1997; Laurutis and Robinson, 1986; Phillips et al., 1995; Volle and Guitton, 1993). If the SEF indeed codes for head displacement, one would expect the stimulation to evoke consistent head displacements at least in some SEF sites. However, as shown in our results, even though the stimulation duration was extended up to 600 ms, these head displacements remained highly variable for any given site (e.g. Fig. 4). That is, there is no site-specific maximum head amplitude encoded in the SEF. This result is in sharp contrast to the stimulation-evoked gaze shifts. Given that the stimulation is extended beyond the end of gaze, the site-specific maximum gaze amplitude would be evoked independent of the duration of the extended stimulation (Freedman et al., 1996; Stanford et al., 1996). Nonetheless, our finding does not preclude the possibility that other cortical areas may contain a pure head displacement command.

The results of Figures 9 and 14 suggest that head movement control is programmed not based on the desired head displacement per se. The eye positions in the orbits provide the justification for the head to continue to move or to stop from moving. Ultimately, the eyes were rolled to the most flexible oculomotor range, i.e. near the center of the orbits (Goossens and van Opstal, 1999; Tomlinson and Bahra, 1986; Sparks, 1999; Sparks et al., 2001; Guitton et al., 1990). These rationales suggest an alternative eye centering hypothesis with the following predictions (Sparks et al., 2001). First, if the eyes were already centered (or within the flexible oculomotor range), the head should move very little. Second, there must be a lawful relationship existing between the amount of eye deviation in the orbit and the amount of post-gaze-shift head displacement. Our findings (e.g. Fig. 9A) are consistent with these two predictions. On the other hand, in the eye-alone trials, the endpoints of the eyes at gaze completion often fell within the range near the center of the orbits. Thus, little head contribution to eye counter-roll was recruited. The
finding that extended stimulation improved head contribution to centering the eyes in the orbits (e.g. Figs. 9A and 14B) further supports the prediction of this hypothesis.

This physiological eye-centering is not a precise and automated mechanism. If the eyes were to be perfectly centered in the orbits, the data points in Figure 9A should fall on the regression line with the slope of one. This was not the case. In the case of the visually guided gaze shifts (Fig. 14B), the head contribution to eye centering was not precise either. The average post-gaze-shift head movements in general fell short of bringing the eyes to precisely the center of the orbits. On the other hand, depending upon the duration of the stimulation, the magnitude of the head contribution to eye counter-roll was above or below that of the averaged visually guided trials (e.g. 300- vs. 600-ms stimulation trials in Fig. 14B). The results confirm that extended stimulation indeed altered the metrics of head contribution to eye centering.

Due to the concern about possible tissue damage by high current, we did not attempt stimulation with durations exceeding 600 ms with the same current intensity and frequency. We did not know whether continuing stimulation would ultimately counter roll the eyes to the orbital limit of the opposite end. However, the examples provided in Figure 4 (e.g. the first trace of 600-ms stimulation trials in the IEPi condition) and Figure 14A (the first trace of 600-ms stimulation trials) offered some hints. These results suggest that the head movements of higher velocities tended to decrease their velocities to baselines before the stimulation was terminated. In these cases, the eyes approached the center of the orbits sooner, and the head movements stopped accordingly. It appears that extended stimulation was unlikely to drive the eyes to the orbital limit of the opposite end. Future experiments are needed to confirm this assertion.

Head contribution to eye counter-roll is also significant in the head-alone trials (Fig. 11A). When the eyes were deviated in the movement directions, the head movements could be robust and
thus served to counter-roll the eyes away from eccentric positions (Fig. 11A). However, in the other cases, the head movements actually drove the eyes *away* (ipsilaterally) from the center of the orbits (Fig. 11A, downward arrow). The latter head movements were in general small, and the eyes remained within 5° from the center of the orbits. This type of head movement was reminiscent of those evoked in the superior collicular stimulation (Corneil et al., 2002a; Galiana and Guitton, 1992; Pelisson et al. 2001).

Note that the stimulation-evoked head movements were primarily horizontal, whereas the stimulation-evoked gaze shifts tended to have significant vertical components (Fig. 3). That is, both the head contribution to eye counter-roll and the head contribution to gaze shift were limited to the horizontal movements (Figs. 9, 11, and 12). The unique head movement direction in the SEF stands out in comparison with a different cortical field near the SEF, in which electrical stimulation evoked head movement in *all* directions in order to achieve centering the eyes in the orbits (Sparks et al., 2001). Also, the head movement representation in the cortex, especially the SEF, appears different from that of the superior colliculus. The latter tends to contain significant vertical head amplitudes depending upon the direction of the stimulation-evoked gaze shifts (Freedman et al., 1996; Martinez-Trujillo et al., 2003).

**Early-head and head-alone movements**

One may wonder whether the early-head (and head-alone) trials were the animals’ anticipatory movements. Similar argument can be made regarding whether these trials were greatly affected by the eye-head postural constraints. These possibilities are unlikely for several reasons. First, Levinsohn (1909, described in Smith, 1949) who performed clinical assessments using electric stimulation had reported similar observations. In these early investigations, the animals...
were lightly anesthetized and there were no sophisticated task or postural demands. Second, the directions of these stimulation-evoked head movements were not random but primarily horizontal and contralateral with respect to the stimulated side. Note that the reward was not contingent upon the animals holding a particular position or moving in a particular direction following the stimulation. Third, the early-head trials were observed in the non-task mode as well as the task-mode stimulation trials. There were no task or postural constraints in the former trial type, yet the results of both trial types were comparable (Fig. 14). Fourth, the stimulation was conducted in darkness. There was no visual or auditory cue that promoted or repressed conditional movements. None of the stimulation-evoked gaze shifts exhibited the hallmark signature of the visually guided gaze shifts, i.e. corrective saccades. Finally, the stimulation-evoked movements were dramatically different across different cortical regions, even in the same animals under the same task demands. For instance, in our FEF stimulation data, we rarely, if at all, observed trials in which the head movements were initiated prior to gaze shifts (Chen and Sparks, unpublished observations; van der Steen et al., 1986). Also worth mentioning is the fact that these results were obtained on different recording days. The same monkeys could not have been conditioned to suppress one type of movement one day and conditioned to suppress another type of movement the next day. Based on these reasons, it is clear that variables other than animal training and task demands need to be taken into account.

The question is then how could SEF stimulation evoke eye-and-head movements in some trials and head-alone movements in other trials? A two-pathway hypothesis has been proposed to account for similar findings in collicular stimulation studies (monkey: Corneil et al., 2002b; cat: Galiana and Guittot, 1992; Pelisson et al., 2001). These authors argue that two pathways—one head and one eye—may be initiated depending on the threshold of activation. When the
stimulation activates the head-alone (presumably low-threshold) pathway, but fails to activate the eye (presumably high-threshold, omni-pause-neuron (OPN) gated) pathway, early-head or head-alone trials will be observed. The saccadic pulse generators are gated by the OPNs in the nucleus raphe interpositus, which is connected with the SEF (review see Moschovakis et al., 1996; Huerta and Kaas, 1990; Shook et all, 1990). The OPN gating works like an on-off switch. As soon as the gaze shift is over (or prior to the gaze initiation), the OPN gating resumes and the gaze position is prevented from changing (Fuchs et al., 1985; Hepp et al., 1989; Keller, 1981; Moschovakis et al., 1996). Hence, via the activation of the VOR, the head displacement observed is approximately equivalent to (but in opposite sign of) the eye counter-roll in the orbit (Cullen, 2004; Green and Angelaki, 2004; Guittton et al., 1990). These regulations exist in the visually-guided and the stimulation-evoked gaze shifts (Corneil et al., 2002a, b; Freedman et al., 1996; Freedman and Sparks, 1997; Fujii et al., 1995; Guittton et al., 1990; Martinez-Trujillo et al., 2003, 2004; Morasso et al., 1973; Phillips et al., 1995; this study).

Tehovnik and colleagues (Tehovnik and Lee, 1993; Tehovnik and Sommer, 1997) have proposed an oculomotor-suppression hypothesis that too may account for our observations of early-head and head-alone movements. The authors argue that the SEF stimulation within the unresponsive IEP region (referred to as the “termination zone”) either overrides the visual (external) input or inactivates the gaze/eye signal. Their hypothesis predicts the following: 1) no gaze shifts will occur when the IEPPh is deviated in the unresponsive IEP region at stimulation onset and 2) the probability of the visually triggered saccades is a function of the IEPPh from the unresponsive IEP region. Two observations in this study are in line with the two predictions. First, when the IEPPh was deviated in the contralateral direction (i.e. most likely within the unresponsive IEP region; e.g. Figs 4 and 6A), SEF stimulation often evoked the head-alone trials. There were
very few trials that were accompanied by gaze shifts. Second, when the gaze shifts did occur in this case, the head movements often occurred earlier than the gaze shifts. That is, these head movements drove the eyes away (ipsilaterally) from the unresponsive IEPh (contralateral) region (e.g. the IEPc or IEPo conditions in Fig. 13C), thus increasing the probability for the gaze shifts to be evoked by SEF stimulation.

At this point, whether the SEF contains local inhibitory circuitry that is sensitive to IEPh or whether the SEF contains separate head and eye pathways that are sensitive to threshold of activation remains unclear. Nonetheless, the finding that the unresponsive IEPh regions remained largely unchanged in head-unrestrained conditions is consistent with the notion that the movements evoked in the SEF are organized in either head-centered or body-centered frames of reference (Martinez-Trujillo et al., 2004; Schlag and Schlag-Rey, 1987; Tehovnik et al., 1998). Distinguishing these coordinate frames of reference remains open for further studies.

There are established methodologies that can reliably produce the early-head movements. It has been shown that, in normal gaze shifts, the difference between head onset and gaze onset results primarily from target predictability and/or motor set. These situations include experimental tasks in which visual targets are off eccentric, flashed briefly, or there is a conflict between targets that are sequentially presented (Bizzi et al., 1972; Corneil and Eleley, 2005; Guitton et al., 1990; Fuller, 1992; Moschner and Zangemeister, 1993; Roucoux et al., 1981; Zangemeister and Stark, 1982). Whether SEF stimulation evokes different head movements in response to these unique situations remains to be investigated.

The early-head movements are usually slow and often accompanied by a gradually increased activity of agonist neck muscles (Bizzi et al., 1971; Corneil et al., 2002a, b). In contrast, the head movements recruited around the time of gaze shifts typically have burst-like neck muscle
activation patterns. It has been shown that the SEF neurons and those in the neighboring inter-connected cortices are strongly modulated by changes in the motor significance of the instructions; these neurons are often responsive to self-initiated, as opposed to externally guided, movements (Amador et al., 2000; Chen and Wise, 1995, 1996; Fujii et al., 1995; Isoda and Tanji, 2002; Kurata and Wise, 1988; Olson and Gettner, 1995; Stuphorn et al., 2000). It is possible that the independent head movement control in the SEF provides one of the mechanisms supporting these physiological functions.

It is of interest that the head-alone movements were more often evoked rostrally compared to caudally in the SEF map (Fig. 15). This rostral representation of head movement in the SEF appears consistent with the somatotopic organization of the supplementary motor cortices adjacent to the SEF, in which the forelimb and hindlimb representations are located rostrally and caudally, respectively (review see Tanji, 1994; Luppino et al., 1991; Mitz and Wise, 1987). Nevertheless, this apparent correlation cannot resolve the issue of whether the SEF is intermixed with the supplementary motor cortices or whether the SEF contains a unique head representation in its map.

The SEF is extensively connected with many other cortical and subcortical areas that are implicated in skeletomotor functions (Huerta and Kaas, 1990; Shook et al., 1991). Somatosensory mapping studies have indicated that the SEF contains neurons responsive to neck manipulations (Rizzolatti et al., 1990; Schlag and Schlag-Rey, 1987; Luppino et al., 1991). This pattern of anatomical connections in the SEF is drastically different from that in the FEF, as the latter is heavily connected with visual and oculomotor regions (Huerta and Kaas, 1990; Schall et al., 1993; Schiller and Chou, 2000; Shook et al., 1991). It is feasible that, like the neighboring complex of supplementary motor cortices, the SEF contains mechanisms that permit extensive cross-talks between different motor apparatuses, thus higher-order movement controls can be achieved (Bon
Comparison with the superior colliculus

There are similarities in the stimulation-evoked head movements between the SEF and the superior colliculus. First, the stimulation-evoked head movements in both the SEF and the superior colliculus are primarily contralateral (Freedman et al., 1996; Corneil et al., 2002a, b; Guitton et al., 1990; Martinez-Trujillo et al., 2003; this study). Second, both the SEF and the superior colliculus have large-amplitude sites in which unresponsive IEP regions exist (Freedman et al., 1996; Russo and Bruce, 1993; Schlag and Schlag-Rey, 1987; Tehovnik and Lee, 1993; Guitton, 1990). Third, the early-head and head-alone trials could sometimes be evoked by electrical stimulation in both the SEF and the superior colliculus (Corneil et al., 2002a, b; Galiana and Guitton, 1992; Pelisson et al., 2000). These similarities should not be surprising considering that the SEF is heavily connected with the intermediate and deep layers of the superior colliculus, the function of which is associated with the initiations of gaze shifts and head movements (Huerta and Kaas, 1990; Moschovakis et al., 1996; Shook et al., 1991; Schall et al., 1993).

It is worthy noting that there exist extensive network interactions between the eye plant and head plant via the VOR (Bizzi et al., 1971; Guitton et al., 1990; Morasso et al., 1973; Moschovakis et al., 1996). As a result, the executed movements of the eye and head are coordinated via vestibular regulation such that the movements observed are not necessarily equivalent to the commands that are issued (review see Sparks, 1999). Since both outputs of the SEF and the superior colliculus are subject to regulation by the same brainstem mechanisms, one should be cautioned in making direct data comparison between the head-restrained and head-unrestrained
There are at least three major differences in the stimulation-evoked head movements between the SEF and the superior colliculus. First, the head movements evoked in the SEF have little vertical components whereas those evoked in the superior colliculus have significant vertical components (Freedman et al., 1996; Corneil et al., 2002a, b; Guitton et al., 1990; Martinez-Trujillo et al., 2003; this study). Second, Corneil et al. (2002b) found that high current stimulation in the superior colliculus tended to evoke eye-and-head movements, whereas subthreshold current (as low as 10 µA) stimulation tended to evoke early-head or head-alone movements. Interestingly, we had never found such a differential effect in the SEF. We found that the higher currents (typically suprathreshold currents, e.g. 100-150 µA) simply improved the detectability of these slow, pre-gaze head movements that otherwise remained undetected (e.g. Fig. 4). Third, it has been shown that the optimal stimulation frequency for the collicular stimulation to evoke the site-specific maximum saccades is 500 Hz, if not higher (head-unrestrained monkeys: Freedman et al., 1996; head-restrained monkeys: Stanford et al., 1996). Given that all other variables remain unchanged, the probability for the collicular stimulation to evoke saccades is a monotonic saturating function of the stimulation frequency. By contrast, the optimal frequency for the SEF to evoke saccades is within a relatively low and narrow range (100-200 Hz); increasing the stimulation frequency higher than 200 Hz often decreased the probability for the SEF stimulation to evoke saccades (Tehovnik and Lee, 1993; Tehovnik and Sommer, 1997).

In light of the above notion, we carried out testing in the stimulation-evoked head movements in the SEF (e.g. Fig. 16). As shown in the Results, under some circumstances (i.e. IEPc and IEPO conditions) SEF stimulation often evoked head-alone movements in the absence of gaze. We tested under these unique circumstances the effect of stimulation frequency in 10 SEF sites (n=
In each tested site, the stimulation current and duration remained constant. In 8 of these sites in which both 100-Hz and 200-Hz stimulations were evaluated, 100-Hz stimulation evoked the largest head displacements in half of the sites and 200-Hz stimulation, the other half. An example of the testing is illustrated in Fig. 16. In 6 sites, 200-Hz and higher frequencies (400-Hz [n= 4], 800-Hz [n= 1], and 1000-Hz [n= 1]) were evaluated. In all 6 sites, frequencies higher than 200-Hz decreased the head displacements by 18-79% as compared to that evoked by 200-Hz stimulation. Thus, the optimal stimulation frequency for evoking head movements (this study) and for evoking saccades (Tehovnik and Lee, 1993; Tehovnik and Sommer, 1997) appeared within similar ranges.

The stimulation parameters required to evoke movements are a function of many physiological variables, such as cortical depth, task induction, gaze amplitude, eye positions, and head positions (Freedman et al., 1996; Stanford et al., 1996; Tehovnik and Sommer, 1997; this study). Stimulation frequency also interacts with other stimulation parameters, such as current, pulse duration, and polarity (Tehovnik et al., 2005). Thus, one cannot easily compare the results across different studies. Note that the electrically evoked movements are definitely not natural movements. For instance, corrective saccades are absent in these stimulation-evoked eye-head combined movements. Nonetheless, stimulation-evoked movements serve to demonstrate the manifestation of the movement commands existing in the SEF.

**Remarks**

It is pertinent to measure the stimulation-evoked pre- and post-gaze-shift head movements in the SEF under adequate control. Without consistent postural stability, such as the task control performed in this study, these low-velocity head movements could easily be misidentified or
ignored. One should be aware of the fact that these head movements may be intermixed with the eye-head combined gaze shifts. The existence of the head movements independent of gaze places constraints on interpreting the stimulation data in the SEF.

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FIGURE LEGENDS

**Figure 1.** Schematic flow charts illustrating onsets and offsets for the targets (indicated as “Red,” “Green,” and “Yellow”) and the microlaser (indicated as “laser”) in the control trials (A) and stimulation trials (B). The open rightward arrows indicate the epochs when the targets were illuminated, whereas the filled rightward arrows indicate the epochs when the targets were extinguished. The vertical filled arrow in A corresponds to the onset of electrical stimulation in B, whereas the open arrow corresponds to the onset for a visual (Yellow) target. Note in trial B, stimulation was delivered 200 ms following the extinction of all visual targets and microlaser; these visual sources remained extinguished throughout the period of electrical stimulation (300-600 ms) and the subsequent period of 500-800 ms.

**Figure 2.** Examples of horizontal position (A) and velocity (B-D) traces of the stimulation-evoked movements in a (left) SEF site. A: Horizontal position traces for gaze (G), eye (E), and head (H) when IEPh was centered in the orbits (IEPo). The horizontal bar indicates the duration of electrical stimulation, 300 ms in this case. Upward deflection indicates rightward movement, whereas downward deflection indicates leftward movements. B: Horizontal velocity traces of head, gaze, and eye for the same data displayed in A. The arrowhead and the arrow indicate the onset and the offset of the evoked head movements. C and D: Horizontal velocity traces for eye, gaze, and head when IEPh was in the direction ipsilateral (IEPi) or contralateral (IEPc) to the stimulated side, respectively. Stimulation: 120 µA, 200 Hz, and 300 ms. E: Horizontal velocity traces for eye, gaze, and head of a control trial (IEPo) in the same block. The filled and open arrows correspond to those plotted in Figure 1A. The open box below the traces indicates the period in which the red
and green targets and the microlaser were re-illuminated, as shown in Figure 1. All traces are plotted in the same horizontal scale.

**Figure 3.** Amplitude and velocity of the stimulation-evoked movements in the SEF. **A** and **B:** Horizontal and vertical components of the head displacement (A) and peak velocity of the horizontal head (Hh) movements plotted as a function of horizontal head displacement (B). Only the trials in which the total head displacement exceeded 2° were included. **C** and **D:** Horizontal and vertical components of the eye displacement (C) and peak velocity of the horizontal eye (Eh; re head) movements plotted as a function of horizontal eye displacement (D). Positive values in A and C reflect movement in the rightward (i.e. contralateral from the side of stimulation) or upward direction. The central line of box plots indicates the median; each side of the box indicates either 25% or 75% of the total. The whisker at both ends indicates 1% or 99% of the total. Data from the stimulation sites (n= 78) of both monkeys were included in the plots.

**Figure 4.** Effects of stimulation duration (top panels: 300 ms; bottom panels: 600 ms) on the velocities and durations of stimulation-evoked head movements, separated for IEPi (range: -28°: -15°, left panels), IEPo (range: -6°: 6°; middle panels), and IEPc (range: 15°: 28°, right panels) conditions in one SEF site. The horizontal velocity traces for head and gaze are plotted in black and gray, respectively. Upward deflection indicates rightward movement, which is contralateral to the stimulated (left) SEF. Shaded regions indicate the epoch in which the electrical stimulation was delivered. Arrowheads show the head onsets, and arrows indicate the head offsets. The trials in which staircase gaze shifts occurred and those in which the gaze shift latency was longer than 300 ms were excluded from the analysis. Stimulation: 120 µA, 200 Hz, and 300 (and 600) ms.
Figure 5. Examples of the effect of stimulation duration on the onset (A1 and B1) and offset (A2 and B2) latencies of the stimulation-evoked head movements in two SEF sites. Open bars are 300-ms trials (N = 56 in site A and N = 53 in site B). Filled bars are 600-ms stimulation trials (N = 31 in site A and N = 37 in site B). Gray bars indicate the overlap bins between the two trial types. Data in B were obtained in the same site as in Figure 4. Stimulation: Site A: 100 µA and 200 Hz; Site B: 120 µA and 200 Hz.

Figure 6. Correlation between the onset latency of horizontal head movement and IEPh. Data points represent means and S.D. of all stimulation trials. Bin width: 10°. Positive IEPh values indicate that the eyes were contralateral with respect to the stimulated side, whereas negative values indicate that the eyes were ipsilaterial with respect to the stimulated side.

Figure 7. Effects of stimulation duration (A: 300 ms, B: 500 ms, and C: 600 ms) on the offset latencies of the stimulation-evoked head movements. Only the head movements at least 200 ms in duration were included in the plots. Arrows indicate the time point when the stimulation train was terminated.

Figure 8. Examples of horizontal gaze (G) and horizontal head (H) position traces of the eye-and-head trials in which SEF stimulation evoked both gaze shifts and head movements, illustrating the metrics of horizontal head contribution to eye counter-roll (HcEch; A). B and C: Positive correlation between horizontal head contribution to eye counter-roll and EPh at gaze offset in two SEF sites. Extended stimulation prolonged the horizontal head contribution to eye counter-roll
(600-ms stimulation: open squares and solid regression lines; 300-ms stimulation: open triangles and dashed regression lines). Site C is the same as that illustrated in Figure 4. EPh: horizontal eye position; EPv: vertical eye position.

**Figure 9.** Positive correlation between horizontal head contribution to eye counter-roll (HcEch) and horizontal eye positions (EPh) following gaze offset (A) and lack of correlation between vertical head contribution to eye counter-roll (HcEcv) and vertical eye positions (EPv) following gaze offset (B). Data were obtained from the eye-and-head trials, separated for different stimulation durations (300-ms: triangle, 500-m: plus, and 600-ms: open square) for all sites. Positive values in A indicate the (right) positions contralateral to the stimulated (left) side; positive values in B indicate the (up or down) positions in the direction of movements. Only trials with head displacements of at least 2° were included. Data points represent means and S.E.M. Bin width: 5°.

**Figure 10.** Examples of horizontal head and gaze position traces of the head-alone trials illustrating the metrics for the horizontal head displacement (A). B and C: Positive correlation between horizontal head displacement and EPh at gaze offset in two SEF sites. Extended stimulation prolonged the head displacements (600-ms stimulation: open squares and solid regression lines; 300-ms stimulation: open triangles and dashed regression lines). Site C is the same as that illustrated in Figure 4.

**Figure 11.** Positive correlations between horizontal head displacement and eye positions at head onset (A) and weak correlation between vertical head displacement (Hv) and eye positions
(EPv) at head onset (B). Data were obtained from head-alone trials, separated for different stimulation durations (300, 500, and 600 ms). Positive values in A indicate the (right) positions contralateral to the stimulated (left) side; positive values in B indicate the (up or down) positions in the direction of movements. Data points represent means and S.E.M. Bin width: 5°. Only the trials with head displacements of at least 2° were included.

Figure 12. Examples of head and gaze position traces of the eye-and-head trials illustrating the metrics of horizontal head contribution to gaze shifts (HcGh; upper traces in A) and vertical head contribution to gaze shift (HcGv; lower traces in A). B: Systematic varying IEPh shifted the horizontal head contribution to gaze shift as a function of horizontal gaze amplitude. C: Vertical head contribution to gaze shifts was negligible despite the variability of vertical gaze amplitude and IEPh. Data were separated for IEPi (squares), IEPo (asterisks), and IEPc (triangles). Bin width: 5°.

Figure 13. Effect of IEPh on the distributions of the latency difference between head onset and gaze onset (top histograms and box plots) and horizontal head contribution to gaze shifts (bottom scatter plot). Data were obtained from the eye-and-head trials, separated for IEPi, IEPo, and IEPc. Box plots follow the same format as Figure 2.

Figure 14. Examples traces of horizontal head velocities and horizontal gaze shifts of the stimulation-evoked movements during the non-task mode stimulation (A). The range of the IEPh and the IHPh at stimulation onset are shown on the right of the traces. Stimulation parameters: 120 µA and 200 Hz. B: Positive correlation between horizontal head contribution to eye counter-roll and EPh at gaze offset of all non-task mode stimulation trials (300-ms stimulation: triangle, n= 128;
600-ms stimulation trial: open square, n= 46; mean ± S.E.M.). Data points represent the average values in 5° bins (horizontal initial head position (IHPh) range: -10°: 10°). Also included in B are visually guided gaze shift trials obtained from the control trials (open circle, n= 1233; mean ± S.D.). The shaded region indicates the range of all data obtained from the visually guided gaze shifts trials.

Figure 15. Stimulation sites (A) and the distribution of eye-alone (E-alone; B), head-alone (H-alone; C), and eye-and-head (E-and-H; C) trials in the SEF of a monkey. The vertical dashed line in A indicates the (chamber) coordinate which is approximately in line with the caudal end of the arcuate sulcus. Ar: arcuate sulcus; Ce: central sulcus; Pr: principal sulcus. The size of the symbols in B and C is plotted in proportion to the number of trials indicated in the lower-left corner in each panel.

Figure 16. Effects of stimulation frequency on the stimulation-evoked horizontal head displacements (upper traces in A) and velocities (lower traces in A) in a SEF site. Each trace represents the average position or velocity of the stimulation-evoked head movements and gaze shift (gray) in IEPc condition. Data were obtained from the head-alone trials, separated for different stimulation frequencies. B: Systematic effect of stimulation frequency on the horizontal amplitude of the stimulation-evoked head movements. Data were separated for IEPh conditions (IEPc: filled squares, IEPo: open squares). Control trials (open triangles) were obtained from the interleaved, non-stimulation trials of the same block. Each data point represents the average (mean ± S.E.M.) of 3-6 trials for the stimulation trials or the average of 10 trials in the control trials. Note that the horizontal head displacements were measured in every trial regardless of whether a head
movement was detected. In the stimulation trials, the head movements were measured from stimulation onset to head offset (when the head movements were detected) or from stimulation onset to 500 ms following the stimulation onset (when the head movement was not detected). In the control trials, the head movements were measured as the head displacement during the 500-ms epoch starting at the time point comparable to the stimulation onset in the stimulation trials (see Methods).
FIGURE 1

A

Red/laser
800-1200
Green
600-800
400-500
Green
500-700
400-600
Yellow

B

Red/laser
Green
200
300-600
500-800
Yellow

400 ms
FIGURE 3

A: Scatter plot showing the relationship between $H_v$ displacement ($^\circ$) and $H_h$ displacement ($^\circ$).}

B: Scatter plot showing the relationship between $H_h$ peak velocity ($^\circ$/s) and $H_h$ displacement ($^\circ$).

C: Scatter plot showing the relationship between $E_v$ displacement ($^\circ$) and $E_h$ displacement ($^\circ$).

D: Scatter plot showing the relationship between $E_h$ peak velocity ($^\circ$/s) and $E_h$ displacement ($^\circ$).
FIGURE 5
FIGURE 7

A  300 ms
N= 1031

B  500 ms
N= 386

C  600 ms
N= 368

H_0 offset latency (ms)
FIGURE 10

A

H

H_h displ.

G

10°

600 ms

B

H_h displacement (°)

EP_h at head onset (°)

600 ms

300 ms

C

EP_h at head onset (°)

300 ms
FIGURE 12
FIGURE 13

$H_c G_h (°)$

$H_h \text{onset} - G_h \text{onset}$

$H_h \text{onset} - G_h \text{onset}$ (ms)

$IEP_c$

$IEP_o$

$IEP_i$
FIGURE 14

A. Visually guided EP at G offset (°)

B. Visually guided HcEh (°)

EPh at Gh offset (°)
FIGURE 15
FIGURE 16

A

H

10°

25%

600 ms

B

H_h displacement (°)

Frequency (Hz)

IEPc
IEPo
control