

Neck Muscle Responses to Stimulation of Monkey Superior Colliculus. II. Gaze Shift Initiation and Volitional Head Movements

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Corneil, Brian D., Etienne Olivier, and Douglas P. Munoz. Neck muscle responses to stimulation of monkey superior colliculus. II. Gaze shift initiation and volitional head movements. *J Neurophysiol* 88: 2000–2018, 2002; 10.1152/jn.00960.2001. We report neck muscle activity and head movements evoked by electrical stimulation of the superior colliculus (SC) in head-unrestrained monkeys. Recording neck electromyography (EMG) circumvents complications arising from the head's inertia and the kinetics of muscle force generation and allows precise assessment of the neuromuscular drive to the head plant. This study served two main purposes. First, we sought to test the predictions made in the companion paper of a parallel drive from the SC onto neck muscles. Low-current, long-duration stimulation evoked both neck EMG responses and head movements either without or prior to gaze shifts, testifying to a SC drive to neck muscles that is independent of gaze-shift initiation. However, gaze-shift initiation was linked to a transient additional EMG response and head acceleration, confirming the presence of a SC drive to neck muscles that is dependent on gaze-shift initiation. We forward a conceptual neural architecture and suggest that this parallel drive provides the oculomotor system with the flexibility to orient the eyes and head independently or together, depending on the behavioral context. Second, we compared the EMG responses evoked by SC stimulation to those that accompanied volitional head movements. We found characteristic features in the underlying pattern of evoked neck EMG that were not observed during volitional head movements in spite of the seemingly natural kinematics of evoked head movements. These features included reciprocal patterning of EMG activity on the agonist and antagonist muscles during stimulation, a poststimulation increase in the activity of antagonist muscles, and synchronously evoked responses on agonist and antagonist muscles regardless of initial horizontal head position. These results demonstrate that the electrically evoked SC drive to the head cannot be considered as a neural replicate of the SC drive during volitional head movements and place important new constraints on the interpretation of electrically evoked head movements.

INTRODUCTION

Large, accurate, and rapid gaze shifts demand intricate coordination between the eye and head (eye-in-space = eye-in-head + head-in-space). The mammalian superior colliculus (SC) is an important structure in gaze-shift generation as it is the final node in the oculomotor network encoding gaze shifts in a spatial, topographic map (see Guitton 1992 for review).

Models of gaze control suggest that the SC provides the command for the impending gaze shift (Galiana and Guitton 1992; Goossens and Van Opstal 1997; Guitton and Volle 1987; Guitton et al. 1990; Lauritis and Robinson 1986; Phillips et al. 1995; Tomlinson 1990), but how this gaze command is parsed into the component eye and head motor commands remains contentious. Do the elements downstream from the SC distribute a common drive to both the eyes and head (Galiana and Guitton 1992; Guitton et al. 1990) or are the eyes and head driven independently (Phillips et al. 1995)? The eye-head kinematics during gaze shifts do not display the inviolable coupling expected from a common driver (Bizzi et al. 1972; Corneil and Munoz 1999; Freedman and Sparks 1997b; Fuller 1992; Goossens and Van Opstal 1997; Herst et al. 2001; Moschner and Zangemeister 1993; Phillips et al. 1995; Ron and Berthoz 1991; Ron et al. 1993; Tweed et al. 1995; Zangemeister and Stark 1982; Zangemeister et al. 1982). However, common drive models incorporate multiple drives to the head of which one also drives saccadic eye movements. Single-unit studies have not resolved this issue because different reports show activity profiles in downstream areas consistent with gaze control (Cullen and Guitton 1997; Cullen et al. 1993; Paré and Guitton 1998) or with controlling only the eye component (Ling et al. 1999; Phillips et al. 1999).

Compared with eye movements, it is difficult to infer precisely the neural drive to the head using head movement kinematics given the substantial inertia and complex musculoskeletal anatomy of the head and neck (Richmond and Vidal 1988, 2001; Winters 1988; Zangemeister and Stark 1981), the kinetics of muscle force generation (see Zajac and Gordon 1989 for review), and the redundancy of the system for orienting movements. These uncertainties are circumvented by recording the electromyographic (EMG) activity in neck muscles, enabling sensitive, precise, and objective quantification of the gross activity of neck muscle motoneurons.

The companion paper (Corneil et al. 2002) described the neck EMG responses evoked by SC stimulation in head-restrained monkeys and provided preliminary evidence for a dual parallel influence of the SC on neck muscle motoneurons: neck EMG could be evoked without gaze shifts, but gaze-shift generation usually augmented the neck EMG response. Given that the neural

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activity within the SC encodes gaze shifts (Freedman and Sparks 1997a), our head-restrained results could be explained if SC efferents contact functionally distinct classes of spinal-projecting neurons in the brain stem that are distinguished by their activity profiles in relation to gaze shifts. One objective of this paper is to test two predictions raised by these findings in monkeys whose heads are unrestrained. First, because neck EMG responses in the restrained preparation could be elicited independent of gaze shifts, SC stimulation should drive head movements without gaze shifts. Many of the models cited in the preceding text (e.g., Galiana and Guitton 1992; Guitton et al. 1990; Phillips et al. 1995) have speculated a SC drive to the head that bypasses the gaze-shifting circuitry, but direct neurophysiological evidence in monkeys is lacking (see Péliisson et al. 2001 for recent data from cats). Second, because neck EMG responses could be augmented by gaze-shift generation in the restrained preparation, a transient EMG response and/or head acceleration should accompany gaze-shift onset even if the head is already in motion. If true, this would suggest that some elements downstream from the SC distribute a drive to both the eyes and head, as suggested by the models of Guitton et al. (1990) and Galiana and Guitton (1992).

A second objective of this paper is to perform a comparison of the EMG patterns that accompany volitional (reported in Corneil et al. 2001) and electrically evoked head movements. Such a comparison may place important constraints on the use of SC stimulation toward the understanding of the neural control of orienting head movements. During volitional horizontal head orienting, both the muscles activated and the relative timing of these activations vary systematically with the initial position of the head. For example, the activation times of agonist muscles are mostly synchronous when the head begins near center yet are staggered by upward of 50 ms when the head begins at a position opposite to the direction of the ensuing gaze shift (Corneil et al. 2001). The systematic nature of these timing differences suggests that information about the head position on the body modulates the transformation of a gaze-related command (represented within the SC) into the spatiotemporal pattern of neck EMG activity during volitional orienting. Stimulation of the SC could be a valuable technique to study this transformation provided the spatiotemporal patterns of neck EMG activity evoked by stimulation resemble those accompanying volitional head movements. Furthermore, stimulation in the restrained preparation evoked reciprocal activation of agonist and antagonist muscles during stimulation as well as stimulation offset transients that are not seen during volitional head-fixed gaze shifts (Corneil et al. 2002), and we therefore sought to determine whether such unnatural patterns were an artifact of the restraint of the head or of SC stimulation.

Some results have been reported previously in abstract form (Corneil et al. 1998, 1999).

METHODS

Experimental procedures

All the surgical, experimental, and data-handling procedures were described in the companion paper (Corneil et al. 2002); only relevant differences are mentioned here. All procedures were approved by the Queen's University Animal Care Committee in compliance with the guidelines of the Canadian Council on animal care. The experiments described in this paper were performed on three male rhesus monkeys

(*Macaca mulatta*, monkeys *z*, *r*, and *m*) weighing 5.4–8.0 kg. The monkeys' weights were monitored daily, and their general health was under the close supervision of the university veterinarian. All monkeys underwent the first surgery (implanting gaze coil and SC cylinder), and monkeys *z* and *r* underwent the second surgery (implanting chronically indwelling EMG electrodes; see Table 1 of Corneil et al. 2002). Because some experiments examined whether head movements could be evoked without gaze shifts, EMG data were not always required (i.e., evoked head accelerations imply changes in neck EMG). Accordingly, portions of the data set were collected from monkey *r* prior to the second surgery and from monkey *m*. However, additional data were collected from monkey *r* after the second surgery, allowing us to examine the EMG patterns underlying evoked head movements without gaze shifts. The total data set for this paper includes data with neck EMG from monkeys *r* and *z* and data without neck EMG from monkeys *m* and *r*.

Monkeys were comfortably placed in a primate chair customized for head-unrestrained experiments and wheeled into a dark, sound-attenuated room. The monkeys wore a customized primate vest (Lomir Biomedical) that enabled their torso to be tethered comfortably to the chair. This setup was effective at preventing large horizontal rotations of the trunk (estimated to be $\pm 10^\circ$) without restraining the head or neck, which was very important given the dependencies of neck muscle activity on head-on-torso position (Corneil et al. 2001). Further, the top module of the chair could be detached to allow completely unencumbered head movements.

In addition to the targets presented in the central (approximately equal to $\pm 35^\circ$), part of the monkey's visual field, visual stimuli could also be presented on two side grids that had light-emitting diodes (LEDs; intensity: 4.7 cd/m²) positioned at $\pm 45^\circ$, 60, and 90° in azimuth from center, either at $\pm 0^\circ$, 30, or 45° of elevation.

Microstimulation parameters

The monkey's head was restrained prior to lowering the stimulating electrode. A customized hydraulic microdrive (MO-95; Narishige) was secured to the SC cylinder, and tungsten microelectrodes were lowered through guide tubes secured inside the cylinder. Leads were anchored with a Velcro strap to the outside of the cylinder for strain relief during head movements, and the head was released. Stimulation consisted of a train of constant current 0.3-ms biphasic pulses delivered at a pulse rate of 300 Hz (see Corneil et al. 2002 for a rationale for these parameters). Stimulating currents ranged from 1.5 to 70 μ A and were referenced to the threshold current, *GT100*, required to evoke gaze shifts at short latency (less than ~ 50 ms) on 50% of stimulation trials with a 100-ms train. Stimulation train duration was set to either 100 or 300 ms. Occasionally, EMG responses were first evoked in the restrained preparation, and then the head was released. This ensured that electrode was in the same place for comparisons across restrained and unrestrained preparations.

As in the companion paper, the terms *stimulation site* refers to a unique stimulation position within the three dimensions of the SC (rostrocaudal, mediolateral, and dorsoventral), *electrode penetration* denotes a dorsoventral collection of stimulation sites that were visited during the same experimental session, and *stimulation location* denotes the unique two-dimensional position of the electrode penetration on the SC motor map as determined by the position of the guide tube.

Behavioral paradigms

The monkeys were trained on a fixation task and a gaze-shifting task for a liquid reward. The fixation task was identical to that described in the Corneil et al. 2002, excepting the use of fixation points (FPs) on the side panels, larger fixation windows ($\leq 10 \times 10^\circ$), and a 1,500-ms fixation interval to ensure the head was stable at stimulation onset. This task was used to obtain a wide range of initial eye and head positions at stimulation onset. As in the head-restrained

condition, we saw no evidence from the baseline levels of EMG activity prior to stimulation that the animals were preparing for stimulation onset in any way as would have been expected if the animals were trying to reduce the size of the evoked head movements.

In separate blocks, the gaze-shifting task required the monkeys to look from a central FP to a peripheral target presented randomly at one of eight preselected locations. Peripheral targets were between 30 and 90° away from the FP and were arranged symmetrically around the central FP on the front and side panels. The gaze-shifting task (as opposed to the fixation task) prevented the monkeys from adopting a customary head position biased in the direction of the evoked head movements. Trial onset was signaled by the removal of the background light and, after a period of 250 ms, by the appearance of the central FP. The monkeys had 1,000 ms to look at this FP and were then required to keep their gaze within a $3 \times 3^\circ$ fixation window for between 800 and 1,500 ms, at which point the central FP was extinguished. On half the trials, SC stimulation began 200 ms later. The peripheral target appeared at the end of the stimulation train, hence the interval from FP disappearance to target appearance was either 300 or 500 ms (the gap interval), depending on the duration of stimulation. We employed a gap interval because head movements either without or prior to gaze shifts were evoked readily in such conditions (unpublished observations). Control trials without stimulation were run on the remaining half of trials, and the interval between FP disappearance and target appearance was set to be identical to the gap interval in stimulation trials. Regardless of evoked gaze shifts, the monkeys were required to look to the target within 500 ms and keep their gaze in a computer-controlled window centered around the target of between 5×5 and $10 \times 10^\circ$ depending on target eccentricity.

Monkey r was also run on a variant of the gaze-shifting task without SC stimulation. This task required the monkey to first look to and fixate the peripheral target for 500 ms as in the control trials in the preceding text, after which the central FP reappeared. To be rewarded, the monkey had to re-fixate the central FP for an additional 500 ms. This variant of the gaze-shifting task was used to measure the EMG activity that accompanied volitional head movements beginning from a variety of positions for comparison to the EMG patterns evoked by SC stimulation.

In *monkeys r* and *m*, a systematic approach to map out the dorsal-ventral course of SC stimulation sites was used as described in Corneil et al. 2002, although with a longer train duration (300 ms) and with the gaze-shifting task. Each site within a depth series was separated by 500 μ m, and at each site, the GT100 current threshold was determined. We then determined the current level necessary to evoke head movements with a 300-ms duration train. The site was classified as a "HOM site" (for head-only movement) if the current thresholds to evoke head movements was $\geq 25\%$ less than the GT100 level. A normalized score for each depth series was calculated by dividing the number of "HOM sites" by the total number of sites within the depth series. We also defined the extent of the sites endowed with the lowest GT100 levels.

Following completion of the depth series, the electrode was returned to the dorsal-most depth endowed with the lowest GT100 current level, and variants of the fixation task were run to study the effects of manipulations in gaze position (9 possible FP locations spanning $\pm 90^\circ$ in azimuth and $\pm 40^\circ$ in elevation) with the stimulating current set to $1.5 \times$ GT100.

Data collection and analysis

The vertical and horizontal rotation of the gaze and head (henceforth referred to as gaze and head "position" signals) and EMG signals (when available) were recorded at 500 Hz. The flexible EMG ribbon-cable leading from the connector to the signal processing electronics did not encumber head movements. To measure head position in space, a search coil was attached to a small plastic cylinder that also held a flexible tube through which the animal was rewarded (total

weight = 28 g). With the weight of the EMG ribbon cable (10 g) and the weight of the microdrive (34 g), the weight of all equipment added to the monkey's head was 72 g. We did not observe any restrictions in how the monkeys moved their heads with the equipment attached and noted that the monkeys occasionally generated vigorous head shakes where the peak velocity of the head exceeded 1,500°/s. The coil system (CNC Engineering) yoked the two horizontal fields together, hence the relationships between induced current and horizontal gaze and head coil position were linear over a range of $\pm 90^\circ$ from center. Gaze coil signals were calibrated by having the monkey fixate targets placed at known eccentricities. Head-coil signals were calibrated without the monkey by anchoring the head coil to a calibration mechanism.

Off-line, horizontal and vertical eye positions were reconstructed by subtracting the calibrated head signal from the calibrated gaze signal. The accuracy of this subtraction was ensured by noting that the eye signal moved by an amount equal but opposite to the head signal after the gaze landed on a peripheral target, but while the head still moved toward the target. Gaze, eye, and head velocity and head acceleration traces were obtained by differentiation or double-differentiation, respectively, of the position signals. Computer software determined the beginning and end of each gaze shift using velocity and acceleration thresholds and template-matching criteria (Waitzman et al. 1991). EMG responses were quantified by their response latency and the peak magnitude above baseline as described in Corneil et al. 2002. All trials were inspected with an interactive graphics package enabling viewing and marking of the eye, head, gaze, and EMG traces. For trials with a head movement, marks were inserted on the horizontal and vertical head position and velocity traces to demarcate the start and end of the head movement (determined by a 5°/s velocity threshold) and the peak velocity. Trials were excluded if the head was moving $> 5^\circ$ /s at stimulation onset. In some trials, marks were inserted onto individual EMG traces to quantify temporal aspects of the signal. Although no strict quantitative criteria were used, sudden changes in neck EMG were easily delineated.

RESULTS

Neck EMG responses to SC stimulation in the unrestrained preparations

COMPARISON TO STIMULATION IN THE RESTRAINED PREPARATION. We delivered stimulation to the SC of head-unrestrained monkeys in 483 sites distributed throughout 36 different stimulation locations (11 in *monkey z* with neck EMG, 9 in *monkey m* without neck EMG, and 16 in *monkey r* either with or without neck EMG). Stimulation at 64% of all sites evoked head movements, stimulation at 93% of applicable sites evoked neck EMG (when measured), and stimulation at 91% of all sites evoked gaze shifts. As discussed in the following text, SC stimulation did not necessarily culminate in head movements in spite of evoked neck EMG, presumably because of the head's inertia. Stimulation commonly evoked responses in obliquus capitis inferior (OCI), rectus capitis posterior major (RCP maj), and splenius capitis (SP cap; Fig. 1, A and C), and less frequently in sternocleidomastoid, biventer cervicis, complexus and atlantoscaphularis anterior. The EMG responses evoked in these latter four muscles resembled those evoked in a restrained preparation (Corneil et al. 2002) and will not be described.

In both unrestrained and restrained preparations, stimulation facilitated activity in agonist muscles turning the head contralateral to the stimulating electrode, and suppressed activity in antagonist muscles (Fig. 1, A and C vs. B and D, respectively). On 13 separate occasions in 13 different stimulation

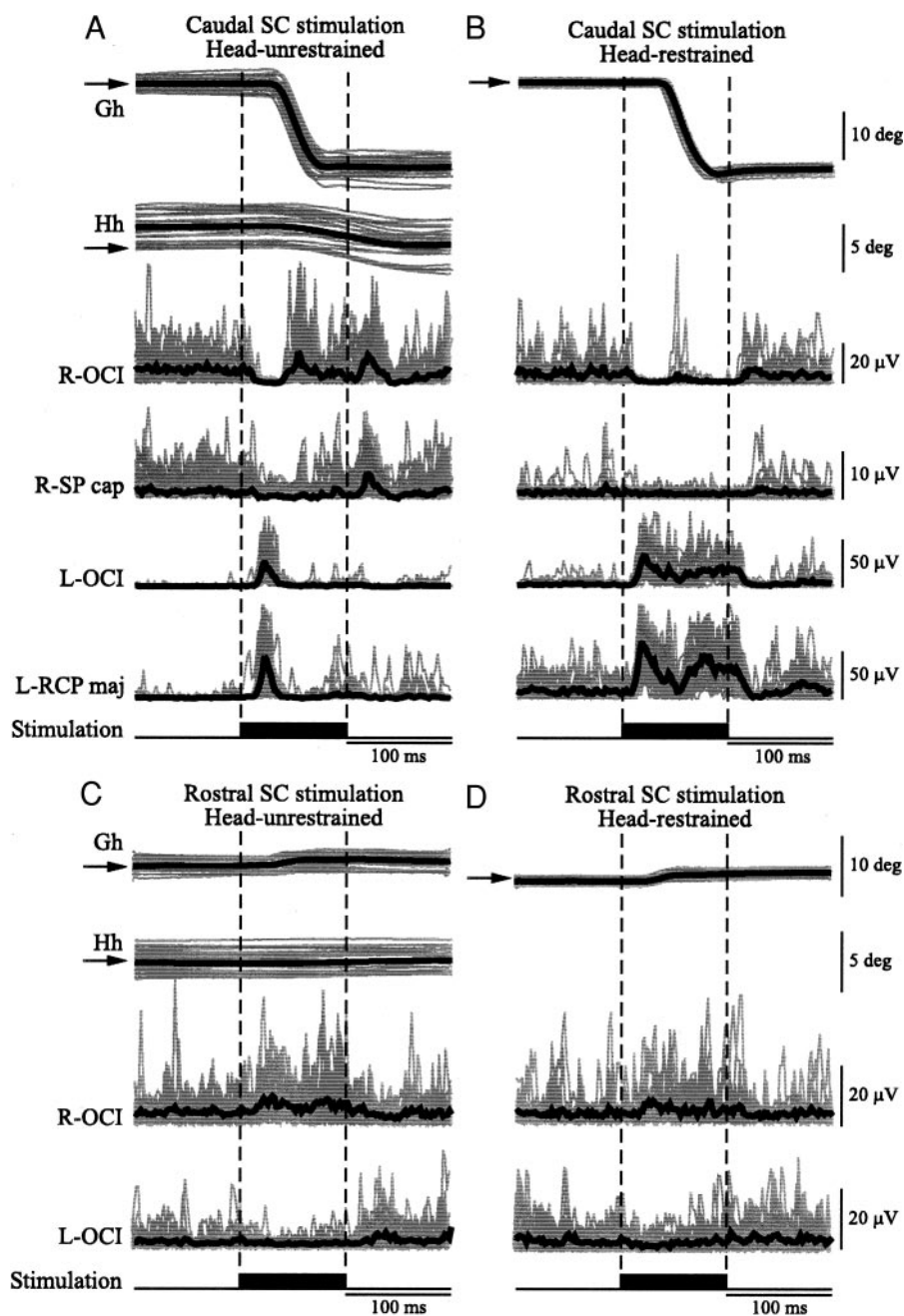


FIG. 1. Comparison of neck EMG evoked following delivery of 40 μ A into caudal right superior colliculus (SC) of monkey *z* (A and B) or 20 μ A into rostral left SC of monkey *r* (C and D). For both pairs of examples (A vs. B, C vs. D), data from the unrestrained preparation (A and C) was obtained immediately after the data from the restrained preparation (B and D), using the same stimulation parameters. Care was taken to release the head as gently as possible. Gh and Hh, horizontal position traces for the gaze and head, respectively; positive deflections indicate rightward movements. Stimulation always evokes a gaze shift and neck EMG but did not evoke a head movement in C. Stimulation was passed for 100 ms in all examples (horizontal black bar and dashed, vertical black lines). Thick, black lines, the average traces, averaged over each of the component traces (thin, gray lines; 21 responses in A, 30 responses in B, 27 responses in C, 30 responses in D). Horizontal arrows, straight ahead. The R- or L- denotes the right or left muscle, respectively. Scale bars to the right of B and D apply for traces on the same row.

locations, unrestrained stimulation was applied immediately after restrained stimulation, allowing us to be confident that the stimulation site remained identical. As shown in Fig. 2, the response latencies and peak magnitudes of the evoked EMG responses, and the latencies of the gaze shift relative to stimulation onset, were approximately equal in both preparations (Fig. 2, A–C; paired *t*-test, $n = 13$; latencies: $P = 0.1875$; peak magnitudes: $P = 0.36$. Signed-rank test for gaze-shift latencies: $P = 0.59$). However, the qualitative appearance of the evoked neck EMG could differ. For example in Fig. 1, A and B, the antagonist (right) muscles had a higher baseline level of activity prior to unrestrained stimulation (Fig. 1A), but the agonist (left) muscles had a higher baseline level of activity prior to restrained stimulation (Fig. 1B). These differences presumably stemmed from slight differences in initial head

position (Corneil et al. 2001) and accounted for aspects of the evoked EMG responses: following the initial EMG responses, the agonist muscles remained active for the duration of the stimulation train in the restrained (Fig. 1B), but not unrestrained (Fig. 1A), preparation.

Evoked head movements generally began within 40–70 ms after stimulation onset. However, evoked neck EMG did not always culminate in observable head movements. For example, stimulation in the rostral SC evoked significant neck EMG responses in both preparations (Fig. 1, C and D), but no head movements were evoked in the unrestrained preparation (Fig. 1C). Across 19 different stimulation locations studied in the unrestrained preparation, the location of the electrode along the rostrocaudal axis of the SC determined both the magnitude of the evoked EMG activity (as reported in Corneil et al. 2002)

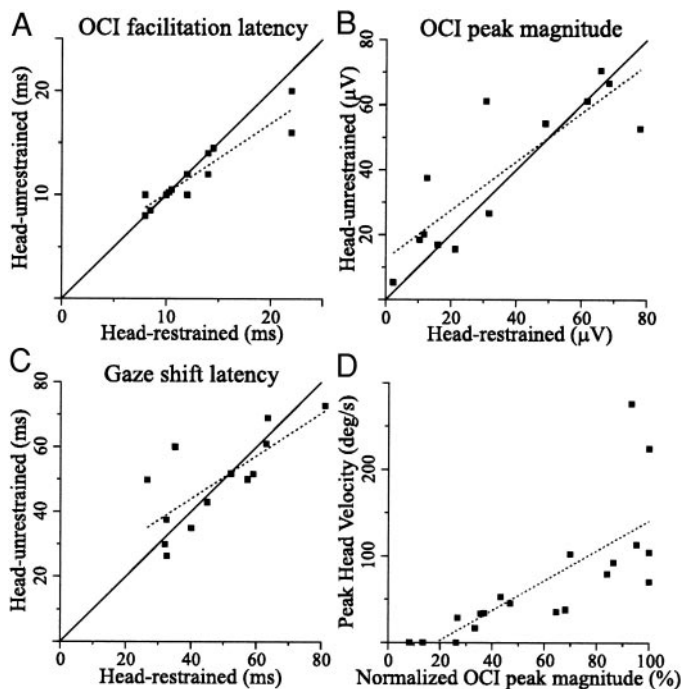


FIG. 2. A–C: comparison of facilitation latency (A), peak EMG magnitude above baseline in contralateral obliquus capitis inferior (OCI; B), and evoked gaze-shift latency (C) after stimulation in the restrained or unrestrained preparation. Each point is derived from a different stimulation location and is taken only from sites in which unrestrained stimulation followed immediately restrained stimulation (7 sites in *monkey z*, 6 sites in *monkey r*). Diagonal black lines, the lines of unity. D: peak velocity of the evoked head movement as a function of the peak EMG magnitude in OCI, normalized to the largest magnitude observed in that muscle. Data points located on the abscissa denote situations in which the evoked OCI activity was not associated with a head movement. Each point derived from 19 different stimulation locations (11 in *monkey z*, 8 in *monkey r*). Stimulation in all cases consisted of $1.5 \times \text{GT100}$ for 100 ms. Dashed lines, significant ($P < 0.05$) linear regression lines. For A: $r = 0.94$, $m = 0.68$, y intercept = 3.4, $n = 13$; B: $r = 0.85$, $m = 0.75$, y intercept = 12.6, $n = 13$; C: $r = 0.75$, $m = 0.66$, y intercept = 17.54, $n = 13$; D: $r = 0.75$, $m = 1.73$, y intercept = -37.9, $n = 19$.

and whether an observable head movement would be evoked. Plotting the peak velocity of the evoked head movement versus the peak magnitude of the agonist OCI activity revealed an intuitive relationship between these two parameters: head velocity increased as stimulation evoked more vigorous EMG responses (Fig. 2D). However, in three different stimulation locations, each of which encoded gaze shifts $<10^\circ$, SC stimulation evoked small EMG responses in the absence of observable head movements (points lying on abscissa in Fig. 2D). Thus although evoked neck EMG usually culminated in head movements, this was not always true when stimulation was delivered to the rostral SC.

COMPARISON TO EMG PATTERNS ACCOMPANYING VOLITIONAL HEAD MOVEMENTS. We compared the EMG patterns accompanying volitional head movements to those evoked by SC stimulation, as shown for representative examples in Fig. 3 (these examples were matched for gaze and head kinematics as closely as possible). Figure 3A illustrates the same data as Fig. 1A except aligned on gaze-shift onset). Note the similarities in the amplitude and timing of the gaze and head movements as well as in the magnitude and timing of the EMG activity in the agonist muscles relative to gaze-shift onset. In general, the antagonist muscles were much more active during evoked

versus volitional head movements. The *arrow* in Fig. 3A points to the increase in antagonist muscle activity that occurred during stimulation; this feature was synchronized with decreased activity in the agonist muscles. The *asterisk* in Fig. 3A denotes the phasic increase in antagonist activity that occurred after stimulation offset. These features frequently ($\sim 50\%$ of all stimulation trials) appeared in evoked EMG patterns (Corneil et al. 2002) but were never observed in an extensive sampling of volitional head movements during trained gaze shifts (Corneil et al. 2001).

We initially sought to perform a detailed quantitative comparison of the magnitude of EMG activity during evoked and volitional head movements beginning from center. To do this, one would have to match closely the direction and duration of both the evoked and volitional gaze shifts to presume that the gaze shifts were controlled by the same region of the SC. Further, because the magnitude of EMG responses during volitional head movements varies substantially with the acceleration of the head (Corneil et al. 2001), and the kinematics of evoked head movements vary with stimulation frequency and duration (Freedman et al. 1996), the kinematics of both the evoked and volitional head movements would also have to be closely matched. In practice, such matching of gaze and head kinematics was quite difficult. Thus although stimulation over multiple stimulation sites evoked activity in the synergy of muscles usually recruited during volitional head movements, we were not able to compare directly the magnitude of evoked

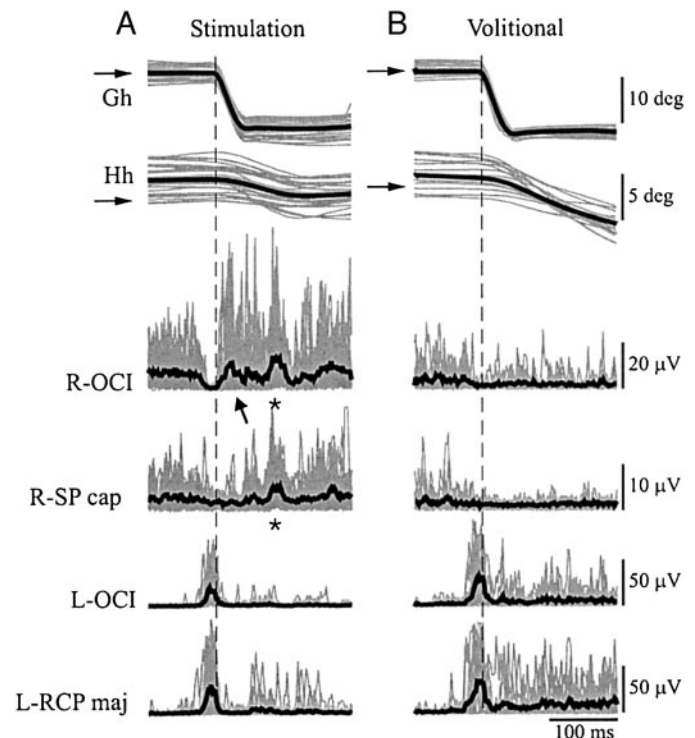


FIG. 3. Comparison of neck EMG evoked after delivery of $40 \mu\text{A}$ into caudal right SC of *monkey z* for 100 ms (A: same data as in Fig. 1A, but aligned on gaze-shift onset) with that generated volitionally also aligned on gaze-shift onset (B). Same format as Fig. 1, except that dashed vertical black lines are aligned on gaze-shift onset. Care was taken to match the gaze and head kinematics in A and B as closely as possible. The arrow and asterisks in A denote features of the stimulation-evoked neck EMG that are not observed during volitional movements.

EMG activity with that accompanying volitional head movement.

Variations in head position

To examine the variations in evoked neck EMG responses with changes in the initial head position, monkeys looked to FPs located within $\pm 90^\circ$ in azimuth from center. We describe the EMG data in reference to the initial position of the head. However, because the position of the eyes, head, and gaze covaried (i.e., leftward gaze fixations were achieved by leftward eye and head positions), we could not segregate the individual contributions of eye, head, and gaze position on the evoked responses. Prior to stimulation onset, the initial head position could vary by more than $\pm 60^\circ$ from center as shown in Fig. 4. With the head near center (Fig. 4, *center column*), stimulation evoked the typical patterns of agonist muscle facilitation and antagonist muscle suppression and also evoked a 15–20° gaze shift and a smaller accompanying head movement. Changing the initial head position altered the evoked EMG activity: the activity evoked in the agonist muscles

increased progressively as the head was positioned contralateral to the side of stimulation (i.e., in the direction of the ensuing head movement; Fig. 4, 2 *right columns*), and got progressively weaker as the head was moved to the other side (Fig. 4, 2 *left columns*). Such changes mirrored the levels of baseline activity prior to stimulation onset, which themselves were related to holding the head in the eccentric posture (see Corneil et al. 2001).

This experiment was performed in a total of six different stimulation locations in *monkey r* (Fig. 5A). In all locations, stimulation (between 12.5 and 40 μA for 100 ms) evoked large and consistent EMG responses. However, because the parameters of stimulation were set only to evoke gaze shifts within ≤ 50 ms from stimulation onset (using our criteria for establishing the GT100), stimulation of 100 ms only occasionally evoked observable head movements that lagged gaze-shift onset. While unfortunate, we do not view the absence of head movements as a major shortcoming, because the evoked EMG responses always preceded both the evoked gaze shift and occasional head movements. Using the amplitude of the

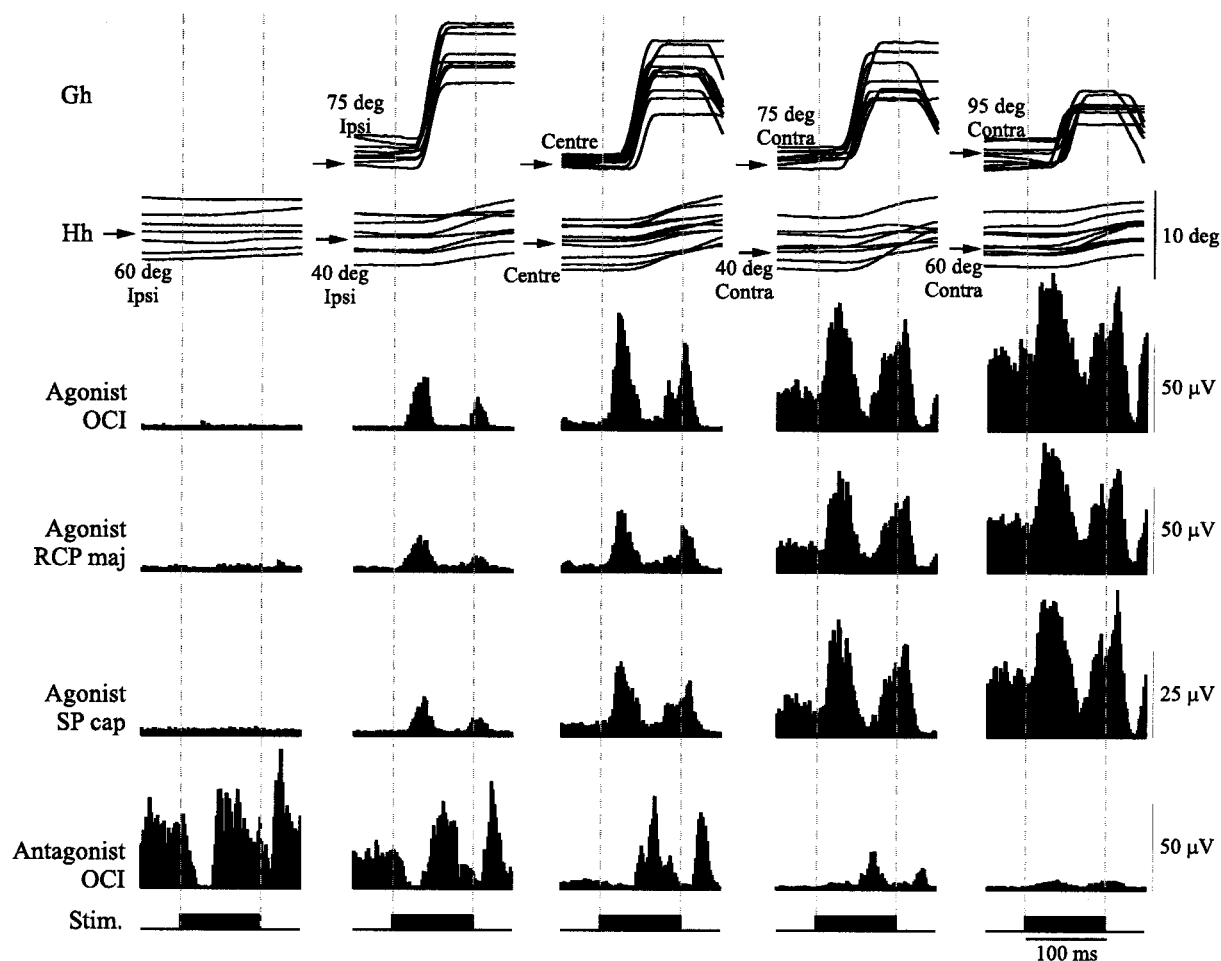


FIG. 4. Average EMG histograms (2-ms bins) evoked by SC stimulation while the *monkey r* attained different horizontal gaze positions while looking at fixation points (FPs) located within $\pm 90^\circ$ of azimuth from center. Horizontal head position varied by $\pm 60^\circ$. Stimulation at central FP evoked a gaze shift of approximately 20° left and 5° up, accompanied by a leftward head movement. Arrows to the left of the gaze (Gh) and head traces (Hh) denote the position listed with each collection of traces. The scale bars to the right of the figure apply for all traces. The average histograms were derived from between 6 and 11 individual trials. Positional data are referenced as being either ipsilateral or contralateral to the side of stimulation. Gaze data for the furthest ipsilateral position was not obtained because the coil signal saturated.

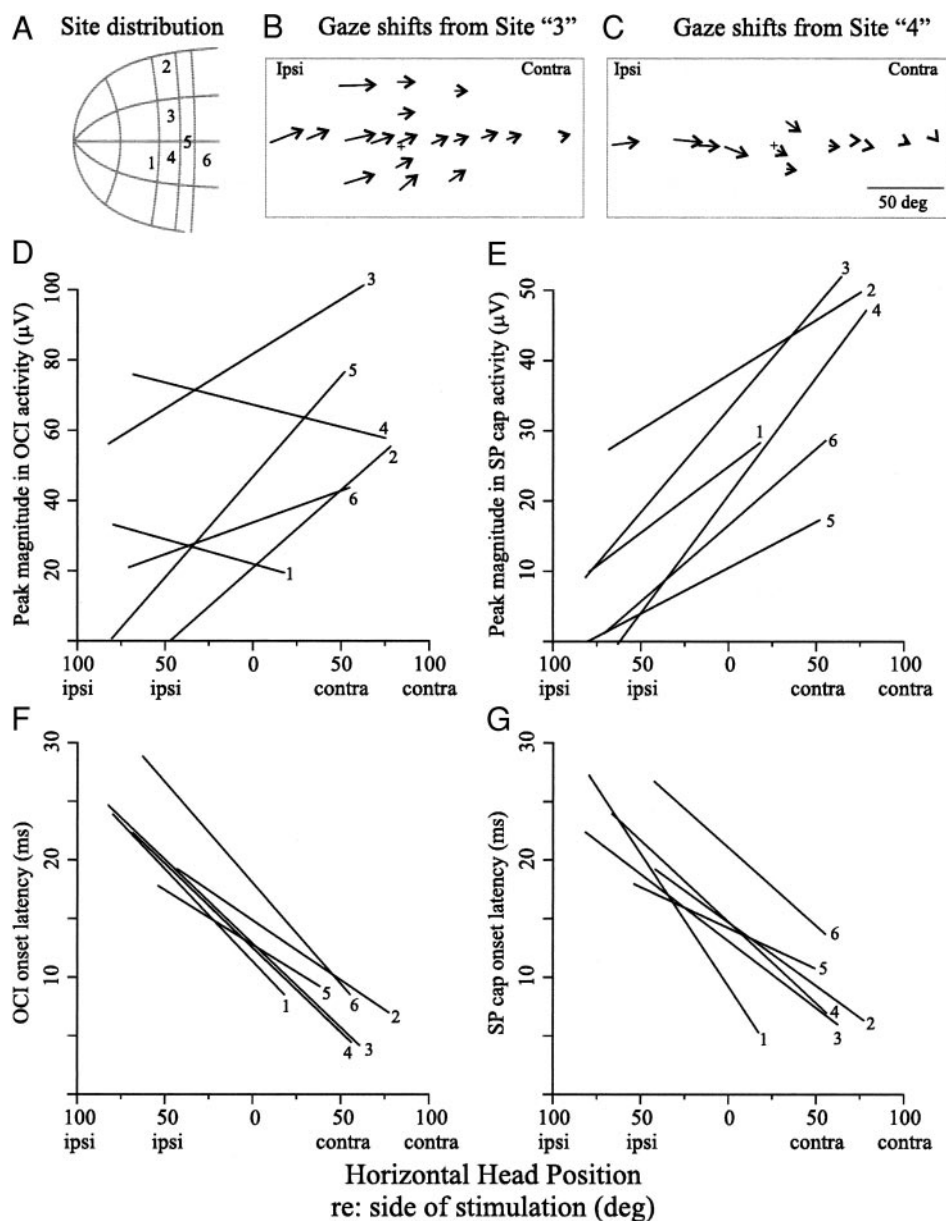


FIG. 5. Quantification of the effects of varying head position on the peak magnitude above baseline (*D* and *E*) or latency (*F* and *G*) of the evoked activity in the agonist OCI (*D* and *F*) or SP cap (*E* and *G*); results were pooled across both SC in *monkey r*. —, the linear regression of the given parameter vs. horizontal head position (all significant at $P < 0.05$), defined relative to the side of the stimulating electrode. Data obtained from 6 different stimulation locations in *monkey r*. The numbers beside the lines reveal the location of the stimulating electrode within the SC as shown in *A* (see Fig. 9*A* for values of the isoamplitude and isodirection lines). *B* and *C*: the pattern of evoked gaze shifts evoked from sites "3" and "4," respectively.

evoked gaze shift as a proxy for evoked head movements, we presumed that larger head movements would have been evoked if stimulation was prolonged (Freedman et al. 1996; Klier et al. 2001). At most of these sites, there was a tendency for the amplitude of the evoked gaze shifts to decrease as the gaze was positioned contralateral to the side of stimulation (Fig. 5, *B* and *C*), consistent with some previous findings (Klier et al. 2001; Segraves and Goldberg 1992).

To summarize the variations in the evoked EMG with head position, we plotted the linear regression lines of the relationship between the peak magnitude or latency of the evoked responses in the agonist OCI and SP cap muscles versus the initial horizontal head position (Fig. 5, *D–G*). In all cases for SP cap (Fig. 5*E*) and for all but two cases for OCI (Fig. 5*D*), the magnitude of the evoked response above baseline increased as the head attained more contralateral positions relative to the side of stimulation even while the amplitude of the evoked gaze shift (and presumably the amplitude of the head move-

ment if stimulation was prolonged) decreased. The latency of facilitation also changed with the initial head position, becoming progressively shorter in all cases for more contralateral head positions for both OCI (Fig. 5*F*) and SP cap (Fig. 5*G*). Note that the two exceptional cases in which contralateral head positions resulted in a decreasing peak OCI magnitude derived from the more rostral stimulation locations (sites "1" and "4").

Another interesting observation from Fig. 5 is that the onset latencies of the OCI and SP cap muscles are nearly equal regardless of the initial position of the head. If true, this differs from what is observed during volitional head movements in which the interval between the onset of the agonist OCI and SP cap muscles increases as the head attains more ipsilateral positions relative to the side of the SC under consideration [Fig. 6*A*; i.e., this interval increases for more centripetal head movements as reported in Corneil et al. (2001)]. Calculation of the interval between the onset of the agonist OCI and SP cap following SC stimulation confirmed that these muscles were

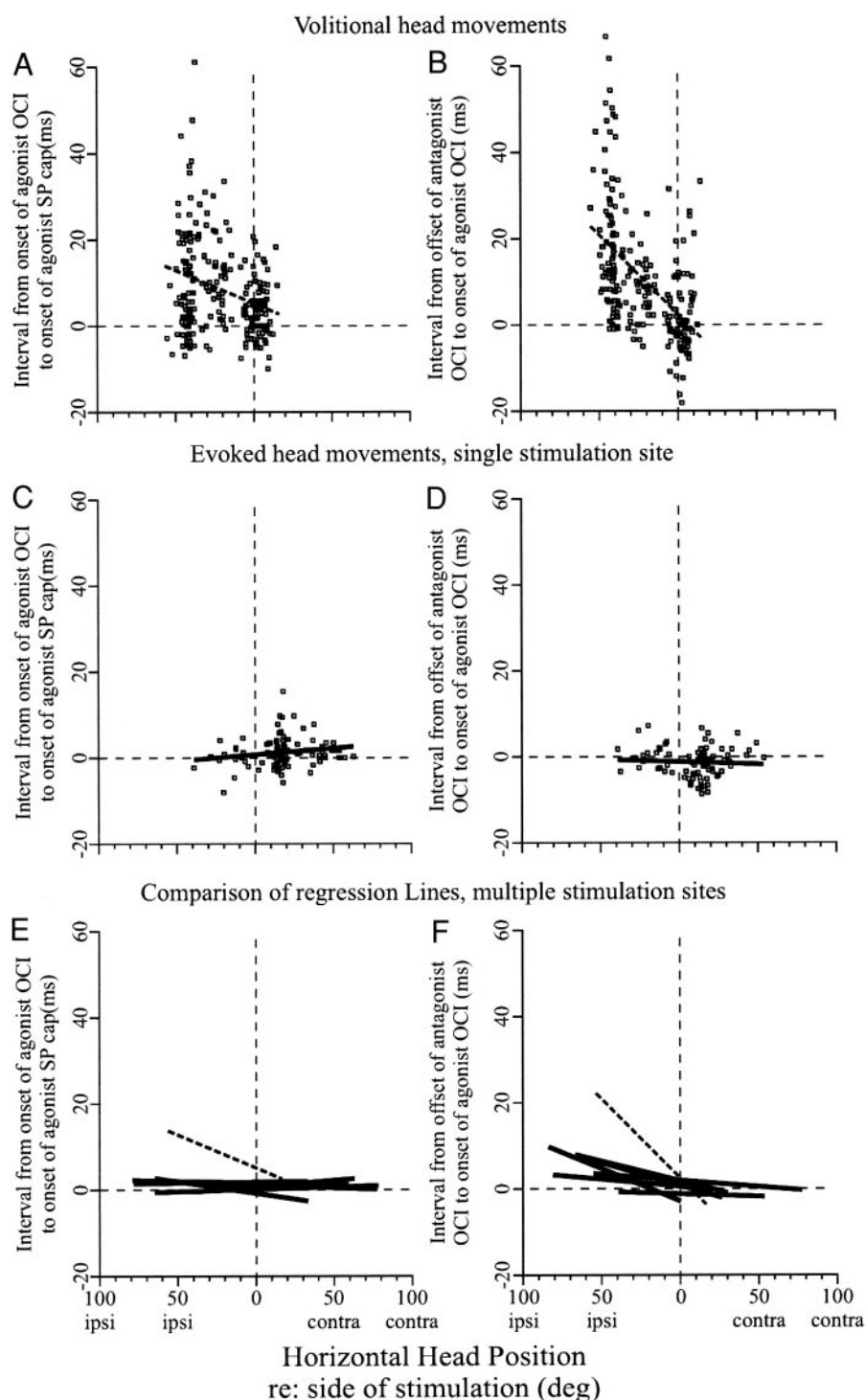


FIG. 6. Comparison of the intervals between EMG events with variations in initial horizontal head position for either volitional head movements (A and B) or head movements evoked by SC stimulation (single site: C and D; multiple sites: E and F). The intervals measure either the time between the onset of the agonist OCI and SP cap muscles (A, C, and E) or between the offset of the antagonist OCI to the onset of the agonist OCI muscle (B, D, and F). □, data from a single head movement. —, linear regressions for either volitional (---, significant at $P < 0.05$) or evoked (—, not significant) head movements. Data from leftward and rightward head movements were pooled together, and the muscle timings and head positions are referenced to the side of stimulation or presumed SC activation for consistency with Fig. 5. Data in A and B were taken from volitional head movements that accompanied horizontal gaze shifts of between 20 and 60° in amplitude. The amplitude of such volitional head movements averaged 29.6°. The gaze shifts evoked by stimulation in C and D averaged 30°. E and F: comparison of the regression lines for the same intervals obtained from volitional head movements (same data as A and B) or evoked head movements obtained from 6 different stimulation sites (6 —). The amplitude of the evoked gaze shifts ranged between 14 and 30°.

recruited nearly synchronously regardless of initial head position (1 site: Fig. 6C, all 6 sites: Fig. 6E). We also calculated the interval between the offset of the antagonist OCI and the onset of the agonist OCI and observed again that this interval changed markedly with head position for volitional but not evoked head movements (Fig. 6, B, D, and F). Overall, the lack of change with head position of the relative response latencies evoked by SC stimulation differs substantially from volitional head movements, in which the intervals between muscle responses can vary by ≥ 40 ms depending on head position.

Low-current, long-duration stimulation can evoke head movements prior to or without accompanying gaze shifts

Low-current SC stimulation can evoke neck EMG responses without gaze shifts when the head is restrained (Corneil et al. 2002). Here we explore the possibility that such stimulation could culminate in head movements. Accordingly, we decreased the stimulation current to levels below GT100 and prolonged stimulation duration to allow more time for presumably weak forces to overcome the head's inertia. Unequiv-

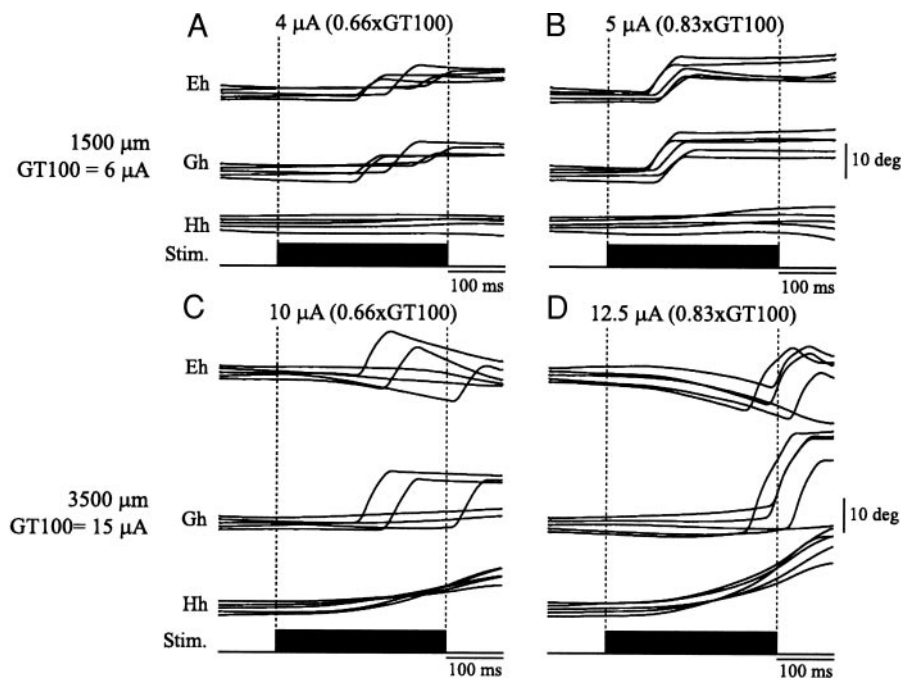


FIG. 7. Horizontal eye (Eh), gaze (Gh), and head (Hh) position traces in response to 300 ms of stimulation at different current levels (0.66 or $0.83 \times$ GT100) and depths within a single electrode penetration in *monkey r* (prior to implantation of EMG electrodes). Listed depths are relative to dorsal extent of SC. At dorsal sites (A and B), stimulation evoked gaze shifts within 100–300 ms without evoking any preceding head movements. At more ventral sites (C and D), stimulation evoked head-only movements (HOMs) prior to gaze shifts that were directed contralateral to the side of stimulation. Gaze stability was maintained during HOMs by compensatory eye movements.

cally, such stimulation could elicit head movements without or in advance of gaze shifts. Such *head-only movements* (HOMs),¹ were observed in all three monkeys and initially studied quantitatively in *monkeys m* and *r* without EMG electrodes. The underlying patterns of neck EMG activity were confirmed later in *monkey r* (see following text). The traces in Fig. 7 illustrate gaze, eye, and head movements from two different stimulation sites located within the same electrode penetration. At a relatively dorsal site, low current stimulation drove gaze shifts 150–275 ms after stimulation onset (Fig. 7A). A slightly higher current level decreased gaze-shift latencies to ~100–150 ms (Fig. 7B). Any accompanying head movements evoked from this site were very small and lagged gaze-shift onset. At a more ventral site, low current stimulation occasionally evoked gaze shifts within 200–300 ms; however, these gaze shifts were preceded by head movements (i.e., HOMs) in the direction contralateral to the stimulating electrode (Fig. 7C). As current intensity increased, the HOMs became faster (Fig. 7D). A compensatory eye movement, presumably mediated by the vestibuloocular reflex, maintained gaze stability during HOMs.

To address the neural mechanisms underlying HOMs, we analyzed their peak velocity and direction prior to gaze-shift onset. We studied HOM velocity because the acceleration of these movements was very small. Further, because gaze-shift latency decreased for increasing stimulation currents, the amplitude of HOMs did not display a straightforward relationship with stimulation current. Statistical analyses confirmed that the peak velocity of HOMs increased with higher stimulation currents (Kruskal-Wallis ANOVA on repeated-measure ranks for velocities at the 3 lowest current intensities used at each

site; Fig. 8A: $\chi^2(2) = 19.2$, $P < 0.0001$; B: $\chi^2(2) = 17.6$, $P < 0.0001$). We also found that the radial direction of HOMs did not differ from the direction of the head movements elicited during gaze shifts evoked by current levels $1.5 \times$ GT100 (paired t -tests; Fig. 8C: $t(14) = 0.60$, $P = 0.56$; D: $t(21) = 0.90$, $P = 0.38$). Note that the distribution of points in Fig. 8, C and D, clustered around the horizontal axes near $0^\circ/360^\circ$ and 180° , reflecting the tendency for evoked and volitional head movements during oblique gaze shifts to have greater horizontal than vertical components (Freedman et al. 1996; Glenn and Vilis 1992). These results demonstrated that the kinematics of HOMs were not random but were dictated by stimulation location and current.

DISTRIBUTION OF SC SITES EVOKING HOMs. Low-current, long-duration stimulation evoked HOMs in a total of 98 of 266 (37%) stimulation sites in two monkeys. The 98 “HOM sites” were distributed in 18 of 22 stimulation locations (7 of 9 in *monkey m* and 11 of 13 in *monkey r*) and were found more frequently, but not exclusively, in caudal stimulation sites (Fig. 9A). Figure 9B illustrates the dorsoventral distribution of HOM sites, leveled to the dorsal-most depth endowed with the lowest GT100 (shaded regions). The dorsoventral distribution of HOM sites varied with stimulation location: HOM sites in the rostral SC resided at ventral sites, whereas HOM sites in the caudal SC could be found at most both dorsal and ventral depths. Figure 9 bore a resemblance to Fig. 4 of the companion paper (Corneil et al. 2002), which described the prevalence and location of “EMG sites” in the restrained preparation (i.e., where the threshold for evoking neck EMG was less than that for gaze shifts), emphasizing the obvious relationship between EMG sites in a restrained preparation and HOM sites in an unrestrained preparation.

HEAD ACCELERATION AND EMG BURSTS ALIGNED ON GAZE-SHIFT ONSET. Although the gaze axis remained stable during HOMs due to compensatory eye movements, on many occasions gaze shifts were elicited well after (>150 ms) the onset

¹ The term *head-only movement* is perhaps not an optimal term because such movements could be followed by evoked gaze shifts during the stimulation train. A more accurate term would be *early head movements*; however, we have already used this term earlier in regard to human head movements (Corneil and Munoz 1999; see also Pélisson et al. 2001) and therefore chose an alternative term here to avoid confusion.

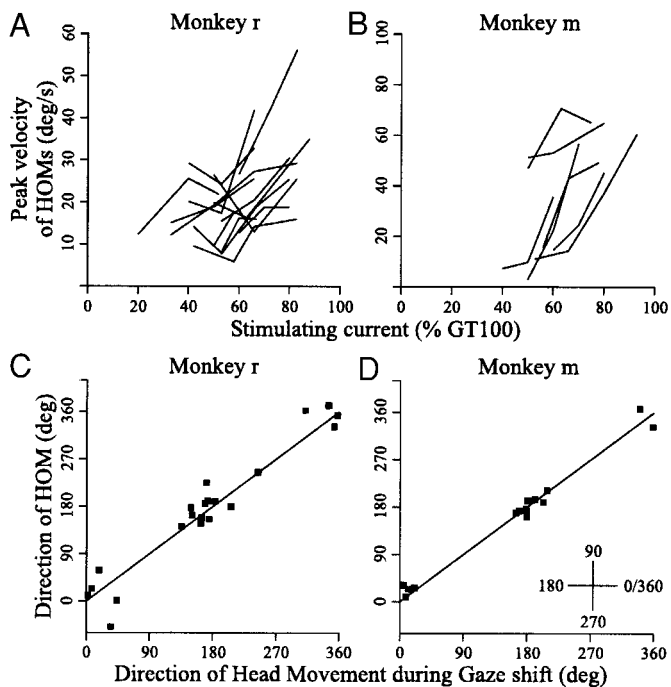


FIG. 8. Quantification of the metrics of HOMs elicited in monkeys *r* (A and C) and *m* (B and D) at multiple sites throughout the SC. A and B: peak vectorial velocity of the HOM as a function of the level of stimulating current, normalized to GT100. Each line connects values derived from a single stimulation site in which ≥ 3 different current levels were tested. Multiple sites could be located in the same electrode penetration. C and D: direction of the head during an HOM as a function of the direction of the head movement elicited during gaze shifts evoked by 100 ms of stimulation at $1.5 \times$ GT100. All points are drawn from different stimulation sites, but could be within the same electrode penetration. A direction of 0 or 360° denotes a straight rightward movement, 90° a straight upward movement, and so on. Values on the y axis were assigned to values either <0 or $>360^\circ$ depending on the value of the x axis to minimize wrapping. —, lines of unity.

of the stimulation train (e.g., Fig. 7, C and D). Examples of gaze shifts preceded by HOMs are shown aligned on stimulation onset in Fig. 10, A and B. Realignment of these traces on gaze-shift onset revealed an additional acceleration of the head that peaked ~ 30 ms after gaze-shift onset (Fig. 10, C and D). This transient head acceleration appeared in both individual and averaged traces.

The head acceleration accompanying gaze-shift onset is quantified over multiple stimulation locations in Fig. 11. Each light line in Fig. 11, A and B, presents the averaged head acceleration trace obtained in a different stimulation location (8 for monkey *m*, 11 for monkey *r*). In spite of large differences in the absolute magnitude of acceleration, most head acceleration traces displayed a significant transient peak ~ 30 ms after gaze-shift onset (the method for assigning significance is described in the legend for Fig. 11). As shown in Fig. 11C, the mean time of the 52 significant peak head accelerations was 35 ± 14 ms (range: 14–60 ms) after gaze-shift onset. Figure 11D shows a comparison of the peak head acceleration over a 50-ms range either before or after gaze-shift onset. Statistical analysis revealed that the peak acceleration after gaze-shift onset was significantly greater (signed-rank test, $P < 0.0001$).

To observe the pattern of neck muscle activity underlying the gaze-aligned acceleration of the head, we repeated a search for HOMs in monkey *r* after the implantation of EMG electrodes. When aligned on stimulation onset, the EMG activity in

agonist muscles displayed a gradual increase that presumably drove the HOMs (Fig. 12A). Realignment of these traces on gaze-shift onset revealed phasic EMG bursts in the agonist muscles that peaked around the time of gaze-shift onset, as well as a peak acceleration of the head some 30 ms later (Fig.

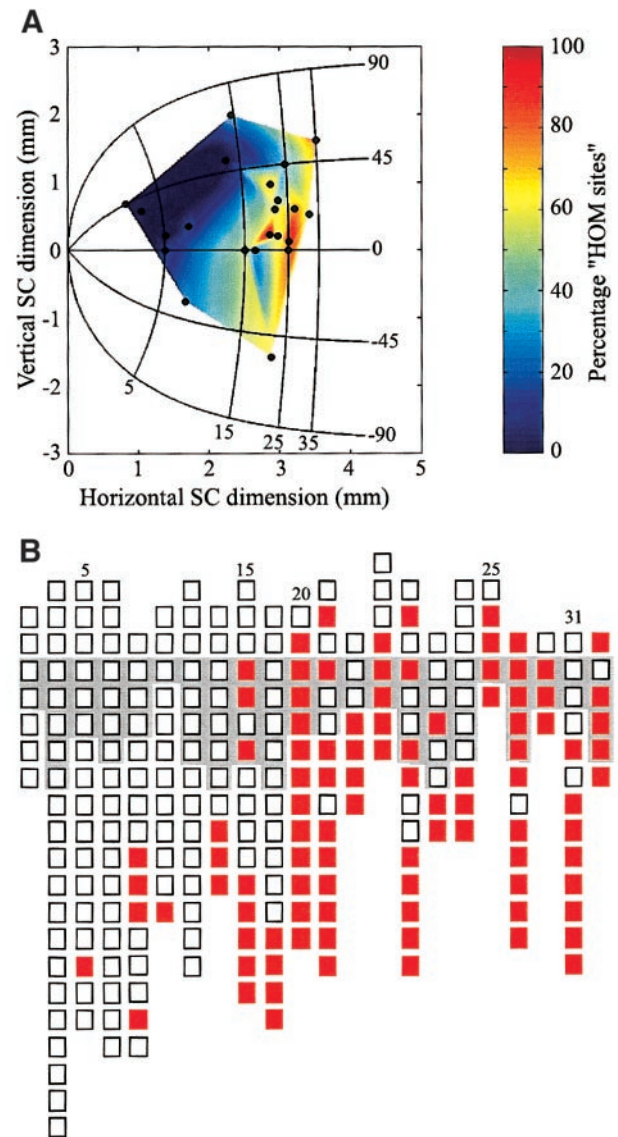


FIG. 9. A: SC map of the proportion of sites within a depth series at which HOMs could be evoked without or prior to gaze shifts ("HOM sites") expressed as a percentage of the total number of sites within the depth series. SC view taken from above, such that abscissa represents the rostrocaudal (horizontal) axis and the ordinate represents the mediolateral (vertical) axis, with positive values indicating medial. Superimposed on the map are iso-amplitude and -direction lines; the corresponding value of each line is placed within either the lower or rightward portion of the map, respectively. Filled circles, the estimated location of the stimulating electrode, based on the vector of the evoked gaze shift and the equations of Van Gisbergen and colleagues (1987). The color contour plot interpolates data between these dots. Data are pooled across monkeys *m* and *r*. B: representation of completed depth series in monkeys *r* and *m*. Each column summarizes data from a different depth series obtained in 500- μ m increments and is arranged from left to right in order of the increasing amplitude of gaze shifts evoked by 100 ms of stimulation at $1.5 \times$ GT100 (the amplitude is denoted above some columns). Red squares, sites at which HOMs were evoked; empty squares, sites at which HOMs were not evoked. Gray shading, regions within each penetration endowed with the lowest GT100. All columns are leveled to the most dorsal of such sites.

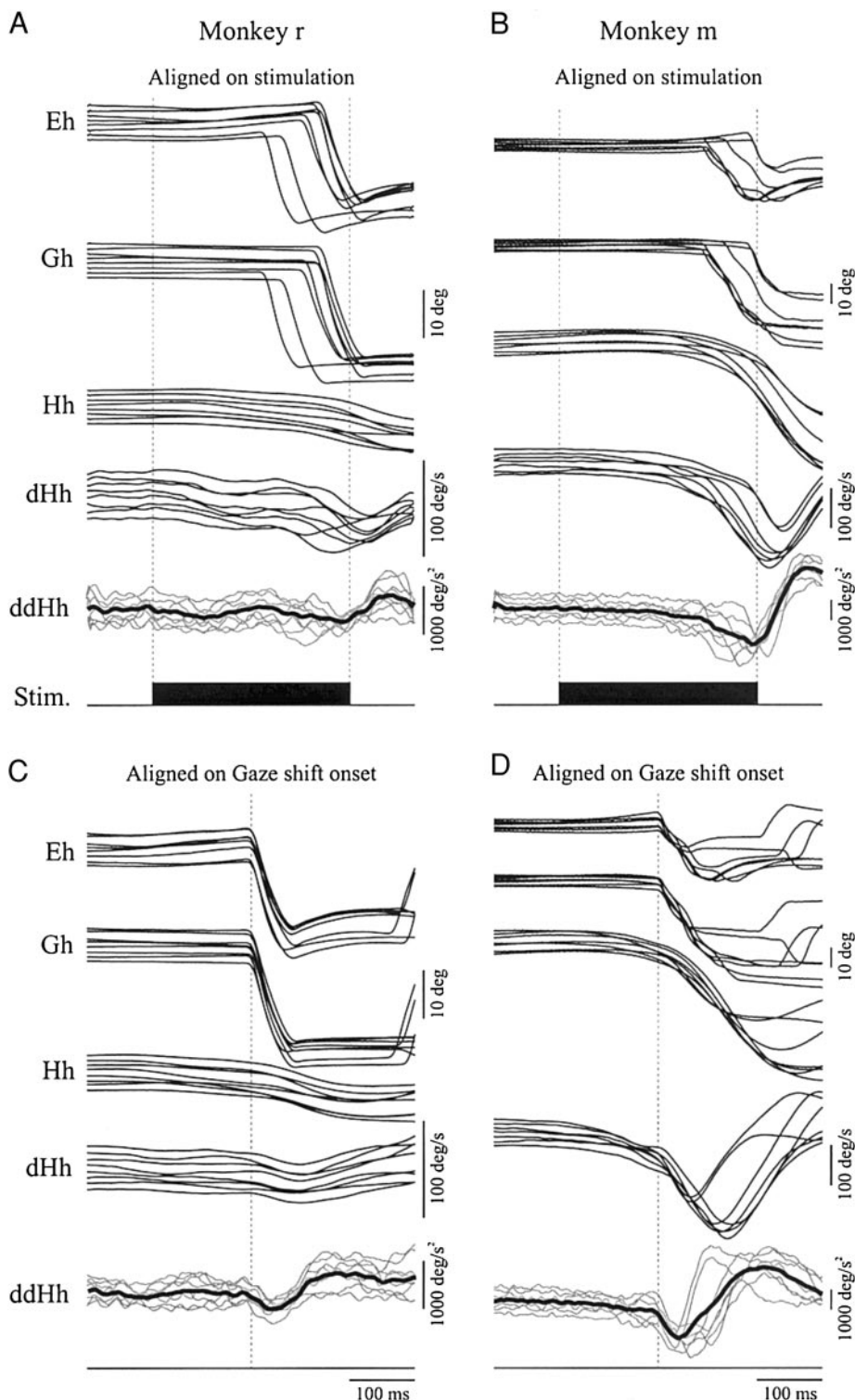


FIG. 10. Horizontal eye (Eh), gaze (Gh), and head (Hh) position and horizontal head velocity (dHh) and acceleration (ddHh) following 300 ms of stimulation into the right SC of *monkeys r* (A and C) and *m* (B and D). Traces aligned on stimulation (A and B: black rectangles and vertical dashed gray lines) or gaze-shift onset (C and D: vertical dashed gray lines). Black or gray thin lines, the individual responses staggered in sequence; thick, black lines in acceleration traces denote the averages of the individual traces. Gaze-shift onset is associated with an acceleration of the head (C and D).

12B). The overall pattern of the aligned EMG activity consisted of the typical pattern of agonist muscle facilitation and antagonist muscle suppression.

Similar observations were made in a total of 18 stimulation sites distributed over six stimulation locations in *monkey r* (Fig. 13A). In 16 of the 18 examples, the activity of the agonist OCI around the time of gaze-shift onset was significantly greater than the activity spanning -150 to -50 ms prior to

gaze-shift onset (i.e., 5 consecutive points ≥ 2 SDs above the activity prior to gaze-shift onset) and the acceleration of the head was significant in 15 of 18 examples (using the criteria described in Fig. 11). Hence, gaze-shift onset after HOMs usually evoked both a significant EMG response and a significant acceleration of the head. A direct comparison of the timing of these events is shown in Fig. 13B and revealed that EMG onset preceded peak head acceleration. Relative to gaze-

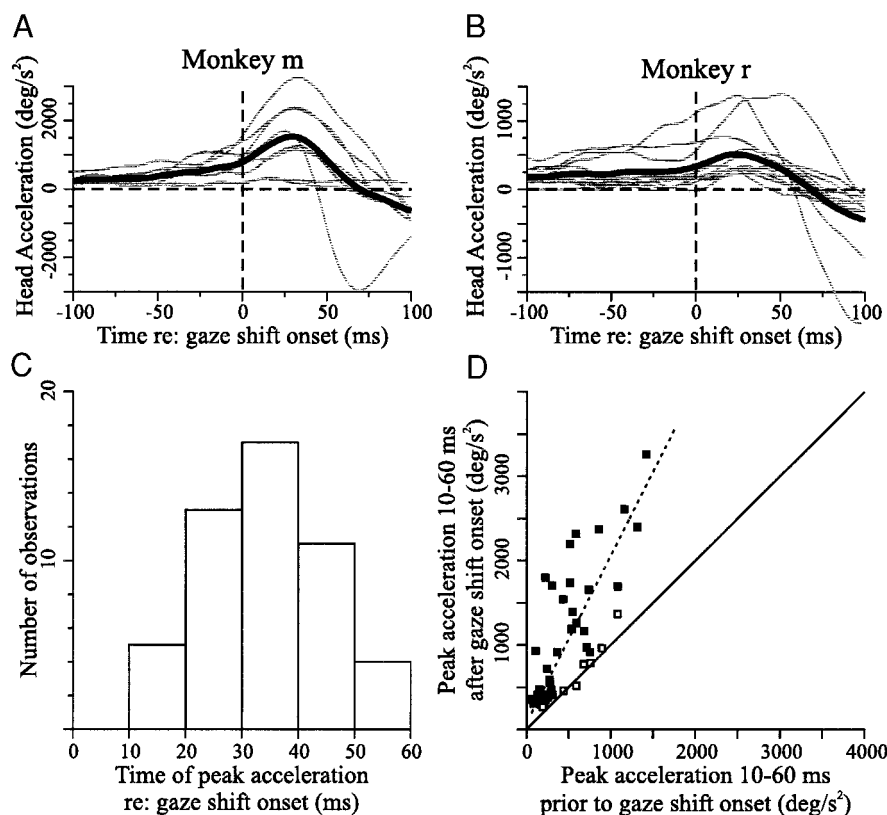


FIG. 11. Quantification of the acceleration of the head linked to gaze-shift onset. *A* and *B*: each light gray line denotes the averaged head acceleration trace aligned on gaze-shift onset obtained from a different stimulation location (8 for *monkey m* in *A*, 11 for *monkey r* in *B*), averaged from ≥ 3 individual traces. For inclusion, a HOM had to precede gaze-shift onset, and the gaze-shift latency had to be within 150–300 ms after stimulation onset. These criteria allowed separation of the head acceleration due to a HOM from that due to gaze-shift onset. Thick black lines denote the mean waveform of the individual averages. *C*: histogram of the time of significant peak head accelerations, relative to gaze-shift onset. Significance was assigned to the observed peak acceleration by extrapolating the least-squares regression line calculated from the 50 ms preceding gaze-shift onset forward to the time of the peak acceleration, and then determining whether the observed peak acceleration exceeded the predicted acceleration by twice the SD of the least squares regression line. Multiple stimulation sites could come from a given stimulation location, but each stimulation site was separated by $\geq 500 \mu\text{m}$. *D*: comparison of the peak head acceleration in the 50-ms interval either before or after gaze-shift onset. ■, significant peak accelerations after gaze-shift onset. □, nonsignificant points. ---, the linear regression for all data points. —, the line of unity.

shift onset, the mean onset time of the EMG response was -10 ± 12 ms (range: -34 to 10 ms, $n = 16$) and the mean time of the peak head acceleration was 29 ± 11 ms (range: 14 – 52 ms, $n = 15$). The mean difference between the time of the EMG onset and the peak head acceleration was 41 ± 18.3 ms (range: 16 – 72 ms, $n = 15$). We confirmed the transient nature of the EMG burst aligned with gaze-shift onset by integrating the EMG activity over 3 30-ms intervals spanning time periods before (pregaze), during (perigaze), or after (postgaze) the onset of the gaze shift (Fig. 13, *A*, *C*, and *D*). Statistical analysis demonstrated that the integrated EMG activity in the perigaze interval was significantly greater than the activity in either the pregaze or postgaze intervals [paired t -test; peri vs. pre, $t(17) = -7.7$, $P < 0.0001$. peri vs. post, $t(17) = -4.7$, $P = 0.0002$]. Taken together with the head acceleration data shown in Figs. 11 and 13, these data confirm that gaze shifts that followed HOMs were associated frequently with phasic EMG bursts and accompanying accelerations of the head.

DISCUSSION

This report is the first to describe the head movements and neck EMG responses evoked by SC stimulation in monkeys free to move their heads. We emphasize three important results. First, the latencies and magnitudes of the neck EMG responses to stimulation are essentially identical in head-restrained and -unrestrained preparations. Second, while recording neck EMG assesses the neuromuscular drive to the head plant, head biomechanics, and muscle force development also impact the kinematics of the head movements. Simultaneous recording of head movements with evoked neck EMG enables

the identification of seemingly counter-intuitive patterns of EMG activity, particularly compared with the EMG patterns accompanying volitional head movements. Third, low-current, long-duration SC stimulation evoked patterns of neck EMG and head movements that suggested the presence of two parallel influences from the SC onto neck muscles, only one of which is regulated by the circuitry controlling gaze shifts. These results, together with the results from the companion paper (Corneil et al. 2002), establish the combination of SC stimulation, neck EMG and head movement recording as a powerful technique toward understanding orienting head movements. Importantly, comparing the evoked EMG responses to those accompanying volitional head movements place specific constraints on the interpretation of head movements evoked by SC stimulation.

Considerations of head biomechanics and the kinetics of muscle force development

Our results indicate that head movements, unlike eye movements, cannot be used as proxies to estimate precisely the neural drive to the head plant; doing so ignores the complexity of the cascade from an EMG signal through force development to movement in a multiarticular and viscoelastic system. Muscle length, velocity, morphometry, histochemistry, and contraction history sculpt muscle force; plant mechanics, musculoskeletal architecture, interaction torques, and co-contraction patterns impact multiarticular movements (see Loeb and Gans 1986; Zajac and Gordon 1989 for review). Failure to appreciate some of these points has confused the interpretation of eye-head gaze shifts in the past. For example, head movements are not evoked if SC stimulation is too short in duration (Cowie

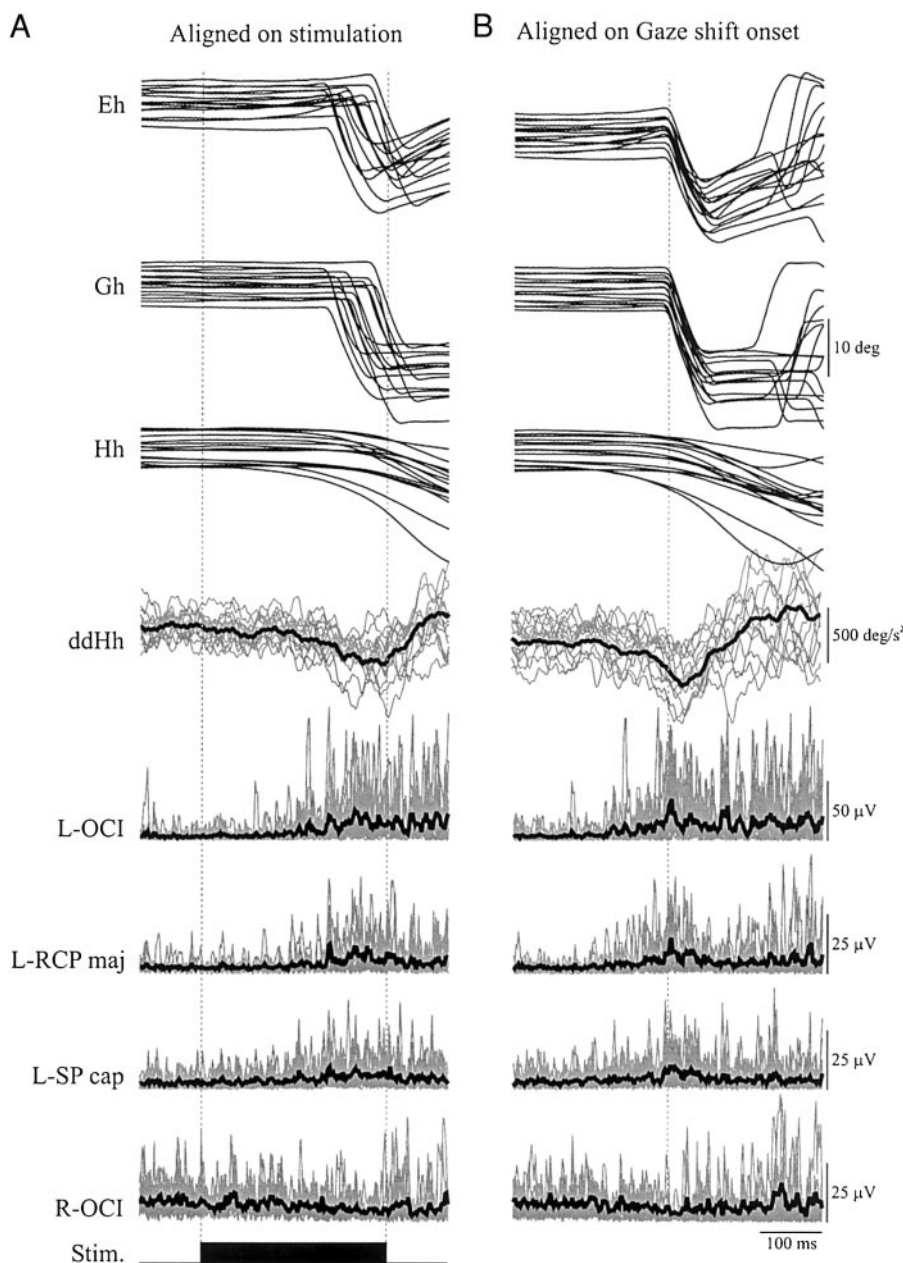


FIG. 12. Eye (Eh), gaze (Gh), and head position (Hh) and head acceleration (ddHh) traces, and EMG traces in response to prolonged stimulation in the right SC of monkey *r*. *A*: aligned on the stimulation. *B*: aligned on gaze-shift onset. Same format as Fig. 10.

and Robinson 1994) or is delivered to the rostral SC (Stryker and Schiller 1975), yet the results presented here (Figs. 1 and 2) and in the companion paper (Corneil et al. 2002) emphasize that such stimulation very likely did evoke neck EMG responses. The absence of evoked head motion therefore does not infer the absence of a neural drive to neck muscle motoneurons, presumably because of the head's inertia. Furthermore, the velocity at which neck muscles contract complicates the interpretation of the seemingly smooth head movement that accompanies sequential gaze shifts evoked by prolonged stimulation trains (Freedman et al. 1996; Stryker and Schiller 1975) because any transient EMG responses linked to the onset of sequential gaze shifts would be delivered to muscles that are actively shortening, consequently developing less force. Considerations of biomechanics and the muscle kinetics are more than a historical issue and apply to a contemporary debate regarding whether frontal cortex stimulation drives head move-

ments either during the evoked gaze shift or not (Sparks et al. 2001; Tu and Keating 2000). Recording neck muscle EMG circumvents such concerns by directly measuring the neural signal issued to the head plant. For example, it should be quite easy to observe whether the EMG responses to frontal cortex stimulation occur before, during, or after the evoked gaze shifts. Thus recording neck EMG enables one to resolve the time of arrival of the motor command at the head plant at a temporal resolution that far surpasses what can be achieved by measuring head kinematics.

Head-restrained vs. -unrestrained stimulation and a comparison with volitional head movements

Comparing the neck EMG responses evoked by SC stimulation across the head-restrained and -unrestrained preparations revealed only small qualitative differences presumably related

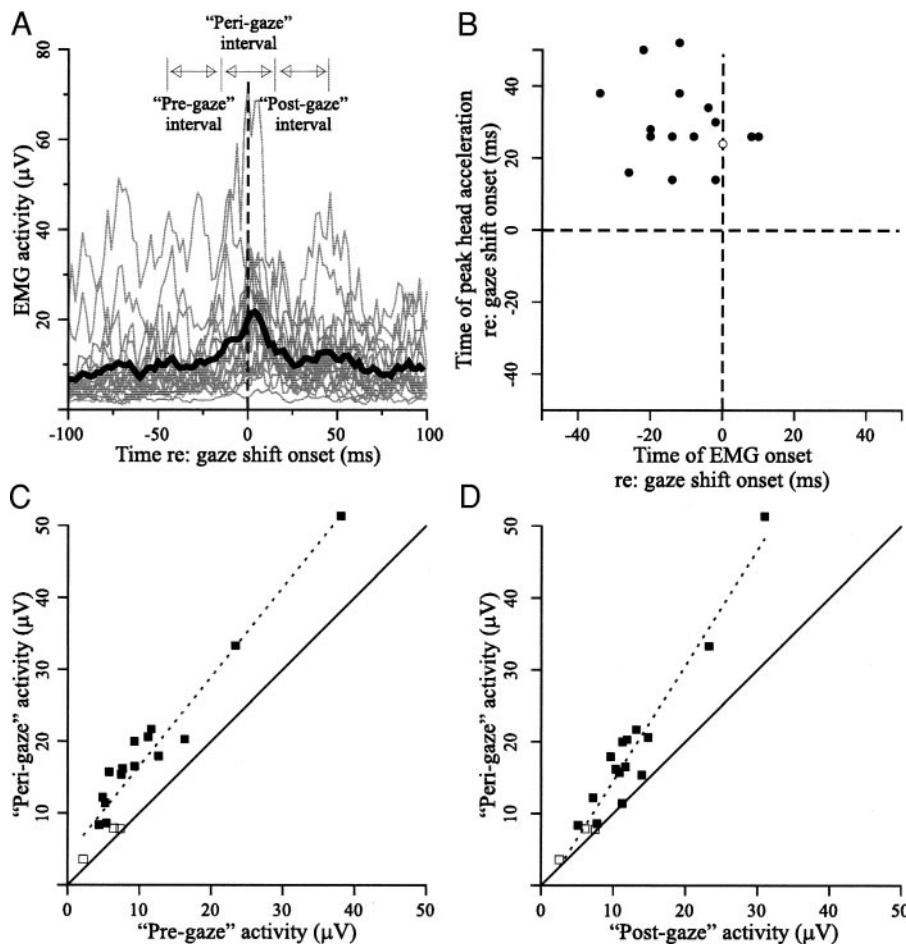


FIG. 13. Quantification of the transient EMG burst associated with gaze-shift onset following a HOM. *A*: 18 light gray lines denote the averaged EMG traces for the contralateral OCI muscle aligned on gaze-shift onset (vertical black dashed line), each obtained from a different stimulation site distributed throughout 6 stimulation locations in monkey *r*. Each average trace was derived from ≥ 3 individual traces (same criteria as described for Fig. 8). The text and lines near the top of the graph depict the 3 30-ms intervals over which EMG activity was integrated. Relative to gaze-shift onset, the "pre-gaze" interval spans -45 to -15 ms, the "peri-gaze" interval spans -15 to +15 ms, and the "post-gaze" interval spans +15 to +45 ms. Thick black line, the mean waveform of these 18 individual averages. *B*: scatter plot contrasting the time of the peak head acceleration vs. the onset of the EMG burst, both relative to the time of gaze-shift onset (horizontal and vertical dashed lines). Data is plotted only if the peak of the aligned EMG activity was significantly above the baseline period (ranging -150 to -50 ms before gaze-shift onset). Empty circle, an example in which the peak head acceleration was not significantly different from the baseline acceleration. Solid circles, examples with significant peak head accelerations. *C* and *D*: scatter plots contrasting the EMG activity integrated over the peri-gaze interval vs. either the EMG activity integrated over the pre-gaze (*C*) or post-gaze (*D*) intervals. Solid or empty squares, examples in which the EMG activity was either significant or not significant, relative to the baseline EMG activity. Dashed lines, linear regression lines; solid diagonal lines, unity lines.

to differences in initial eye or head position (Figs. 1 and 2). Importantly, this point validates the combination of neck EMG recording with head-restrained stimulation as a simplified means to address aspects of the neuromuscular control of the head.

Surprisingly, a comparison of the neck EMG patterns evoked by SC stimulation with those that accompany head movements during volitional gaze shifts places specific constraints on the interpretation of evoked head movements. For example, although SC stimulation initially recruits seemingly natural synergies of agonist muscles, the reciprocal patterning of EMG activity during stimulation and the poststimulation increase in antagonist muscle activity are not observed during volitional head movements (Fig. 3) (see also Corneil et al. 2002). Furthermore, SC stimulation evokes synchronous responses across agonist and antagonist muscles regardless of initial head position (Figs. 4 and 5). The EMG patterns during volitional head movements that begin from eccentric head postures display an elegant staggering in muscle recruitment that presumably exploits the elastic recoil from the eccentric posture and prevents lengthening contractions in the antagonist muscles (Corneil et al. 2001). Apparently, the mechanisms that stagger muscle recruitment are disrupted by SC stimulation (Segraves and Goldberg 1992).

This leads us to conclude that the neuromuscular patterns underlying evoked and volitional head movements are quite different in spite of their similar kinematics. The kinematic similarities of evoked and volitional head movements persist

probably because the head's inertia imposes a low-pass filter characteristic which smoothes out the consequences of the differences in muscle recruitment. The mechanisms underlying these recruitment differences are unknown, but several explanations are possible. For example, the SC receives abundant information from neck muscle spindles (Edney and Porter 1986; Richmond and Abrahams 1975; Richmond and Bakker 1982), thus it is possible that stimulation activates a different region of the SC when the head begins in different positions. Alternatively, unnatural temporal patterns of SC activity induced by stimulation, abnormal recruitment of downstream or parallel structures in the brain stem, cerebellum, or cervical spinal cord, or disrupted feedback signals during the movement (Coimbra et al. 2000) could also underlie our results. Regardless, the interpretation of the head movements evoked by SC stimulation must be done in light of our findings.

Variations in evoked neck EMG with initial head and eye position

The patterns of evoked neck EMG changed with different initial head positions in the unrestrained preparation (Fig. 4 and 5) and with different initial eye positions in the restrained preparation (Corneil et al. 2002). For both, the magnitude of the agonist EMG responses increased and the response latencies decreased as the head or eye attained positions contralateral to the side of SC stimulation (i.e., in the direction of the ensuing gaze shift). Our head-restrained results relate to the

effect reported by Freedman and colleagues (1996) that the latency to head movement decreases and the head contribution to the gaze shift increases when the eyes are initially deviated in the direction of the ensuing gaze shift with the head beginning near center.

Other aspects of the evoked neck EMG responses are more surprising and again emphasize the risk in using head kinematics to infer the neuromuscular drive to the head plant. Previous studies have shown that stimulation in the caudal SC can generate a convergent pattern of gaze and head movements (Segraves and Goldberg 1992; see Klier et al. 2001 for an interpretation of these movements in retinal coordinates). Although it is perhaps unfortunate that we could not examine the neuromuscular origins of head convergence because our stimulation duration was too short, we could still interpret the evoked EMG patterns in relation to the convergence of gaze shifts and assume that the head would also have converged if longer stimulation durations were used. When convergent gaze patterns were elicited, the magnitude of the evoked EMG response on the agonist muscles increased while the amplitude of the evoked gaze shift decreased. This might seem somewhat paradoxical because one might have expected the magnitude of the evoked EMG response to covary with the amplitude of the evoked gaze shift (and presumably the amplitude of the evoked head movement if stimulation was prolonged). However, such a scenario ignores biomechanical and kinetic factors associated with head postures deviated in the direction of the ensuing gaze shift: such postures are presumably associated with increased elastic recoil back to center and also place the agonist muscles on less forceful segments of their force-length curves. Thus even though the magnitude of evoked EMG responses increased, the consequent turning forces developed by the head plant likely decreased.

We make one final point in regards to the coordinate transformations that occur between the gaze-related command represented at the SC and the body-centered coordinates defined by neck muscle activity. This transformation presumably begins downstream from the SC at various brain stem centers specialized for the control of either horizontal or vertical movements. Our comparison between volitional and evoked head movements suggests that at least the final stage of the natural operation of this transformation is rendered inoperative by SC stimulation. Instead, SC stimulation appears to elicit a generic signal that simultaneously facilitates agonist muscles and suppresses antagonist muscles. Indeed, a simple explanation for the variations of evoked neck EMG with eye or head position is that this generic signal sums with the preexisting baseline EMG activity determined by both head position (Figs. 4 and 5) and eye position (Corneil et al. 2002). Overall, the unnatural spatiotemporal patterns of EMG activity evoked by SC stimulation suggests that SC stimulation cannot be used to study the natural transformation from gaze-related signals in the SC into body-centered signals at the neck muscles.

Head-only movements

The patterns of evoked head movements and neck EMG confirmed the predictions from the restrained preparation of a parallel drive from the SC onto neck muscle motoneurons (Corneil et al. 2002). One drive, the *independent drive*, was not regulated by the circuitry controlling gaze shifts and mediated

the evoked EMG responses and HOMs observed prior to or without gaze shifts (Fig. 4) (Corneil et al. 2002). The *dependent drive* was synchronized with gaze-shift generation and mediated the transient EMG bursts and head accelerations linked to gaze-shift onset (Figs. 10–13) (Corneil et al. 2002). Apparently, in spite of neck EMG activity evoked by an independent drive, gaze-shift initiation recruits other neural elements that also influence the activity of neck muscle motoneurons.

The three-dimension topography of sites from which HOMs were evoked (Fig. 9) resembled the distribution of EMG-only sites discerned from the restrained preparations (Fig. 4 in Corneil et al. 2002), emphasizing their obvious causal relationship. Further, the metrics of HOMs were determined by stimulation current and location (Fig. 8) as found for head movements during gaze shifts evoked by higher stimulation currents in a number of species (owls: du Lac and Knudsen 1990; cats: Paré et al. 1994; monkeys: Freedman et al. 1996). Phenomena similar to HOMs in monkeys have been described qualitatively before following stimulation of the SC (Cowie and Robinson 1994; Freedman et al. 1996), frontal eye fields (Tu and Keating 2000), and supplementary eye fields (Sparks et al. 2001), and a recent study in cats reported that HOMs can be evoked by low-intensity stimulation of the SC (Pélisson et al. 2001). While the prevalence of sites from which HOMs were evoked might be surprising considering they had not been quantitatively analyzed before, recall our use of prolonged low current stimulation was predicated on the discovery of EMG sites in the restrained preparation (Corneil et al. 2002).

There is compelling evidence in a host of nonprimate species that the role of the SC is not limited to rapid, saccadic-like orienting. In the rodent, electrical stimulation can evoke two types of contralateral orienting head movements: either a fast saccade-like head movement or a slower movement whose kinematics are dependent on stimulation parameters (King et al. 1991). Slower head movements also follow the rapid head movement elicited by stimulation of the optic tectum in owls (du Lac and Knudsen 1990), similarly SC stimulation in head-fixed cats drives both fast and slow eye movements (Grantyn et al. 1996), and SC stimulation in head-free cats can drive HOMs (Pélisson et al. 2001). The slow eye movements in cats are not simply aberrations from electrical stimulation but form a part of the oculomotor repertoire (Missal et al. 1993) and are encoded by tecto-reticulo-spinal cells driving both eye and head movements (Olivier et al. 1993; see Grantyn et al. 1993 for review). Eye-head coordination similar to HOMs is also observed during visually guided orienting in cats (Pélisson et al. 2001). Our observations in the monkey complement these findings by showing that signals from the SC can impart multiple influences on the head. Of course, confirmation of our results awaits recording studies in behaving animals. Specifically, we predict that some components of SC firing should be related to neck muscle activity and head movements in the absence of gaze shifts. Numerous studies in humans and monkeys have emphasized the lability of eye-head coupling during gaze shifts (see Fuller 1992; Stahl 1999; see Herst et al. 2001 for review), and a more recent study has specifically demonstrated an orienting command to the head in the absence of gaze shifts (Corneil and Munoz 1999). Although the SC is traditionally thought of as a gaze-orienting structure, the complexity of the downstream circuitry apparently endows the

oculomotor system the flexibility to orient the eye and head either separately or together depending on the behavioral context.

Neural mechanism for a parallel SC drive to the head

Figure 14 presents a simplified neural mechanism as a framework in which to discuss our results and propose future experiments. This mechanism supposes that the neural drive to the head is determined by two drives from the SC: a dependent pathway gated by the pontine omni-pause neurons (OPNs) that drives both the eyes and head during gaze shifts and an independent pathway that bypasses this gate and accesses neck motoneurons more directly. Similar embodiments of such a parallel drive from the SC can be found in earlier models (Galiana and Guitton 1992; Goossens and Van Opstal 1997; Guitton et al. 1990). The location of stimulation within the SC determines the strength of both drives, underlying the topography described in the companion paper (Corneil et al. 2002), and eye and head position signals affect the head premotor circuitry, mediating the known effects of eye and head position on tonic neck EMG.

The discharge of SC saccade-related neurons displays a dichotomy important for the relevance of this mechanism. Besides high-frequency bursts of activity before saccades, some saccade-related neurons exhibit low-frequency activity well before gaze onset when the location of potential target is predictable (Basso and Wurtz 1997, 1998; Dorris and Munoz 1998; Dorris et al. 1997; Glimcher and Sparks 1992; Munoz and Wurtz 1995). In unrestrained preparations, increasing target predictability leads to head movements that precede gaze shifts (Bizzi et al. 1972; Fuller 1992; Moschner and Zangemeister 1993; Munoz et al. 1991; Zangemeister and Stark 1982; Zangemeister et al. 1982), and we hypothesize that low-frequency SC activity accesses the head plant via the independent pathway. Specifically, the locus and intensity of such activity should encode the kinematics of the head movement or the magnitude of neck EMG activity. If true, then low-frequency SC activity would serve a concrete motor function of moving the head, or at least distributing a drive to the head premotor system, prior to a predictable gaze shift. Correlating low-frequency SC activity with neck EMG will test this hypothesis.

Gaze-shift onset is preceded by a cascade of neural events: cessation of OPN activity and a concomitant activation of the

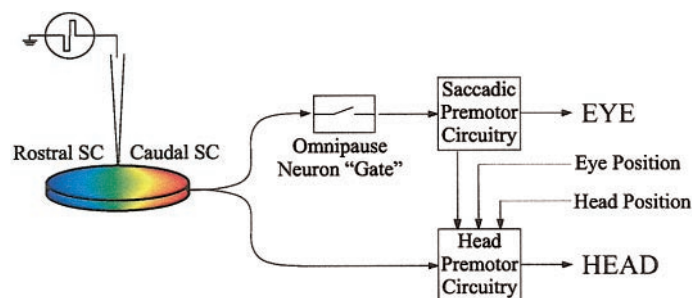


FIG. 14. Schematic of a mechanism for parallel SC drives to head, 1 of which is gated by the omni-pause neurons and engaged only when a gaze shift is generated. The color of the different SC regions denotes the strength of the projections onto neck muscle motoneurons, becoming stronger for more caudal locations. See DISCUSSION for further details.

long-lead burst neurons culminate in the discharge of medium-lead burst neurons (see Fuchs et al. 1985; Hepp et al. 1989; Keller 1981; Moschovakis et al. 1996). Tectal efferents project to both saccadic and head premotor areas, and some reticulospinal cells discharge a phasic burst at gaze-shift onset shifts while other reticulospinal neurons do not (cats: Grantyn and Berthoz 1987a,b; Grantyn and Grantyn 1982; Grantyn et al. 1992; Isa and Naito 1995; Vidal et al. 1983; monkeys: Scudder et al. 1996a,b; Whittington et al. 1984). In cats, subpopulations of reticulospinal cells either do or do not have collateral branches that project to extraocular motoneurons (Grantyn et al. 1992; Isa and Itouji 1992). Our mechanism predicts that gaze-shift onset delivers a drive to both the eye and head. This viewpoint is debatable and defines a crux differentiating between models employing common-drive elements and those postulating independent control of the eye and head.

Discriminating whether a given brain stem element controls the eye, head, or gaze in monkeys is complicated by the similarities of eye and gaze trajectories. For example, the pause duration of OPNs in monkeys correlates better to eye than gaze duration (Phillips et al. 1999), but this finding has been debated on the grounds of how well the movement components are defined (see Paré and Guitton 1998). Recording neck EMG provides an alternative approach by establishing the functional contribution of a given element to the neuromuscular control of the head. For example, if OPNs inhibit a common element driving both the eyes and head (cats: Cullen et al. 1993), then OPN stimulation during gaze shifts should inhibit the active agonist neck muscles. Long-duration (50–100 ms) OPN stimulation during gaze shifts in cats interrupts gaze and head trajectories (Paré and Guitton 1998); however, preliminary results in monkey demonstrate interruptions only to the eye and gaze but not head, trajectories (Coble et al. 1994; Sparks et al. 2002). The influence, or lack thereof, of OPN stimulation on head kinematics in these species is difficult to interpret because of the head's inertia and because OPN stimulation could work through an axon reflex of tectal efferents, which then access the head plant via an independent pathway (Gandhi and Keller 1997). A comparative analysis of neck EMG response latencies to SC and OPN stimulation could establish the hierarchy of signal flow, if it exists, in both species; indeed a similar approach has established the signal flow from the SC to extraocular motoneurons (Keller et al. 2000; Miyashita and Hikosaka 1996).

The understanding of head premotor events downstream from any "common" elements is further advanced in cats than monkeys (see Isa and Sasaki 2002 for review). Premotor processing transforms a topographic movement representation into the neuromuscular sequence that accounts for the forces resisting movement as well as the physiological and structural properties of neck muscles. An intermediate step of this transformation segregates the movement into cardinal components in the pontomedullary reticular formation and mesencephalon (owls: Masino and Knudsen 1993; cats: Fukushima 1987; Isa and Naito 1994, 1995; Isa and Sasaki 1992a,b; Sasaki et al. 1999). The descending spinal systems from these areas contact a specific subpopulation of neck muscle motoneurons (Isa and Sasaki 1992a,b; Iwamoto and Sasaki 1990; Sasaki 1999; Shinoda et al. 1996) forming functional neck muscle synergies hard-wired via descending brain stem systems (Shinoda et al. 1996; Siegel and Tomaszewski 1983). We suspect these syn-

ergies are recruited by SC stimulation. Evidence from volitional head movements in cats and monkeys suggests that such synergies are sculpted by the kinetic requirements of the particular movement (Corneil et al. 2001; Thomson et al. 1994, 1996). Apparently, such sculpting mechanisms are not available during SC stimulation.

General conclusions

Our results suggest the need for caution on two fronts. First, electrical stimulation of the SC does not evoke completely natural patterns of evoked neck EMG. In spite of the kinematic similarities between evoked and volitional head movements, the assumption that evoked head movements equate to volitional head movements is unfounded. Second, our evidence for parallel drives from the SC to the head plant complicates the application of traditional measures to assess eye-head coupling during gaze shifts, such as correlating eye, head, and gaze metrics or kinematics because actions of the independent pathway could obscure actions of the dependent pathway. We are not saying that correlational approaches should be abandoned but instead that certain questions, such as whether a given brain stem element drives the head during a gaze shift, would be better addressed at a neural level and recording neck muscle EMG represents an optimal approach to measure objectively the final form of the neural drive to the head plant.

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