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Gaze shifts evoked by stimulation of the superior colliculus in the head-free cat conform to the motor map but also depend on stimulus strength and fixation activity

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Abstract In our previous paper we demonstrated that electrical microstimulation of the fixation area at the rostral pole of the cat superior colliculus (SC) elicits no gaze movement but, rather, transiently suppresses eye-head gaze saccades. In this paper, we investigated the more caudal region of the SC and its interaction with the fixation area. In the alert head-free cat, suprathreshold stimulation in the anterior portion of the SC but outside the fixation area evoked small saccadic shifts of gaze consisting mainly of an eye movement, the head's contribution being small. Stimulating more posteriorly elicited large gaze saccades consisting of an ocular saccade combined with a rapid head movement. At these latter stimulation sites, craniocentric (goal-directed) eye movements were evoked when the cat's head was restrained. The amplitude of eye-head gaze saccades elicited at a particular stimulation site increased with stimulus duration, current strength, and pulse rate, until a constant or "unit" value was reached. The peak velocity of gaze shifts depended on both pulse rate and current strength. The movement direction was not affected by stimulus parameters. The unit gaze vector evoked, in the head-free condition, by stimulating one collicular site was similar to that coded by efferent neurons recorded at that site, thereby indicating a retinotopically coded gaze error representation on the collicular motor map which is not revealed by stimulating the head-fixed animal. Evoked gaze saccades were found to be influenced by fixation behavior. The amplitude of evoked gaze shifts was reduced if stimulation occurred when the hungry animal fixated a food target. Electrical activation of the collicular fixation area was found to mimic well the effects of natural fixation on evoked gaze shifts. Taken together, our results support the view that the overall distribution and level of collicular activity contributes to the encoding of the metrics of gaze saccades. We suggest that the combined levels of activity at the site being stimulated and at the fixation area influence the amplitude of evoked gaze saccades through competition. When stimulation is at low intensities, fixation-related activity reduces the amplitude of evoked gaze saccades. At high activation levels, the site being stimulated dominates and the gaze vector is specified only by that site's collicular output neurons, from which arises the close correspondence between the unit-evoked gaze saccades and the neurally coded gaze vector at that site.

Key words Superior colliculus · Microstimulation
Gaze saccades · Tecto-reticulo-spinal neurons
Fixation · Cat

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Introduction

The superior colliculus (SC) is a midbrain structure composed of several layers. Its superficial layers contain visually responsive neurons that are organized into a retinotopic map subtending up to 80° of the contralateral visual field (Feldon et al. 1970). In the intermediate layers, immediately below the area centralis and foveal representations in cat and monkey, respectively, are neurons that discharge tonically during attentive fixation (Munoz and Guitton 1989, 1991; Munoz et al. 1991; Munoz and Wurtz 1992, 1993a). In cat, these are efferent neurons that send descending projections into the predorsal bundle. In our companion paper (Paré and Guitton 1994), we demonstrated that electrical mi-

crostimulation applied to the fixation area of cat SC suppresses both eye and head motion. We also presented evidence that neurons situated in this particular collicular area may exert their role in fixation control via a direct projection onto brainstem cells that inhibit the saccadic burst generator.

The intermediate and deep layers outside the fixation area of the SC are considered important to the control of saccadic shifts of gaze (reviewed in Guitton 1991, 1992). Gaze is defined here as the "eye position relative to space" (eye position relative to head + head position relative to space). Which of either the eye or the head, or both, are controlled by the SC may depend on the degree of eye motility available to the animal. In cat, an animal with a restricted oculomotor range ($\pm 25°$), some output neurons of the intermediate and deep layers project to brainstem areas that control eye and head movements (Grantyn and Grantyn 1982; Olivier 1992; Olivier et al. 1993; reviewed in Grantyn 1988). These neurons discharge prior to saccadic gaze shifts – composed of combined eye and head movements – having a specific range of directions and amplitudes (Munoz et al. 1991). Electrical stimulation evokes saccadic gaze shifts that have been claimed to be topographically organized into a gaze motor map (Roucoux et al. 1980). No direct comparison, however, has been made between the evoked gaze shift vectors and the corresponding neural activity. One objective of this paper was to determine whether, for a particular collicular site in cat, the gaze shift vector "preferred" by output neurons corresponds to that produced by electrical stimulation.

Experiments such as those summarized above have led to the view that saccadic gaze shifts are represented in the SC by a motor map and that information concerning amplitude and direction is exclusively extracted from the locus of activity on this motor map irrespective of whether it is produced by natural or electrically induced activity. This view, however, must be reconciled with recent evidence that the effects of electrical stimulation are not all-or-none. In the head-restrained monkey, the amplitude of evoked saccadic eye movements depends on current strength at near-threshold stimulus intensities (Schiller and Sandell 1983; Sparks and Mays 1983; van Opstal et al. 1990). It is only for stronger currents that saccade amplitude reaches a constant value that is close to, but somewhat larger than, that preferred by collicular saccade-related neurons recorded at the same site. In the barn owl (Du Lac and Knudsen 1990) and rat (King et al. 1991), the amplitude of head rotations elicited by stimulation of the optic tectum and SC, respectively, have been found to vary with current strength, pulse rate, and duration of the stimulus. In the cat whose head is fixed, an influence of stimulus current strength and duration upon the amplitude of saccadic eye movements has been reported by Straschill and Reiger (1973), Stein et al. (1976), and Guitton et al. (1980). Roucoux et al. (1980) also noted anecdotally that, in the head-free cat, head movement amplitude varies with stimulus duration. These observations suggest that knowing the location of the active neuronal population on the motor map may not be sufficient to deduce the resulting saccade vector, and thus appear to be at variance with the notion whereby the SC encodes saccades only by a spatial code. While the effects of varying the stimulation parameters on the properties of eye saccades (in the head-fixed monkey) and head movements (in the owl and rat) have been systematically quantified, there have been no comparable studies of SC-evoked saccadic shifts of gaze accomplished by coordinated eye-head movements. The second objective of the present investigation was to determine the influence of stimulus parameters on gaze saccades evoked by stimulating the SC of the head-free cat.

In a related phenomenon, it has been reported that saccadic eye movements elicited from the primate SC are smaller if the stimulation train occurred during active fixation (Schiller and Sandell 1983; Sparks and Mays 1983). Our final objective, related to observations in the accompanying paper (Paré and Guitton 1994), was to investigate the effects of attentive fixation on the characteristics of electrically evoked gaze shifts and to test whether artificial activation of the collicular fixation area mimics the effects of natural fixation.

In general, our results suggest that the collicular gaze motor maps of the cat derived by microstimulation and cell discharges, respectively, are coextensive and that the dependence of gaze saccade amplitude on stimulus parameters may be due to the presence of concurrent activity in the SC fixation area. The generation of the saccade vector represented at one collicular site appears to depend on whether the motor-related activity of neurons at that site can override the fixation-related activity in the rostral fixation area. A brief description of a part of this study has been presented elsewhere (Crommelinck et al. 1990).

Materials and methods

The data described here were obtained from eight alert cats (referred to in the text by the letters *G*, *H*, *L*, *M*, *Q*, *S*, *V*, and *Y*, respectively). In addition to the present study, four of the animals (cats *G*, *L*, *V*, and *Y*) were also used in the studies of SC fixation-area stimulation and collicular projection to omnipause neurons (OPNs) that were conducted in the accompaning paper (Paré and Guitton 1994). Some of the methods used in the present study have been described in the latter.

Surgical procedures

The cats were surgically prepared under general anesthesia, induced by pentobarbital sodium (Nembutal) or halothane, and aseptic conditions. A wire coil for the measurement of eye position with the search-coil technique was sutured to the sclera of one eye. The connector for the eye-coil wire and an attachment for a coil monitoring head position were embedded in a dental acrylic explant that was anchored to the skull with stainless steel bolts. A head-holding device was cemented at the rear of the explant. The head of the animal could be immobilized by securing this device to an immobile structure attached to the recording table. In three

animals (cats *H*, *M*, *Q*), electrodes made of fine, flexible 25-μm wires (Teflon-insulated; California Fine Wire) were implanted in each SC during the same surgical procedure (see Guitton and Munoz 1991). In cats *G*, *L*, *S*, *V*, and *Y*, rigid bipolar concentric electrodes (Kopf NEX-25) were implanted in a second procedure, when the animal was slightly anesthetized (ketamine hydrochloride 10 mg/kg i.m. supplemented by 2–5 mg/kg). As described in the accompaning paper, the movement vectors represented in both SC were mapped out, and stimulating electrodes were placed in collicular layers, for which electrical stimuli evoked eye movements with minimal threshold intensity, and were implanted chronically, fixed in place with dental acrylic.

Experimental procedures

During stimulation sessions, the alert animal was placed in a loosely fitting cloth bag and placed in a restraining box. The recording table was surrounded by a large curtain isolating it from the rest of the laboratory. The laboratory lights were dimmed and no fixation target was provided, save for the experiments involving interaction between stimulation-induced saccades and attentive fixation. In this latter condition, the hungry animal fixated a stationary food target positioned in front of it. The stimulus pulse train was applied in order to evoke gaze shifts either when the animal was fixating the food target or when no food target was presented. Electrical stimulation to evoke gaze shifts was also applied with simultaneous activation of SC fixation areas by bilateral electrical stimulation. The positions of eye and head relative to space were monitored by the search-coil-in-magnetic-field technique. In the head-fixed cat, the eye coil measured directly the eye position in the orbit. In the head-free animal, the eye position relative to head was obtained by subtracting the head-coil signal from the signal of the eye coil, which then measured gaze position.

For three animals (cats *G*, *Q*, and *S*), we determined the amplitude versus peak velocity relation of natural gaze saccades triggered by visual stimuli. Data were collected from gaze saccades made when the hungry cat oriented to food targets manually displaced from either side of a tangent opaque barrier positioned in front of it (Guitton et al. 1990; Munoz and Guitton 1991). The gaze saccades obtained from the three cats were grouped into amplitude bins, having widths of 5°. The mean and standard error of each bin were used to represent the data.

Electrical stimulation

A train of cathodal pulses generated by a stimulator (Grass S88) and constant-current stimulus isolation units (Grass PSIU6) was used to stimulate the deeper layers of the SC. Train duration, pulse rate, and current strength were systematically varied. Current strength was monitored on an oscilloscope and was measured by taking the voltage across a 10-kΩ resistance in series with the stimulating electrode; it ranged from 5 to 80 μA. The range of pulse rates was 100–600 pulses/s, train duration varied between 25 ms and 1 s. Strength-duration curves were generated at several stimulation sites (Fig. 1). The current threshold required to evoke a gaze shift decreased with increasing pulse duration until a duration of about 0.3 ms. Accordingly, this duration was chosen to reduce possible tissue damage.

Stimulation trials aimed at evoking gaze shifts started with the animal's head and gaze aligned with the body axis. Each parameter set (see Results) was applied at least ten times in a block, but values of the parameters in each block were randomized. In order to prevent drowsiness, the animal was fed once or twice each block. In those cases where the amplitude of the electrically elicited gaze saccades was larger than 40°, we stimulated when the cat was looking eccentrically.

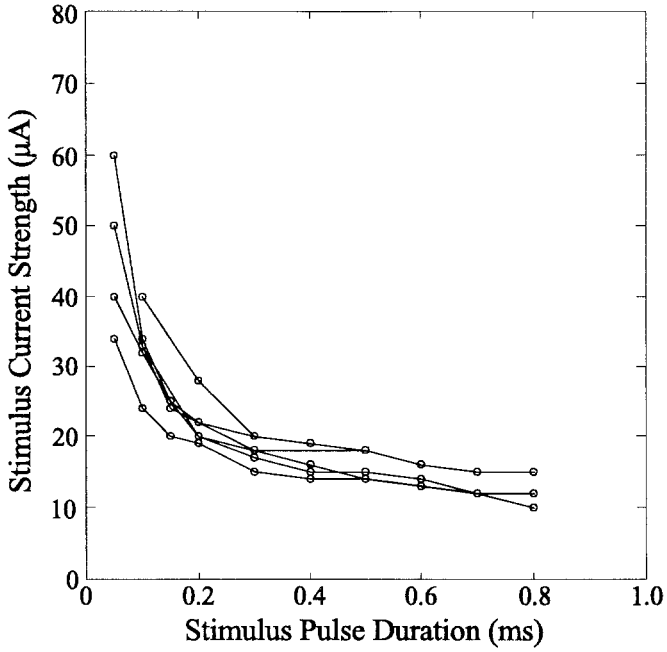


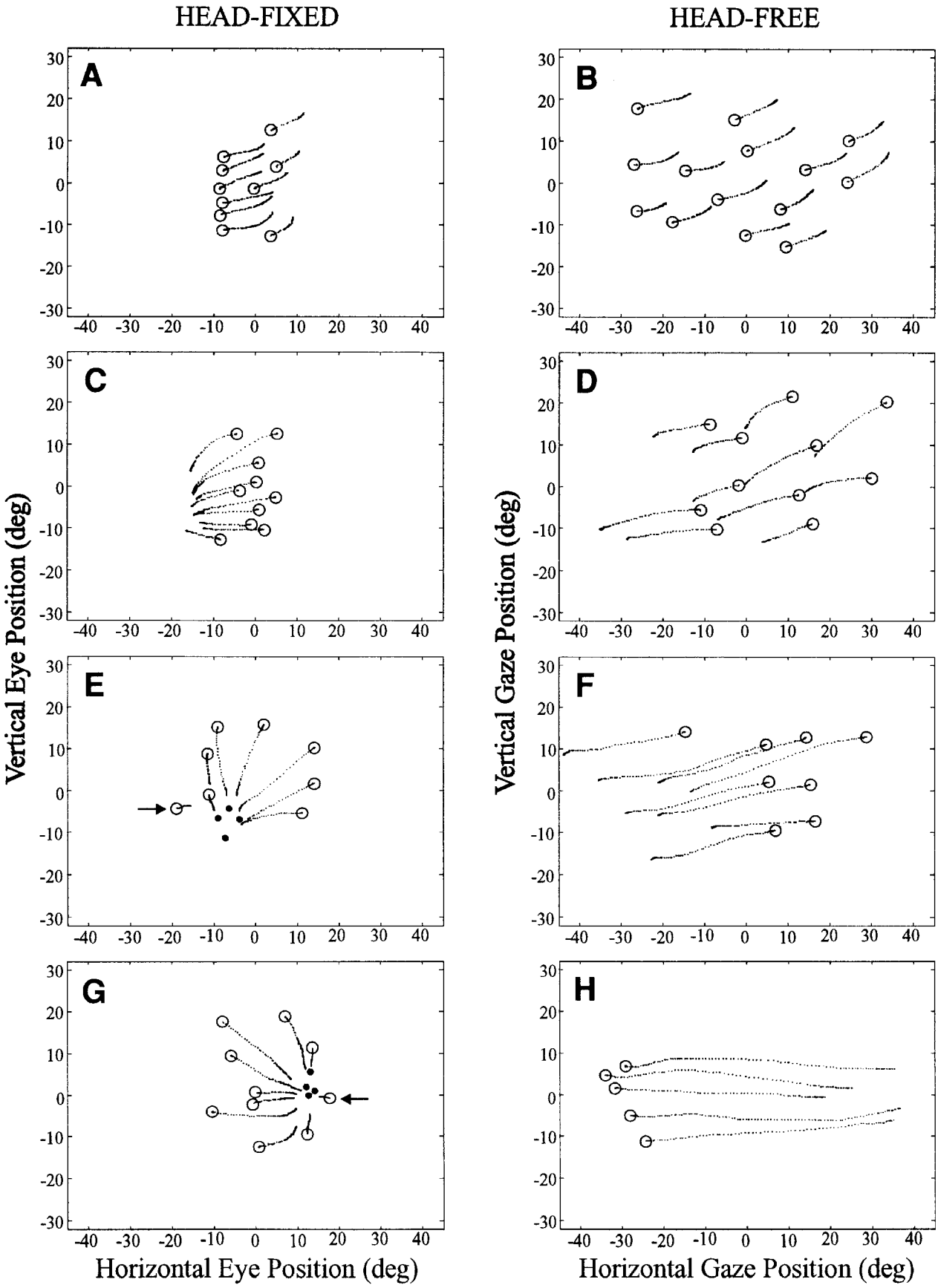
Fig. 1 Strength-duration curves for six stimulation sites in two cats (*G* and *S*). Each point gives the combination of current strength and pulse duration required to evoke an eye-head gaze shift in 50% of the stimulus presentations, using a train of 500 ms in duration and a pulse rate of 300 pulses/s.

Data analysis

Position signals were low-pass filtered at 250 Hz, digitized by a PDP-11/73 computer at 500 Hz and stored for off-line analysis. The digitized and calibrated data were displayed on a large oscilloscope screen. An interactive graphic program (courtesy of Dr. R.M. Douglas, Ophthalmology Department, University of British Columbia, Canada) allowed the investigator to scroll through the data and to select sections to be analyzed. With the use of cursors which were manually displaced, the time of onset and offset of selected eye and/or gaze saccades was delineated using the movement velocity traces which were derived from position traces by calculating the instantaneous rate of change in position across five data points. The onset of a movement was defined as the moment when the velocity first reached 20°/s, and the offset was taken as when the velocity fell again to this value. In those cases where a second movement occurred before the velocity of the first one decreased to the criterion level, the end of the first movement (the only one considered for analysis) was set at the moment midway between the deceleration phase of the first movement and the acceleration phase of the second one. The computer software measured and stored the following parameters: vectorial amplitude, direction, latency, duration, and vectorial peak velocity. The vectorial peak velocity was computed using the equation $V_r^2 = V_h^2 + V_v^2$, where V_h is peak velocity of the horizontal component, V_v is peak velocity of the vertical component, and V_r is peak velocity of the resultant vector. The peak velocity values obtained from this equation were compared with the values of the peak velocity derived from the real vector computed from the point-by-point vector summation of the horizontal and vertical components. No significant difference was observed, most oblique saccades being straight.

Results

As we will show in later sections, the amplitude and velocity of electrically evoked gaze shifts depended on


HEAD-FIXED
HEAD-FREE
A
B
C
D
E
F
G
H
Vertical Eye Position (deg)
Vertical Gaze Position (deg)
Horizontal Eye Position (deg)
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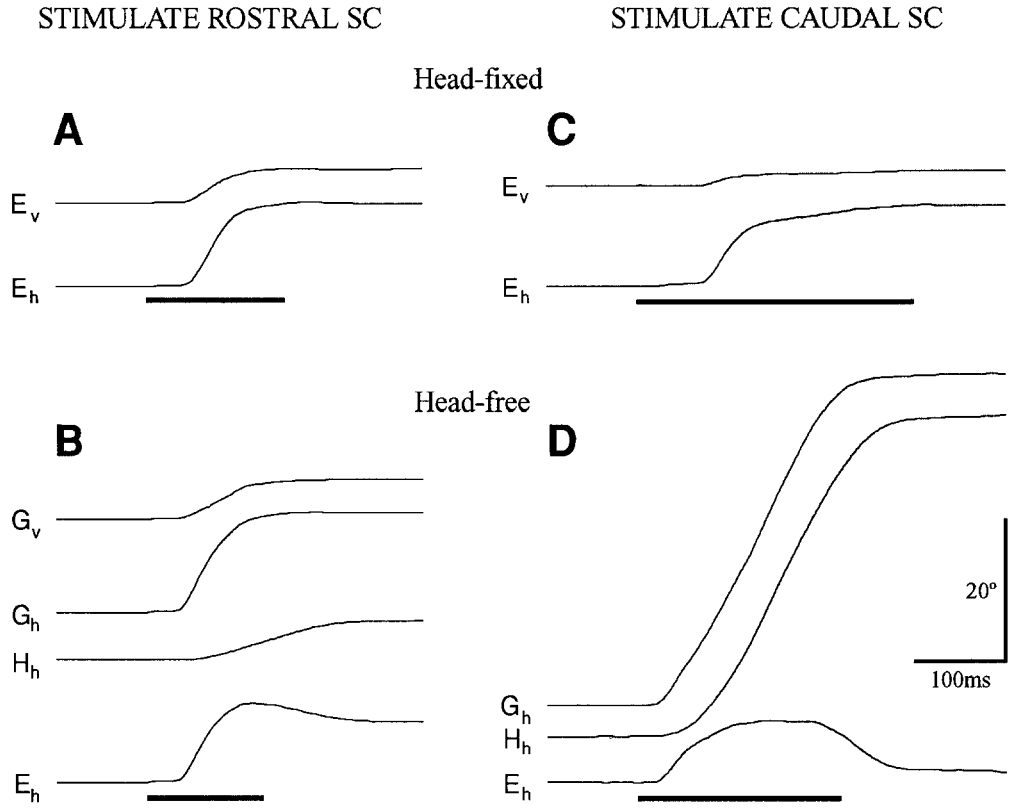


Fig. 3A–D Time course of electrically elicited eye and eye-head gaze saccades. **A,B** Data from a rostral site (*Q53*); **C,D** data from a caudal site (*Q46*). *top*, head-fixed condition; *bottom*, head-free condition. Examples **A,B,C,D** are selected from the *x-y* plots of Fig. 2A,B,G,H, respectively. Stimulation period is indicated by the *horizontal bar* below the movement traces. G_h, G_v, H_h, E_h, and E_v are the position traces of gaze, head, and eye in the horizontal (subscript *h*) and vertical (subscript *v*) planes. *Upward deflections on traces* indicate movements up and to the right, respectively

stimulus duration, pulse rate, and current strength. Before considering these effects, we will briefly review the general organization of the collicular motor map as revealed by suprathreshold stimulation and long stimulus trains in both head-fixed and head-free conditions.

General characteristics of eye, head, and gaze saccades evoked by collicular stimulation

Extensive parametric experiments were performed in seven cats (*G*, *H*, *L*, *Q*, *S*, *V*, and *Y*). In total, 17 locations in the deeper layers of the SC were studied. Figure 2 shows trajectories of eye saccades (head-fixed) and gaze saccades (head-free) evoked by suprathreshold electrical stimulation (2 times current threshold, 300 pulses/s) at different collicular sites selected along the rostrocaudal axis so as to give nearly horizontal gaze saccades. In the head-fixed condition, three types of saccade trajectories were distinguished: retinocentric (Fig. 2A), converging (Fig. 2C), and craniocentric (Fig. 2E,G). Similar patterns of SC-induced eye movements have been described before (Guitton et al. 1980; McIlwain 1986), thereby confirming our collicular electrode placements.

In the head-fixed animal, eye saccades, directed contralaterally to the stimulated site, were evoked by stimulating sites located in rostral regions of the SC, but excluding the fixation area (Fig. 2A). These saccades are described as roughly retinocentric, because the initial position of the eyes had a negligible influence on the direction of the evoked saccades. The amplitude of the saccades was, however, slightly dependent on the initial eye position (see McIlwain 1986, 1990). The trajectory as a function of time of one of the saccades of Fig. 2A is shown in Fig. 3A. When stimulation was applied to the same site in the head-free condition (Figs. 2B, 3B), the evoked gaze saccades had amplitudes and directions very similar to the eye saccades elicited in the head-fixed condition. For these rostral sites, the evoked head movement contributed little to the gaze shift because of its slow rise time. In both head-fixed and head-free conditions, long stimulus durations produced a staircase series of saccades (e.g., Fig. 4) having a similar direction but of decreasing amplitude as the gaze reached eccentric positions.

Craniocentric saccades were evoked, in the head-fixed animal, from stimulation sites located more caudally in the SC (Fig. 2E,G). The direction and amplitude of these eye saccades were systematically modified by initial eye position. The eye was directed to a particular

Fig. 2A–H Trajectories of eye and eye-head gaze saccades produced by electrical stimulation of different collicular sites in the rostrocaudal direction. *Left column*, cat is head-fixed; *right column*, head-free. **A,B** Stimulation site located in rostral regions (site *Q53*); **C,D** intermediate regions (site *S4*); **E–H** caudal regions (sites *G2* and *Q46*, respectively). The trajectory of saccades are projected onto the animal's frontal plane. Zero on *x*- and *y*-axis represents the straight-ahead position, the center of the oculomotor range. *Empty circles* indicate the initial gaze position; gaze position was sampled at 2-ms intervals. *Black dots* in **E** and **G** indicate gaze positions at which no movement was elicited. Current strength was 2 times threshold and pulse rate was 300 pulses/s

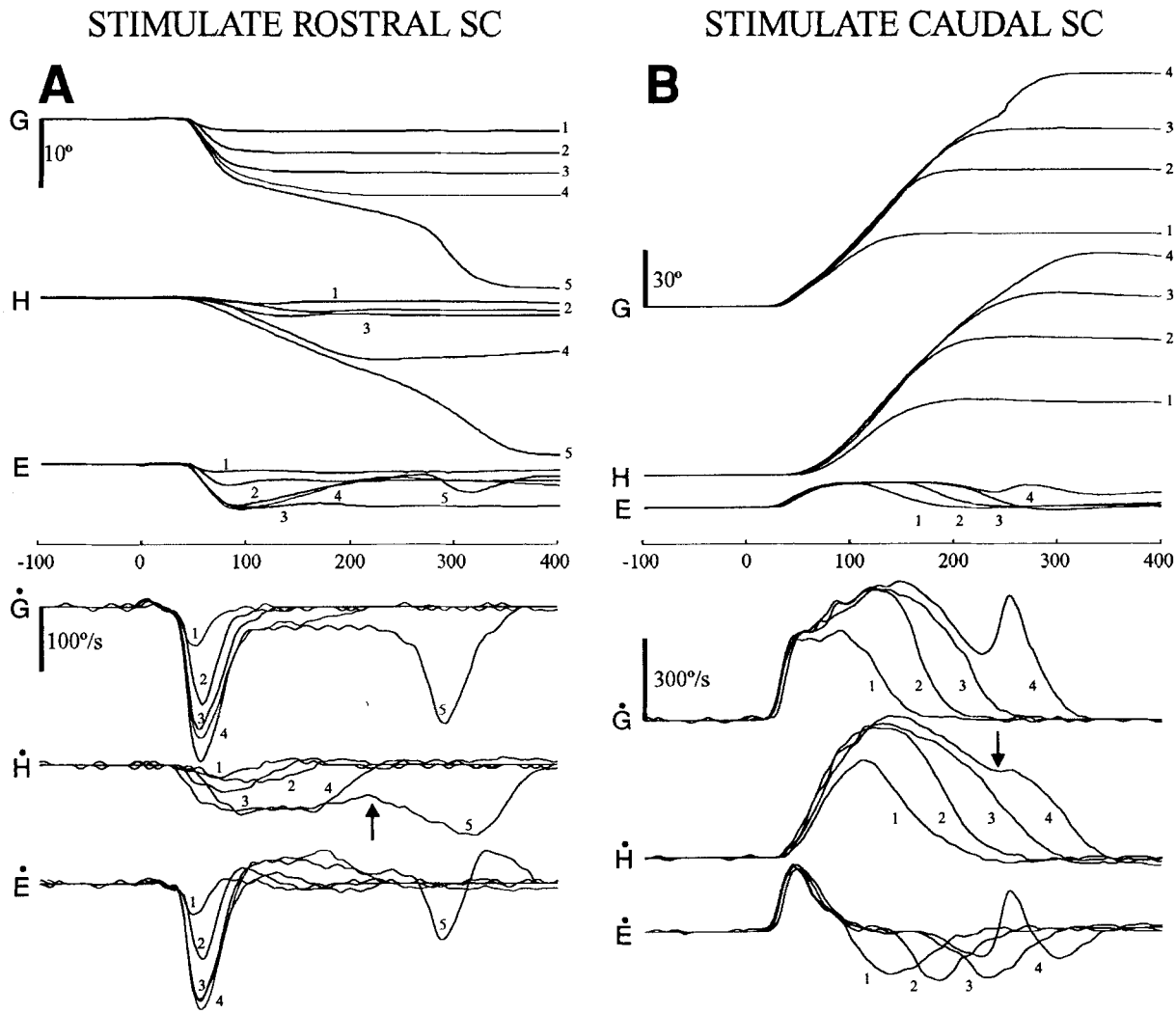


Fig. 4A,B Effect of varying the duration of the stimulus pulse train on eye-head gaze saccades. **A** Data from stimulation of a rostral site (*Q20*). Train durations were 25 (1), 50 (2), 75 (3), 125 (4), and 300 ms (5). Current strength and pulse rate were 40 μA (2 × threshold) and 300 pulses/s. **B** Data from stimulation of a caudal site (*Q46*). Train durations were 100 (1), 150 (2), 200 (3), and 250 ms (4). Current strength and pulse rate were 30 μA (2 × threshold) and 400 pulses/s. The horizontal components of position and velocity traces are plotted as a function of time, in milliseconds. Zero on time calibration indicates the onset of the stimulus. *G*, *H*, *E* and $\dot{G}$, $\dot{H}$, $\dot{E}$ are, respectively, the position and velocity traces of gaze, head, and eye

region of the orbit frequently referred to, in the literature, as the "goal." Ipsiversive eye movements could occasionally be elicited (arrows in Fig. 2E,G), and, when the eye was in the goal region, stimulation failed to evoke eye movements. By comparison with more rostral regions, long stimulus trains could not, in the head-fixed cat, elicit multiple saccades from these caudal sites (Fig. 3C). When the animal's head was unrestrained, stimulation evoked coordinated eye and head movements, resulting in large saccadic gaze shifts whose trajectories appeared independent of the initial position of the visual axis in space (Figs. 2F,H, 3D). Head motion made an important contribution to these gaze shifts. The movement of the eye in the orbit was an eye saccade followed by a plateau or ramp of low velocity. The eye movement usually started from approximately a central position, and during the plateau phase the eye position was at the goal position defined in the head-fixed condition. Long-duration stimuli elicited staircases in gaze position in the head-free animal (e.g., Fig. 4B). The mean direction of the gaze saccades corresponded roughly to the vector between the primary position and the goal position observed in the head-fixed stimulation condition.

Figure 2C shows several saccades elicited, in the head-fixed cat, from a site located between the rostral and caudal regions of the SC. These saccades tended to combine the properties of those evoked from the more anterior and posterior sites. They were directed toward the contraversive side but tended to converge toward a point beyond the limits of the oculomotor range. Multiple saccades were seldom seen when long stimulus trains were used. Combined eye-head gaze saccades elicited from these sites (Fig. 2D) had amplitudes between those of the anterior and posterior sites.

These results complement those reported for the

head-fixed cat by Guitton et al. (1980) and McIlwain (1986, 1990), and for the head-free cat by Roucoux et al. (1980). In general, evoked gaze saccades made head-free, but not eye saccades made head-fixed, had vectors which appeared to conform to the organization of the retinotopically coded motor map of the SC. This will be demonstrated more directly in a later section, where we compare gaze vectors produced by neural and electrical activity.

Dependence of electrically evoked gaze saccades on stimulus parameters

Stimulus duration

Varying stimulus duration generated systematic changes in the amplitude of eye, head, and gaze saccades. Figure 4 shows, for two collicular sites located in the rostral (*Q20*) and caudal (*Q46*) regions, respectively, a series of combined eye-head gaze shifts evoked with stimuli of different durations. In general, the amplitude of gaze saccades increased with stimulus duration until it attained a constant value (see below). In the rostral region, the dependency of gaze saccade amplitude on stimulus duration was due mainly to a variation in the amplitude of the saccadic eye movement. Because of a small contribution of head motion, stimulation in the head-fixed and head-free conditions produced similar results. In caudal SC regions, the evoked gaze shift was strongly influenced by the amplitude and velocity of the head saccade, since the eye movement in the orbit was of small amplitude compared with the displacement of gaze (see also Fig. 3D). Thus, the dependence of head saccade amplitude on stimulus duration strongly influenced gaze motion, the eye remaining at the plateau position (Fig. 4B).

In these two regions, if stimulation duration was sufficiently lengthened, a second gaze saccade occurred after a short and variable period, varying from 25 to 150 ms. The duration of this intersaccadic period was inversely proportional to the pulse rate or the current strength of the stimulus. During this period, gaze displacements could continue with a ramp-like motion (Fig. 4) in which velocity increased with the stimulus pulse rate or current strength. In contrast to the staircase gaze shifts, the head trace appeared more continuous, but the presence of distinct head movements could

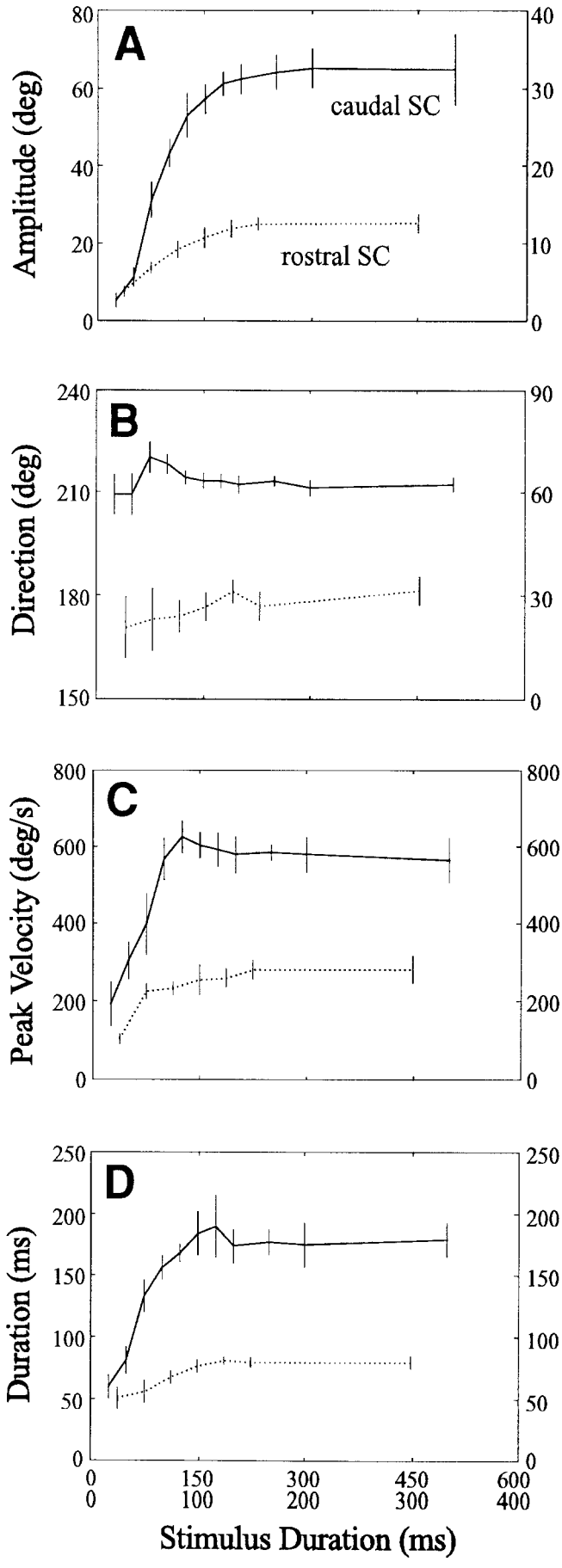


Fig. 5A–D Quantitative effect of stimulus duration on combined eye-head gaze saccades. The mean value of amplitude, direction, peak velocity, and duration of gaze saccades are plotted as a function of stimulus duration. *Vertical bars* indicate ± 1 standard deviation. *Dotted lines*, data from stimulation of a rostral site (*Q53*); current strength and pulse rate were 35 μA (2 × threshold) and 300 pulses/s. *Solid lines*, data from stimulation of a caudal site (*Q31*); current strength and pulse rate were 50 μA (2 × threshold) and 300 pulses/s. *Right y-axis* and *bottom x-axis*, rostral site; *left y-axis* and *top x-axis*, caudal site

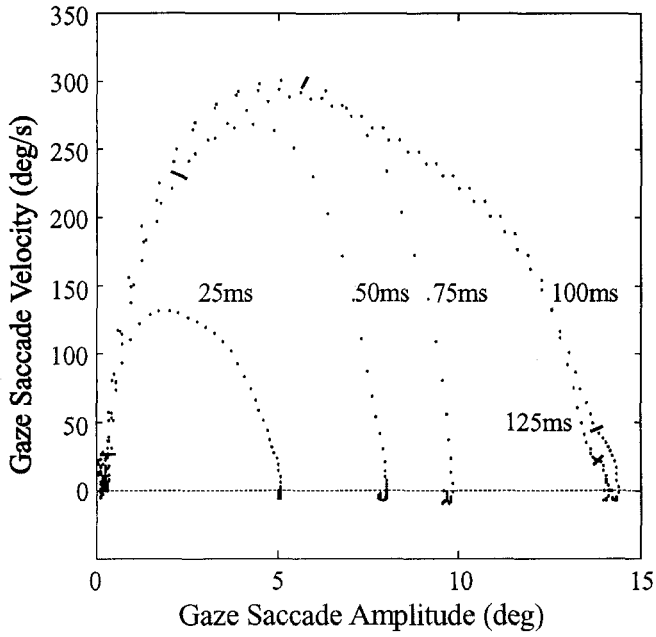


Fig. 6 Phase plane plot of gaze velocity versus gaze position over the course of stimulation-induced saccades. Results from a rostral site (*Q53*). Each curve represents a single saccade evoked with the stimulus duration indicated. Current strength was 35 μA (2 × threshold) and pulse rate was 300 pulses/s. The *small bar* on each curve indicates the end time of the stimulation train

still be discerned, particularly on the head velocity trace (arrows in Fig. 4). The smoothing effect on head motion was most probably due to the large inertia of the head.

The effects of stimulus duration on parameters of gaze saccades elicited from two other rostral (*Q53*, dotted lines) and caudal (*Q31*, solid lines) sites are shown quantitatively in Fig. 5. Figure 5A shows that the amplitude of the gaze saccade increased monotonically with train duration until a peak value was reached, the unit gaze saccade. That value varied with the location of the stimulating electrode on the SC's motor map. Also, the stimulus duration necessary to evoke the unit gaze saccade was shorter for small movements than for large saccades. The movement direction was unaffected by variations of stimulus duration (Fig. 5B). The peak velocity of the saccade initially increased with stimulus duration but remained relatively constant for additional increases, even though the saccade amplitude still increased (Fig. 5C). This suggests that saccades evoked by stimulus durations shorter than the duration required to elicit the unit gaze saccade were in fact unit saccades whose trajectories were truncated. This interpretation was also supported by two additionnal observations: (1) gaze saccades elicited with different train durations had almost identical position and velocity profiles for the initial part of the movement (Fig. 4); and (2) phase plane plots of gaze velocity versus gaze position over the course of saccades evoked from the same site but with different stimulus durations were identical until the stimulus end time, at which point the gaze saccades started to decelerate (Fig. 6).

Stimulus pulse rate and current strength

Variations in the pulse rate or current strength of the stimulus affected in the same way eye, head, and gaze saccades elicited from both rostral and caudal SC. Threshold currents for all the stimulation sites ranged from 8 to 25 μA (with a stimulus pulse rate of 300 pulses/s). Threshold pulse rate was around 100 pulses/s (at 2 times current threshold). The threshold current was inversely proportional to stimulus pulse rate and vice versa. Figure 7 shows examples of combined eye-head gaze shifts elicited from rostral (*Q53*) and caudal (*Q46*) sites, respectively, with stimuli of different pulse rates, but of fixed current strength. For low rates, saccades were small and had low velocity. If the stimulus train was long enough, a succession of small gaze saccades could also be evoked with these near-threshold stimuli (asterisk in Fig. 7B). As the stimulus pulse rate increased, the amplitude and velocity of eye, head, and gaze shifts increased until saturation values were reached.

Figure 8 shows quantitatively the effects of stimulus pulse rate on properties of gaze saccades evoked, in two animals, from one rostral (site *S6*, dotted lines) and one caudal (site *G5*, solid lines) site. These results were obtained for a stimulus current twice threshold; the threshold current being defined at a pulse rate of 300 pulses/s. Gaze amplitude (Fig. 8A) increased with the pulse rate of the electrical stimulus until it attained the constant "unit" value. The shape of the function linking gaze saccade amplitude with stimulus pulse rate was dependent on stimulus current strength. Figure 9A illustrates results obtained at one caudal site (*Q46*) where we tested the effect of stimulus pulse rate on gaze saccade amplitude for three different current strengths (1.2, 2, and 3 times threshold). At low currents the amplitude increased slowly with pulse rate, whereas at larger currents the increase was rapid. The effect of current strength and pulse rate on evoked saccades could be traded off. This is addressed in more detail with regards to Fig. 9B, which will be considered in the discussion.

For a given percentage increase in pulse rate, the increase in peak velocity was usually greater than in amplitude. In most cases, peak velocity continued to increase even though amplitude had saturated (Fig. 8C, caudal site *G5*). In other cases, velocity covaried with amplitude and saturated at about the same pulse rate (Fig. 8C, rostral site *S6*). The maximum values of peak velocity, like amplitude, depended on the stimulation site. Saccade direction (Fig. 8B) was unaffected by variations in stimulus pulse rate. It depended solely on the location of the stimulating electrode. Saccades evoked at low frequencies exhibited long and variable latencies (Fig. 8D). Nonetheless, the similar direction of these saccades with the ones elicited at higher pulse rates indicates that they probably resulted from activation of the same collicular site (see Glimcher and Sparks 1993). In all cases, gaze saccade latency was reduced with increase in pulse rate; at high stimulation frequency the mean latency was always less than 40 ms.

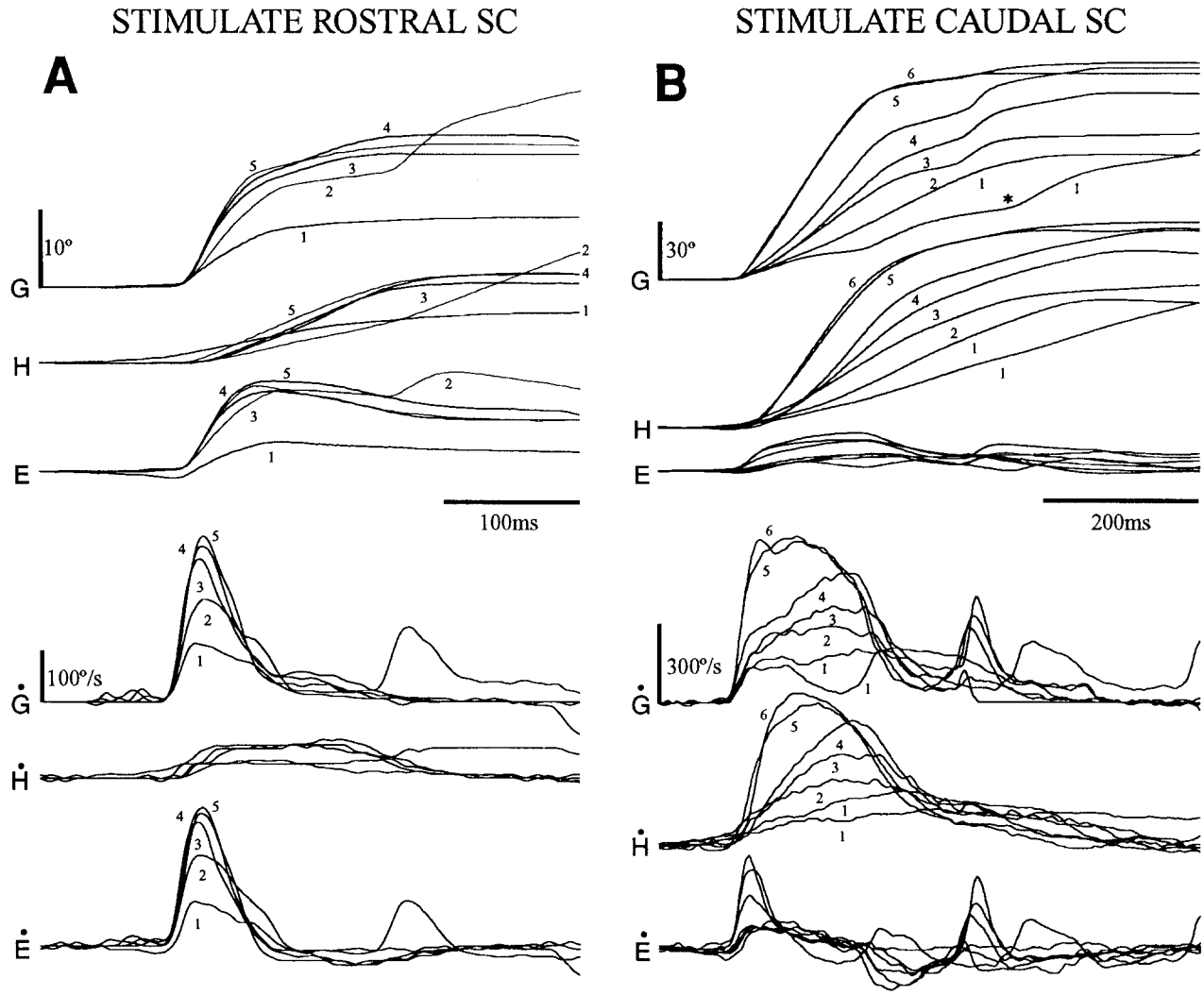


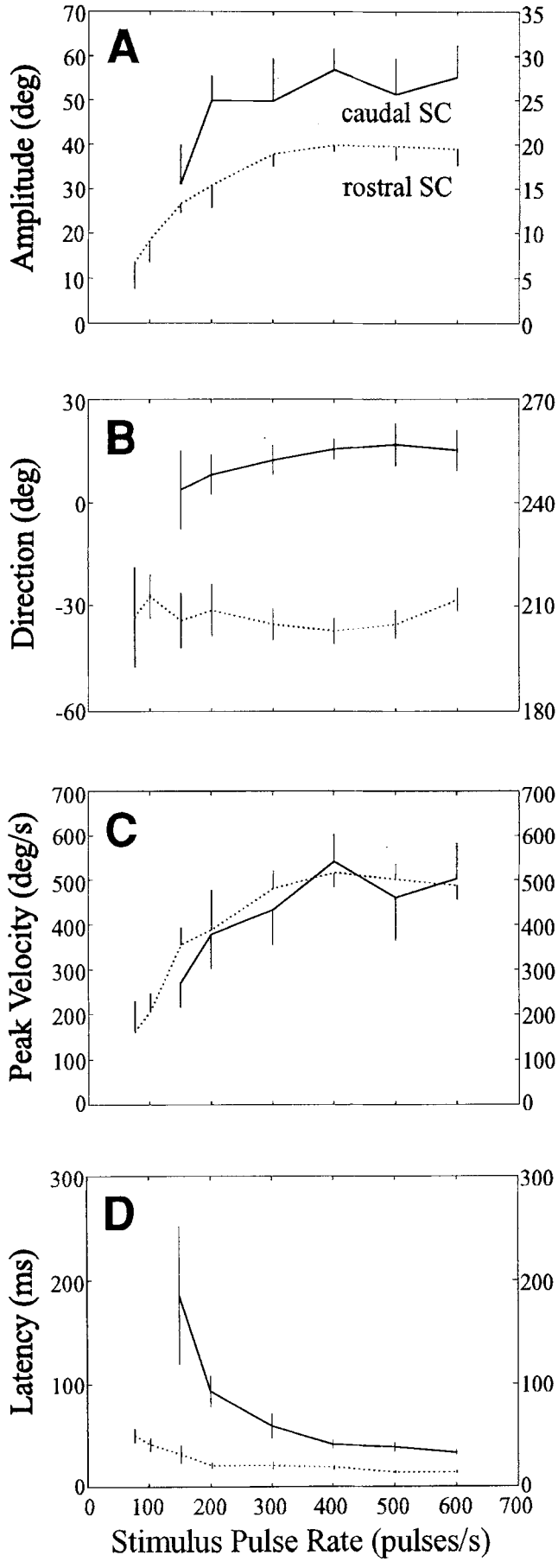
Fig. 7A,B Effect of stimulus pulse rate on eye-head gaze saccades. The horizontal components of position and velocity traces are aligned on the onset of the gaze saccades. **A** Data from stimulation of a rostral site (*Q53*); **B** data from stimulation of a caudal site (*Q46*). Current strength was 35 μA (2 × threshold). Pulse rates were 100 (1), 200 (2), 300 (3), 400 (4), 500 (5) and 600 pulses/s (6). The stimulus duration was variable but always outlasted the gaze saccade duration; the beginning of a second saccade can be seen in a few traces. (*Symbols* as in Fig. 4)

Comparison between natural and electrically evoked gaze saccades

To evaluate the kinematic properties of gaze saccades evoked at the 17 sites studied, we have plotted the maximum peak velocity obtained at each site against the corresponding maximum amplitude (Fig. 10). These values were obtained by using strong stimulation: maximum stimulus pulse rates of 500–600 pulses/s and current strength 2 times threshold. Both the amplitude and peak velocity of gaze saccades increased from rostral to caudal SC regions. For a given amplitude, the maximum peak velocity of electrically evoked gaze saccades was either comparable with or larger than the peak velocity of natural gaze saccades triggered by visual stimuli, averaged for three of the cats (*G*, *Q*, and *S*).

Comparison between gaze vectors produced by electrical stimulation and by neural activity

In cat, collicular efferent neurons outside the fixation area – tecto-reticular and tecto-reticulo-spinal neurons – have been shown to be implicated in gaze control (Grantyn and Berthoz 1985, 1988; Munoz and Guitton 1989, 1991; Guitton and Munoz 1991; Munoz et al. 1991; Olivier 1992). For a given collicular location, these output neurons generate a burst discharge that precedes gaze shifts within a specific range of amplitudes and directions. There is an optimal vector for which the burst intensity is the highest. That burst can be preceded by a sustained discharge of low frequency. For a given collicular site, that sustained discharge is present whenever the position of the visual axis is within a particular range of directions and amplitudes from a target of interest – the gaze position error field for that site (Munoz and Guitton 1991; Munoz et al. 1991). For a given neuron, the optimal vector of the movement field



and its gaze position error field are similar and are organized topographically into a motor map that controls eye-head gaze shifts.

The gaze vector evoked by suprathreshold stimulation of a collicular site and the gaze vector "preferred" by output neurons located at that site were compared. Data for ten collicular sites in two animals (cats *M* and *Q*) were available. The data on the movement fields of the neurons in cat *Q* have been published by Munoz and Guitton (1991) and Munoz et al. (1991). Data on movement fields and evoked vectors in the additional cat *M* were taken from Munoz (1988). In these experiments, the optimal gaze vector of one efferent neuron was first determined and electrical stimulation was subsequently applied through the same electrode. The comparison was made between gaze shifts that had the same starting position. Figure 11A shows that for most of the SC motor map there is good agreement between the mean value of the gaze amplitude coded by a specific efferent neuron and the maximum amplitude evoked at that site. For gaze shifts larger than 40°, the evoked amplitude was somewhat larger than the neurally determined one. In addition, Fig. 11B indicates that on average there is also correspondence between the mean directions of the preferred and evoked movements. Linear regression analysis showed a high correlation coefficient for the two relationships $r = 0.96$ and 0.98, respectively.

Dependence of electrically evoked gaze saccades on fixation behavior

The amplitude of a gaze shift evoked from one SC site depended not only on stimulus parameters, as we have shown above, but also on whether or not the animal was attentively fixating. We studied the effects of attentive fixation on gaze saccades evoked by stimulation of five collicular sites, one in each of five cats (*H*, *L*, *Q*, *S*, and *Y*). Electrical stimuli were given when the hungry animal was looking at a food target. Properties of the resulting evoked gaze shifts were compared with control gaze saccades evoked by electrical stimuli applied when the animal's attention was not solicited by food targets. Figure 12 shows results obtained from cat *H* (site *H1*). During control trials, saccades of relatively constant amplitude were evoked (Fig. 12A). When the animal was fixating its food reward, the evoked gaze shifts were reduced in size and were followed by return saccades (Fig. 12B). In addition, stimulation during fixation

Fig. 8A–D Quantitative effect of stimulus pulse rate on combined eye-head gaze saccades. *Dotted lines*, data from stimulation of one rostral site (*S6*); *solid lines*, data from stimulation of one caudal site (*G5*). The mean values of amplitude, direction, peak velocity, and latency of gaze saccades are plotted as a function of stimulus pulse rate. Vertical bars indicate ± 1 standard deviation. Current strength (2 × threshold) was 50 μA (rostral site) and 40 μA (caudal site). Stimulation duration outlasted the gaze saccade duration. *Right y-axis*, rostral site; *left y-axis*, caudal site

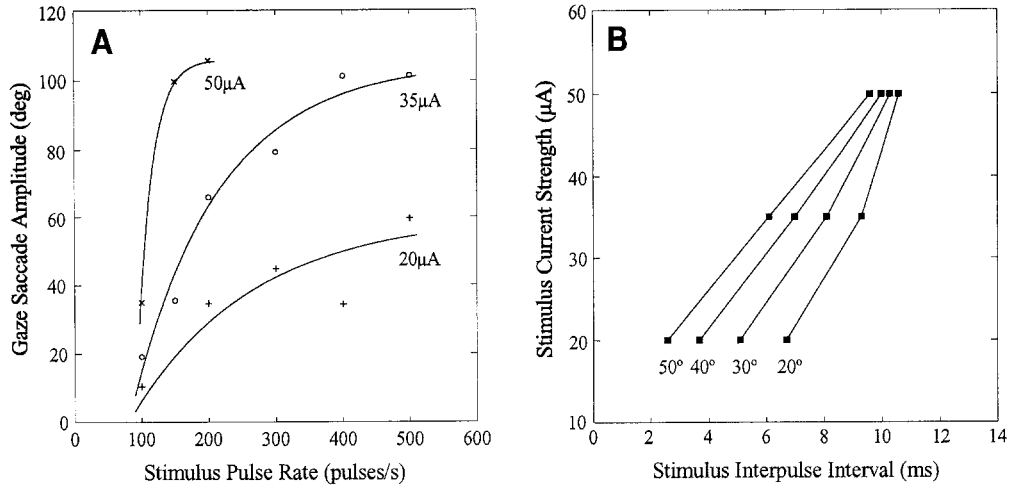


Fig. 9 **A** Mean value of eye-head gaze saccade amplitude as a function of stimulus pulse rate for different currents. Data from stimulation of a caudal site (*Q46*). Current strengths are: 1.2 (+, 20 μA), 2 (o, 35 μA), and 3 (×, 50 μA) times threshold. An exponential function was fitted to the data points. **B** Data from **A** replotted as a relation between stimulus current strength and interpulse interval. Each curve represents saccades having the same amplitude (20, 30, 40, and 50°)

Table 1 Effect of attentive fixation on the amplitude of stimulation-induced gaze saccades in five cats (*H, L, Q, S, Y*). *Ratio* is the ratio of gaze saccade amplitude evoked in fixation and no-fixation trials

Stimulation site	Stimulation parameters		No-fixation amplitude			Fixation amplitude			Ratio (%)
	Current (μA)	Rate (pulses/s)	Mean (deg)	SE	*n*	Mean (deg)	SE	*n*	
Q 31	30	100	63.0	2.2	(10)	15.4	1.2	(12)	24
S 4	40	300	12.0	0.8	(25)	7.0	0.9	(21)	58
S 4	50	300	17.1	1.3	(20)	10.6	1.1	(11)	62
L 2	40	100	1.3	0.4	(31)	0.3	0.2	(13)	23
L 2	40	200	3.4	0.2	(30)	2.4	0.1	(14)	70
L 2	40	300	3.2	0.2	(11)	2.6 NS	0.3	(6)	
H 1	60	75	11.8	0.7	(19)	2.0	1.1	(10)	17
H 1	60	100	13.3	0.5	(14)	7.4	0.6	(20)	56
H 1	60	200	14.3	0.4	(20)	7.9	0.4	(16)	55
H 1	60	400	15.3	0.3	(12)	11.6	0.3	(16)	76
*Y*2	40	100	17.2	1.1	(24)	4.1	0.9	(7)	24
*Y*2	40	125	26.2	2.4	(8)	5.8	0.7	(8)	22
*Y*2	40	150	35.4	1.6	(27)	15.8	2.0	(5)	45
*Y*2	40	200	48.7	0.8	(27)	39.8	3.9	(5)	82
*Y*2	40	300	52.4	1.5	(24)	55.2 NS	0.4	(5)	

The difference between mean saccade amplitude evoked in fixation trials and in no-fixation trials was significant (Student *t*-test, $P<0.01$), except for the last set of stimulation parameters of sites *L2* and *Y2* (*NS*)

could at times produce no movement. We also observed that gaze saccades evoked in fixation trials could bring the eyes to the same eccentricity as that attained by saccades elicited in no-fixation trials, but these were accomplished by a succession of small gaze displacements. In these cases, the head trajectory was also fragmented. In all cats and at all stimulated sites, attentive fixation reduced significantly the amplitude of evoked gaze saccades (Table 1). The amplitude of gaze saccades evoked during fixation trials was from 22 to 82% of the size of saccades evoked in control trials. The biggest reduction was seen when the intensity of the electrical stimulus was near threshold.

We investigated whether artificial activation of the SC fixation area could reproduce these fixation-induced reductions in amplitude of electrically evoked gaze shifts. For this purpose we exploited our observations described above and illustrated in Figs. 7–9 that gaze saccade amplitude is dependent on stimulus pulse rate. The relationships between the amplitude of evoked gaze shifts and the pulse rate of the stimulus applied at a caudal SC site were compared during different conditions (Fig. 13): (1) in control trials, as in Fig. 8, when the animal's attention was not solicited by a food target and when the fixation areas were not electrically stimulated; (2) when the cat attentively fixated a stationary target, as in Fig. 12; and (3) when the cat was not required to fixate but the fixation areas were electrically stimulated. In the latter experiments, an 800-ms train was delivered bilaterally through two stimulating electrodes, each located in the fixation area of a SC. After a 100-ms delay, a stimulus was applied through the electrode located in the caudal region. Results obtained in cat *Y* indicate that stimulation of the SC fixation areas produced a reduction in gaze saccade amplitude that was comparable with the effect of natural attentive fixation behavior. It was only for intense stimulation of the caudal region that artificial fixation activity, as well as natural fixation behavior, had no effect on the characteristics of the evoked gaze shifts.

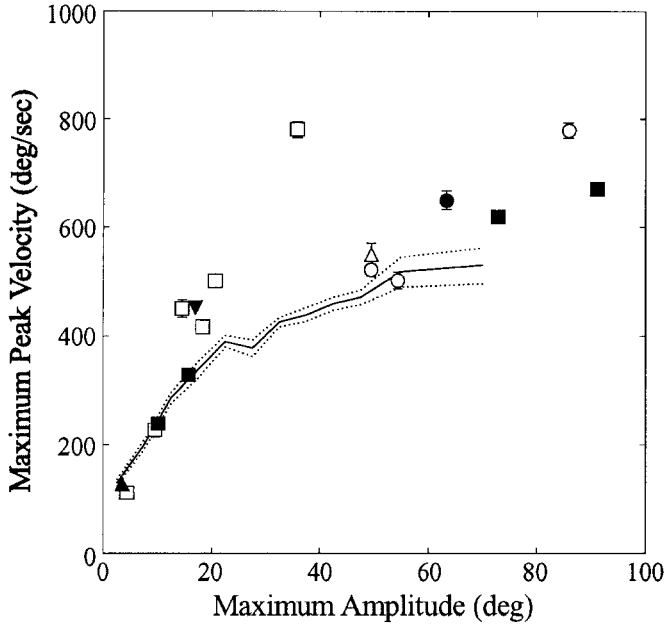


Fig. 10 Kinematic properties of electrically elicited gaze saccades evoked at the 17 sites studied. Relationship between the maximum peak velocity obtained at each site versus the corresponding peak value in amplitude. The main sequence relationships for natural, visually triggered gaze saccades of three cats (*G*, *Q*, and *S*) is shown as the mean (*solid curve*) ± standard error (*dotted curves*). Each *symbol* represents one stimulation site in: cat *G* (○); cat *H* (▼); cat *L* (▲); cat *Q* (■); cat *S* (□); cat *V*(△); cat *Y*(●). *Vertical and horizontal bars* indicate ±1 standard error. Symbols lacking a horizontal or vertical bar denote standard error equal to or less than the size of the symbols

Discussion

In this paper we have shown: (1) that stimulating the SC in the head-free cat generates a command for a saccadic gaze shift that is similar to that specified by collicular output neurons located at the site being stimulated; (2) that for a particular stimulation site, gaze amplitude, but not direction, is dependent on stimulus train duration, pulse rate, or current strength, gaze velocity being dependent on stimulus pulse rate and current strength; and (3) that artificial activation of the SC fixation area acts similarly to attentive fixation and reduces the amplitude of evoked gaze saccades.

Stimulation of the cat's SC: relation to neural discharges

A comparison of movements obtained by electrical stimulation of the SC in the monkey (Stryker and Schiller 1975; Segraves and Goldberg 1992), barn owl (Du Lac and Knudsen 1990), and cat suggests that a prime role of the SC's deep layers is to generate orienting movements of the visual axis. The relative contributions of eye, head, and body motion presumably depend on the amplitude of the evoked gaze shift and on the relative degree of mobility of the eyes, head, and body (reviewed in Guitton 1991).

Studies undertaken in the head-restrained monkey (Schiller and Stryker 1972; van Opstal et al. 1990) have reported that SC-evoked eye saccades are in register with the optimum movement vectors of saccade-related neurons recorded at the site of stimulation. The original studies of gaze saccades electrically evoked from the SC in the head-free cat suggested a topographical coding of

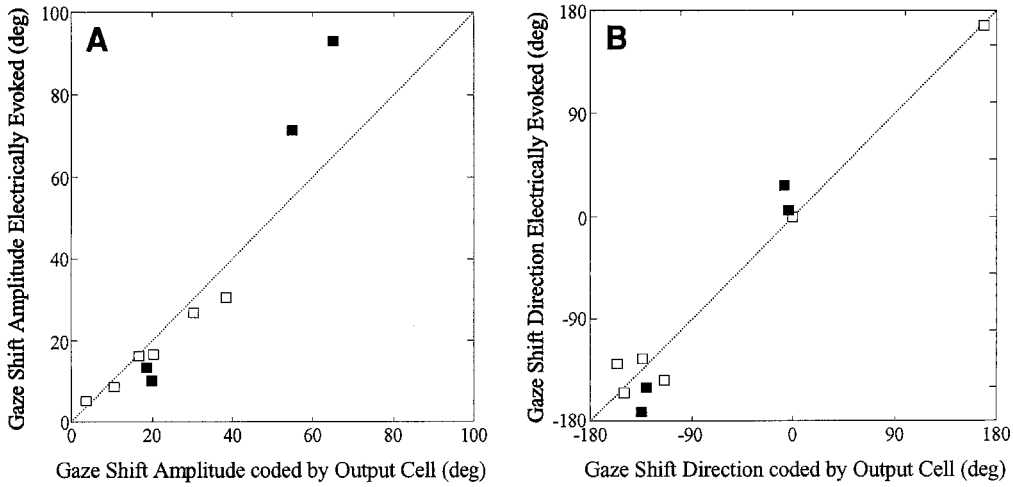


Fig. 11A,B Comparison between the metrics of gaze saccades evoked by suprathreshold stimulation and those coded by collicular output neurons recorded at the site where stimulation was applied (see text). **A** Peak amplitude (unit value) of electrically evoked gaze saccades versus the preferred gaze amplitude of a nearby physiologically identified output neuron for ten collicul ar sites. **B** Mean direction of electrically evoked gaze saccades as a function of the gaze direction preferred by an output neuron at the site of stimulation. Data show that natural cell discharges and suprathreshold electrical activity produce similar gaze shifts. Each symbol represents one stimulation site in: cat *M* (□); cat *Q* (■). (Data for cat *M* were taken from Munoz (1988))

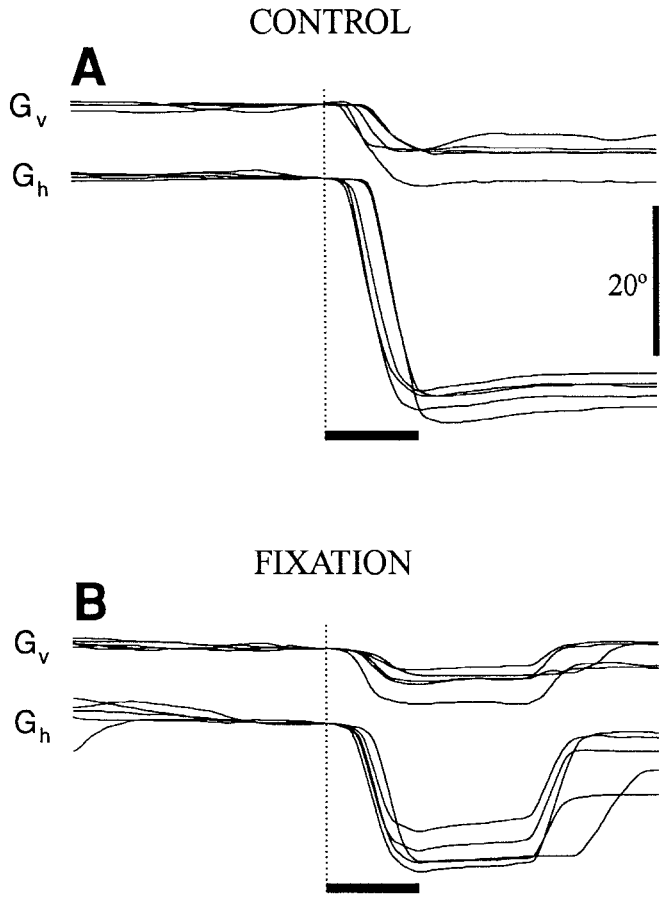


Fig. 12A,B Effect of fixation behavior on the amplitude of eye-head gaze saccades evoked at one collicular site. Data from cat *H* (site *H1*). **A** Gaze saccades elicited when no target was presented to the animal (control trials). **B** Gaze saccades elicited when the animal attentively fixated a food target (fixation trials). Stimulus parameters were 60 μA, 200 pulses/s and 100 ms train duration. (G_v gaze horizontal, G_h gaze vertical)

the gaze vectors (Roucoux et al. 1980). Similarly, the optimum gaze saccade vectors of cat tecto-reticulospinal neurons were shown to be organized topographically in a motor map controlling gaze shifts (Munoz and Guitton 1991; Munoz et al. 1991). It was not known, however, whether the two maps, deduced respectively from electrical stimulation and natural cell discharges, were coextensive. Our results suggest that they are, at least for amplitudes about less than 40°. At the caudal edge of the map, stimulation produced gaze vectors larger than those neurally encoded at these sites. A very nonlinear representation of amplitude in this zone may explain that result; the electrical activation of a circular area of tissue would recruit more neurons that discharge for larger amplitudes, hence shifting caudally the center of gravity of the presaccadic activity.

Our results also show that there is a graded relation between the level of activity artificially induced in the SC and the velocity of electrically evoked saccades, even when the amplitude of the latter has attained the unit or saturation value. A similar phenomenon occurs in natural conditions. Many collicular cells discharge with a burst whose onset precedes saccadic movements. The intensity of the burst and the movement velocity can covary. For saccades made in the absence of direct sensory guidance, such as to remembered or predicted visual targets, the burst frequency is weaker, than for saccades to visible targets (Sparks and Porter 1983; Rohrer et al. 1987; Munoz et al. 1991). Correspondingly, saccades to predicted and remembered targets are slower than to visible targets (Bronstein and Kennard 1987; Smit et al. 1987; Smit and van Gisbergen 1989; Guitton et al. 1990). In addition, there are more cells in the SC that burst before visually triggered saccades than before saccades to auditory targets (Jay and Sparks 1987). Correspondingly, saccades to auditory targets are slower

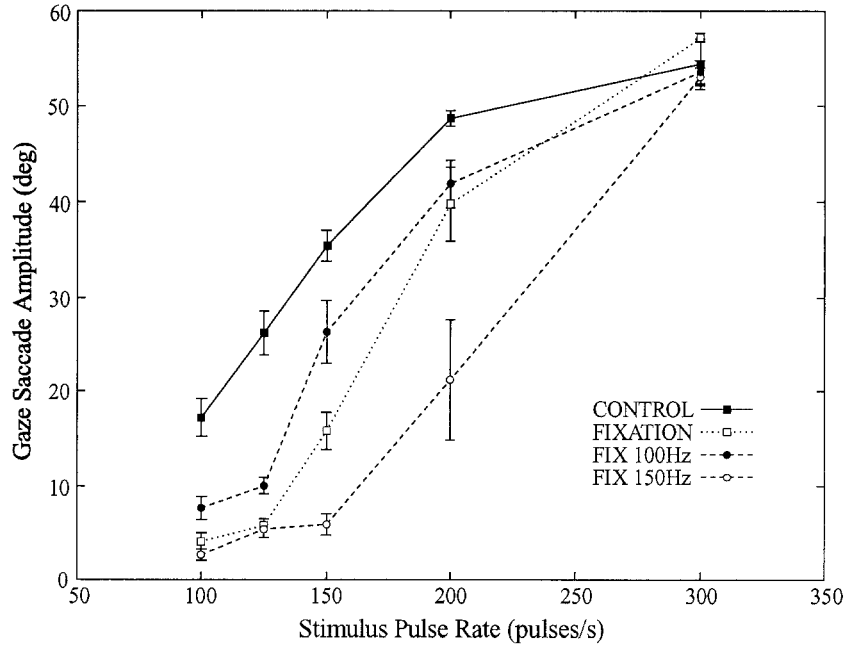


Fig. 13 Effects of bilateral electrical stimulation delivered to the superior colliculus (SC) fixation areas on the amplitude of gaze saccades evoked at one collicular site. Data from cat *Y* (site *Y2*). *Solid line and filled squares*, gaze saccades evoked when no target was presented to the animal (control trials); *dotted line and open squares*, gaze saccades evoked when the animal fixated a food target (fixation trials); *dashed lines, filled and open circles*, gaze saccades evoked when the collicular fixation areas were simultaneously stimulated (at either 100 or 150 pulses/s). *Symbols* represent mean values and *vertical bars* represent ± standard error. Stimulus current strength was 40 μA and 60 μA for the caudal SC site and the fixation area, respectively

than those to visual targets (Zambarbieri et al. 1982). Furthermore, when a zone of the SC is reversibly deactivated, saccadic eye movements, with a vector corresponding to the locus of the activated zone, are still possible but their velocity is reduced (Hikosaka and Wurtz 1985, 1986; Lee et al. 1988). Together, these observations suggest that saccadic velocity is influenced by the level of activity and number of collicular neurons recruited in a particular task. Electrical stimulation mimics well these effects.

Influence of stimulus parameters on electrically evoked saccades

The first systematic studies of saccadic eye movements evoked by electrical stimulation of the SC's deep layers, in the alert monkey, suggested that the amplitude and direction of evoked eye saccades are determined mainly by the collicular site being stimulated and are little influenced by stimulus parameters (Robinson 1972; Schiller and Stryker 1972). Later studies have suggested a more complex picture. Sparks and Mays (1983) provided some evidence that saccade amplitude depends on current strength: for small currents, amplitude was smaller and more variable than that associated with higher currents. Van Opstal et al. (1990) found a monotonic increase, to a saturation value, of saccade amplitude with current, saccade direction being independent of current strength. Saccades evoked by low stimulation currents also were slower than visually driven saccades of equivalent amplitude. This observation led van Opstal et al. (1990) to hypothesize that small-amplitude saccades associated with low currents were large saccades that were truncated but would have continued to their saturation value had the duration of the stimulus train been longer. However, they did not study the effect of varying train duration. Our results do not corroborate this hypothesis: stimulation with long trains and low currents still produced smaller gaze shifts; long trains evoked a staircase series of small movements (see Fig. 7).

Trade-off between stimulus current strength and pulse rate

Our results show that to maintain a given amplitude of an electrically evoked gaze shift as the current decreases, the frequency of stimulation must be increased. For amplitudes less than the saturation level, the stimulus current strength and interspike interval are linearly related (Fig. 9B). In the "counter model" of brain stimulation (Yeomans 1990), a given response level is determined by the total number of action potentials (firing frequency × number of axons excited) produced by focal microstimulation of a nerve. For the ideal fiber bundle, the number of axons excited is proportional to the current strength of the stimulus. It follows that, for a fixed response level, stimulus current strength is inversely proportional to firing rate or proportional to interpulse interval. Figure 9B shows that gaze saccade amplitude, below the saturation level, is proportional to the total number of action potentials induced by SC microstimulation. This observation concurs with the counter model and is further supported by the observation that gaze amplitude is proportional to stimulus train duration (Figs. 4,5). Head movements evoked by SC and optic tectum stimulation in barn owl and rat, respectively, also appear to obey the counter model's rule (Du Lac and Knudsen 1990; King et al. 1991). However, in spite of these conclusions, the assumptions leading to the counter model seem weak when applied to the SC, since this structure is nonhomogeneous and the spread of activity due to focal stimulation is largely synaptic (McIlwain 1982). Synaptic transmission is enhanced by repeated stimulation, and thus increasing stimulation intensity or frequency could lead to a spread of the area of activity as well as an increase in the firing rates of active neurons.

Effects of fixation on electrically evoked gaze shifts

We have shown that when collicular stimulation was delivered while the head-free cat attentively fixated a food target, the amplitude of the evoked gaze shifts was reduced. These results are in agreement with previous reports that, in the primate, fixation of a visual target significantly reduces the amplitude of saccadic eye movements evoked by SC stimulation (Schiller and Sandell 1983; Sparks and Mays 1983). Furthermore, we demonstrated that simultaneous, bilateral electrical stimulation of the SC fixation areas reduces the amplitude of gaze shifts electrically evoked from the SC in similar proportion to that obtained during natural attentive fixation (see Fig. 13).

How does SC fixation activity attenuate gaze shifts coded by activity elsewhere in the SC? Saccadic eye movements electrically evoked from the SC are known to interact with concurrent stimulation of other collicular sites (Robinson 1972; McIlwain 1986). An interaction between electrically and visually triggered saccades has also been observed (Schiller and Sandell 1983; Sparks and Mays 1983; Schlag-Rey et al. 1987; Pélisson et al. 1989). When two visual stimuli are presented simultaneously at different positions in the visual field, the saccadic system often generates average responses in which the saccade is directed to an intermediate position between the two targets (Coren and Hoenig 1972; Findlay 1982; Ottes et al. 1984; He and Kowler 1989). Taken together, these studies suggest that the responses are the vector-weighted average of the saccades that each stimulus elicits. For stimulation experiments, the weighting factor is the relative intensity of the stimuli.

One interpretation for the smaller gaze shifts elicited during fixation is that there is a vector averaging between activities in the collicular fixation areas (representing a 0° amplitude movement) and at the site being

stimulated. Physiologically, this may be implemented as follows. In cat, saccade-related SC output neurons are inhibited when the animal attentively fixates (Munoz and Guitton 1991). In primate, a recent report (Munoz and Wurtz 1993c) has demonstrated that collicular fixation neurons and saccade-related neurons mutually inhibit each other. Orientation-related activity is then suppressed by fixation-related activity and the gaze vector encoded at one site may be revealed only for strong stimulation. Thus, competition between activity created at a stimulation site that commands orientation and activity in the fixation areas could explain the graded relation, observed at low-level stimulation, between the amplitude of evoked gaze saccades and stimulus pulse rate or current strength. In parallel with this intracollicular mechanism, an interaction between motor and fixation signals originating from the SC could be taking place in the brainstem via the direct projection of the SC fixation areas onto omnipause neurons OPNs (see accompaning paper, Paré and Guitton 1994) which in turn inhibit oculomotor burst neurons, and which could also impede head motion (Guitton et al. 1990).

Apart from the SC, the frontal eye field and the supplementary eye field also contain neurons exhibiting fixation-related activity (Bon and Luchetti 1992; Schlag et al. 1992; Segraves 1992) and it has been shown that both areas access the raphe interpositus nucleus containing OPNs (Stanton et al. 1988; Shook et al. 1990). The demonstration by Segraves (1992) that electrical stimulation of the frontal eye field does not excite OPNs but rather inhibits them at long latencies suggests, however, that cortical fixation activity may not reach directly these brainstem neurons. Rather, it may be processed through the SC fixation areas which are tightly connected with OPNs, thereby implying a dominant role for collicular fixation activity.

The generation of goal-directed saccades in the head-fixed cat

Why does electrical stimulation applied to caudal SC regions produce large gaze saccades when the cat's head is unrestrained, whereas craniocentric (goal-directed) eye saccades are elicited in the head-fixed condition? McIlwain (1986) suggested that goal-directed eye saccades could be obtained, as a result of current spread, by the combination of retinotopically coded saccades and centering movements that are obtained by stimulation of very caudal regions of the cat SC. This suggests that goal-directed saccades are artifactual, but this explanation seems unlikely, because we showed here that in the head-free condition, gaze saccades evoked from the caudal SC, using the same stimulus parameters as in the head-fixed condition, conform to the motor map defined by output cells. In an alternative explanation of goal-directed eye movements, McIlwain (1988, 1990) proposed that during electrical stimulation the computation of target position with respect to the head is defective. The main difficulty with this proposal is that, according to the equation provided by McIlwain, stimulation of collicular sites encoding gaze saccades whose amplitudes are larger than the oculomotor range – SC sites for which stimulation produces craniocentric eye movements – would produce eye movements converging toward a goal lying outside the oculomotor range of the cat. This is not what observations made by ourselves and others indicate. Furthermore, accurate knowledge of eye, head and target position is important to the generation of gaze shifts (Guitton 1992), and collicular stimulation in the head-free cat yields gaze shifts that largely conform to the motor map defined by the discharge of efferent neurons.

A different interpretation of the goal-directed eye movement phenomenon is provided if a saturation element is placed between the SC and the eye saccade burst generator, thereby providing a neural saturation in eye position. In normal gaze shifts, a neural saturation in eye position is known to exist in cats, monkeys and humans (Guitton et al. 1984; Laurutis and Robinson 1986; Tomlinson and Bahra 1986; Guitton and Volle 1987; Becker and Jürgens 1992). The model of Galiana and coworkers (Guitton et al. 1990; Galiana and Guitton 1992; Lefèvre and Galiana 1992) incorporates such a saturation and predicts, in the head-fixed condition, retinocentric eye saccades by "stimulating" the rostral portion of the SC and craniocentric eye saccades by "stimulating" caudal regions. In this view, goal-directed saccades are not an artifact but an expression of real circuit behavior when motion of one of the mobile segments, the head, is impeded, thereby preventing completion of the gaze shift.

In general, our results suggest that electrical stimulation of the SC produces realistic effects: (1) the kinematic properties of evoked gaze saccades and of natural ones are comparable; (2) there is concordance between evoked gaze shift vectors and those "preferred" by local SC output neurons; (3) increasing stimulus pulse rate increases gaze velocity, just as increased output cell activity does; and (4) the effects of electrically activating the collicular fixation area are similar to those produced by natural fixation behavior.

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