Activity of Cells in the Deeper Layers of the Superior Colliculus of the Rhesus Monkey: Evidence for a Gaze Displacement Command

EDWARD G. FREEDMAN1 AND DAVID L. SPARKS1,2
1Institute of Neurological Sciences and the 2Department of Psychology, University of Pennsylvania, Philadelphia, Pennsylvania 19104–6196

Freedman, Edward G. and David L. Sparks. Activity of cells in the deeper layers of the superior colliculus of the rhesus monkey: evidence for a gaze displacement command. J. Neurophysiol. 78: 1669–1690, 1997. When the head is free to move, microstimulation of the primate superior colliculus (SC) evokes coordinated movements of the eyes and head. The similarity between these stimulation-induced movements and visually guided movements indicates that the SC of the primate is involved in redirecting the line of sight (gaze). To determine how movement commands are represented by individual collicular neurons, we recorded the activity of single cells in the deeper layers of the superior colliculus of the rhesus monkey during coordinated eye-head gaze shifts. Two alternative hypotheses were tested. The “separate channel” hypothesis states that two displacement commands are generated by the SC: one signal specifying the amplitude and direction of eye movements and a second signal specifying the amplitude and direction of head movements. Alternatively, a single gaze displacement command could be generated by the SC (“gaze displacement” hypothesis). The activity of collicular neurons was examined during three behavioral dissociations of gaze, eye, and head movement amplitude and direction (metrics). Subsets of trials were selected in which the amplitude and direction of either gaze shifts or eye movements or head movements were relatively constant but the metrics of the other two varied over wide ranges. Under these conditions, the separate channel and gaze displacement hypotheses make differential predictions about the patterns of SC activity. We tested these differential predictions by comparing observed patterns with predicted patterns of neuronal activity. We obtained data consistent with the predictions of the gaze displacement hypothesis. The predictions of the separate channel hypothesis were not confirmed. Thus microstimulation data, single-unit recording data, and behavioral data are all consistent with the gaze displacement hypothesis of collicular function—the hypothesis that a gaze displacement signal is derived from the locus of activity within the motor map of the SC and subsequently is decomposed into separate eye and head displacement signals downstream from the colliculus.

INTRODUCTION

The high-velocity, conjugate eye movements evoked by electrical stimulation of the primate superior colliculus (SC) when the head is restrained are remarkably similar to naturally occurring, visually guided saccadic eye movements. The relationships between movement amplitude and peak velocity and between movement duration and amplitude are comparable for visually guided and stimulation-induced movements (Robinson 1972; Schiller and Stryker 1972). The amplitude and direction (metrics) of stimulation-induced saccades depend on the location of the stimulating electrode within the SC1 and systematic changes in electrode location produce systematic shifts in the amplitude and direction of evoked movements. Thus it was hypothesized (Robinson 1972) that saccade direction and amplitude are encoded anatomically by the location of motor-related activity.

Chronic single-unit recording experiments in head-restrained monkeys have provided insight into how commands for saccadic eye movements are represented by the activity of individual collicular neurons. Many neurons in the intermediate layers of the SC discharge maximally before saccades of a particular direction and a particular amplitude but are broadly tuned; cells discharge in association with movements having a large range of different amplitudes and directions but discharge less vigorously in association with saccades having directions and amplitudes that differ from that of the preferred movement (Sparks 1978; Sparks et al. 1976; Wurtz and Goldberg 1972). These properties of single SC cells are illustrated schematically in Fig. 1, A and B. Cells with movement-related activity are organized topographically based on the metrics of the preferred movement, and the map formed by the systematic variations in the tuning of SC cells corresponds with the map of stimulation-induced saccade amplitude and direction produced by systematic changes in the location of the stimulating electrode (Schiller and Stryker 1972).

Because each neuron is active before a broad range of saccades, it follows that a large population of collicular neurons discharges before any particular saccade (McIlwain 1975; Sparks et al. 1976). The profile of population activity is characterized by a spatial and temporal distribution of activity (Sparks and Mays 1980). The motor-related activity of neurons in the center of the population begins earlier and is more vigorous; the activity of cells on the fringe of the active population is less vigorous and may follow, rather than precede, saccade onset (Fig. 1, C and D). Note that a single neuron can be a member of active populations centered at different loci in the SC map (Fig. 1E). Thus the gradations in the vigor of motor-related discharge of a single cell, which may be observed when movements of different amplitudes and/or directions are made, occur because the observed cell is in different locations relative to the center.

1 The amplitude and direction of stimulation-induced saccades with the head restrained and stimulation-induced gaze shifts when the head is unrestrained depend on the parameters of stimulation (cf. du Lac and Knudsen 1990; Freedman et al. 1996; Pare et al. 1994; Stanford et al. 1996; van Opstal et al. 1990).
FIG. 1. A: schematic representation of superior colliculus (SC) motor map; rostral pole to the left; iso-amplitude lines are indicated (5, 10, 20, 40, 80). Shaded region represents the movement field of a hypothetical cell (●) located at a SC site representing 20° movements along the horizontal meridian (Horiz.). Dark stippling, movements associated with high firing rates; light stippling, lower firing rates. B: firing rate of this hypothetical cell plotted as a function of movement amplitude for movements along the horizontal meridian (preferred direction), and firing rate plotted as a function of movement direction for movements having the preferred vectorial amplitude. C: representation of the active population of cells during movements of 20° directed along the horizontal meridian. D: firing rates and burst lead time (time from burst onset to movement onset) of 5 hypothetical cells (a±e) in different locations relative to the center of the active population are illustrated. E: representation of the changes in the location of the active population of SC cells during movements (a±e) of different amplitude (directed along the horizontal meridian). F: hypothetical activity during the 5 different movements (a±e) of a cell located at the SC representation of 20° horizontal movements. G–I: behavioral dissociations of gaze, eye, and head movement amplitude and direction (see text for details).

of the active population (Fig. 1F), not because movement amplitude and direction are encoded by the frequency of cell discharge. As illustrated in Fig. 1, B and F, similar rates of neuronal activity can be associated with movements of many different amplitude and directions.

Results of recent microstimulation experiments (Freedman et al. 1996; see also Segraves and Goldberg 1992), conducted in monkeys with unrestrained heads, indicate that the primate SC generates a command to redirect gaze (change the direction of the line of sight), rather than a command to move only the eyes. Stimulation of sites in the caudal SC evokes gaze shifts that involve coordinated movements of the eyes and head. The stimulation-induced eye-head movements are remarkably similar to visually guided gaze shifts of the same direction and amplitude; the relationship between the amplitude of the gaze shift and peak gaze velocity and gaze amplitude and gaze duration are comparable for stimulation-induced and visually guided movements.

The SC could contribute to the generation of coordinated eye-head movements in two ways: 1) the SC could specify the amplitude and direction of eye movements relative to the head, based on the locus of activity within a map of eye displacement, and specify separately the amplitude and direction of head movements based on the locus of activity within a map of head displacement ("separate channel" hypothesis); or 2) the SC could specify the amplitude and direction of the desired gaze shift, based on the locus of the active population within a gaze displacement map ("gaze displacement" hypothesis).

The primary goal of the present study was to determine how signals for the control of gaze are represented in the SC by recording the activity of individual neurons during coordinated eye-head movements. As noted above, in head-restrained animals, movement amplitude and direction are specified by the location of the active population of cells within the motor map not by the discharge rate of collicular neurons. The same discharge rate is associated with a large number of saccadic movements having quite different amplitudes and directions (Fig. 1). By extension, in animals with unrestrained heads, information about the amplitude and direction of eye, head, or gaze movements may be specified by the loci of active populations within collicular motor maps but not by the frequency of discharge of individual neurons. Thus an understanding of how signals for the control of gaze are represented within the colliculus must come from an analysis of the location of collicular activity during different gaze shifts rather than from standard correlations of the discharge rate of single cells with the amplitude (or direction) of gaze, eye, or head movements.

The problem of determining how movements of the eyes and head are represented within the SC is exacerbated by the fact that gaze, eye, and head movement amplitudes and directions do not vary independently, but in general are highly correlated (for reviews, see Berthoz 1985; Fuller 1992; Roucoux and Crommelinck 1988). However, three conditions have been identified in which gaze, eye, and head movement metrics can be dissociated (Freedman and Sparks 1997). Each of these dissociations is illustrated schematically in Fig. 1, G–I. The dissociation in Fig. 1G occurs...
during movements initiated with the eyes in the center of the orbits and directed along the horizontal meridian. Under these conditions, head movement amplitude increases linearly with increases in gaze amplitude from 40 to 90°, but eye movement amplitude saturates at ~35°. Another dissociation of gaze, eye, and head movement metrics occurs as a result of the relatively small vertical amplitude of head movements observed during oblique gaze shifts (Freedman and Sparks 1997; Glenn and Vilis 1992; Tweed et al. 1995).

It is possible to select a group of movements in which the direction and amplitude of head movements are relatively constant but the direction of the associated eye and gaze movements vary over a wide range (Fig. 1H). A third dissociation of gaze, eye, and head movement metrics occurs because of the inverse effects of initial eye position on the amplitude of eye and head movements observed during constant amplitude gaze shifts (Freedman and Sparks 1997). As shown schematically in Fig. 1I, gaze shifts having relatively constant amplitude and direction can be composed of different combinations of eye and head movements depending on the initial orbital positions of the eyes; eye amplitude increases and head amplitude decreases as the eyes begin in more eccentric (contralateral to movement direction) positions. The separate channel and gaze displacement hypotheses make differential predictions about the region of activity in the SC when gaze, eye, and head movement metrics are separable.

We recorded the activity of single SC cells and compared observed changes in discharge rates with the changes predicted by the alternative hypotheses. Our results are inconsistent with the hypothesis that eye and head displacement signals are represented simultaneously by different populations of SC cells. The data are consistent with the alternative, that a single gaze displacement signal is derived from the locus of the active population of cells within the SC.

METHODS

Subjects and surgical procedures

Preparation of the subjects (two female Macaca mulatta) for single-unit recording began, during an aseptic surgery, with the implantation of a scleral coil (Fuchs and Robinson 1966; Judge et al. 1980) for monitoring gaze. A stainless steel cylinder, centered on the midline at stereotaxic anterior-posterior position zero and perpendicular to the horizontal stereotaxic plane, served as the receptacle for a hydraulic microdrive and was secured to the skull in a separate aseptic surgical procedure. General anesthesia (isoflurane) was used during all surgical procedures. Postoperative analgesics were administered as directed by the attending veterinarian. All surgical and experimental protocols were approved by the University of Pennsylvania Animal Care and Use Committee and are in accordance with the National Institutes of Health Guide for the Care and Use of Animals.

Behavioral training and experimental apparatus

During training and experimental sessions animals were seated in a primate chair designed to permit unrestricted movements of the head by restraining the subject with a canvas vest secured loosely around the neck and to the inside of the chair. The flexibility of the vest allowed complete head mobility but prevented subjects from reaching equipment mounted on the head. In addition, the chair prevented movements of the hips and restricted upper body rotations to approximately ±20°. Animals were monitored using an infrared video system (Sanyo Electric). Typically, they sat with hips and shoulders aligned and parallel to the fronto-parallel plane. The only impediment to head movements was the mass (~250 g) of the reward delivery system, head coil, x-y positioner, and microdrive (Kopf), which were mounted on the head. We observed no differences in gaze or head movements during sessions with and without the x-y positioner and microdrive.

Subjects were positioned 84 cm from a tangent screen such that the center of the screen was aligned with the midsagittal plane. Subjects were positioned vertically so that when they fixated the screen center, the line of sight was in a horizontal plane. Visual targets (~10 min diam) could be back projected at any location (1° resolution) on a tangent screen that subtended ±45° horizontally and ±40° vertically. Positioning of the target was accomplished by deflecting a laser beam (Uniphase) with a pair of mirrors attached to orthogonal galvanometers (General Scanning). Targets were gated on and off with an acoustical-optical shutter (IntracAction). During some sessions, an LED array (2° resolution) having the same dimensions and positioned in the same location was used to present targets.

Changes in gaze (defined as the 2-dimensional rotation of the eyes relative to a fixed, external frame of reference) were measured using the standard scleral coil. Head movements were measured using an identical coil mounted daily on the animal’s head. The uniform portion (±2%) of the two magnetic fields (in spatial and phase quadrature) was estimated by measuring the voltage induced in a search coil at different locations within the field. This portion of the magnetic fields was approximately a 20-cm diameter sphere centered within the field generating coils (85-cm diam). Infrared video observations did not reveal head translations large enough to bring the coils out of the uniform portion of the magnetic fields, and the coil signals are translation invariant within this region. The gaze coil was calibrated by having the animal fixate different locations on the screen. The head coil was calibrated (on the animal) by restraining the head at known positions and adjusting the signal gain and offset appropriately. The two coil signals were sampled at 500 samples/s and stored for off-line analysis. The head and gaze signals were corrected for the nonlinearities inherent in the coil system (after Judge et al. 1980), and eye position relative to the head was calculated off-line by subtracting the head signal from the gaze signal (although see Huebner et al. 1995 for a discussion of problems with this calculation resulting from the difference in axes of eye and head rotation).

A hydraulic microdrive (Kopf) was used to lower parylene-coated tungsten electrodes (MicroProbe) into the SC perpendicular to the horizontal stereotaxic plane. Standard physiological techniques were used for amplification (Bak Electronics) and filtering (Krohn-Hite) of neural signals. Activity of single cells was isolated using a time/amplitude window discriminator (Bak Electronics). Neural spikes were converted into standard pulses and interspike intervals, timed with 100-μs resolution, and were stored for off-line analysis.

Behavioral tasks

Subjects were trained to perform the two tasks illustrated in Fig. 2. During the remembered-target task (Fig. 2A), subjects were required to maintain fixation (within a computer-defined targeting window ±5°) of the initial target (α: fixation interval), during the presentation of a secondary target (β: delay interval), and for an additional period (γ: memory interval) after the extinction of the secondary target. The duration of the fixation interval varied from 800 to 1,200 ms (100-ms increments), the secondary target duration varied from 400 to 800 ms (50-ms increments), and the mem-
gaze and eye position were defined as the time at which velocities exceeded or fell below 40°/s; velocity criterion for head movement onset was 25°/s, criterion for head offset was 15°/s. Movements were checked automatically and onsets and offsets marked according to these criteria. All marks were inspected visually on a trial-by-trial basis and could be adjusted manually if necessary. Two measures of head movement were obtained: total head movement amplitude and the head contribution to the gaze shift, defined as that portion of the total head movement that occurred during the gaze shift. Firing frequency criteria were used to mark burst onset (4 consecutive interspike intervals < 20 ms) and offset (2 consecutive interspike intervals > 100 ms). These values could be adjusted manually if necessary. Some cells had high tonic firing rates that preceded the onset of the motor-related burst, and for these cells, burst onset was defined by beginning the search for the onset criterion during the motor burst and searching backward in time until the firing frequency fell below the criterion level. This minimized incorrect definitions of burst onset because of fluctuations in the prelude activity. Burst end was defined using a separate frequency criterion.

Movement fields

Movement fields were obtained by plotting average firing rate (calculated as spikes/s during a period beginning 20 ms before movement onset and continuing until the end of the motor burst) as a function of horizontal and vertical movement amplitude during the delayed gaze shift task. Because cells in the caudal colliculus are active during a wide range of movements, plots of movement fields with 4° resolution were based on data obtained from ~1,000 trials. The general procedure used for data collection began by randomly selecting a secondary target from an initial 12 (horizontal) × 2 (vertical) array of potential targets. In this initial array, the horizontal displacement of targets ranged from 0 to 88° at 8° intervals. The horizontal position of the initial (fixation) target was typically eccentric relative to the midsagittal plane of the body to achieve large target displacements (see Freedman and Sparks 1997 for details). Each of the 24 targets was presented at least three times before the vertical components were changed and targets from a new 12 × 2 array were presented. The vertical displacement of targets ranged from down (−40°) to up (+) 40° with 8° separation. Thus 131 different targets (secondary targets could not be presented at the same location as the initial target) were each presented at least three times during this first phase of data collection. The resolution of the movement field then could be increased by presenting a second set of 131 targets that was shifted horizontally and vertically by 4°. Finally, for cells with movement fields that extended beyond ±40° vertically, the location of the initial target could be moved (up and/or down) to extend the range of vertical target displacements. Separation of targets began at 4° when rostral cells, with smaller movement fields, were recorded and target displacement was increased until the movements were outside the cell’s movement field.

Calculation of the motor index

To distinguish between cells with and without motor related activity, a “motor index” was computed by comparing activity (using the remembered target task) during two temporal epochs (Fig. 2C). The “precue” interval (I) began 150 ms before the cue to initiate a movement (marked by the heavy vertical line) and was 150 ms in duration. Because the duration of the memory interval was variable and unpredictable, subjects were unable to accurately anticipate the occurrence of the cue, and activity preceding the cue was not temporally correlated with the movement. The “perimovement” interval (II) began 20 ms before movement onset and extended for 150 ms. By definition, activity during this interval
was correlated temporally with the onset of the movement. The ratio of average firing rate during epoch II divided by the average firing rate during epoch I was calculated for those trials having ≥90% of the maximal activity observed during the perimovement interval. The mean ± SD of the ratios from ≥15 and at most 35 individual remembered-target trials were used for the calculation of the motor index for each cell in our sample. For convenience, the motor index was defined as >100 when the denominator was zero. The motor index identifies the presence or absence of motor-related activity; it is not useful for comparing the relative vigor of the motor burst across cells.

**Localization of recording sites**

Both subjects continue to be active in ongoing experiments so anatomic localization of recording sites is not possible. Localization of recording sites is based on stereotaxic coordinates of the electrode track and on the physiological properties of the cells recorded along each track. All cells were located between 1.0 and 2.8 mm below the depth at which visual activity was first encountered in the SC. Electrical stimulation was performed routinely after recording from isolated cells and saccadic eye movements or coordinated eye/head gaze shifts were evoked at all sites. The amplitude and direction of the electrically-evoked movements were similar to the amplitude and direction associated with the most vigorous activity of the cell recorded at the same site (see Freedman et al. 1996).

**Experimental rationale**

Our analysis of the activity of single cells was based on three behavioral dissociations of gaze, eye, and head metrics and a consideration of the differential predictions that arise from the competing hypotheses. These predictions, for each behavioral dissociation, are illustrated in Fig. 3. The first behavioral dissociation (Fig. 3A) occurs because a subset of movements can be selected in which eye movement amplitude is relatively constant but gaze and head amplitudes vary. In Fig. 3B, the shaded region represents the hypothetical locus of the active population of cells during three different movements (a–c; vertical lines in Fig. 3A and rows in Fig. 3B). According to the gaze displacement hypothesis, a signal of desired gaze displacement is derived from the locus of the active population within a gaze motor map. During gaze shifts of increasing amplitude (a–c), the center of the active population of cells in this map shifts systematically toward more caudal regions as shown schematically in Fig. 3B, left (gaze column, rows a–c). While recording the activity of a single SC cell, positioned in the map at a locus representing movements along the horizontal meridian having amplitudes of 50° (●), a weak motor burst would be observed in association with movements to a because this particular cell would be near the edge of the active population during movements of this amplitude and direction. For the larger gaze shifts to b, the center of the active population would be shifted caudally, the hypothetical cell would be closer to the center of the active population, and a more vigorous motor burst would accompany these movements. During even larger gaze shifts to c, the active population would be centered at the same location as the cell and vigorous bursts would be associated with these gaze shifts. For this hypothetical cell, the gaze displacement hypothesis predicts that the vigor of the motor-related activity will increase as a function of increasing gaze amplitude (see the following text for extension to more general predictions) as illustrated in Fig. 3C (upper left). Note that this relationship is observed, not because gaze amplitude is coded by the discharge rate of this cell, but because the position of the cell relative to the center of the active population changes as movement metrics change. The gaze displacement hypothesis also makes explicit predictions about the relationship between eye movement amplitude and discharge rate for this cell. Discharge rate will vary with changes in gaze amplitude (within the framework of the gaze displacement hypothesis) but eye movement amplitude is relatively constant for this subset of trials and the resulting relationship should have a slope of zero (Fig. 3C, gaze column, middle). Because increments in gaze amplitude are associated with larger head movements, for this subset of trials, the predicted relationship between head amplitude and discharge rate (3C, gaze column, bottom) is the same as that for the relationship between gaze amplitude and discharge rate.

The separate channel hypothesis assumes that there are two separate populations of active cells: one encoding eye displacement (Fig. 3B, eye column) and a second encoding head displacement (Fig. 3B, head column). During movements to a–c, eye amplitude and direction are relatively constant and the separate channel hypothesis assumes that the locus of the active population in a collinear map encoding eye displacement is fixed (Fig. 3B, eye column, a–c). The vigor of the motor-related burst of a hypothetical cell (●) within the eye displacement map should be constant during eye movements associated with this set of gaze shifts because the location of the cell relative to the center of the active population does not change. The relatively constant discharge rate predicted by the separate channel hypothesis for this cell will be associated with a large range of gaze (3C, eye column, top) and head (3C, eye column, bottom) movement amplitudes. However, a plot of eye movement amplitude as a function of firing rate should reveal a small cluster of points because there will be only small variations in eye movement amplitude associated with small variations in discharge rate (3C, eye column, center). During this subset of movements (a–c) both gaze amplitude and head movement amplitude increase, and as a result the second set of predictions made by the separate channel hypothesis, that cells encode head displacement, are identical to the predictions of the gaze displacement hypothesis (compare Fig. 3, B and C, head and gaze columns); if the activity of cells were examined only during this subset of movements, no distinction could be made between these alternatives.

A similar analysis for the second method of dissociating gaze, eye, and head metrics (Fig. 3D) is illustrated in Fig. 3 (E and F). These panels represent gaze shifts in which head movement amplitude and direction are relatively constant but the amplitude and direction of gaze and eye movements vary. For this set of movements, the location of a population of cells encoding head movement amplitude and direction should not vary (Fig. 3E, head column, a–c), and one of the predictions of the separate channel hypothesis is that during this subset of trials, the firing rate of a hypothetical cell that codes head displacement will not vary (3F, head column, bottom). The active populations encoding either eye or gaze displacement should vary systematically (Fig. 3E, gaze and eye columns) and the discharge rates of single cells within these active populations also should vary (Fig. 3, E and F, gaze and eye columns). During this subset of movements, both gaze and eye movement direction covary, and as a result, one set of predictions of the separate channel hypothesis, that some cells encode eye displacement, are identical to the predictions of the gaze displacement hypothesis (Fig. 3, E and F, gaze and eye columns); therefore, these hypotheses are not dissociable if only this subset of movements were considered.

The third dissociation of gaze, eye, and head metrics occurs as a result of the inverse effects of initial eye position of the amplitude of the eye and head components of constant amplitude gaze shifts (Fig. 3G). The gaze displacement hypothesis predicts that under these circumstances, the position of the active population within the SC map will remain constant (Fig. 3H, gaze column) and a plot of gaze amplitude as a function of firing rate of a hypothetical cell would result in a small cluster of points (Fig. 3I, gaze column, top). Because both eye and head amplitude vary, the gaze displace-
The separate channel hypothesis predicts that activity in the eye displacement map will shift systematically (to more caudal regions) when the eyes begin in more eccentric positions (eye movement amplitude increases), whereas the population of active cells within the map of head displacement will be centered in progressively more rostral regions for the same subset of movements. These predictions are shown in the eye and head columns of Fig. 3, H and I.

Note that the predictions outlined above will depend on the location of the test cell. In the examples above, the cell is located in a region of the SC representing $5^\circ$ amplitude movements and, as a result, as gaze and head amplitudes increase from 20 to $50^\circ$ (Fig. 3A), the gaze displacement hypothesis predicts that firing rate will increase monotonically because the cell is progressively closer to the center of the active population as gaze amplitude increases. However, if the cell in question were located at the representation of $20^\circ$ for the same three movements, the relationship between gaze amplitude and firing rate would be reversed. As gaze amplitude increased, the cell would be further from the center of the active population and firing rate would decline. The predictions described above can be made more general if the amplitude and direction of movements are expressed relative to the amplitude and direction of the cell’s preferred movement (i.e., the difference between preferred amplitude and direction and the actual amplitude and direction of any particular movement). Because the maximal burst of any cell will be associated with movements of the preferred direction and amplitude, as movements are made that deviate from the preferred metrics, discharge rates will decline. As a result the relationship between firing rate and gaze amplitude relative to the movement field center (e.g., Fig. 3C) should have a negative slope regardless of the cell’s location in the SC. The generalized predictions of the separate channel and gaze displacement hypotheses will be used below (RESULTS).

RESULTS

We obtained high-resolution movement field or activity field data from 36 single neurons in the deeper layers of the superior colliculi of two rhesus monkeys. The activity of isolated cells was recorded during coordinated eye-head gaze shifts. With the head unrestrained, during the remembered target task (Fig. 4, A–D), the 36 cells fell into three general groups: cells with only visual and/or sustained activity but

![Figure 3](http://jn.physiology.org/)

**Figure 3.** A, D, and G: replotted schematic diagrams illustrating the behavioral dissociations of movement metrics (see Fig. 1 and related text). B: hypothetical locations of the active population of cells in the SC map as predicted by the alternative hypotheses during movements indicated in A (a–c). □, active population; ●, location of hypothetical cell used to illustrate the specific predictions of the alternatives. Column marked gaze outlines the locus of the active population according to the gaze displacement hypothesis during movements (rows a, b, and c). Similarly, eye and head columns illustrate the loci of active populations according to the separate channel hypothesis. C: specific predictions of the hypotheses (columns) are outlined for the test cell in B. Gaze, eye, and head movement amplitudes (rows) are plotted as functions of hypothetical firing rate. D: schematic of a second behavioral dissociation of movement metrics. E: loci of active populations in SC map during three movements (D: a–c) according to the alternative hypotheses (columns: gaze, eye, and head). F: specific predictions of gaze, eye, and head amplitude (rows) when plotted as a function firing rate of test cell (● in E). G: schematic of a third behavioral dissociation of movement metrics. H: loci of active populations in SC map during three movements (G: a–c) according to the alternative hypotheses (columns: gaze, eye, and head). I: specific predictions of gaze, eye, and head amplitude (rows) when plotted as a function firing rate of test cell (● in H).
FIG. 4. Examples of different activity profiles exhibited by 4 different cells recorded during coordinated eye-head gaze shifts. In each panel, 5 trial averages of horizontal gaze position (top), horizontal head position (middle), and horizontal eye position (bottom) are illustrated; vertical amplitudes were less than $\pm 10^\circ$ in all examples and are not shown. Below the position traces, instantaneous frequency histograms showing the activity from the 5 individual trials are plotted. Onset of secondary target (T ON), extinction of secondary target (T OFF), and movement initiation cue (Cue) are marked in each panel. Scale bar for all panels is given in A. Motor indices for each cell are provided in the text.

no motor-related activity; cells with only motor-related activity; and cells with visual, sustained, and motor-related activity. The first group of cells ($n = 10$) had motor indices $<1.0$. An example of one such cell is presented in Fig. 4A, which illustrates five individual trials made during the remembered target task to a target located along the horizontal meridian. Average horizontal gaze (top), head (middle), and eye (bottom) position for the five trials are plotted above the five instantaneous frequency histograms from each trial. As shown, the firing rate of this cell increased from $\sim 50$ to $\sim 500$ spikes/s, $\sim 70$ ms after the onset of the secondary visual target (T ON). Firing rates declined during the next 100 ms to $\sim 300$ spikes/s. This tonic firing rate ($\sim 300$ spikes/s) was maintained through the memory interval (from T OFF to Cue) while the subject continued to fixate the initial target. Tonic activity declined after the onset of the movement and ceased $\sim 150$ ms later. As illustrated, there was no increase in discharge rate temporally coupled with the onset of the movement, and this cell had a motor index of $0.68 \pm 0.3$, indicating that there was a reduction of activity during the perimovement interval compared with the precue interval. The activity profile of this cell was typical of the 10 cells in this group.

Cells with motor indices $>1.0$ and $<30$ ($n = 21$) define the second group. These cells had phasic increases in firing rates associated with the movement and also had sustained activity during the memory interval. An example of a cell from this group is illustrated in Fig. 4B [motor index (MI) = $2.9 \pm 0.8$]. The average horizontal gaze, eye, and head positions during five trials are shown above the individual frequency histograms. This cell exhibited a large transient increase in activity associated with the presentation of the
secondary visual target and a smaller transient increase in discharge rate temporally coupled with the extinction of the secondary target (T_{off}). Tonic firing (~150 spikes/s) was maintained throughout the memory interval. Unlike the cell shown in Fig. 4A, compared with the 150-ms precue interval, this cell had a small increase in discharge rate coupled with the onset of the movement. Figure 4C depicts a cell (MI = 14.3 ± 2.4) that maintained a tonic discharge rate (~100 spikes/s) beginning with the presentation of the secondary target and usually continued through the memory interval. A high-frequency burst of activity was coupled temporally with movement onset and ended in association with the end of the gaze shift.

A third group (n = 5) of cells had no activity other than that associated with movement onset (motor indices of these cells were defined as >100). An example of a cell from this group is illustrated in Fig. 4D.

Correlation of motor activity with eye, head, and gaze movements

When the head is unrestrained, large amplitude gaze shifts are composed of coordinated eye and head movements, and on any particular trial motor activity occurs in conjunction with a gaze shift, an eye movement, and a head movement. Figure 5A plots the average discharge rate of the motor-related burst (beginning 20 ms before movement onset to the end of the phasic activity) of a single caudal collicular cell as a function of horizontal (abscissa) and vertical (ordinate) gaze amplitude. This panel illustrates the motor activity observed during 722 gaze shifts made to different targets while the subject performed the delayed gaze shift task. A burst of activity was associated with gaze shifts ranging in horizontal amplitude from 15 to 75° and ranging in vertical amplitude from 45° below the horizontal meridian (−) to 45° above the horizontal meridian (+). The most vigorous activity occurred before and during gaze shifts with horizontal components of ~72° and vertical components of ~15°. Hereafter, movements are described as if they were vectors in a Cartesian coordinate system. For example, the coordinates (72, 15) describe the gaze shifts associated with the most vigorous motor activity in Fig. 5A. The motor activity of the same cell is replotted (Fig. 5B) as a function of the horizontal and vertical amplitudes of the eye components of the same 722 gaze shifts. The most vigorous motor activity was associated with eye movements having coordinates of approximately 35, 15. When the activity of this cell is replotted (Fig. 5C) as a function of the horizontal and vertical amplitudes of the head movements that occurred during the same 722 trials, the most vigorous motor activity was associated with movements having coordinates (45, 5).

Based on the movement metrics associated with the cell’s most vigorous discharge, this cell could be contributing maximally to the generation of a desired gaze displacement command with coordinates (75, 15), a desired eye displacement command with coordinates (35, 15), or a desired head displacement command with coordinates (45, 5).

Figure 5 emphasizes the need for analyzing neuronal activity during subsets of movements in which gaze, eye, and head movements are dissociable. If a given gaze shift always were associated with exactly the same eye and head components, it would not be possible to determine whether motor activity was related to the gaze shift or to the eye or head components of the gaze shift. However, as a result of the dissociations of gaze, eye, and head movement metrics, it is possible to test the differential predictions of the hypotheses outlined above (see METHODS). These analyses require that cells are active during coordinated eye-head movements. Seven of the 26 cells with motor-related activity were located in the rostral SC and were only active for small amplitude gaze shifts accomplished with saccadic eye movements and did not meet this requirement.

Gaze, eye, and head movement metrics can be dissociated when gaze shifts are directed along the horizontal meridian and initiated with the eyes centered in the orbits. Under these conditions (Fig. 6B), eye amplitude (■) is a saturating function of gaze amplitude, but head amplitude (○) increases linearly as a function of gaze amplitude. It is possible, therefore, to select a subset of movements (between arrows in Fig. 6B) in which eye movement amplitude is relatively constant but gaze and head movement amplitude vary over a wide range. For this subset of movements, the separate channel hypothesis predicts that the location of the population of cells encoding eye displacement will be relatively constant. As a result, the discharge rate of a single cell within this active population will be relatively constant because its location relative to the location of the active population is not changing3 (Fig. 6C4). The constant discharge rate of this cell (predicted by the separate channel hypothesis) will be associated with a large range of gaze amplitudes (Fig. 6C2) and head movements (Fig. 6C6). The separate channel hypothesis also predicts that the locus of the active population of cells encoding head movement metrics will change systematically during the selected trials because head movement amplitude increases linearly with gaze amplitude for the selected range of movements. Thus the relative position of individual cells within the active population will change systematically (Fig. 3), and this hypothesis predicts systematic variations in discharge rates (Fig. 6C5). These changes in discharge rate will be associated with a small range of eye movement amplitudes (Fig. 6C3) and a large range of gaze amplitudes (Fig. 6C1). As illustrated in Fig. 3, the gaze displacement hypothesis predicts that the location of the active population of cells encoding gaze metrics will vary systematically during the selected movements. The gaze displacement hypothesis predicts that the rate of discharge of a single cell will be related to the amplitude of the gaze shift (Fig. 6C1). This range of discharge rates will be associated with eye movements having

2 Note that the predictions of the separate channel hypothesis regarding cells encoding eye displacement are identical to the predictions of the hypothesis that the SC is involved only in generation of saccadic eye movements. The results of electrical stimulation of the SC with the head unrestrained are inconsistent with this eye-only hypothesis because they demonstrate the role of the SC in generation of coordinated eye-head movements. Nonetheless, the predictions of this hypothesis are a subset of the predictions of the separate channel hypothesis.

3 Note that in this and subsequent figures, movement amplitudes and directions are expressed relative to the movement field center, making the predictions independent of cell location within the SC motor map. The distance from the center of the movement field in this and subsequent figures is calculated separately as a function of the gaze, eye, or head movement fields.
FIG. 6.  A: schematic illustrating 1 of the behavioral dissociations of eye and gaze and head movement amplitude and direction (see INTRODUCTION for details).  B: during movements directed along the horizontal meridian with the eyes initially centered in the orbits, eye movement amplitude (●) and head movement amplitude (○) are plotted as a function of gaze shift amplitude.  C: general predictions of the alternative hypotheses are illustrated schematically in C, 1–6. Gaze and head metrics are not dissociable under these conditions (see text for details).  D: for a subset of trials like those marked in B (●), collected while recording from cell s7, predictions of the hypotheses are tested by plotting (●) gaze amplitude (D), eye amplitude (E), and head amplitude (F) as functions of firing rate (see Table 1 for details). In D–F, the results of this analysis for a second cell (t6) are shown (○) for comparison.

relatively constant amplitudes (Fig. 6C3). If the activity of a cell were examined only during this subset of trials, it would not be possible to distinguish between cells encoding head displacement and gaze displacement.

In Fig. 6, gaze amplitude (D), eye amplitude (E), and head amplitude (F), relative to the movement field center,
are each plotted as a function of firing rate for cell s7 (●).
For cell s7, the correlation between gaze amplitude and firing rate (D) was −0.74, and the line of best fit had a slope of −0.32 (n = 58). The correlation between eye amplitude and firing rate for this cell was −0.05, and the slope of this relationship was −0.00. The correlation between head amplitude and firing rate (Fig. 6F, ●) was −0.54 and the slope of this relationship was slope −0.26. For comparison, in Fig. 6, D–F, data from a second cell (t6) are also shown (○).
This cell was selected because it had the lowest correlation (r = −0.40) between gaze amplitude and firing rate in our sample. The pattern of results for the two cells illustrated and for the remaining 17 cells (see Table 1) were inconsistent with the hypothesis that some cells in the SC encode eye displacement, one of the predictions of the separate channel hypothesis. The pattern of results for all 19 cells was consistent with the gaze displacement hypothesis. Because gaze and head metrics were not dissociable under the behavioral conditions of this analysis, results were also consistent with the hypothesis that some SC cells encode head displacement, a second prediction of the separate channel hypothesis (but see below).

For the analysis illustrated in Fig. 6, gaze amplitude and head amplitude covaried. Although the activity of cells was not related to changes in eye movement metrics, changes in discharge rates could represent commands related to either gaze or head movement metrics. Thus the activity of the same cells was examined during a different subset of trials in which the amplitude and direction of head movements was relatively constant but the direction of associated eye (○) and gaze (●) movements varied over a wide range (Fig. 7B). In Fig. 7, the direction of gaze (D), eye (E), and head (F) movements are plotted as a function of firing rate for cell s7 (●). Under these conditions, the separate channel hypothesis predicts that the location of the active population of cells encoding head movement metrics will remain relatively constant and that the discharge rates of cells involved in specifying head amplitude and direction will similarly remain relatively constant (Fig. 7C6). This relatively constant discharge rate of cells encoding head metrics will be associated with gaze shifts (Fig. 7C2) and eye movements (Fig. 7C4) that vary in direction over a wide range. Alternatively, the gaze displacement hypothesis predicts that the location of the active population of SC cells

### TABLE 1. Correlation of firing rate with eye and gaze amplitude and correlation of firing rate with vertical head and gaze amplitude

<table>
<thead>
<tr>
<th>Cell No.</th>
<th>MI</th>
<th>r_y</th>
<th>r_o</th>
<th>r_s</th>
<th>s_l_y</th>
<th>s_l_o</th>
<th>s_l_s</th>
<th>n</th>
<th>r_y</th>
<th>r_o</th>
<th>r_s</th>
<th>s_l_y</th>
<th>s_l_o</th>
<th>s_l_s</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>T2</td>
<td>1.1 ± 0.6</td>
<td>−0.62</td>
<td>−0.62</td>
<td>−0.02</td>
<td>−0.26</td>
<td>−0.27</td>
<td>−0.00*</td>
<td>131</td>
<td>−0.54</td>
<td>−0.07</td>
<td>−0.52</td>
<td>−0.23</td>
<td>−0.01*</td>
<td>−0.25</td>
<td>95</td>
</tr>
<tr>
<td>T3</td>
<td>7.7 ± 2.1</td>
<td>−0.53</td>
<td>−0.49</td>
<td>−0.37</td>
<td>−0.28</td>
<td>−0.21</td>
<td>−0.07*</td>
<td>22</td>
<td>−0.53</td>
<td>−0.01</td>
<td>−0.55</td>
<td>−0.26</td>
<td>−0.00*</td>
<td>−0.25</td>
<td>31</td>
</tr>
<tr>
<td>T4</td>
<td>3.7 ± 1.1</td>
<td>−0.40</td>
<td>−0.34</td>
<td>−0.20</td>
<td>−0.19</td>
<td>−0.15</td>
<td>−0.01*</td>
<td>81</td>
<td>−0.51</td>
<td>−0.31</td>
<td>−0.59</td>
<td>−0.21</td>
<td>−0.03*</td>
<td>−0.19</td>
<td>56</td>
</tr>
<tr>
<td>T5</td>
<td>3.2 ± 1.1</td>
<td>−0.54</td>
<td>−0.59</td>
<td>−0.20</td>
<td>−0.18</td>
<td>−0.21</td>
<td>−0.01*</td>
<td>71</td>
<td>−0.51</td>
<td>−0.09</td>
<td>−0.54</td>
<td>−0.31</td>
<td>−0.01*</td>
<td>−0.32</td>
<td>102</td>
</tr>
<tr>
<td>T6</td>
<td>14.2 ± 2.4</td>
<td>−0.40</td>
<td>−0.36</td>
<td>−0.45</td>
<td>−0.11</td>
<td>−0.11</td>
<td>−0.02*</td>
<td>95</td>
<td>−0.54</td>
<td>−0.13</td>
<td>−0.52</td>
<td>−0.26</td>
<td>−0.04*</td>
<td>−0.29</td>
<td>89</td>
</tr>
<tr>
<td>T7 &gt;100</td>
<td>0.56</td>
<td>−0.48</td>
<td>−0.32</td>
<td>−0.30</td>
<td>−0.21</td>
<td>−0.03*</td>
<td>71</td>
<td>−0.51</td>
<td>−0.09</td>
<td>−0.54</td>
<td>−0.31</td>
<td>−0.01*</td>
<td>−0.32</td>
<td>102</td>
<td></td>
</tr>
<tr>
<td>T8 &gt;100</td>
<td>0.54</td>
<td>−0.58</td>
<td>−0.05</td>
<td>−0.35</td>
<td>−0.34</td>
<td>−0.42</td>
<td>−0.07*</td>
<td>60</td>
<td>−0.70</td>
<td>−0.10</td>
<td>−0.77</td>
<td>−0.26</td>
<td>−0.1*</td>
<td>−0.25</td>
<td>51</td>
</tr>
<tr>
<td>T9 &gt;100</td>
<td>0.68</td>
<td>−0.65</td>
<td>−0.32</td>
<td>−0.21</td>
<td>−0.24</td>
<td>−0.02*</td>
<td>101</td>
<td>−0.90</td>
<td>−0.10</td>
<td>−0.90</td>
<td>−0.19</td>
<td>−0.01*</td>
<td>−0.22</td>
<td>66</td>
<td></td>
</tr>
<tr>
<td>T10 3.5 ± 1.1</td>
<td>−0.46</td>
<td>−0.40</td>
<td>−0.07</td>
<td>−0.19</td>
<td>−0.21</td>
<td>−0.02*</td>
<td>36</td>
<td>−0.51</td>
<td>−0.01</td>
<td>−0.66</td>
<td>−0.24</td>
<td>−0.01*</td>
<td>−0.21</td>
<td>86</td>
<td></td>
</tr>
<tr>
<td>T12 11.1 ± 1.4</td>
<td>−0.62</td>
<td>−0.57</td>
<td>−0.58</td>
<td>−0.18</td>
<td>−0.25</td>
<td>−0.06*</td>
<td>61</td>
<td>−0.46</td>
<td>−0.30</td>
<td>−0.42</td>
<td>−0.17</td>
<td>−0.03*</td>
<td>−0.17</td>
<td>53</td>
<td></td>
</tr>
<tr>
<td>T13 &gt;100</td>
<td>0.47</td>
<td>−0.45</td>
<td>−0.25</td>
<td>−0.34</td>
<td>−0.31</td>
<td>−0.03*</td>
<td>63</td>
<td>−0.56</td>
<td>−0.33</td>
<td>−0.55</td>
<td>−0.31</td>
<td>−0.14</td>
<td>−0.32</td>
<td>85</td>
<td></td>
</tr>
<tr>
<td>S6 1.1 ± 0.8</td>
<td>−0.58</td>
<td>−0.50</td>
<td>−0.12</td>
<td>−0.19</td>
<td>−0.18</td>
<td>−0.01*</td>
<td>80</td>
<td>−0.47</td>
<td>−0.54</td>
<td>−0.47</td>
<td>−0.21</td>
<td>−0.06*</td>
<td>−0.24</td>
<td>124</td>
<td></td>
</tr>
<tr>
<td>S7 7.7 ± 1.3</td>
<td>−0.74</td>
<td>−0.54</td>
<td>−0.05</td>
<td>−0.32</td>
<td>−0.26</td>
<td>−0.00*</td>
<td>58</td>
<td>−0.43</td>
<td>−0.05</td>
<td>−0.39</td>
<td>−0.14</td>
<td>−0.00*</td>
<td>−0.18</td>
<td>49</td>
<td></td>
</tr>
<tr>
<td>S8 14.3 ± 3.8</td>
<td>−0.61</td>
<td>−0.58</td>
<td>−0.09</td>
<td>−0.13</td>
<td>−0.15</td>
<td>−0.00*</td>
<td>100</td>
<td>−0.87</td>
<td>−0.10</td>
<td>−0.81</td>
<td>−0.14*</td>
<td>−0.03*</td>
<td>−0.12*</td>
<td>45</td>
<td></td>
</tr>
<tr>
<td>S9 25 ± 2.3</td>
<td>−0.45</td>
<td>−0.45</td>
<td>−0.08</td>
<td>−0.19</td>
<td>−0.18</td>
<td>−0.00*</td>
<td>107</td>
<td>−0.59</td>
<td>−0.30</td>
<td>−0.62</td>
<td>−0.24</td>
<td>−0.07*</td>
<td>−0.20</td>
<td>89</td>
<td></td>
</tr>
<tr>
<td>S10 33.3 ± 1.7</td>
<td>−0.47</td>
<td>−0.45</td>
<td>−0.32</td>
<td>−0.20</td>
<td>−0.03*</td>
<td>32</td>
<td>−0.48</td>
<td>−0.17</td>
<td>−0.45</td>
<td>−0.24</td>
<td>−0.03*</td>
<td>−0.30</td>
<td>63</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S12 &gt;100</td>
<td>−0.89</td>
<td>−0.62</td>
<td>−0.42</td>
<td>−0.40</td>
<td>−0.36</td>
<td>−0.03*</td>
<td>134</td>
<td>−0.78</td>
<td>−0.19</td>
<td>−0.76</td>
<td>−0.18</td>
<td>−0.03*</td>
<td>−0.16</td>
<td>189</td>
<td></td>
</tr>
<tr>
<td>S13 2.9 ± 0.8</td>
<td>−0.51</td>
<td>−0.47</td>
<td>−0.31</td>
<td>−0.24</td>
<td>−0.21</td>
<td>−0.03*</td>
<td>171</td>
<td>−0.49</td>
<td>−0.28</td>
<td>−0.41</td>
<td>−0.24</td>
<td>−0.03*</td>
<td>−0.23</td>
<td>91</td>
<td></td>
</tr>
<tr>
<td>S15 33.3 ± 1.7</td>
<td>−0.45</td>
<td>−0.41</td>
<td>−0.05</td>
<td>−0.21</td>
<td>−0.26</td>
<td>−0.00*</td>
<td>39</td>
<td>−0.58</td>
<td>−0.23</td>
<td>−0.51</td>
<td>−0.23</td>
<td>−0.05*</td>
<td>−0.21</td>
<td>43</td>
<td></td>
</tr>
</tbody>
</table>

Correlation coefficients (r) and slopes of the lines of best fit for the analyses illustrated in Figs. 6 and 7 for cells with motor-related activity and for cells without motor-related activity. Cell identification number, number of trials used for the correlations, and motor indices (MI) are given for each cell that met the analysis criteria (see text for details). MI are means ± SD. *, slopes are not statistically different than zero (P > 0.95).
will vary systematically during this subset of movements in which gaze shift directions vary, and as a result, the hypothesis predicts that the discharge of single cells will be related to changes in gaze movement metrics (Fig. 7C1). In addition, the gaze displacement hypothesis predicts that the variations in cell discharge rates will be associated with relatively constant amplitude and direction head movements (Fig. 7C5) and eye movements having a variety of directions (Fig. 7C3).

For cell s7, the correlation between gaze shift direction and firing rate was −0.43, and this relationship had a slope of −0.14. This was one of the lower correlation coefficients (range: −0.37 to −0.90) of the 19 cells (see Table 1). The correlation between head movement direction and firing rate (Fig. 7F, black) was −0.05 and had a slope of −0.00. The correlation between eye movement direction and firing rate (Fig. 7E) was −0.39, and the line of best fit had a slope of −0.18. Results of this same analysis for cell t9 (gray) selected for the high correlation between gaze direction and discharge rate (−0.90), are also illustrated in Fig. 7, D–F, for comparison (see Table 1 for details of this and other cells). The pattern of results illustrated in Fig. 7 and Table 1, in which head movement metrics were dissociated from gaze and eye movement metrics, was inconsistent with the set of predictions of the separate channel hypothesis that some cells encode head displacement. The results were consistent with the predictions of the gaze displacement hypothesis, and because eye and gaze metrics were not dissociable within this subset of movements, results are also consistent with one set of predictions of the “separate channel” hypothesis that some cells encode eye metrics.

Activity was recorded from 19 collicular cells with motor-related activity under conditions in which eye movement amplitude and direction were dissociated from head and gaze metrics (Fig. 6) and under conditions in which head metrics were dissociable from eye and gaze metrics (Fig. 7). In all 19 cases, neuronal activity was related to the amplitude and direction of gaze shifts. When gaze and eye movement metrics were dissociable (Fig. 6), only a weak relationship between neuronal activity and eye movement metrics was observed. When gaze and head movement metrics were dissociable (Fig. 7), the activity of the same 19 cells was correlated poorly with head movement metrics. As stated, the only consistent relationship between cell discharge and movement metrics was the relationship between discharge and gaze movement metrics, as predicted by the gaze displacement hypothesis.

As illustrated in Fig. 8B, it is possible to select a single group of movements in which, during gaze shifts having relatively constant amplitudes and directions, the amplitude and direction of the eye and head components vary inversely as a function of the initial positions of the eyes in the orbits. The gaze hypothesis predicts that there should be little variation in firing rate associated with constant vector gaze shifts, and plotting gaze amplitude as a function of firing rate should result in a cluster of points that do not covary (Fig. 8C1). This hypothesis also predicts that if firing rate is plotted as a function of the initial position of the eyes in the orbits, the line of best fit should have zero slope (Fig. 8C2). The separate channel hypothesis predicts that eye movement amplitude will vary systematically as a function of firing rate (Fig. 8C3, ——), and discharge rate will decrease as a function of initial eye position (Fig. 8C4). The separate channel hypothesis also predicts that, for some cells, head movement amplitude will vary systematically as a function of firing rate (Fig. 8C5, ——) and, under these conditions, the firing rate will increase systematically as a function of initial eye position (Fig. 8C6). The predictions of the gaze displacement hypothesis for the relationships between firing rate and eye and head movement amplitude also are shown in Fig. 8. C3 and C5 (——). For cell s7, the correlation between firing rate and initial eye position was 0.13 (n = 61), and the slope of this relationship was 0.06 (Fig. 8E). Slopes of the lines of best fit for the 13 cells with motor-related activity meeting

---

In addition to the requirements of the previous analyses, this analysis requires that gaze shifts having similar amplitude and direction are made when the eyes began in different orbital positions. Thirteen of the 26 cells with motor-related activity met these criteria.
the requirements of this analysis ranged from 0.03 to 0.33 (see Table 2 for details). As indicated, if either eye or head movement amplitude and direction were encoded by the locus of SC activity, discharge rates should vary systematically as a function of initial eye position during groups of trials in which eye and head amplitude vary (see Table 2). Figure 8, F and G, plot eye and head amplitude, respectively, as functions of firing rate for the same subset of trials in which gaze amplitude and direction are relatively constant. As illustrated, there was variability in both eye (range: 22–47°) and head (range: 27–61°) movement amplitude but little variability in firing rate for this subset of trials; eye amplitude and head amplitude varied systematically as a function of initial eye position (correlation coefficients were −0.78 and 0.72, respectively). Thus during gaze shifts of relatively constant amplitude and direction, SC cells with motor-related activity showed little variation in discharge rates even though the amplitudes of the associated eye and head movements varied over wide ranges. These results are inconsistent with the predictions of the separate channel hypothesis, but this is the pattern of activity expected if the site of activity of collicular cells generates a gaze displacement command.

**Gaze movement fields**

In general, the movement field structure of cells in the caudal colliculus, recorded during head unrestrained gaze shifts was similar to that of more rostral collicular cells recorded when the head was restrained (Sparks et al. 1976). Cells were broadly tuned and were active before and during a wide range of movements. As the eccentricity of the preferred movement increased, the range of movements during which the cell was active increased. One notable difference between activity of cells in the caudal and rostral SC is the peak discharge rate of motor-related activity. During the perimovement interval, the peak discharge rate observed for cells in the caudal SC did not exceed ~600 spikes/s (see for example, Fig. 4). In contrast, it has been reported that cells in the rostral SC recorded with the head restrained can have instantaneous discharge rates that exceed 1,200 spikes/s (for example, Sparks et al. 1976).

Gaze movement fields for six of the 26 cells identified as having motor-related activity are shown in Fig. 9. Five of these cells were recorded from the left colliculi, one from the right SC (Fig. 9D). The cells were selected to show...
mally active for rightward movements with amplitudes were active for a larger range of movements than were rostral activity that declines when movements larger than the pre-illustrated in Fig. 9A was maximally active before and during movements with coordinates of \((5, 4)\). Activity was reduced for all movements with directions and/or amplitudes that differed from these preferred coordinates. Similarly, the cell illustrated in Fig. 9D was maximally active for movements with coordinates of \((-5, -5)\), and motor activity was reduced for movements that differed in amplitude and/or direction. Figure 9, B and E, plots the movement fields of two cells with maximal motor activity for movements of \((30, 15)\) and \((35, 0)\), respectively. These more caudal cells were active for a larger range of movements than were rostral cells. In Fig. 9B, the cell had a burst \(\geq 50\%\) of the maximal firing rate for movements ranging in horizontal amplitude from 15 to 40° and ranging in vertical amplitude from 0 to 25°, but the activity of the cell declined dramatically for movements outside this range. The cell in Fig. 9E was maximally active for rightward movements with amplitudes \(\sim 35°\) directed along the horizontal meridian. Movements in the best direction with amplitudes of 60 or 70° still were associated with vigorous motor bursts, but the firing rate during these movements was reduced compared with firing rates observed for movements of the preferred direction and amplitude. In Fig. 9, C and F, the movement fields of cells from the caudal SC are shown. The peak activity observed for these cells occurred during \(\sim 75\sim 80°\) gaze shifts, movements made to targets displaced at the limits of our apparatus. The preferred movements of the cells illustrated in Fig. examples from rostral (Fig. 9, A and D), intermediate (Fig. 9, B and E), and caudal (Fig. 9, C and F) regions of the colliculus. In each panel, contour lines are superimposed on the movement field data (see caption for details). The cell

<table>
<thead>
<tr>
<th>Cell No.</th>
<th>Firing Rate</th>
<th>Gaze Amplitude</th>
<th>Eye Amplitude</th>
<th>Head Amplitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>T3</td>
<td>35</td>
<td>0.2</td>
<td>0.33</td>
<td>-0.95</td>
</tr>
<tr>
<td>T4</td>
<td>51</td>
<td>0.01</td>
<td>0.13</td>
<td>0.21</td>
</tr>
<tr>
<td>T5</td>
<td>43</td>
<td>0.02</td>
<td>0.17</td>
<td>0.2</td>
</tr>
<tr>
<td>T7</td>
<td>86</td>
<td>0.2</td>
<td>0.24</td>
<td>0.25</td>
</tr>
<tr>
<td>T8</td>
<td>47</td>
<td>0.1</td>
<td>0.10</td>
<td>0.07</td>
</tr>
<tr>
<td>T9</td>
<td>59</td>
<td>0.2</td>
<td>0.26</td>
<td>0.08</td>
</tr>
<tr>
<td>T10</td>
<td>81</td>
<td>0.15</td>
<td>0.03</td>
<td>0.1</td>
</tr>
<tr>
<td>S3</td>
<td>37</td>
<td>0.19</td>
<td>0.11</td>
<td>0.17</td>
</tr>
<tr>
<td>S7</td>
<td>61</td>
<td>0.13</td>
<td>0.06</td>
<td>0.13</td>
</tr>
<tr>
<td>S8</td>
<td>68</td>
<td>0.1</td>
<td>0.09</td>
<td>0.15</td>
</tr>
<tr>
<td>S9</td>
<td>71</td>
<td>0.08</td>
<td>0.34</td>
<td>0.04</td>
</tr>
<tr>
<td>S12</td>
<td>38</td>
<td>0.01</td>
<td>0.13</td>
<td>0.13</td>
</tr>
<tr>
<td>S13</td>
<td>47</td>
<td>0.15</td>
<td>0.10</td>
<td>0.13</td>
</tr>
</tbody>
</table>

A. Cells with motor-related activity

B. Cells without motor-related activity

Correlation coefficients (\(r\)), and slopes of lines of best fit for regressions of firing rate, gaze, eye, and head movement amplitude on initial eye position (see text). Data from analysis of cells with and without motor-related activity are shown. Motor indices for all cells are provided in Table 1 with the exception of cell s3 (MI = 33.3 ± 4.1).

GAZE-RELATED ACTIVITY IN THE MONKEY SC

TABLE 2. Correlation of initial eye position to firing rate, gaze, eye, and head amplitudes

9C and F, were directed slightly above the horizontal meridian. The vigor of the motor burst for these two cells (and an additional 7 similar cells) increased monotonically as gaze amplitude increased. As a result, the preferred amplitude of these cells remains undefined; preferred amplitudes could be \(\pm 80°\). In rhesus monkeys, when the head is unrestrained, the functional limit of eye movements relative to the head is about \(\pm 35°\) (cf. Freedman and Sparks 1997). The preferred amplitude of these caudal SC cells exceeds the amplitude of movements that are accomplished by movements of the eyes, even if the initial positions of the eyes were \(35°\) contralateral to movement direction.

The movement field structure of some collicular cells with clearly defined movement field centers and motor-related activity that declines when movements larger than the preferred amplitude are made (e.g., Fig. 9, A, B, and D), have been called closed or bounded. The vigor of the motor burst of some cells continues to increase as movement amplitude increases, and the resulting movement field structure is called open or unbounded. A correlation between open movement field structure and the presence of activity (>30 spikes/s) preceding the onset of the motor burst by \(\geq 100\) ms has been reported, and cells with this activity profile have been called buildup cells (Munoz and Wurtz 1995a). In our sample of cells, we observed no consistent relationship between the motor index and the structure of the movement field. Twenty-one of 26 motor cells had motor indices between 1.0 and 30 and satisfied the definition of buildup cells. Thirteen (62%) of these 21 cells had closed movement fields. The classification of movement field structure as open or closed is problematic because the range of movements

made while recording from any particular cell necessarily is restricted. In Fig. 9, C and F, cells with open movement fields are illustrated. Motor activity of these cells could decline for movements >85°, and these cells could have been classified incorrectly as having open movement fields because of the failure to observe larger movements. Similarly, if only movements ≤40° were observed while recording from the cell illustrated in Fig. 9B, this cell also might have been classified incorrectly as having an open movement field structure. This problem is exacerbated when the head is restrained, because the range of observable movements is restricted further.

**Temporal correlation of motor activity and movement onset**

In addition to the relationship between the locus of the active population and the metrics of gaze, eye, and head movements, the temporal distribution of activity within the collicular map may provide insight into the mechanisms for specifying movement metrics. For instance, when the head is restrained, the onset of the motor-related burst of activity is correlated with the onset of saccadic eye movements. The degree to which the burst precedes the onset of saccades depends on the amplitude and direction of a particular movement relative to the center of the recorded cell’s movement field. The longest intervals from the onset of the motor burst to the onset of the movement (burst lead time) are associated with movements having the cell’s preferred amplitude and direction. Burst lead time is reduced when movements either larger or smaller than the preferred amplitude are made, and lead time also is reduced when movements having the preferred vectorial amplitude but directions that differ from the preferred direction are made (Sparks and Mays 1980; see also Peck 1990). Figure 10 illustrates a similar analysis for caudal SC cells recorded during head-unrestrained gaze shifts. In Fig. 10A, the time from burst onset to gaze shift onset is plotted as a function of gaze shift direction (for movements having the preferred vectorial amplitude) for three representative cells (t3, □; t9, ○; s10, ●). As shown, burst lead time was longest during movements into the center of each cell’s movement field. The motor burst precedes movement onset by progressively shorter intervals as movements deviate from the preferred direction. The difference between burst lead time for movements into the movement field center and movements having directions that deviated from the preferred direction was statistically significant (P < 0.05) for 24 of 26 cells.

In Fig. 10B, burst lead time is plotted as a function of gaze shift amplitude for movements of different amplitudes in the preferred direction of each cell (same cells as in Fig. 10A). Burst lead time was longest during movements into the center of each cell’s movement field and declined for movements that deviated from the preferred amplitude. The difference between burst lead time for movements into the movement field center and movements smaller than the preferred amplitude was statistically significant (P < 0.05) for 15 of 21 cells recorded while a sufficient number of movements smaller than the movement field center were made; some cells in the rostral SC had too few movements smaller than the movement field center for this analysis. Similarly, for movements larger than the preferred amplitude there was a significant difference (P < 0.05) in mean burst lead time for 13 of 17 cells. Nine caudal cells had no movements with amplitudes larger than the movement field center.

---

**FIG. 9.** Gaze movement fields for 6 different cells. A and D: cells shown from rostral colliculus. B and E: examples shown of cells from intermediate regions of the SC. C and F: movement fields of cells from caudal regions of the SC. Cell identification number (cell #) indicates the subject (t or s). For each cell, the total number of individual movements that make up the movement field (N) is shown. Color bars for each panel provide the z-axis scale (spikes/second). Firing rates for movements that fell into the same 1 × 1° window were averaged to produce each point in the movement field in B, C, E, and F. 0.5 × 0.5° windows were used in panels A and D. Motor indices for each cell were A, 33.3; B, >100; C, >100; D, 3.1; E, 3.2; F, 7.7. In all panels, contour lines (distance weighted least squares) having 35 spikes/s increments starting at 0 are superimposed on the movement field data.
From data illustrated above, we can extrapolate the temporal distribution of SC activity (see INTRODUCTION). For any particular movement, the first cells to become active are those at the center of the active population (longest burst lead times). Cells distal to the center become active later than those at the center (burst lead time is reduced for movements that deviate from the preferred amplitude and/or direction). Because burst lead time is reduced for movements larger and smaller than movements of the preferred amplitude and for movements directed above and below the preferred direction, these data suggest that activity spreads in all directions away from the center.

In general, during large amplitude gaze shifts (>50°), head movement onset was correlated highly with the onset of the gaze shift, and as a result, burst onset was correlated with both gaze and head movement onset during these movements. However, during smaller movements, the relative timing of eye and head movements was more variable, and the head movement often occurred after the completion of the gaze shift. For the 19 cells with motor-related activity during coordinated eye-head movements, 10 had maximal bursts during gaze shifts smaller than ~50° in amplitude. During movements of the preferred amplitude and direction for each cell, the onset of the motor burst never was correlated highly with the onset of the head movement (correlation coefficients ranged from 0.02 to 0.3).

Temporal correlation of motor activity and movement end

Unlike the onset of motor-related activity in the SC, the relationship between the end of the motor burst and the end of the movement did not depend on the vector of the movement relative to the center of the movement field. For all of the cells with motor indices ≥ 1.0, the end of the motor burst was correlated highly with the end of the gaze shift. Figure 11A plots burst end as a function of gaze shift end for 700 movements used to describe this cell’s movement field. The lowest correlation between burst offset and gaze shift offset of the 26 cells with motor-related activity was r = 0.62 (n = 352). This lower correlation may reflect the restricted range of measurements available for this particular cell. For the remaining 25 cells, correlation coefficients were all >0.89. The relationships between burst offset and gaze shift offset for all 26 cells were similar; pooling data across cells and across monkeys resulted in a correlation coefficient of 0.95, with a slope of 1.01 (n = 4806), and Y intercept 25.3 ms. This positive intersection of the line of best fit with the ordinate suggests that the motor-related burst ended on average 25 ms before the end of the gaze shift.

The end of the eye contribution to the gaze shift and the end of the gaze shift were coupled tightly (see Freedman and Sparks 1997). Correlations between the end of the eye movement and the end of the motor burst (Fig. 11B) ranged from 0.62 to 0.97 for the 26 cells with motor-related activity. The end of the head movement was related only loosely to the end of the motor burst. Figure 11C plots the relationship between head movement end and motor burst end for the cell displaying the highest correlation. Correlation coefficients ranged from 0.13 to 0.49.

FIG. 11. The time from the movement initiation cue to the end of the motor burst is plotted as a function of the time from the cue to the end of the gaze shift (A), the end of the eye movement (B), and the end of the head movement (C). This example had the highest correlation between head movement offset and burst offset in our sample. See text for other details.

Cells without motor-related activity

Ten cells had motor indices <1.0 (e.g., Fig. 4A). During remembered target trials, these cells had tonic firing rates that continued throughout the memory interval; these cells had no movement-related modulation in discharge rates. Plots of the activity of three cells during the perimovement interval as a function of horizontal and vertical gaze amplitude are illustrated in Fig. 12. Because the term movement field is inappropriate, activity field is used to describe these plots. The tonic level of activity of the cell illustrated in Fig. 12A was highest before movements to the left, declining during oblique gaze shifts and during smaller amplitude movements. A similar gradient of tonic activity was displayed by the cell illustrated in Fig. 12B; activity declined...
GAZE-RELATED ACTIVITY IN THE MONKEY SC

for all movements that deviated from the direction or amplitude of the optimal movement (−35, −25). The cell illustrated in Fig. 12C was not active for movements <35°, but was active for larger movements and discharge rate increased with increasing movement amplitude up to ~80°. Of the 10 cells in our sample without motor-related activity, 4 had activity field structures like that illustrated in Fig. 12B. Maximal discharge occurred before movements of a particular amplitude and direction and decreased systematically as movement metrics deviated from the optimal direction or amplitude.

The function of the tonic discharge of these SC cells is unknown. Nonetheless, the rate of tonic activity during the memory interval is correlated with the metrics of the movement. In this series of experiments, because gaze, eye, and head movement metrics were dissociable, we were able to determine whether tonic discharge of these cells was correlated with the metrics of the gaze shift or the eye or head movement. We found that the sustained discharge was a good predictor of the amplitude and direction of the ensuing gaze shift but a poor predictor of the amplitude and direction of either the eye or head components of gaze (see Tables 1 and 2). However, because visual signals of secondary target displacement and gaze metrics are coupled tightly (cf. Freedman and Sparks 1997), the results of these analyses cannot reject an alternative hypothesis that tonic discharge is a visual signal that persists after extinction of the secondary target. Nonetheless, if sustained activity is involved in specification of movement metrics, the sustained activity we observed is related to the amplitude and direction of the impending gaze shift not to movements of the eyes or head.

DISCUSSION

We recorded from single cells in the deeper layers of the primate superior colliculus during head-unrestrained gaze shifts to test the differential predictions of two hypotheses regarding the role of the SC in the control of coordinated eye-head movements. The differential predictions were assessed during three behavioral dissociations of gaze, eye, and head movement metrics (Freedman and Sparks 1997). In each dissociation, subsets of trials were selected in which either the metrics of eye movements or head movements or gaze shifts were relatively constant, but the metrics of the other two parameters varied systematically over wide ranges. For every cell in our sample that met the criteria for these analyses, data were inconsistent with the hypothesis that the SC generates two separate displacement signals specifying both the displacement of the eyes and head. Data were consistent with the alternative hypothesis that a single gaze displacement signal is derived from the locus of the active population of cells in the SC. This finding, its relationship to previous studies of the collicular displacement command, and possible alternative interpretations of results are discussed in the next section.

Previous findings

Microstimulation of the optic tectum or superior colliculus of a variety of species results in coordinated movements of the eyes and head (Dean et al. 1986; du Lac and Knudsen 1990; Ellard and Goodale 1986; Ewert 1984; Freedman et

FIG. 12. Tonic rate of firing during the perimovement interval is plotted as a function of the horizontal and vertical components of the gaze shift. These cells did not have motor-related activity. Motor indices (MI), number (n) of trials are given for each cell (cell number in A: t11; B: t16; C: s4). Firing rates for movements that fell into the same 1 × 1° window were averaged to produce each point in the movement field. In all panels, contour lines (distance weighted least squares) having 35 spikes/s increments starting at 0 are superimposed on the movement field data.
al. 1996; Harris 1980; Hess et al. 1946; Kashin et al. 1974; King et al. 1991; Northmore et al. 1988; Paré et al. 1994; Roucoux and Crommelinck 1976; Roucoux et al. 1980; Sahibzada et al. 1986; Salas et al. 1994; Schaefer 1970; Schapiro and Goodman 1969; Segreaves and Goldberg 1992; Straschill and Reiger 1973; Syka and Radl-Weiss 1971). These data indicate that the SC is involved in the generation of coordinated eye-head movements not exclusively in the generation of saccadic eye movements. Understanding how the commands for coordinated eye-head movements are represented by the activity of cells in the SC is essential for understanding the neural control of orienting gaze shifts. Because a determination of whether the activity of cells is related to eye movements, head movements, or gaze shifts cannot be made from recordings obtained when the head is restrained, it was necessary to record the activity of single collicular cells during head-unrestrained gaze shifts.

Little evidence is available concerning the representation of gaze, eye, and head displacement commands by the activity of individual SC cells. Straschill and Schick (1977) reported that some cells \((n = 15)\) in the cat SC discharged before and during head movements, increased discharge rates with increasing head velocity, and discharged during maintained contralateral head abduction. However, there was no attempt to determine if activity was more tightly coupled with the metrics of the gaze shift or the head movement. Harris (1980) noted that the activity of several \((n = 4)\) cat collicular cells was coupled temporally to the onset of coordinated eye-head movements. Activity was coupled to head, eye, and gaze onset, although in one example (Fig. 12B of Harris 1980), the cell did not discharge when a gaze shift was made without an associated head movement. However, because the cells did not generate vigorous motor bursts and activity was not obviously correlated with head amplitude or velocity, it is not clear that these cells were involved in encoding head movement metrics, and this hypothesis was not tested directly. Also in the cat, Peck (1990) reported that several cells \((n = 5)\) generated bursts temporally correlated with head movements (activity of other cells was associated with coordinated eye-head gaze shifts), but the increase in activity followed the onset of head movements, making these cells unlikely candidates for the initiation of head movements. Alternatively, observations that activity in the cat SC is correlated temporally with head movements could reflect the presence of sensory signals from neck muscle afferents (cf. Abrahams and Rose 1971). Robinson and Jarvis (1974) reported that in the monkey, the onset of motor activity was related weakly to head movement onset but tightly coupled with eye (or gaze) movement onset.

Intuitively, it seems that one strategy for dissociating gaze, eye, and head movement metrics is to compare coordinated eye-head movements (made with the head unrestrained) with movements of only the eyes (made with the head restrained). Comparing the activity of a single SC cell during movements made under these two conditions might be a fruitful approach for determining whether a cell’s activity is related to movements of the eyes or to movements of the head or to changes in gaze. However, interpretation of the results of such an experiment is not straightforward. Consider a single example in which the discharge of a cell associated with a 40° gaze shift composed of a 10° head movement and 30° eye movement is identical to the discharge associated with a 30° eye movement made when the head is restrained. The most obvious interpretation is that the activity of the cell is encoding eye displacement; discharge was identical during identical movements of the eyes. However, in the absence of further evidence, two other interpretations are possible. One interpretation is that the activity of the cell represents a command for a 40° gaze shift. Cell discharge is the same because the subject attempted to make a 40° gaze shift in both situations; only a 30° movement was observed when the head was restrained because the restraint prevented the execution of the command to move the head. Only the eye component of the collicular gaze command was observed, but cell discharge was the same because the collicular command was the same. This interpretation cannot be dismissed because, even in subjects that have been performing oculomotor tasks with the head restrained for several months, movements of the eyes are associated with vigorous neck muscle activity (Lestienne et al. 1984; Vidal et al. 1982), indicating that the head movement command is generated even though no head movements are possible. Yet another plausible interpretation is that the activity of the cell represents a 10° head movement command. The same head movement command was generated in the two cases, but, in the second case, the execution of the command was prevented because the head was restrained. If the possibility exists that the activity of collicular cells can encode a motor command that is not executed, multiple interpretations of the data obtained from a single cell, during head-restrained and -unrestrained conditions, are plausible (see Stanford and Sparks 1994 for an example of conditions in which SC activity is dissociated from movement metrics). Two reports are available in which comparison of SC activity during head-restrained and -unrestrained movements was used in attempts to determine which command signals are generated by collicular neurons (Munoz et al. 1991; Robinson and Jarvis 1974). For the reasons mentioned above, no valid conclusions can be based on these findings. Similarly, the observation that cells in the rostral colliculus discharge before small changes in the direction of gaze accomplished by only movements of the eyes (saccades) does not necessarily indicate that cells in the rostral SC are generating an eye displacement command. These cells could be generating a gaze displacement command that usually is executed with movements of only the eyes. Experiments in which small amplitude gaze shifts are accomplished with different combinations of eye and head movements are needed to distinguish between these possibilities.

Gaze displacement and separate channel hypotheses

The separate channel hypothesis (Cowie and Robinson 1994; May and Porter 1992) is based primarily on anatomic data demonstrating two output pathways originating in the upper and lower sublayers of the stratum griseum intermediale (SGI). The pathway from the upper SGI projects to pontine regions implicated in the control of eye movements, and the pathway originating in the lower SGI projects to pontine regions implicated in head movement control. Because of these anatomic connections, the separate channel
hypothesis assumes that an eye displacement signal is derived from the locus of SC activity in the upper SGI and a head displacement signal is derived from the locus of activity in the lower SGI and that these separate signals are sent to different pontine regions. Consequently, the separate channel hypothesis makes clear predictions about the locus of activity within these separate regions of the SC when the metrics of eye and head movements are dissociated (see METHODS).

An alternative hypothesis, that a gaze displacement command is derived from the locus of SC activity, is based primarily on the results of electrical stimulation. Stimulation of a particular SC site using constant stimulation parameters produces gaze shifts having relatively constant amplitudes and directions (cf. Freedman et al. 1996; Paré et al. 1994). This constancy does not depend on a particular eye movement being associated with a particular head movement; similar gaze shifts can be composed of eye and head components that vary over a wide range (Freedman et al. 1996). This finding is in direct conflict with the separate channel hypothesis, which predicts that electrical stimulation (at a single SC site, using constant parameters) will evoke movements composed of a fixed eye displacement coupled with a fixed head displacement. This follows from the separate channel hypothesis because the locus of activity in upper SGI (which generates an eye displacement command) and lower SGI (which generates a head displacement command) will be determined by the site of stimulation, which, under these conditions, is fixed. Thus the results of collicular stimulation are inconsistent with the predictions of the separate channel hypothesis but are consistent with the hypothesis that a unitary signal of desired gaze displacement is derived from the locus of collicular activity and that this signal is decomposed into separate displacement commands for the eye and head downstream from the SC.

Based on these alternative hypotheses, activity related to gaze, eye, or head movement metrics could be observed in the SC. Under conditions in which the metrics of eye movements are constant but gaze and head movement metrics vary, the separate channel hypothesis predicts that the population of active cells encoding a signal of eye displacement will be in a fixed location within the map, but the locus of a set of cells encoding head displacement will vary. When head movement metrics are fixed but eye and gaze metrics vary, the separate channel hypothesis predicts the locus of activity of cells encoding head displacement will remain constant but the locus of activity of cells encoding eye displacement will vary. In both circumstances, the gaze displacement hypothesis predicts that the location of the active population of cells encoding gaze displacement will vary. When gaze metrics do not vary but eye and head movement metrics do, the gaze displacement hypothesis predicts that the locus of active cells within the SC will be constant, but the separate channel hypothesis predicts that the loci of the two active populations will vary. Three behavioral conditions have been identified in which dissociations of gaze, eye, and head movement metrics are observed. As a result, we were able to test the explicit predictions of the alternative hypotheses outlined above (see Fig. 3 and related text).

For the 19 cells with motor-related activity that met the criteria for these analyses, we found no evidence of activity that was consistent with the predictions of the separate channel hypothesis. In addition, for each of these cells, activity was consistent with the predictions of the gaze displacement hypothesis. Similar analyses of the tonic rate of firing of cells without motor-related activity revealed that the discharge of these cells was coupled more tightly to the amplitude and direction of the ensuing gaze shift than to the metrics of either the associated eye or head movements.

The data obtained from 27 cells (19 with and 8 without motor-related activity) that met the criteria for testing the differential predictions of the two hypotheses were inconsistent with the predictions of the separate channel hypothesis. It is possible that due to sampling biases and the small sample size, cells with activity related to the metrics of either the eye or head movements were not observed. However, this presupposes that the SC contains three distinct displacement signals (gaze, eye, and head displacement) and that we recorded activity from only cells generating a gaze displacement signal. Our data indicate that the SC contains a signal related to gaze displacement. Given the constraints of interpretation of previous results outlined above, there exists no compelling evidence that the SC generates an eye displacement command. Until evidence is provided for the existence of eye or head displacement signals, it is parsimonious to assume that a single gaze displacement signal is derived from SC activity.

As indicated above (RESULTS and Table 1), the correlation between discharge rate and gaze amplitude was generally fairly low. In the analyses described in Figs. 6 and 7, variance in discharge rate accounted for between ~20 and ~80% of the variance in gaze amplitude. These relatively low correlation coefficients are not unexpected because, as summarized above, the metrics of movements are not coded by the frequency of firing of SC cells. What is more important to note is that the pattern of activity in the three behavioral dissociations is always consistent with the predictions of the gaze displacement hypothesis and never consistent with the predictions of the separate channel hypothesis.

The analyses on which these conclusions are reached depend on several assumptions. First, we assume that it is the locus of motor-related activity within the SC map that specifies movement metrics. This assumption is supported by existing data from the head-restrained subject (see INTRODUCTION) and by the results of electrical stimulation in the head-unrestrained subject (cf. du Lac and Knudsen 1990; Freedman et al. 1996; Paré et al. 1994). Second, the predictions of the alternative hypotheses are based on the assumption that the weighted average of the collicular output derived from the active population is constant throughout the movement (see below). If this were not the case, the assessment of the location of SC activity used in this report would be flawed. Third, we assume that movements observed when the head is unrestrained, during the delayed gaze shift task, accurately reflect the displacement command represented by the locus of motor-related activity in the SC. This need not be the case, for example, during remembered target trials (Stanford and Sparks 1994) or when the head is restrained (Freedman et al. 1996), movement metrics may not reflect the collicular command.

A potential alternative to both the separate channel and gaze displacement hypotheses, based primarily on the linear summation hypothesis of Bizzi and colleagues (Bizzi et al.'
Temporal correlations of motor activity with gaze, eye, and head

One of the predictions of the separate channel hypothesis is that there are some SC cells that encode desired head displacement. One might expect that the activity of these cells would be correlated temporally with the onset and offset of the head movement. Motor activity, in all the cells we sampled, was correlated temporally better with the onset and end of gaze shifts than with the onset and end of head movements (see also Robinson and Jarvis 1974).

The relationship between the onset of motor-related activity and the onset of gaze or eye movements depends on the amplitude and direction of the ensuing movement relative to the amplitude and direction of the cell’s preferred movement (Fig. 10) (see also Sparks and Mays 1980). The motor-related burst precedes the onset of the movement by a longer interval during movements of the preferred amplitude and direction and this interval is reduced for movements that deviate from the preferred metrics. Extrapolating from the relative timing of the burst of a single cell during a wide range of movements to the timing of the motor burst for the active population of cells in the SC (see INTRODUCTION) leads to the conclusion that motor activity in the SC spreads radially outward from the center of the active population (see also, Gandhi et al. 1994). These findings conflict with reports that activity spreads unidirectionally toward the rostral collicular pole (e.g., Munoz and Wurtz 1995b; Munoz et al. 1991).

Recent experiments using electrical stimulation of the SC indicate that maintaining collicular activity is required for stimulation-induced movements to continue until the specified amplitude and direction are accomplished (Freedman et al. 1996; Stanford et al. 1996). Stimulation data also demonstrate that cessation of SC activity is not required for movements to end; movements end when the specified amplitude and direction are accomplished despite continuing SC activity (Freedman et al. 1996; Robinson 1972; Schiller and Stryker 1972). When recording motor activity from single units in the SC of the head-unrestrained monkey, we observed that the cessation of motor activity in the superior colliculus is correlated highly with the end of the gaze shift; because the end of the gaze shift and the end of the eye movement are coupled tightly, the end of the motor burst also is correlated highly with the end of the eye movement. This high correlation is independent of the amplitude and direction of gaze shifts relative to the cell’s preferred movement and was observed across cells and across subjects. The observation that this correlation does not depend on the amplitude and direction of movements relative to the movement field center suggests that there is a general cessation of motor activity over large regions of the collicular motor map associated with the end of the gaze shift. The high correlation between the cessation of motor activity in the SC and the end of the gaze shift could occur because cessation of SC activity causes the movement to terminate or because signals related to the end of the movement produce a general reduction of SC activity throughout the motor map. Explicit tests are required to distinguish between these alternatives.

As illustrated in Fig. 11, the finding that the cessation of SC activity does not terminate the head movement could indicate that an extracollicular signal, continuing after SC activity ceases, also is involved in driving head movements during coordinated gaze shifts. A potential source of this secondary drive is a signal related to eye position in the orbit. Several reports (e.g., André-Deshays et al. 1988; Lestienne et al. 1984; Vidal et al. 1982) have described a relationship between orbital position and ipsilateral neck muscle activity, and such a signal could serve to “pull” the head toward the direction of the line of sight after the gaze shift ended. Another possibility is that after the gaze displacement signal derived from the SC is decomposed into separate eye and head displacement signals, which serve as reference signals for separate eye and head comparators (see Freedman and Sparks 1997; Freedman et al. 1996; Philips et al. 1995; Tweed et al. 1995), the head signal is maintained, despite cessation of SC activity, until head error is reduced to zero.

Using the analyses described in this report, we found that a gaze displacement signal is generated by at least some cells in the primate superior colliculus. A similar analysis needs to be applied to neuronal activity in the rostral SC under conditions in which gaze, eye, and head movement metrics can be dissociated during small amplitude gaze shifts. It also might be applied to studies of other species to determine whether the functional organization of the SC is the same in other animals. Finally, because the data in this report and the results of microstimulation of the primate SC indicate that the colliculus generates a gaze displacement command (Freedman et al. 1996), a new mapping of this structure is required; the current motor map, based on head-restrained microstimulation data (Robinson 1972), is not an accurate representation of the coordinated eye-head gaze shifts encoded by activity in the superior colliculus of the rhesus monkey.

The authors thank the anonymous reviewers for helpful comments on the original version of this manuscript. We also are grateful for the programming skills and expertise of K. Pearson.

This research was supported by National Eye Institute Grant R37-EY01189 and The McKnight Foundation Endowment Fund for Neurosci-
ence. E. G. Freedman was supported by National Institute of Mental Health training grant T32-MH-17168.

Present address and address for reprint requests: E. G. Freedman, Physiology and Biophysics, 357290, School of Medicine, University of Washington, Seattle, WA 98195.

Received 13 August 1996; accepted in final form 27 May 1997.

REFERENCES


SPARKS, D. L., HOLLAND, R., AND GUTHRIE, B. L. Size and distribution of
SPARKS, D. L. AND MAYS, L. E. Movement fields of saccade-related burst 
STANFORD, T. R., FREEDMAN, E. G., AND SPARKS, D. L. The site and parame-
ters of microstimulation: evidence for independent effects on the proper-
ties of saccades evoked from the primate superior colliculus. J. Neuro-
STANFORD, T. R. AND SPARKS, D. L. Systematic errors for saccades to 
remembered targets: evidence for a dissociation between saccade met-
rics and activity in the superior colliculus. Vision Res. 34: 93–106, 
1994.
STRASCHILL, M. AND Reid, P. Eye movements evoked by focal stimula-
STRASCHILL, M. AND SCHICK, F. Discharges of superior colliculus neurons 
during head and eye movements of the alert cat. Exp. Brain Res. 27: 
SYKA, J. AND RADMIL-WEISS, T. Electrical stimulation of the tectum in freely 
Tweed, D., Glenn, B., and Vils, T. Eye-head coordination during large 
VAN OPSTAL, A. J., VAN GISBERGEN, J. A. M., AND SMIT, A. C. Com-
parison of saccades evoked by visual stimulation and collicular electrical 
Vidal, P.-P., Roucoux, A., and Berthoz, A. Horizontal eye position-
related activity in neck muscles of the alert cat. Exp. Brain Res. 46: 448– 
453, 1982.
WURTZ, R. H. AND GOLDBERG, M. E. Activity of superior colliculus in 
behaving monkey. III. Cells discharging before eye movements. J. Neuro-