Role of Superior Colliculus in Adaptive Eye–Head Coordination During Gaze Shifts

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Role of superior colliculus in adaptive eye–head coordination during gaze shifts. J Neurophysiol 92: 2168–2184, 2004. First published June 9, 2004; 10.1152/jn.00103.2004. The goal of this study was to determine which aspects of adaptive eye–head coordination are implemented upstream or downstream from the motor output layers of the superior colliculus (SC). Two monkeys were trained to perform head-free gaze shifts while looking through a 10° aperture in opaque, head-fixed goggles. This training produced context-dependent alterations in eye–head coordination, including a coordinated pattern of saccade–vestibuloocular reflex (VOR) eye movements that caused eye position to converge toward the aperture, and an increased contribution of head movement to the gaze shift. One would expect the adaptations that were implemented downstream from the SC to be preserved in gaze shifts evoked by SC stimulation. To test this, we analyzed gaze shifts evoked from 19 SC sites in monkey 1 and 38 sites in monkey 2, both with and without goggles. We found no evidence that the goggle paradigm altered the basic gaze position–dependent spatial coding of the evoked movements (i.e., gaze was still coded in an eye-centered frame). However, several aspects of the context-dependent coordination strategy were preserved during stimulation, including the adaptive convergence of final eye position toward the goggles aperture, and the position-dependent patterns of eye and head movement required to achieve this. For example, when initial eye position was offset from the learned aperture location at the time of stimulation, a coordinated saccade–VOR eye movement drove it back to the original aperture, and the head compensated to preserve gaze kinematics. Some adapted amplitude–velocity relationships in eye, gaze, and head movement also may have been preserved. In contrast, context-dependent changes in overall eye and head contribution to gaze amplitude were not preserved during SC stimulation. We conclude that 1) the motor output command from the SC to the brain stem can be adapted to produce different position-dependent coordination strategies for different behavioral contexts, particularly for eye–head position, but 2) these brain stem coordination mechanisms implement only the default (normal) level of head amplitude contribution to the gaze shift. We propose that a parallel cortical drive, implemented upstream or downstream from the motor output layers of the superior colliculus (SC) are often said to code gaze, with coordination of the eye and head taking place downstream, perhaps in the brain stem and cerebellum (Freedman 2001; Fuchs et al. 1985; Guitton 1992; Optican and Robinson 1980; Pelisson et al. 2003; Robinson and Fuchs 2001; Sparks et al. 2001; Waitzman et al. 2002), but it is much less clear whether these lower-level mechanisms are themselves responsible for the adaptive and context-dependent aspects of eye–head coordination, or whether higher-level inputs from the cerebral cortex are required. A number of studies have looked for the anatomic sites and brain stem mechanisms of adaptation for saccades (Edelman and Goldberg 2002; Optican 1985; Optican and Robinson 1980; Zee and Optican 1985) as well as for the vestibuloocular reflex (VOR) (Galiana 1986; Miles et al. 1985; Viirre et al. 1988). Several studies have looked at the behavioral aspects of adaptation in eye–head coordination (Ceylan et al. 2000; Crawford and Guitton 1997; Mellvill Jones et al. 1988; Misslisch et al. 1998; Pathmanathan et al. 2001; Phillips et al. 1997; Stahl 2001). However, very few studies have looked directly on the adaptive neural mechanisms for eye–head coordination during gaze shifts. In contrast to behavioral controls (Coimbra et al. 2000), gaze shifts evoked by stimulating the SC of the cat failed to compensate for acutely increased loads on the head. However, this task involved the preservation of normal gaze kinematics rather than the long-term acquisition of new, context-dependent patterns of eye–head coordination. One context-dependent way to change the relative contributions of the eye and head to gaze shifts in the primate is to train subjects to make head-free gaze shifts while looking through a small head-fixed aperture—the “goggles task” (Ceylan et al. 2000; Crawford and Guitton 1997; Misslisch et al. 1998; Stahl 2001). Learning this task forces 2 main changes in the neural control system. First, the amount of head contribution to the gaze shift must increase so that the head moves directly toward the target by about the same amount as the desired gaze shift. Second, in the goggles task, the eye must look through the aperture to foveate the target.

The latter requirement is not as trivial as it might sound. Because the eye and head do not generally rotate in exactly the same direction during oblique gaze shifts (Tweed et al. 1995), an increased head rotation will not automatically recenter the eye. After goggle training, the eye does not simply stay stuck at one position (i.e., by reducing saccade and VOR gain to zero), nor does it simply roll back further in the head because...
of the increased head movement. Rather, the eye engages in a coordinated pattern of saccade and VOR movements such that it ends up at the trained location. If the eye position is initialized at a new aperture location, monkeys trained on a different aperture location continued to drive the eye toward the old (now occluded) aperture location until retrained (Crawford and Guittion 1997). However, despite the complexity of these learning processes, once trained, monkeys are able to switch between the goggles strategy and the normal default eye–head coordination strategy as a function of context (Crawford et al. 1999).

The purpose of this study was to determine whether these context-dependent learning strategies were implemented upstream or downstream from the SC motor command, by training monkeys to switch rapidly between the normal and “goggle” strategies, and then evoking gaze shifts by electrically stimulating the SC in each condition. As shown schematically in Fig. 1A, any context-dependent adaptation in eye–head coordination that is implemented downstream from the SC (i.e., in structures accessed by a fixed output from the SC) should be preserved during SC stimulation (Freedman et al. 1996; Guillaume and Pelisson 2001; Paré et al. 1994). Conversely, context-dependent mechanisms that are implemented only upstream (Fig. 1B) or parallel (Fig. 1C) to the site of stimulation should not be preserved during this paradigm.

This approach required a complex analysis. First we had to identify and quantify the context-dependent changes between normal gaze shifts and the goggles paradigm in the behavioral data. Then, the same analysis was required on the SC stimulation-evoked movements, to see whether the same context-dependent results are observed in these data. Thus this study involves a comparison between 2 comparisons: behavior with/without goggles versus SC stimulation with/without goggles. In this analysis, we focused on several aspects: 1) amplitudes and directions of eye, head, and gaze movements; 2) relative amplitude contributions of eye and head to gaze; 3) dependency of stimulus-evoked movement trajectories on their initial position; 4) amplitude–velocity relationships in eye, head, and gaze; 5) accuracy of placing final eye-in-head position at the goggles aperture; and 6) the patterns of saccade, VOR, and head movement coordination required to achieve the latter. Specific hypotheses will be presented in the results with each section. These results showed that some, but not all, aspects of the adapted eye–head coordination strategy were preserved during SC stimulation, suggesting a more complex model for adaptive eye–head coordination (Fig. 1D) than previously considered. Some of these results were previously reported in abstract form (Constantin et al. 2001, 2003).

M E T H O D S

Animal preparation

All surgical and experimental procedures were approved by the York University Animal Care Committee and were in compliance with the Canadian Council on Animal Care policy on the use of laboratory animals. Two juvenile female monkeys, Macaca fascicularis (henceforth designated M1 and M2), underwent aseptic surgery under general anesthesia (isoflurane 1.5% and ketamine 10 mg/kg). The procedure involved the implantation on the skull of 3 types of devices, fixated with the aid of a dental acrylic cap: 1) one stainless steel recording chamber was placed on the skull at 5 mm anterior and

![FIG. 1. Possible neural sites of adaptation in eye–head coordination after “goggles training.” Cortex (frontal and parietal) provides inputs (solid lines) to the motor layers of the superior colliculus (SC), which in turn is thought to drive areas of brain stem involved in the control of eye muscle motoneurons and neck (head) muscle motoneurons (e.g., Freedman et al. 1996). Frontal cortex gaze control areas also provide a parallel input (dashed lines) to brain stem reticular formation gaze control areas (e.g., Schiller et al. 1979). Here we also consider the possibility of an independent parallel channel for the head. Possible sites of adaptation for our training task are denoted by the schematic “goggle.” A: adaptation to a hypothetical brain stem mechanism that “splits” an SC gaze command into separate eye and head commands. These adaptations should be preserved during SC stimulation. B: adaptation to a similar hypothetical “splitting” mechanism somewhere upstream from the SC output cells, with parallel eye and head channels within the SC. Such adaptations would not be preserved during SC stimulation. C: adaptations within separate, parallel channels from the cortex to separate eye and head control areas downstream from the SC. Again, these adaptations should not be accessible during SC stimulation. D: hybrid scheme that we propose based on our data (see DISCUSSION). Here the adaptation occurs in the oculomotor mechanisms downstream from the SC and in a parallel head drive from cortex.](http://jn.physiology.org/lookup/fig/1)
magnetic fields (Tweed et al. 1990). Coil signals were recorded at a sampling frequency of 100 Hz.

**Pinhole goggles task and training**

The primates were trained only with the head unrestrained. They first learned to fixate and follow “treats” held at a distance of 80 to 100 cm throughout a large range of eye and head movements (Crawford and Guitton 1997). After this initial training, we fit the animals with a pair of opaque plastic goggles, shaped to the contour of each monkey’s face. Initially, a single round aperture was positioned at our best estimate of the center of the mechanical range of the eye, as given by the intersection of a visually measured line between the center of the eye and the auditory canal and a line projected from the pupil, when the monkey was looking straight ahead toward a distant target, with its head restrained. This standard aperture gave the eye a useful visual range of only 10°. We trained the animals to fixate treats through the aperture and then to make horizontal and vertical gaze shifts following the treats, and finally to make oblique gaze shifts. The animals were rewarded with the treats after 4 or 5 gaze shifts. A large and varied range of gaze movements was obtained in an effort to match the large variety of naturally occurring gaze shifts.

The animals were trained in 1-h sessions, until they were able to correctly move the head with the goggles on and look through the aperture for the treats. It took approximately 3 wk of training to establish the basic elements of this task (Crawford and Guitton 1997). The training was continued throughout the subsequent weeks of experiments, and thus the learned behavior was maintained.

**Experiments**

We began experiments when the animals were fully trained on the goggles task, and could switch between the normal and “goggle” strategy of eye–head coordination, and when we identified the location of the SC sites. Before each stimulation experiment, we reinforced the learned goggles behavior and recorded behavioral data (i.e., the eye and head movements evoked by a visual stimulus) in the 2 conditions: without goggles (no goggles: NG) and with goggles (WG).

Single-unit recordings and microstimulations were performed with the use of tungsten microelectrodes (0.5–2 mΩ impedance at 1 kHz), which were advanced using a Narishige model MO-95S hydraulic microdrive modified to fit onto the stage of an MO-99 X–Y placement system. The weight of this entire system was 68 g. Once experiments began, animals bore this same weight on their head during all head-free recording conditions.

We identified SC sites by following a 3-step method. First, we identified the interstitial nucleus of Cajal and oculomotor nucleus (Klier et al. 2002), using the clear saccade-related burst-tonic activity of these nuclei to confirm our stereotaxic coordinate system. Second, we moved our electrode “tracks” posterior toward the expected center of the SC topographic saccade map. At the beginning of each SC experiment we recorded unit activity with the animal’s head restrained to identify any saccade-related burst activity. Finally, electrical stimulations, of various durations, were delivered through the same electrodes at 0.5-mm intervals. Sites that showed bursting activity during contralateral saccades and that evoked contralateral saccades when stimulated at 50 μA, were classified as SC motor sites and investigated further. Exploration of further sites on subsequent days was aided by following the expected topography of the SC (Freedman et al. 1996; Stanford et al. 1996).

Once the SC site was identified, the head was then freed and each identified site was further explored by use of electrical microstimulation trains (50 μA, 200 Hz). In conditions established for our investigations (Klier et al. 2001, 2005) these are the minimal required parameters to consistently evoke maximal eye–head gaze shifts from most SC sites. We held this current strength constant to provide minimal current spread and consistent comparisons between sites and conditions. Stimulation train duration was initially varied in 100-ms steps to find the minimum duration that most consistently produced maximum amplitude (single-step) gaze shifts that resembled natural gaze shifts. In animal M1 this “optimal duration” was 300 ms and in animal M2, 200 ms. These durations were then held constant (with and without goggles). These stimulation parameters are unlikely to evoke gaze shifts from the superficial sensory layers of the SC (Van Opstal et al. 1990) but have been shown to evoke natural-looking eye–head gaze shifts from the deeper motor layers in the monkey (Freedman et al. 1996; Klier et al. 2001, 2003; Van Opstal et al. 1990).

For each site, evoked eye and head movements were recorded in the 2 conditions: “with goggles stimulation” (WGS) and “no goggles stimulation” (NGS). In the NGS condition, we stimulated each SC site (30 to 60 stimulations per site) and recorded the data while the monkey was using an eye–head coordination strategy of its own choosing. In the WGS, we donned the goggles and stimulated the SC again. We moved the electrode by 0.5 mm vertically and repeated the process, in both conditions. After these procedures, we investigated 19 sites from M1 (in 4 tracks) and 38 sites from M2 (in 10 tracks). However, for data analysis we used only those sites that consistently evoked eye + head gaze shifts >10° (i.e., the aperture diameter), which resulted in 12 sites from M1 and 31 sites from M2.

With M2 we also performed the “switching aperture” experiment, which took place at the end of the NGS condition of the experiment. For this additional 10° goggles apertures were positioned 20° up, down, left, and right from the center of the middle aperture. Up until the time of this “switching holes” experiment, these 4 holes were occluded so that the animal was trained only on the center aperture. However, during this experiment we covered the standard central aperture and uncovered the rest of the apertures, one at a time, while monitoring the eye and head positions on the computer. We then delivered the electrical microstimulation when the monkey was looking through each new aperture. This was repeated for each of the 5 apertures, at 7 SC sites.

When the experiments were finished the SC sites were marked with a localized lesion (using a current pulse of 1.5 mA for 15 s) and the brains were removed for histological verification. This confirmed that the stimulation sites reported in this study were situated in the deep motor layers of the SC, extending rostrocaudally from its middle to its caudal border.

**Data analysis**

A computer program was used to convert the coil signals into eye and head position quaternions for head relative to space (Head) and eyes relative to space (Gaze), and then these values were used to calculate the position for the eye relative to head (Eye) (Crawford et al. 1999; Tweed et al. 1990). Quaternions represent positions as a fixed-axis rotation from a reference position (Westheimer 1957). This reference position was chosen when the monkey was looking straight ahead (in the same directions as the forward-pointing magnetic field), in the NG condition. However, for some analyses we required a "WG reference position," taken when the monkey was wearing the goggles and was looking straight ahead and through the aperture.

Quaternions were used because they provide an accurate and convenient representation of eye and head orientations throughout the entire 360° range in all 3 dimensions. Gaze trajectories, angles of rotation, and angular velocities were computed from these quaternions (Crawford et al. 1999; Tweed et al. 1990). The beginning and the end of the stimulation-evoked eye, head, and gaze movements were selected by an experimenter during visual inspection of the movement traces on a computer screen. The saccade and the VOR components of gaze shifts were differentiated visually by marking (on a computer screen) the inflection point at which eye-in-head velocity reversed. We chose the point in the same direction as head movement to receding in the direction opposite to head movement. We never observed "plateau phases" where eye-in-head position held steady between the saccade and VOR, so this inflection point was always
To characterize the typical results of stimulating each SC site, we also calculated the “characteristic vector” (CV) for eye, head, and gaze, using a method described previously (Klier et al. 2001; Martinez-Trujillo et al. 2003). This “characteristic vector” expresses the gaze, head, or eye trajectory that would be expected if the eyes and head were pointing straight ahead at the beginning of the stimulation.

RESULTS

Overview of behavioral data

The purpose of this section is to provide an overview of the behavioral differences between gaze shifts in NG and WG conditions after training, as recorded at the beginning of each experiment. In subsequent sections we will see which aspects of these context-dependent changes are preserved during SC stimulation. The 2 top panels in Fig. 2 show the horizontal components of 2 similar-sized gaze shifts, without (A) and with (B) the goggles, plotted as a function of time. Gaze is plotted along with its constituent eye and head components. As in most head-free gaze shifts, the eye and head move in the same direction during the rapid-saccade portion of the gaze shift (between the dashed vertical lines), and then the eye rolls backward during the subsequent VOR phase. However, during the WG condition (B), notice that the head movement is larger and faster, and that the eye rolls back toward its initial position (at the aperture), such that the overall saccade + VOR eye movement is negligible.

These observations are extended to 2 dimensions (2-D) in Fig. 3, which plots the gaze (A), head (B), eye saccade (C), and eye VOR (D) trajectories, recorded during the behavioral tasks, for both for NG (left column) and WG (right column) conditions. The open circles (○) correspond to the end of the movement trajectories. These trajectories are represented by unit-length vectors parallel to the pointing direction of the eye-in-space, head-in-space, and eye-in-head (i.e., showing gaze direction, facing direction, and eye direction, respectively). The horizontal and vertical components of these vectors are plotted, as one would view them from behind the monkey. These vectors thus define a ±90° sphere indicated by the large circles in A and B. The gaze shifts illustrated here were selected so that their gaze amplitudes were similar in the 2 behavioral conditions (mean 33.5° in WG and 32.4° in NG), to allow for comparison between the corresponding eye and head components.

FIG. 2. Horizontal eye, head, and gaze trajectories. Plot represents the horizontal positions vs. time of eye, head, and gaze during similar leftward gaze shifts, for the 4 experimental conditions. A: behavior data without goggles [no goggles (NG)]. B: behavior data with goggles (WG). C: NG stimulation data. D: WG stimulation data.

FIG. 3. Behavioral data. 2-D trajectories of gaze (A), head (B), and eye (C, D) in the 2 conditions: NG (left column) and WG (right column). Each point corresponds with the tip of the unit-length vector (computed from quaternions), and represents the position in space for gaze (A), head (B), and eye-in-head (C; D), with their vertical and horizontal components projected from behind, onto a 2-D plane. A: gaze trajectories seem of comparable amplitude in NG and WG. B: head movements corresponding to the gaze movements in A. C: eye saccadic movements, which drive the eye toward an eccentric position. D: movements evoked by vestibuloocular reflex (VOR), which maintain the eye on the target, until the end of the head movement. Location of the aperture is marked by the small circle (dotted in NG); (○) represents the end of the movement.
Figure 3B plots the corresponding head movements. The amplitudes of the head movements were much larger in WG (right column: averaged amplitude of head movements is 38.9°), compared with NG (left column: averaged amplitude of head movements is 21.8°). Figure 3C shows that in both the NG and WG conditions, the initial saccade portion of the oculomotor response tended to take the eye away from the central range. However, the behavior during the subsequent VOR phase (Fig. 3D), during which the eyes rolled back while the head continued to move, was different for the NG and WG conditions. In the control NG condition, the VOR tended to roll the eye back only part of the way toward center, such that the range of the final endpoints (●) was still relatively large (left column). In contrast, in the WG condition, the eyes rolled back toward the center, landing within the location of the visual aperture (indicated by the central gray circle).

These basic results (quantified in more detail below) are consistent with previous behavioral observations using the goggles task (Crawford and Guitton 1997) as follows: 1) an increase in the size of head movement for a given gaze shift and 2) a restriction in the final eye-in-head position range. This suggests that the animals had learned 2 qualitatively and quantitatively different patterns of eye–head coordination. Once this was learned, the animals could rapidly switch between these 2 patterns simply by donning or removing the goggles. This allowed us to perform the planned electrophysiological experiments.

Overview of stimulation data

One simple hypothesis could be that all of these state-dependent behavioral changes were implemented downstream from the SC (in a functional sense) and that these changes were “switched on-off” by contextual signals, depending on whether the monkey wore the goggles. Previous studies suggest that electrical stimulation of the SC activates a local population of neurons whose response profile is graded with distance from the electrode tip, presumably simulating a fixed motor output from the SC (Bergeron et al. 2003; Freedman et al. 1996; Guitton et al. 1993; Port et al. 2000; Ranck 1981; Sparks 1993). Therefore if the behavioral adaptations described above are implemented downstream from the SC, they should be preserved during stimulation of its intermediate and deep layers.

Without goggles, the average amplitudes of the stimulation-evoked gaze shifts (averaged for each particular stimulation sites and across individual trials for each site) that met our analysis criteria (eye and head gaze shifts — 10°) ranged from 10.3 to 90.4°, with corresponding average head movement amplitude ranging from 4.5 to 80.3° and corresponding average evoked-saccade amplitudes ranged between 4.5 and 22.9°. Here we provide a qualitative overview of the main results before embarking on a quantitative comparison of the data.

The bottom panel of Fig. 2 shows typical horizontal movement trajectories during movements evoked from one SC stimulation site, in the NGS condition (C) and WGS condition (D), matched in size to the behavioral gaze shifts shown in the top panel. As in the NG behavioral data (A), in the NGS data (C) one can see the natural sequence of a saccadic gaze shift, accompanied by a small head movement, and a slight VOR-related rollback of the eye at the end of the movement.

Moreover, this pattern is changed in the WGS condition (D), where the eye rolls back further toward its initial position (at the aperture), much like the behavioral WG data (B). The effect on head movement is less clear; in this example (D) the head also seems to move a bit more, but as we shall see, this result was not consistent.

Figure 4 extends these observations by plotting the 2-D trajectories of stimulation-evoked gaze shifts from one SC site in the NGS (left column) and WGS (right column) conditions, using the same conditions shown previously in Fig. 3. The
empty circles (○) correspond to the end of the stimulus-evoked movement. On casual inspection, there does not appear to be much difference between the gaze trajectories evoked in the NGS and WGS (A) conditions. More important, unlike the behavioral data, there does not appear to be much difference between the corresponding head movement trajectories in these 2 stimulation conditions (B).

In contrast, there were clear differences between the VOR (D) distributions in these 2 conditions. The VOR returned the eye toward a more restricted range in the WGS condition (D), which appears to roughly coincide with the location of the aperture. These examples suggest that some, but perhaps not all, aspects of the behavioral adaptation were preserved during SC stimulation. To determine with more rigor which aspects were preserved, the following sections pursue these observations with the use of a detailed quantitative analysis of this entire population and additional controls as described in the INTRODUCTION.

Amplitude and direction of stimulus-evoked gaze, head, and eye movements

Previous studies have shown that the amplitude of gaze, eye, and head movements evoked from SC stimulation depend on initial eye and head position (Freedman et al. 1996; Klier et al. 2001; Roucoux et al. 1980). Typical position dependencies can be observed in Fig. 4, but these tend to be much greater for large-amplitude stimulus-evoked movements. We could not independently manipulate eye and head position in this experiment without disrupting our 2 tasks (natural gaze shifts vs. goggles paradigm). Moreover, these tasks could not guarantee a homogeneous and comparable distribution of initial eye and head positions (training monkeys to look at LEDs with goggles becomes unwieldy for more than a few targets). These factors rule out comparisons of movement amplitude based on raw or averaged data. Therefore we calculated the “characteristic gaze vector” (CV) for each site. This CV represents the theoretical movement that would be evoked by stimulation of that site while the eyes and head are looking straight ahead, as calculated by a multiple linear regression on all of the gaze trajectories and initial gaze positions from each particular site (Klier et al. 2001; Martinez-Trujillo et al. 2003). The CV thus accounts for the near-linear dependency of evoked gaze, eye, and head movement components on their initial-position components (Freedman et al. 1996; Klier et al. 2001; Paré et al. 1994; Roucoux et al. 1980), correcting for nonuniform distributions of initial position.

GAZE PREDICTION. Our paradigm does not provide any specific predictions about the effect of the WG condition on the overall gaze shift. However, most “gaze models” of the SC would predict no change (i.e., the goggles would not affect the gaze shifts; Galiana and Guitton 1992; Guitton 1992; Sparks 1999). Characteristic gaze vectors (CVgaze) are plotted in Fig. 5 for NGS (A) and WGS (B), for both M1 (○) and M2 (●). Typical of SC stimulation (Moschovakis 1996; Stanford et al. 1996), the control NGS gaze shifts (A) were mainly horizontal (contralateral to the stimulation site) with various smaller vertical components, and the same was true in the WGS condition (B).
At first glance, the CV_{gaze} values for the WGS condition (B) do not look strikingly different. However, quantitative analysis (average values ± 5SE) revealed that the amplitude of the WGS movements (CV_{gaze} = 20.5 ± 2.7° for M1, CV_{gaze} = 16.3 ± 2.2° for M2) was smaller than that of the control NGS movement (CV_{gaze} = 25.6 ± 3.6° for M1, CV_{gaze} = 19.2 ± 2.6° for M2). This difference was statistically significant in both animals (Student’s t-test, P = 0.009 for M1 and P < 0.001 for M2). This result is summarized in Fig. 5C, which plots the amplitudes of the CV_{gaze} WGS as a function of NGS for each site, with separate regression fits for each monkey. Both animals show a reduction of slopes (0.661 for M1 and 0.790 for M2 with correlations of 0.769 for M1 and 0.915 for M2) from the expected—by default—line of unity. The reasons for this become clear when we look at the underlying eye and head movements.

HEAD PREDICTION. In the behavioral data, the new eye–head coordination pattern in the WG condition included a clear and significant increase in the size of the head movement for a given gaze shift (Figs. 2 and 3). For example, when we pooled the head movements for all of the behavioral data collected from both monkeys, average head amplitude increased from 19.0° (M1) and 14.6° (M2) in the NG condition to 32.4° (M1) and 19.3° (M2) in the WG condition. This increase was statistically significant in both monkeys (Student’s t-test, P < 0.001).

If this increase was implemented downstream from the SC, one would expect it to occur in our stimulation data as well. However, this was not the case (see also Fig. 4). Figure 5D shows the characteristic head movement vectors (CV_{head}) computed for each SC stimulation site for the NGS condition (as described above for gaze). Notice the wide distribution of directions and amplitudes. When these were computed for the WGS condition, we observed no increase between the WGS (E) and the NGS (D) conditions. Indeed, our quantitative analysis revealed a very small but significant decrease in the size of the head movements in the WGS condition. The vectors have a significantly smaller magnitude in WGS (CV_{head} = 15.9 ± 2.5° for M1, CV_{head} = 14.1 ± 1.9° for M2) than in NGS (CV_{head} = 19.9 ± 3.4° for M1, CV_{head} = 16.5 ± 2.5° for M2) (Student’s t-test, P = 0.008 for M1 and P = 0.009 for M2). Again, these results are summarized in Fig. 5F, which shows a reduced slope in the CV_{head} amplitudes for WGS versus NGS in both animals (0.683 for M1 and 0.727 for M2 with correlation factors of 0.886 for M1 and 0.892 for M2). Thus the stimulation-evoked head movements failed to show the increased contribution to the gaze shift observed in the behavioral WG condition.

SACCADe PREDICTION. Based on the behavioral data, it was not clear what to predict for the effects of the WGS condition on saccade amplitude. The goggles paradigm requires that a coordinated saccade–VOR movement place the eye on the aperture location. There are several ways this could happen. Although Figs. 2 and 3 would suggest otherwise, one way this could occur is that there could be a dramatic reduction in saccade gain (i.e., no saccade and no VOR). Therefore for the sake of completeness we also analyzed the CV for the eye-in-head movement up to the end of the saccade part of the gaze shift (or to the end of the first saccade when stimulation produced multiple steps movements), in the same way as above.

Figure 5, G and H show that the CV_{saccade} vectors were smaller than the corresponding overall head movements (D, E) and less compressed in direction along the horizontal axis. Again, there was no obvious difference between the CVs for the NGS and WGS conditions on casual inspection. Statistical analysis showed a slight decrease in the CV_{saccade} amplitude, from 9.3 ± 1.0° for M1 and 6.0 ± 0.7° for M2 in NGS to 4.9 ± 1.0° for M1 and 6.5 ± 0.5° for M2 in WGS. This is summarized in Fig. 5I, which shows that the relationship between saccade amplitudes in the WGS to NGS conditions remained quite linear but with a small offset or reduction between the two tasks (with slopes of 0.86 for M1 and 0.75 for M2 and correlations of 0.75 and 0.75, respectively). Clearly, this reduction in saccade size would contribute little to directing the eye toward the aperture. Again, however, placing the eye on the aperture location depends on the coordination of both the saccade and VOR components, which will be addressed in a subsequent section.

Latencies of the stimulation-evoked movements

One explanation for the slight reduction of the WGS head and gaze movement amplitudes could be that the goggles paradigm produces greater activation of a head (and perhaps eye) fixation system, making it harder to evoke a movement (Tehovnik et al. 1999). If so, then one would expect the latency of stimulus-evoked head and gaze movements to increase with the goggles on. However, this did not occur. The histograms in Fig. 6 illustrate that the population of stimulation-evoked gaze movements (here pooled from both monkeys) had similar latency profiles in the 2 conditions (A and C). The graphs are supported by statistical analysis showing that gaze movement latencies (means ± SE) without goggles (42.9 ± 4.7 ms for M1 and 38.0 ± 1.6 ms for M2) were comparable with the gaze movement latencies with goggles (42.7 ± 4.6 ms for M1 and 37.9 ± 1.8 ms for M2) with P values of 0.94 for M1 and 0.92 for M2. Furthermore, the corresponding stimulation-evoked head movement latencies were comparable in the 2 conditions (Fig. 6, B and D). Analysis of the corresponding head movement latencies for each animal confirmed that the latencies without goggles (84.7 ± 7.6 ms for M1 and 55.8 ± 2.3 ms for M2) were not significantly different (P = 0.36 for M1 and P = 0.67 for M2) than the head movement latencies in the goggle condition (with an average of 92.2 ± 7.5 ms for M1 and average of 54.7 ± 2.0 ms for M2). Thus the reduction in gaze and head amplitudes in the WGS condition was not the result of increased latencies of response to the stimulus.

Relative amplitude contributions of the eye and head to gaze

The preceding analysis implicitly assumes that the same SC sites are activated physiologically during the NG and WG tasks. However, it is conceivable that the topographic profile of SC activity changed between these conditions so that one cannot make within-site comparisons. This conjecture, although seemingly unlikely, is consistent with the observed change in gaze-shift amplitude between the NGS and WGS conditions (Fig. 5). To control for this, one has to compare eye–head contributions for NG and WG as a function of the
amplitude of the gaze shift, for both the behavioral and stimulation data. To do this, we sorted gaze-displacement amplitudes into bins of 10°. Then, within each of these bins we calculated the average gaze, eye, and head amplitudes. Finally, we plotted the average eye and head amplitudes as a function of the average gaze amplitudes (Martinez-Trujillo et al. 2003). Included in this analysis was the entire set of stimulation data. To do this, we sorted gaze-displacement amplitudes into bins of 10°. Trials in which gaze was moving above this speed at stimulus onset, or the head was moving above 20°/s, were rejected.

From this plot, one can see the entire pattern of amplitude contributions of each data set. In the control NG behavioral data, the eye (●) makes about the same contribution as the head (■) up until gaze shift exceeded 25° in M1 and 15° in M2. After that, the relative eye contribution begins to plateau. The main effect of the trained WG condition is to increase the gain of the head contribution (□) and decrease the saccadic eye contribution (○) so that it plateaus much earlier. Statistical analysis (ANCOVA) showed significant differences between the behavioral NG and WG with \( P < 0.001 \), in both monkeys.

If these context-dependent patterns were implemented downstream from the SC, one would expect them to persist during SC stimulation. However, there was no statistical difference between the NGS and WGS curves in panels B and D. During stimulation, the 2 curves appear to be essentially identical (ANCOVA, \( P > 0.5 \)). (Interestingly, they appear to fall between the NG and WG curves for the behavioral data.)

Thus according to both analyses—site-by-site (Fig. 5) and gaze-by-gaze (Fig. 7)—there was no preservation of the behavioral context dependency in amplitude contribution of saccades and head movements during stimulation-evoked gaze shifts.

**Position-dependent patterns of gaze and head convergence**

As noted earlier, a number of studies have noted that gaze shifts evoked from the superior colliculus converge as a function of initial position (Freedman et al. 1996; Gandhi and Keller 1999; Moschovakis et al. 1998; Pelisson et al. 1989). Our preceding analysis accounted for this, but did not look directly at the position dependencies. Such dependencies have recently been quantified to probe reference frame coding in the SC (Klier et al. 2001), and to show the differences in movements evoked with the head fixed and head free (Martinez-Trujillo et al. 2003). Here we used similar methods to ask whether the pattern was influenced by the goggles paradigm. In particular, we were interested to see whether there was any systematic change in reference frame coding by looking at position dependencies in the evoked movements.

As described elsewhere (Martinez-Trujillo et al. 2003) for each stimulation site we calculated a convergence index (CI), which was the slope of the stimulus-evoked displacement as a function of initial position. This was done separately for components orthogonal to the CV (off-axis) as a measure of direction dependency and for components parallel to the CV (on-axis) as a measure of amplitude dependency on position. For reference, a CI\textsubscript{gaze} of 0 denotes fixed-vector coding and −1.0 denotes a goal-in-space code, whereas a retinal code
results in off-axis values ranging from 0 to –1.0 as a function of gaze amplitude. This analysis was done for both the gaze shifts and the head movements for comparison between the NGS and WGS conditions. It was not done for the eye-in-head saccades because, in the goggles paradigm, the range of initial eye-in-head positions was not wide enough to calculate a reliable slope.

Having made these calculations, we then compared the $C_{\text{gaze}}$ for NGS and WGS using the various plotting schemes described in Klier et al. (2001) and Martinez-Trujillo et al. (2003). As these authors reported, the off-axis $C_{\text{gaze}}$ increased as a function of $C_{\text{gaze}}$ magnitude in our NGS data, in a manner consistent with an eye-centered coding scheme. We found no systematic change in this pattern (or any other measures of position-dependent convergence in gaze and head movements) in our WGS data. In both NGS and WGS, SC sites coding small to medium gaze shifts appeared more “fixed vector” (Fig. 4A), whereas sites encoding larger gaze shifts were much more convergent, as reported previously (e.g., Klier et al. 2001).

Because these results were negative and not directly related to our current hypotheses, they are only briefly summarized in Fig. 8, which plots $C_{\text{gaze}}$ (WGS) as a function of $C_{\text{gaze}}$ (NGS) (top row) and $C_{\text{head}}$ (WGS) as a function of $C_{\text{head}}$ (NGS) (bottom row), along both the “on axis” (left column) and “off axis” (right column). As shown in the figure and verified statistically (see figure legend) a few individual stimulation sites showed a substantial change across conditions, but there were no consistently significant trends across sites or between animals (as we saw in our various other “reference frame plots”). Thus we found no evidence that the default position dependency or eye-centered gaze frame of the SC motor code was altered in the WGS condition.

Amplitude–velocity relations

Our behavioral tasks were not designed to directly manipulate the relationships between movement amplitude and velocity, but we reasoned that monkeys might make faster head movements with the goggles to get the visual aperture onto the target more quickly. In the behavioral data set, we observed an increase in head velocity during head movements from an average of 117.1°/s in NG to 177.2°/s in WG (Student’s $t$-test, $P < 0.001$) for M1 and an average of 127.5°/s in NG to 195.4°/s in WG (ANOVA, $P < 0.001$) for M2. This alone was not surprising, given that head velocity varies with head-movement amplitude (Freedman and Sparks 1997; Zangemeister et al. 1981), which was larger in the WG condition. However, even though average head displacements were slightly smaller in the WGS condition, average head velocity ($v$) was still significantly higher (ANOVA, $P = 0.002$ for both monkeys) ($v = 132.0°/s$ for M1 and $v = 118.8°/s$ for M2) compared with the control NGS condition ($v = 111.5°/s$ for M1 and $v = 110.9°/s$ for M2).

Having made this initial observation, we set out to compare eye, head, and gaze velocities between the 2 paradigms on a more even footing (i.e., by plotting them as a function of amplitude). Such plots normally show a characteristic relationship between velocity and amplitude known as the main sequence (Bahill et al. 1975; Freedman and Sparks 1997; Gandhi and Sparks 2001; Zangemeister et al. 1981). Main sequences for the gaze, eye-in-head saccade, and head behavioral data are shown in Fig. 9 (rows 1 and 3). These data have been grouped into bins to simplify the graphic plot, but statistics were done on the raw data. Computing an ANCOVA test for the amplitude and velocity in each condition, we found for the head (right column) a slight but significant increase of velocity as a function of amplitude in the WG head data (open circles) than the NG data (filled circles) with $P < 0.001$. In contrast, the eye data (middle column) showed a significant decrease in velocity as a function of amplitude (ANOVA, $P < 0.001$) in the WG condition, whereas the resulting gaze data (left column) showed a slight and significant decrease (ANOVA, $P < 0.01$) in WG data. These observations were true for the behavioral data in both M1 (1st row) and M2 (3rd row).

More important, some relationships were preserved in the stimulation-evoked movements (Fig. 9, rows 2 and 4). We computed the ANCOVA and again the head velocity in the WGS was significantly higher ($P < 0.001$) than that in the NGS. However, the difference in the 2 conditions (with and without goggles) was not statistically significant for the eye and gaze velocities. Nevertheless it is possible that these modest but significant effects were not a direct signature of “downstream adaptation processes,” but were rather cross-correlated to some other aspect of the paradigm that we cannot control for, such as the difference in the initial combinations of eye and head position (Gandhi and Sparks 2001). Next we
focus on preserved effects that are more central to the adaptations required in the goggles paradigm.

Preservation of the adapted eye-in-head range under stimulation

Thus far, our quantitative data (Figs. 5–9) have largely shown the negative result inconsistent with a downstream implementation of adaptive eye–head coordination. However, we now turn our attention to the most basic aspect of the goggles task: placement of eye position at the aperture at the end of the gaze shift. Figures 2 and 3 suggest that the WG condition caused the saccades and VOR to coordinate in such a way that eye positions end up near the goggles aperture, and that this part of the behavior may be preserved during SC stimulation (Fig. 4).

To illustrate this more directly, Fig. 10 plots post-VOR eye position ranges without (A–C) and with (D–F) the goggles. These plots show data recorded between head-free gaze shifts (i.e., during fixations) when both gaze and head velocity dropped below 10°/s. Each square represents the tip of a 2-D eye “pointing vector,” plotted on a vertical versus horizontal coordinate system. The left column shows a typical example of the behavioral result. Whereas the natural NG range was relatively distributed, particularly in the vertical dimension (A), the post-VOR range for the WG condition was reduced to the size of the central 10° aperture (D). The corresponding frequency-bin histogram for vertical eye position (Fig. 10G) shows that the eye landed more often on the location of the aperture (horizontal black bar) when the animal was wearing goggles.

Was this context-dependent behavior consistently preserved during SC stimulation? The middle and right columns of Fig. 10 show the final (post-VOR) distributions of eye positions from 2 SC stimulation sites (from M2), using the same conventions as in the behavioral data (left column). Note that these will not necessarily provide the same range of positions as the behavioral data because they each result from activation of only one SC site. However, like the behavioral data, in the WGS condition (E, F) the eye appears to converge more toward the head-fixed location of the aperture, compared with NGS (B, C). Again, frequency histograms are provided for vertical eye position in Fig. 10, H and I. These show a greater

**FIG. 10.** Fixation ranges for eye in head in behavioral (A, D) and stimulation (B, C, E, F) conditions. Left column: plots represent the position of the eye in head when the gaze and head velocity were <10°/s, in 2 conditions: NG (A) and WG (D). Last 2 columns: data from 2 putative SC sites, in the 2 experimental conditions: NGS (B and C) and WGS (E and F). Squares represent the tips of eye “pointing vectors,” with horizontal vs. vertical components projected from behind, on a 2-D plane. Bottom panel (G–I): plots of the corresponding frequency bin histograms for the vertical component of the eye range, without (top row) and with goggles (bottom row). Each vertical bar gives the frequency of fixations within 2° bin for the vertical components of the eye fixation positions, relative to the center of the aperture, at the end of the head movements. Aperture location is indicated by the horizontal black bar.

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**FIG. 9.** Amplitude–velocity relationships. Average peak velocity as a function of average amplitude, for both behavior and stimulation data, for Gaze (A, D, G, J), Eye (B, E, H, K), and Head (C, F, I, L) for Monkey 1 (top panel) and Monkey 2 (bottom panel), contrasted without (●) and with (○) goggles.
concentration of final eye positions within the aperture for the WGS condition (gray bars) compared with the NGS condition (horizontal black bar).

To extend these observations to 2-D and document them across all of our stimulation sites, we used a standard Matlab (The MathWorks, Natick, MA) function to fit ellipses to the horizontal and vertical components of the final eye-in-head positions of the NGS data (Fig. 11A) and WGS data (Fig. 11B). For this analysis, all eye positions were normalized with respect to the goggles aperture by using a reference eye position collected while the eye was looking straight ahead through the aperture (see METHODS). Thus a position at 0, 0 in these coordinates would place the eye right through the center of the aperture. Rows 2 and 3 of Fig. 11 show such elliptical fits for all stimulation sites in animals M1 (2nd row) and M2 (3rd row). Comparing the NGS data (left column) to the WGS data (right column) 2 trends should be evident: the WGS ellipses tend to be smaller and better aligned with the origin (the aperture center).

This reveals 2 ways in which the effect of the goggles on final eye position may be quantified. The first way the goggles might have influenced the stimulation-evoked endpoints could have been to shift these ranges toward the center of the aperture. The same is true in the WG behavioral condition, but we did not compare this to the central tendency in the NG behavioral because the latter is arbitrarily related to multiple, unknown SC sites. To locate the central tendency of the stimulus-evoked eye positions, we averaged the vertical and horizontal components of the final stimulation-evoked eye positions, at each site. Again, for these analyses the origin was aligned with the aperture. Figure 12, A and B, plots these data from both monkeys (M1, ○; M2, ●). These averaged eye endpoints covered a wide range in the NGS condition (A). In contrast, the centers of the WGS ranges (B) were more narrowly distributed and largely confined within the range of the aperture. This effect was statistically significant (Student’s t-test, \( P < 0.05 \)) for both the vertical and horizontal components.

Second, as observed above there may have been a reduction in variance in the final eye-in-head ranges during the goggles paradigm. This could be true for both the behavioral and stimulation data. To quantify the scatter of the final eye positions, we computed the SD of the vertical and horizontal fixation ranges of the eye. The results of this analysis for the behavioral condition are shown in Fig. 12, C (M1) and D (M2). The bars show averaged SD values (±SE) for the eye-fixation ranges across experiments. For both monkeys and both eye position components, the distributions were significantly smaller (Student’s t-test, \( P < 0.05 \)) in the WG condition (white bars) compared with NG condition (black bars). Figure 12, E and F, illustrates the averaged values (±SE) for the same analysis across all stimulation sites. As in the behavioral data, the WGS eye ranges (white bars) were significantly smaller (Student’s t-test, \( P < 0.05 \)) than the NGS eye ranges (black bars), in both monkeys, for both the vertical and horizontal components of the eye-fixation position. Thus both aspects of the eye-in-head training procedure—shift in the central tendency toward the aperture and reduction in variance—were preserved in the stimulus-evoked gaze shifts.

Position-dependent aspects of eye–head coordination

With the head free, final eye-in-head position at the end of a gaze shift is determined by a combination of saccade and VOR trajectories (Fuller 1996). In the NGS stimulation condition, this did not result in a recentering of the eye, apparently because the eye and the head had variable starting positions and the saccades and head movements had different amplitudes and directions (Fig. 4). Could it be that the recentering of the eye in the WGS condition was the result of the eye always starting at the aperture location, such that the subsequent recentering was simply a by-product of the saccade and head movement (perhaps) rotating about the same axis, so that the VOR negated the saccade? Or was the eye aimed toward the aperture by a more sophisticated mechanism? As noted above, the initial set of eye-in-head positions in the goggles paradigm was too restrictive to test the position-dependent aspects of this behavior. Therefore to test between these 2 possibilities, we used the “switching holes” paradigm in animal M2.

It was previously shown (Crawford and Guittton 1997) that, once a monkey is trained on one aperture location, it will initially continue to drive the eye toward the old aperture site
Figure 13 illustrates examples of results of this experiment for eye movements evoked by stimulating one of the SC sites with the eye initialized at 3 different aperture locations: right (1), left (2), and down (3). Again, the reference position has been adjusted here so that the location of the original aperture is centered at zero in this coordinate system. Independent of initial eye position, the final eye positions were driven toward the central (now occluded) aperture for which the monkey had been trained. In these examples, the eye obtained the original aperture through a series of small multistep saccades (and intervening VOR segments) that drove the eye well away from the direction of head movement. Once again, because the central aperture was now occluded from vision, this coordinated pattern of saccades and VOR slow phases can be attributed to the perseverance of some context-dependent, learned response rather than just a visual stimulus. Further, this context-dependent adaptation would be situated downstream from the stimulation location (i.e., downstream from the SC).

To quantify these results, we computed a regression of the overall eye displacement (saccade + VOR) as a function of the initial eye position for each stimulation-evoked trajectory, pooling data from all 4 “new” apertures, for each stimulation site (Fig. 13B). This was done separately for the vertical (left column) and horizontal components (right column). If the eye was simply returning to the initial position, the slope would be zero. If the eye returned exactly to the center of some fixed

when confronted with a new aperture location. To find out what happens when the eye started from a different location here, we covered the central aperture and uncovered top, bottom, right, and left apertures, one by one. When the animal was fixating through the new apertures we applied the electrical stimulus to see whether the evoked moments would show the same effect; that is, would the saccade + VOR bring the eye back toward the location of the initial, now covered, aperture? Or, would the saccade + VOR bring the eye back to the new, uncovered, aperture? We were able to do this with 7 stimulation sites before the animal showed signs of “unlearning” the original task, that is, reducing its accuracy for aiming the eye with the original aperture.
location every time, the slope would be $-1$, and an intercept of zero would indicate a landing in the center of the aperture.

The top panels of Fig. 13B show the results from one site, whereas the bottom panels show the regression fits to all 7 sites. On average, slopes were $-0.57 \pm 0.09$ for the vertical and $-0.48 \pm 0.1$ for the horizontal component, with average correlations of 0.45 and 0.25, respectively. This population of 7 sites is perhaps not large enough to prove that initial eye-position dependencies are significantly changed by the goggles paradigm. However, this does cast doubt on the idea that the clustering of final eye positions near the aperture in our larger WGS population (Figs. 4, 8–11) was attributed only to an initial eye position effect—clearly the system was not limited to bringing eye position back to where it started.

Head movements were also influenced by the initial eye position in the switching-aperture paradigm. Moreover, this influence was correlated to the eye movement in a way that is consistent with gaze models of the superior colliculus (Freedman and Sparks 1997, 2000; Guitton et al. 1990). For example, although the gaze shifts evoked from the SC shown in Fig. 13A were all leftward, the overall eye movement and the head movement could be in the same direction (trajectory 1) or—most dramatically—in the opposite direction (trajectory 2). In the latter manner, the overall eye movement was rightward and the overall head movement was leftward. Why would this happen? Viewing Fig. 13A, one can see that when the overall eye movement reversed from leftward (eye trajectory 1) to rightward (eye trajectory 2), the head trajectory (head trajectories 1 and 2) increased to compensate. Likewise, when the overall eye movement took on an upward component (eye trajectory 3), the accompanying head movement took on a downward head component (head trajectory 3), with the result that the gaze kinematics (gaze trajectories 1, 2, and 3) remained consistent in size and direction.

Figure 13C quantifies this inverse eye–head relationship by plotting overall eye displacement as a function of head displacement for individual stimulation trials. Vertical displacements are plotted in the first column and horizontal displacements in the second column, pooled across all of the “switching holes” experiments for that site. Clearly, these eye and head data show a strong negative correlation. Regression fits for all 7 stimulation sites tested this way are shown in the bottom panels of Fig. 13C, confirming this trend. Average slopes were $-0.76 \pm 0.12$ for vertical and $-1.04 \pm 0.13$ for horizontal displacements, with average correlations of 0.26 and 0.41, respectively. Thus during the goggles task in this animal, SC stimulation elicited eye (saccade + VOR)–head movements that compensated for initial position and were specifically coordinated to land the eye on the learned aperture while maintaining gaze kinematics.

**Discussion**

A number of studies have already shown that electrical stimulation of the SC in the head-free cat or monkey evokes gaze shifts that include “natural” patterns of eye–head coordination (Freedman et al. 1996; Guillaume and Pelisson 2001; Klier et al. 2001; Pelisson et al. 2001; Roucoux et al. 1980), apparently with dependencies on initial gaze position consistent with an eye-centered gaze coding scheme (Klier et al. 2001; Martinez-Trujillo et al. 2003). We found no evidence to contradict these basic ideas. The stimulation of the SC produced natural-looking combinations of eye and head movements (Figs. 7, B and D) with basically the same default dependencies on initial gaze and head position (Fig. 8), in both conditions—with or without goggles. Moreover (although we did not have space here to present the data in more detail than Figs. 5 and 8), the goggles paradigm did not alter the basic eye-centered coding scheme that the SC apparently uses to encode gaze targets (Klier et al. 2001). However, this is not what is at issue here. Here we were interested in how these targets are acquired; specifically, in those aspects of eye–head coordination that are directly related to our context-dependent adaptation procedure.

Previous studies of head-free gaze control have emphasized a simple dichotomy: is eye–head coordination implemented upstream or downstream from the SC motor output command (Cowie and Robinson 1994; Cowie et al. 1994; Freedman and Sparks 2000; Galiana and Guitton 1992; Guitton et al. 1990; Stein et al. 1976). A strict adherence to this dichotomous expectation predicts that either all or none of the behavioral adaptations observed in our study would be preserved during SC stimulation. Instead, we found that certain aspects of the adapted eye–head coordination pattern (particularly those required to place the eye at its correct final position) were preserved during SC stimulation, whereas other aspects of the adapted pattern (i.e., the context dependency of eye and head contribution to gaze amplitude) were not preserved. Viewed in terms of the traditional upstream versus downstream dichotomy, we initially found these results surprising, but in the following sections we present a scheme that appears to unify our data.

**Behavioral adaptations in the goggles paradigm**

The current results confirm previous behavioral studies (Ceylan et al. 2000; Crawford and Guitton 1997; Stahl 2001), showing that the goggles paradigm reduced the range of final eye-in-head positions to coincide with the location of the head-fixed aperture, requiring a modified pattern of position-dependent coordination between saccades and VOR movements (Crawford and Guitton 1997). We also confirmed that this is accompanied by an increase in the size and range of head movements (Stahl 2001). Moreover, we have now shown that the velocity–amplitude relationship of these head movements is subtly but significantly changed. These changes were context dependent: once the monkey had learned the task, somehow the “knowledge” that it was or was not wearing the goggles was enough to force a switch between the normal motor strategy and the newly learned strategy. Presumably this results from state-dependent alterations within the brain that are triggered by sensory cues. The question is where this happens and how?

1 Departure of slopes/correlations from the ideal $1/1$ are not surprising, given that the amplitude of stimulation-evoked gaze shifts are known to vary with eye position (Harris 1980; Paré et al. 1994; Roucoux et al. 1980; Schiller and Stryker 1972; Stanford et al. 1996). This causes eye and head contributions to co-vary to some extent with eye position, in opposition to the contra-
Adaptations preserved under SC stimulation

We have shown that several aspects of the context-dependent adaptations described in the preceding section are preserved in gaze shifts evoked by SC stimulation. Some of these (i.e., the task-dependent changes in eye, head, and gaze velocity-amplitude relations) were subtle and may have been secondary to other kinematic aspects of the task (Gandhi and Sparks 2001). Therefore we cannot be confident that these were a signature of downstream adaptation mechanism.

However, other preserved effects were much more robust and clearly task-related, such as the oculomotor mechanisms that allowed the eye to recenter toward the goggles aperture (or not, without the goggles). This effect was not simply a by-product of increased head movement driving the eye further back toward center because increased head movements were not observed during WGS. Nor was it attributed to the eye starting at the aperture location because eye position was still driven toward the original aperture when it was occluded and the eye was initialized at other aperture locations.

Instead, this effect appears to reflect a specific aiming strategy. Specifically, this mechanism requires saccades to place the eye in such a position that the VOR—which simply rotates the eye opposite to the head—then brings the eye back to the right spot (Crawford and Guitton 1997; Crawford and Vilis 1991; Crawford et al. 1999; Tweed 1997; Tweed et al. 1995). Moreover, in the “switching-holes” experiment this strategy included a compensatory position dependency in head movement that tended to preserve gaze kinematics.

To interpret these results, one needs to consider that electrical stimulation of the SC could activate a different profile of neurons than a natural stimulus, including fibers-en-passant and possibly other neurons by antidromic activation. Nevertheless, electrical stimulation of the SC appears to produce a graded-with-distance activation of SC neurons similar to the “hill of activation” seen in physiology (Bergeron et al. 2003; Guitton et al. 1993; Port et al. 2000; Sparks 1993). Additionally, electrical stimulation of the SC generates gaze shifts with fixed trajectories in eye coordinates (Klier et al. 2001). Finally, eye-head coordination kinematics during stimulation are essentially indistinguishable from those seen in natural gaze shifts (Freedman 2001; Freedman and Sparks 2000; Guitton et al. 1990; Klier et al. 2003).

Conservatively, one can presume that low intensity, super-threshold stimulation of the deep motor layers of the SC produces a fixed motor output (Klier et al. 2001) without the normal accompanying pattern of cortical activity, however physiological this may or may not be. With the stimulation parameters that we used (i.e., 50 μA) it is highly unlikely that this current spread with sufficient strength to the superficial visual layers of the SC (anatomically upstream from the cortex) to evoke a “cortical” saccade, so we were more likely observing the isolated motor output command from the deep, motor SC. Based on the known anatomy of the oculomotor system, the most direct targets of this output are likely the brain stem reticular formation and cerebellum (Moschovakis 1996; Robinson 1995), but given that the SC is likely nested in recurrent feedback loops (Bergeron et al. 2003; Guitton et al. 2003; Sparks 1999; Tweed et al. 1995) one cannot exclude the participation of more indirect pathways. Given these caveats, here we conservatively define the targets of this output operationally as the SC “target circuit.”

Given these limitations, our data support the idea that this SC target circuit 1) is uniquely involved in several aspects of eye-head coordination (i.e., saccade–VOR coordination, choosing final eye position, position-dependent eye–head coordination patterns, and head dynamics); 2) is responsible for adaptation in these aspects of eye-head coordination; and 3) is accessible to context-dependent signals that can trigger different learned states. This is consistent with the current understanding of the brain stem implementation of saccades and the VOR, and position dependencies in both of these and of head movement (Coimbra et al. 2000; Crawford and Guitton 1997; Freedman 2001; Guitton 1988, 1992; Isa and Sasaki 2002; Waitzman et al. 2002). Also, it seems likely that the cerebellum is involved in either incorporating some aspects of the learned adaptations, or teaching the brain stem circuits to incorporate these context-dependent adaptations (Goffart and Pelisson 1994; Optican and Quaia 2002; Optican and Robinson 1980; Quaia et al. 1999). Having said this, it seems unlikely that the context-dependent circuits operate in complete independence from the cortex. Presumably, it is the cortex that “recognizes” that the goggles are on or off (through sensory and cognitive signals) and then sends the “context signal” that triggers the different learned states in the lower-level brain stem circuit.

Adaptations not preserved under SC stimulation

During the WGS paradigm head movements were evoked and eye-head coordination was roughly normal (Figs. 4, 5, and 7). Therefore it appears that the SC output circuit is capable of implementing a default level of overall eye-head contribution. However, this eye-head pattern did not change with or without goggles. In contrast to the results described in the previous section, we found no increase in head overall amplitude during SC stimulation with the goggles. Head movement even decreased slightly in WGS. This reduction did not arise from increased head movement latencies, as might have resulted from increased engagement of the fixation system (Tehovnik et al. 1999). So then, what could explain the absence of context-dependent head amplitude contribution in our stimulation results compared with our behavioral results?

This result would be difficult to reconcile with our other stimulation results if there was only one serial pathway for eye-head coordination from the cortex through the SC. Clearly the SC output circuit is able to implement a default level of eye-head coordination (Fig. 7, B and D) and we have shown that some aspects of this circuit are under adaptive control. So it is logically difficult to have the gaze command splitting like this into separate eye and head commands both downstream (Fig. 1A, 1B) from the SC. Our paradigm probably cannot distinguish between coordination mechanisms implemented upstream from the SC (Fig. 1B) and coordination mechanisms within the SC, but again the same “double-splitting” problem argues against this alternative. However, the brain does not just have one serial gaze pathway.

The nonserial alternative arises from the well-known gaze-control pathway from the frontal cortex to the brain stem reticular formation, in parallel to the SC (Schiller and Chou 1998; Schiller and Sandell 1983; Schiller et al. 1979). For the moment, let us assume that this parallel circuit has the capacity...
for separate control of the head (Fig. 1C). Within such a parallel arrangement, some aspects of adaptive eye–head coordination could be implemented in the SC output circuit (Fig. 1A), some aspects could be implemented within the SC, and some aspects—like adaptive head amplitude control—could be implemented in parallel to the SC.

There are several reasons to suspect that the SC output treats the head motor circuits differently than the oculomotor circuits. Specifically, prolonged SC stimulation produces a staircase of discrete, time-separated saccades (Stanford et al. 1996; Van Opstal et al. 1990), but a smooth continuous head movement (Freedman et al. 1996), although some have argued that discrete pulses are at least partially masked by the inertia of the head (Coimbra et al. 2000; Corneil et al. 2002b). Moreover, although SC stimulation yields kinematically normal head movements in most respects (Corneil et al. 2002b; Klier et al. 2003; Roucoux et al. 1980) the underlying pattern of muscle activity is not entirely physiological (Corneil et al. 2002a). Finally, we know that eye and head behavior can be dissociated in a number of ways (Tweed et al. 1995), and it has been suggested that this results from different eye and head SC target circuits in the brain stem (Corneil et al. 2002a,b). So it is very likely that the head control circuit could be accessed with some independence from the gaze/eye control circuit.

We propose that the context-dependent alterations in overall head amplitude contribution observed in our behavioral data are implemented in the parallel circuit from frontal cortex to the brain stem. This parallel circuit would not be activated by SC stimulation, consistent with our data. Taken together with the data described in the previous section, this leads to the scheme illustrated in Fig. 1D, where the oculomotor aspects of the adaptation are implemented downstream from the SC and the head contribution aspects in a circuit parallel to the SC. A variation of this scheme would be to propose 2 independent channels through the superior colliculus—not for the eye and head as proposed previously (Cowie and Robinson 1994)—but rather one that codes gaze with a default level of eye–head coordination, and one that modulates head contribution, perhaps through different populations of neurons or patterns of firing that would not be accessed by electrical stimulation. However, the basic idea is the same.

This parallel coding scheme is consistent with our (human) ability to voluntarily choose between making gaze shifts only with the eyes or with large head movements. Although the latter argument is speculative, it is difficult to believe that such voluntary decisions are made at or downstream from the level of the SC motor layers. Such a cortical control center responsible for overall eye–head contribution would have survival consequences for any primate, say in choosing to move just the eyes and not move the head when hiding from a predator (often called “shifty glances” in humans). In humans, this capacity has apparently generalized to tasks as diverse as reading (Kowler et al. 1991; Vilis 1994) and driving (Land and Tatler 2001).

**Implications for gaze control models**

Models in which the SC codes a gaze command (Galiana and Guitton 1992; Guitton 1988, 1992; Klier et al. 2001; Munoz and Guitton 1989) would seem to predict that all aspects of eye–head coordination are implemented downstream from the SC. Some of our findings in the “switching-holes” experiment were consistent with this prediction, suggesting that complimentary eye–head position dependencies required to preserve gaze kinematics are implemented downstream from the SC. Nevertheless, at first glance, the failure to increase head amplitude in opposition to decreased eye amplitude and the subsequent reduced gaze amplitudes in the WGS seem inconsistent with the SC gaze hypothesis.

Again, these results would contradict the SC gaze model if the gaze control system had only one serial channel. However, if, as hypothesized above (Fig. 1D), a parallel channel is responsible for the increased head amplitude during the goggles task, then a SC site coding a given gaze-shift amplitude would be calibrated to “expect” this parallel input in normal physiology (i.e., to compensate for the reduced overall eye movement implemented downstream from the SC). Thus the gaze trajectory encoded by a given SC site would not be revealed by WGS stimulation (see Quaia et al. 1999 for a similar theoretical consideration of parallel pathways from the SC and cerebellum). This hypothesis could be tested by recording from SC neurons. If the superior colliculus simply encodes gaze, then we predict that the SC will show the same site-specific activity for gaze shifts with and without the goggles. However, it is also possible that additional signals in the SC (such as duration of the SC output response) could influence head movement.

Similarly, the scheme shown in Fig. 1D does not contradict the idea of an eye-centered gaze coding scheme in the SC (Klier et al. 2001). In simple terms, once the SC has determined the target of a gaze shift—in retinal coordinates, for example—and once this target is acquired, a prolonged drive to the head movement would simply serve to recenter the eye through the VOR without changing gaze direction (one can try this for oneself). The matter is more complex when head drive varies during the saccade, when the VOR may be shut off (Martinez-Trujillo et al. 2003), but again this is a problem for coordination rather than spatial coding. As long as the brain stem saccade generator has access to these intended movement signals, it can compensate through the saccade generator to place the eye on target with the right combination of final eye/head orientations (Crawford and Guitton 1997; Tweed 1997; Tweed et al. 1995).

In conclusion, we believe that neither eye–head coordination nor its adaptation can be conceptualized in simple terms as being either downstream or upstream from the SC. The existence of parallel pathways to the brain stem necessitates more complex models of the gaze-control system. Our data suggest that different aspects of adaptation in eye–head coordination are divided between these 2 pathways along the lines most suitable for their normal contributions.

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