

## RESEARCH ARTICLE

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## The collicular code of saccade direction depends on the roll orientation of the head relative to gravity

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**Abstract** This paper investigates the influence of static head tilt on the relation between activity in the motor layers of the superior colliculus (mSC) and saccadic oculomotor output. Based on single-unit recordings and electrical microstimulation in awake rhesus monkeys, we report that head roll changes the direction of the saccade vector generated by the mSC, with respect to a head-fixed coordinate system. Typically, the vector rotates in a direction that is opposite to the head roll direction. This rotation *exceeds* the amount of ocular counterroll that is observed as a result of difference in static head roll positions. We find that the mSC works in an oculocentric coordinate system that is biased in the direction of gravity. It is argued that the modification is a result of processes that occur downstream of or parallel to the mSC.

**Key words** Superior colliculus · Reference frames · Gravity · Saccades · Monkey

### Introduction

Neuronal activity in the motor layers of the superior colliculus (mSC) is tightly correlated with both the timing and the metrics of saccadic eye movements (for review, see Sparks and Hartwich-Young 1989). mSC units are active immediately prior to and during saccades, where each

unit fires optimally for a saccade vector of a specific direction ( $\Phi$ ) and amplitude (Schiller and Koerner 1971; Wurtz and Goldberg 1972). Increasing deviations from this optimum vector result in a gradual decrease in activity. The so-called movement fields of collicular saccade-related burst neurons (SRBNs) are approximately independent of sensory input (Jay and Sparks 1987; Groh and Sparks 1996; see, however, Van Opstal and Frens 1996) and form a neural map of motor space (McIlwain 1982; Ottes et al. 1986).

Depending on the site of stimulation, electrical microstimulation in the mSC leads to saccades with a specific horizontal and vertical displacement component (Robinson 1972), but with no torsional component (Van Opstal et al. 1991; Hepp et al. 1993). This displacement is only weakly dependent on eye position (Azuma et al. 1996). The output of the mSC is therefore, to good approximation an oculocentric two-dimensional eye displacement (or, equivalently, oculocentric target) vector, confined to a plane which is known as “Listing’s plane” (Von Helmholtz 1867; Tweed and Vilis 1990).

The present paper deals with the question of how the collicular output is transformed when the head is statically tilted about the naso-occipital axis (“roll axis”), which is roughly orthogonal to Listing’s plane (see Fig. 2). The answer is not a priori obvious, for the following reasons.

Firstly, head roll causes a counterrotation of the eyes. Typically this static ocular counterroll (OCR) is linearly related to the sine of the head roll angle and has a maximum amplitude of less than 10° (Haslwanter et al. 1992). Thus OCR may necessitate a different coordination of eye muscles for a movement of a given direction. Therefore the signal that is required to transform mSC output into eye displacements may vary, causing a change in the relation between the neural code of the mSC and the final oculomotor output.

Furthermore, the OCR rotates the retina with respect to the head. If the motor map in the mSC is strictly in oculocentric coordinates, then the tuning curves should follow the OCR. However, a directional bias toward gravity is also plausible, since already in an early stage of visual

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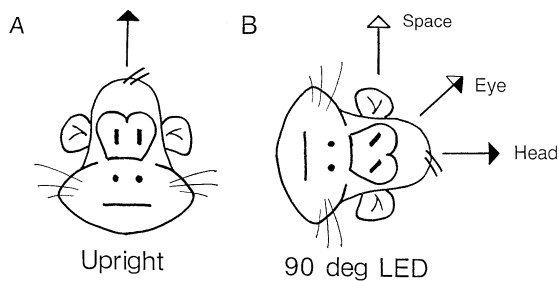
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**Fig. 1A, B** Schematic representation of orientation differences between the three hypothetical coordinate systems. **A** A monkey in the upright position. The arrow indicates “upward” for all coordinate systems. **B** The monkey has been rolled 90° left ear down (LED). Arrows indicate “upward” in the three coordinate systems (see text). The craniocentric coordinate system remains invariant with respect to the head (*Head*), the oculocentric coordinates stay in register with the current eye orientation (*Eye*), and the space-fixed coordinates remain stable relative to gravity (*Space*). Note that, for sake of clarity, ocular counterroll has been largely exaggerated in this figure. In the rest of the paper, the data are presented in a craniocentric reference frame. Thus, a saccade vector that remains invariant to the head will have a directional shift of 0°, whereas a vector that remains invariant to space would have a shift of 90° in this example

processing (areas V2 and V3/V3a) a significant number of neurons display a gravity-fixed orientation tuning (Sauvan et al. 1994; Sauvan and Peterhans 1995).

Thus, three extreme possibilities for the relation between head roll and the mSC output can be conjectured (Fig. 1):

1. The saccade vector, which is encoded by a population of units, remains invariant relative to the head. Thus, the vector is coded in *craniocentric coordinates*.
2. The saccade vector remains invariant to the eye orientation (and therefore to a target on the retina). Due to the OCR this *oculocentric reference frame* systematically deviates from the craniocentric system.
3. The saccade vector remains invariant with respect to gravity (*spatial reference frame*).

Each of these possibilities has its own clear prediction. Since the saccade vector will be described in head-centered coordinates in this paper, the prediction of the craniocentric code would be that no change in the preferred saccade direction occurs as a function of head roll. The prediction of an oculocentric code is a directional shift that equals the amount of ocular counterroll, whereas a spatial reference frame would lead to a directional shift that is equal in size, but opposite in sign to the amount of head roll.

In this study, single-unit activity in the mSC was recorded and microstimulation of mSC was performed during static head roll. Our findings are that the mSC encodes saccade direction in an coordinate system that is biased toward the direction of gravity, clearly exceeding the amount of OCR. The results of this study have been presented in abstract form (Frens et al. 1996).

## Materials and methods

### Subjects

Five rhesus monkeys (*Macacca mulatta*; Br, Ca, Cr, De, and Yu) participated in this study. The experimental protocols were in accordance with the guidelines set by the Veterinary Office of the Canton of Zurich and the *Principles of laboratory animal care* (NIH publication No. 86–23).

The surgical procedures that were applied have been described in detail previously (Hepp et al. 1993). Anesthesia was initiated with sodium pentobarbital. The animals were intubated and breathed N<sub>2</sub>O/O<sub>2</sub>, with the addition of halothane as required. Bolts were chronically implanted to allow for a stable fixation of the head during experiments. Furthermore, a recording chamber was placed over a trephine hole in the skull above the superior colliculi. A custom-made dual search coil (Hess 1990) was chronically implanted on one of the eyes.

The monkey was head-restrained during the course of the experiment. In the upright position, the horizontal stereotaxic plane of the head was pitched down by 15° with respect to the earth-horizontal. Thus, the response plane of the horizontal semicircular canals was positioned orthogonally to the direction of gravity (Böhmer et al. 1985). Before the experiments, monkeys were water-deprived to motivate them to fixate reward-associated targets, needed for the calibration of the eye position signal.

### Setup

#### Eye position recording

Three-dimensional eye position was recorded with the dual search coil technique. The head of the monkey was placed in the center of two alternating magnetic fields (20 kHz), which were in spatial and phase quadrature (Skalar Instruments, Delft, The Netherlands). Eye position was calibrated before every experimental session, following the procedures described by Hess et al. (1992).

#### Turntable

The monkeys were positioned in a computer-driven three-dimensional turntable (Henn et al. 1992), that could be positioned rapidly and reliably in the various roll and pitch positions needed for the experiments. All rotation axes met at the point where the monkey's head was centered.

#### Recording and stimulation

Recording of single-unit activity as well as electrical microstimulation in the mSC were done with varnished tungsten microelectrodes (impedance typically 1 MΩ at 1 kHz). Neurons were selected that had a short, transient burst in relation to saccadic eye movements, and that could therefore be considered as typical saccadic burst neurons. Because the monkeys made spontaneous eye movements in the light, no further classification could be made (visuomotor, quasivisual, pure motor); however, so-called buildup cells (Munoz and Wurtz 1995) were not investigated. Additionally, our analysis method required off-line selection of those cells that had a clear circumscribed movement field and that had a peak activity well above baseline.

Single-unit activity was detected by exceeding a threshold and stored, together with the eye-position signals and other relevant parameters, at a sample rate of 833 Hz. For electrical microstimulation, 70-ms trains of 0.2-ms pulses at 500 Hz were used, which were repeated every 2 s.

#### Protocol

Two experimental protocols were used:

1. *Single-unit recording*. The activity of units in the mSC was recorded, while the monkey made spontaneous eye movements in

the light. The monkeys (Yu, Cr) were positioned either upright or put in different static roll positions over an angle of  $\pm 40^\circ$ . If time permitted, the monkey was subsequently statically pitched over the same angles ( $\pm 40^\circ$ ). During data acquisition the monkey was stimulated to make saccades throughout its oculomotor range, by presenting natural visual and auditory stimuli (such as finger clicks and movements of the experimenters) throughout the visual field.

**2. Electrical stimulation during static roll.** The mSC was locally activated by electrical microstimulation in the dark, while the monkeys (De, Yu, Ca, Br) were positioned in various static roll positions, ranging from  $-120$  to  $120^\circ$ . One monkey (Yu) was also positioned in various pitch positions. Current intensities were well above threshold ( $20\text{--}100\ \mu\text{A}$ ) and generally in the order of  $50\ \mu\text{A}$ . For each stimulation site, one fixed stimulation intensity was used for all roll positions.

### Localization of the mSC

In all animals oculomotor landmarks such as the riMLF, oculomotor rootlets, or the trochlear nuclei were localized by single-unit recordings. If necessary, stereotaxic coordinates were then corrected for possible misalignments of the recording chamber or for individual variability. The electrode was then aimed in stereotaxic coordinates at the mSC, where units with typical saccadic movement fields were encountered in a spatial distribution as given by electrical stimulation (Robinson 1972; see also Ottes et al. 1986).

At the conclusion of all experiments, electrolytic or chemical lesions (kainic acid) were set. Animals were given an overdose of pentobarbital and perfused. Histological examination supported the *in vivo* coordinates of anatomical structures in all cases.

### Data analysis

#### Ocular counterroll

We determined Listing's plane for each roll position separately. OCR was defined as the shift of the plane along the axis of stimulation (see Fig. 2). The angle between the roll axis and the primary position was always smaller than  $15^\circ$ . Thus, stimulation was always in good approximation orthogonal to Listing's plane.

#### Saccade characteristics

During off-line analysis, on- and offsets of saccadic eye movements were marked automatically in the calibrated eye-position signal on the basis of a velocity and an acceleration criterion. All markings were checked by eye and, if necessary, corrected. Subsequently, saccade vectors were calculated. For the selection of saccades that were evoked by electrical microstimulation, care was taken to exclude movements that were evoked during or shortly after a spontaneous saccade.

The direction of a saccade ( $\Phi$ ) was defined as the slope of the line through the craniocentric onset and offset position of the saccade. The torsion displacement components of the saccades were negligible, so that

$$\Phi = \arctan \frac{V_{\text{off}} - V_{\text{on}}}{H_{\text{off}} - H_{\text{on}}}$$

where  $H_{\text{on}}$  ( $V_{\text{on}}$ ) and  $H_{\text{off}}$  ( $V_{\text{off}}$ ) are the horizontal (vertical) components of the saccadic onset and offset positions. By definition,  $\Phi = 0^\circ$  is rightward, and  $\Phi = 90^\circ$  is upward.

#### Neuron activity

To determine the preferred direction ( $\Phi_0$ ) in the recorded activity of a unit, we fitted a Gaussian profile through the saccade directions ( $\Phi$ ) and the associated neural activity ( $F$ ).

$$F = F_0 \exp - \frac{(\Phi - \Phi_0)^2}{2\sigma_0^2}.$$

Such a fit uses three fit parameters: the preferred direction  $\Phi_0$ , the estimated peak activity  $F_0$ , and the width of the Gaussian,  $\sigma_0$ .

$F$  was defined as the mean firing rate in a window between 20 ms prior to saccade onset and 20 ms before saccade offset (Van Opstal et al. 1995). Our results proved to be independent of the exact time window used. Using a window between 20 ms prior to saccade onset and saccade offset did not change the value of the fitted preferred direction significantly.

The data set of saccades on which the fit was based was selected on the basis of a direction and an amplitude criterion. Saccades that were used for the fit had a direction that was less than  $60^\circ$  off the estimated preferred direction ( $\Phi_{\text{est}}$ ).  $\Phi_{\text{est}}$  was determined by taking the mean of all saccade directions, weighted by their associated values of  $F$ .

The amplitudes of the saccades had to be in a range that led, in the close proximity of  $\Phi_{\text{est}}$ , to an activity of more than half of the maximum recorded firing rate. We allowed this relatively broad range of amplitudes to be included in the fit, because the shape of collicular movement fields is such that the preferred direction of a unit is *independent* of the saccade amplitude range (see Ottes et al. 1986). Thus, the resulting large set of data points gives the most reliable fit of  $\Phi_0$ , even though the absolute estimate of  $F_0$  is systematically too low.

The statistical reliability of the individual fit parameters ( $\Phi_0$ ,  $F_0$  and  $\sigma$ ) was determined by means of the Monte Carlo bootstrap procedure (Manly 1991; Press et al. 1992). As a measure for the overall fit quality, we took the mean linear correlation coefficient between the measured activity and the prediction of the fit ( $\bar{r}$ ). Cells that could not be fitted in a highly significant way in all three roll positions ( $P(\bar{r} < 0.8) > 10^{-3}$ ) were excluded from subsequent analysis. Unreliable fit results were due to either undersampling of the whole movement field or too much inherent scatter in the cell's response.

## Results

### Effects of static head roll on saccades

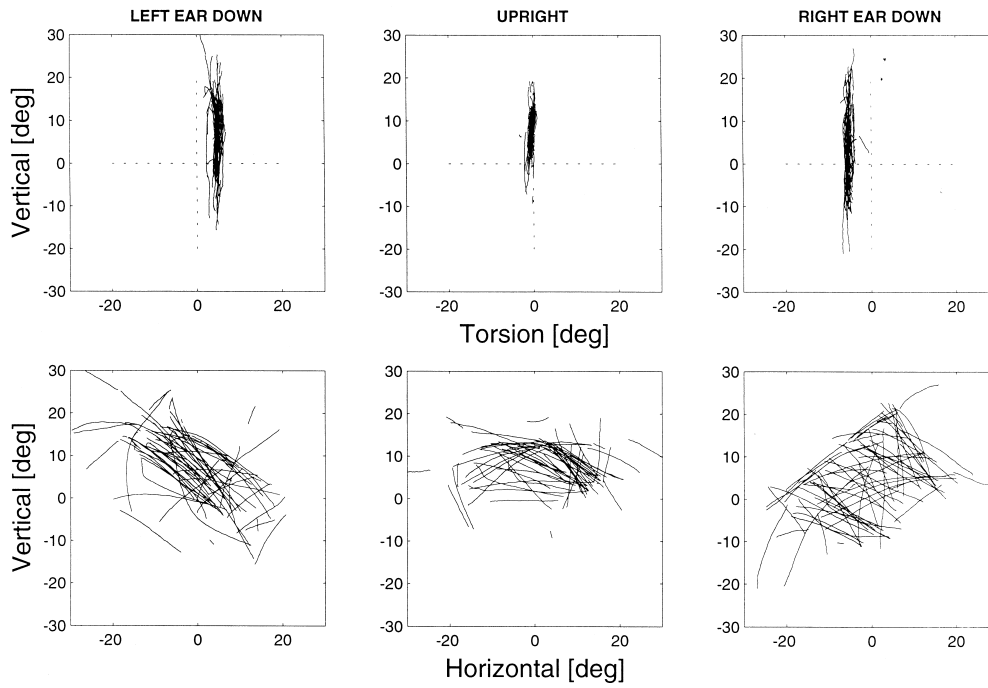
As expected, the roll of the head caused a counterroll of the eyes, which could be measured by the shift of Listing's plane (Fig. 2). During saccadic eye movements at any head roll angle, the eyes stayed to good approximation in the shifted Listing's planes.

As shown in Fig. 3, the dynamic characteristics of the saccadic eye movements were not affected by the static head roll. Saccades in all head orientations had equal main-sequence characteristics and were equally straight ( $P > 0.05$ ; two-dimensional Kolmogorov-Smirnov test).

### Single-unit recordings

We were able to record a total number of 33 saccade-related burst neurons (Cr, 25; Yu, 8) in the three roll positions ( $[-40, 0, 40]^\circ$ ), while the monkeys made spontaneous eye movements in the light. The estimated preferred amplitudes of the units varied over the whole saccadic range ( $2^\circ$  to more than  $35^\circ$ ).

The preferred direction of a unit was determined in each position by fitting a Gaussian to the direction-firing rate relation (see Materials and methods). Figure 4 shows the data and the fits of a typical unit in the three roll positions.



**Fig. 2** Saccade trajectories in three dimensions – monkey Cr. *Top* The vertical components of saccades as a function of the torsional components. The saccades were recorded, while the monkey was rolled 40° left ear down (*left*), upright (*middle*), and 40° right ear down (*right*). Note the torsional offset, in the *left and right* panels, which is due to ocular counterroll. However, the torsional components remain equally small in all head orientations. The *dashed horizontal line* shows the axis about which the monkey was rolled, which is roughly orthogonal to Listing’s plane. The *dashed vertical line* at torsion 0° serves as a visual reference for comparing the torsional offset in the different panels. *Bottom* The same vertical components, but now as a function of the horizontal component. For sake of clarity, all panels show 100 randomly selected saccade trajectories, drawn from the full data set of 800–1000 movements

We defined the change in preferred direction:

$$\Delta\Phi_0 = \Phi_0^{\text{LED}} - \Phi_0^{\text{RED}}$$

where  $\Phi_0^{\text{LED}}$  and  $\Phi_0^{\text{RED}}$  are the fitted preferred directions in the 40° left- and right-ear-down roll positions, respectively. Figure 5 shows the obtained values of  $\Delta\Phi_0$  for the 26 units that had highly significant fit results in all three roll angles [ $P(\bar{r} < 0.8) \leq 10^{-3}$ ; see Materials and methods]. It should be noted that the value of  $\Phi_0$  in the upright position was always between the values obtained in the right- and left-ear-down positions.

The mean value of  $\Delta\Phi_0$  was  $-16.1 \pm 1.6^\circ$ , where the minus sign indicates that the direction shift was in the opposite direction of the change in head orientation. This was significantly different from 0° ( $P \leq 10^{-4}$ ) and significantly more than the measured mean static OCR difference between the left- and right-ear-down positions ( $-8.1 \pm 0.2^\circ$ ;  $P \leq 10^{-4}$ ). Thus, the shift in orientation exceeded the predictions both of a head-centered code (prediction:  $\Delta\Phi = 0^\circ$ ; solid line in Fig. 5) and of an eye-cen-

tered code (prediction:  $\Delta\Phi$  equals the ocular counterroll difference; dashed line in Fig. 5). On the other hand, it was considerably smaller than the prediction of a space-fixed reference frame ( $\Delta\Phi = -80^\circ$ ; dotted line in Fig. 5;  $P \leq 10^{-4}$ ).

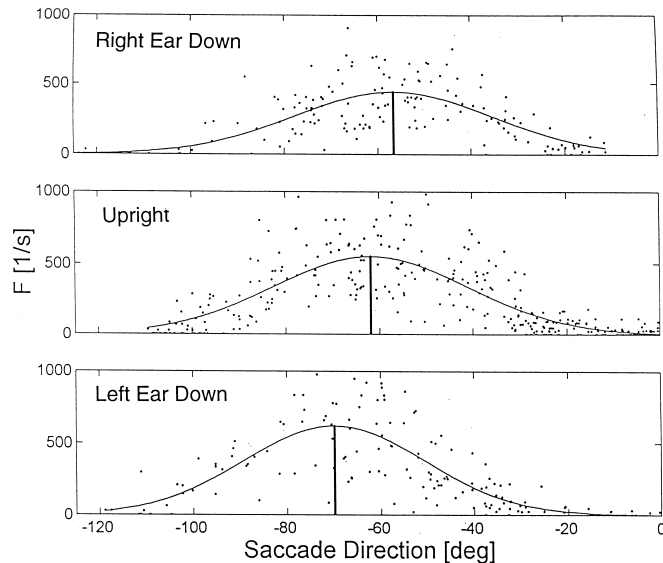
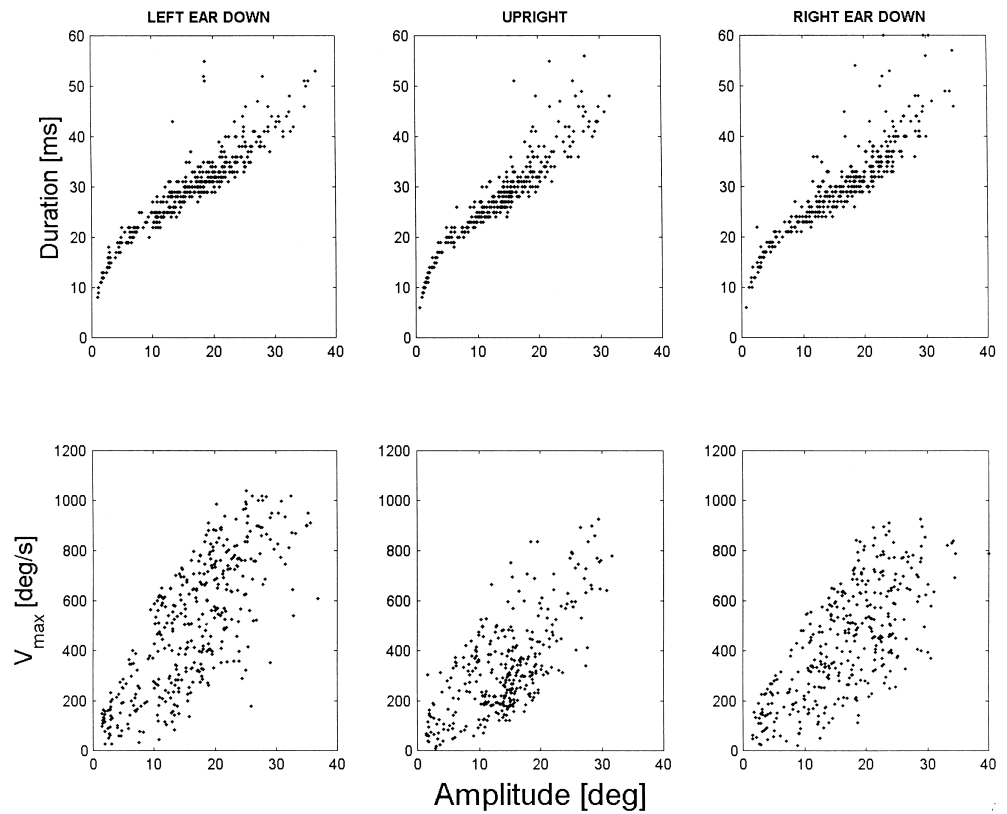
On an individual basis, all neurons changed their preferred direction by less than 80°, whereas 23 of 26 neurons displayed an orientation shift that differed significantly from 0° ( $P \leq 0.01$ ) and 21 of 26 showed an orientation shift that significantly exceeded the OCR difference. Nonetheless, the  $\Delta\Phi_0$  of each neuron was most closely related to the prediction of an oculocentric coordinate system ( $\Delta\Phi = \text{OCR}$ ). There was no correlation between the values of  $\Delta\Phi_0$  and the OCR differences measured during the recording of the neurons ( $r = 0.07$ ;  $P > 0.05$ ). Furthermore, the value of  $\Delta\Phi_0$  was independent of the preferred direction or the estimated preferred amplitude of a unit (Fig. 6).

As a control, the monkeys were pitched to  $\pm 40^\circ$ , during the recordings of eight cells. This did not result in a systematic shift in preferred directions (not shown). Neither of the other fit parameters, peak activity ( $F_0$ ) and the width of the Gaussian ( $\sigma_0$ ) varied systematically as a function of either roll or pitch.

### Microstimulation

We stimulated 13 sites in the mSC of four monkeys (De, 6; Yu, 3; Br, 2; Ca, 2) while they were positioned in static roll orientations in the dark. The range of tilts varied from monkey to monkey, mainly due to what the monkey accepted. Monkey Yu, who was extensively trained for work in any body position, could be rolled to body orientations up to  $\pm 120^\circ$  off-vertical.

**Fig. 3** Main sequence relations – monkey Cr. Top The relation between saccade amplitude and duration (top row) and saccade peak velocity (bottom row), while the monkey was rolled 40° left ear down (left), upright (middle), and 40° right ear down (right). The dynamic characteristics were identical for all three orientations. Note the relatively large scatter in peak velocities, which is due to the fact that saccades have been pooled over directions and starting points



**Fig. 4** Representative example of single-unit activity in the three roll positions – cell CR5802. The firing rate ( $F$ ) of a collicular saccade-related burst neuron as a function of saccade direction, together with the fitted Gaussian profile. Data points were selected from a relatively wide amplitude range, which explains the large scatter in individual firing rate values. However, such a large data set is optimal for the estimate of  $\Phi_0$  (see text). Rolling the monkey from 40° right ear down (upper panel) to upright (middle) to 40° left ear down (lower panel) results in a preferred direction (indicated by the thick lines) that shifts systematically in the opposite direction.  $\Delta\Phi_0$  of this neuron is  $-13.0 \pm 1.9^\circ$  ( $P(\Delta\Phi_0 = 0) < 0.01$ ); the ocular counterroll difference during this measurement was  $-8.0 \pm 0.9^\circ$

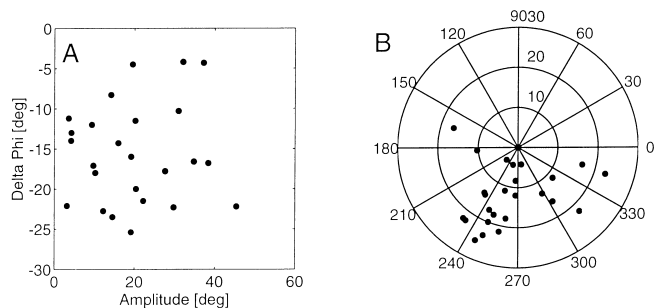
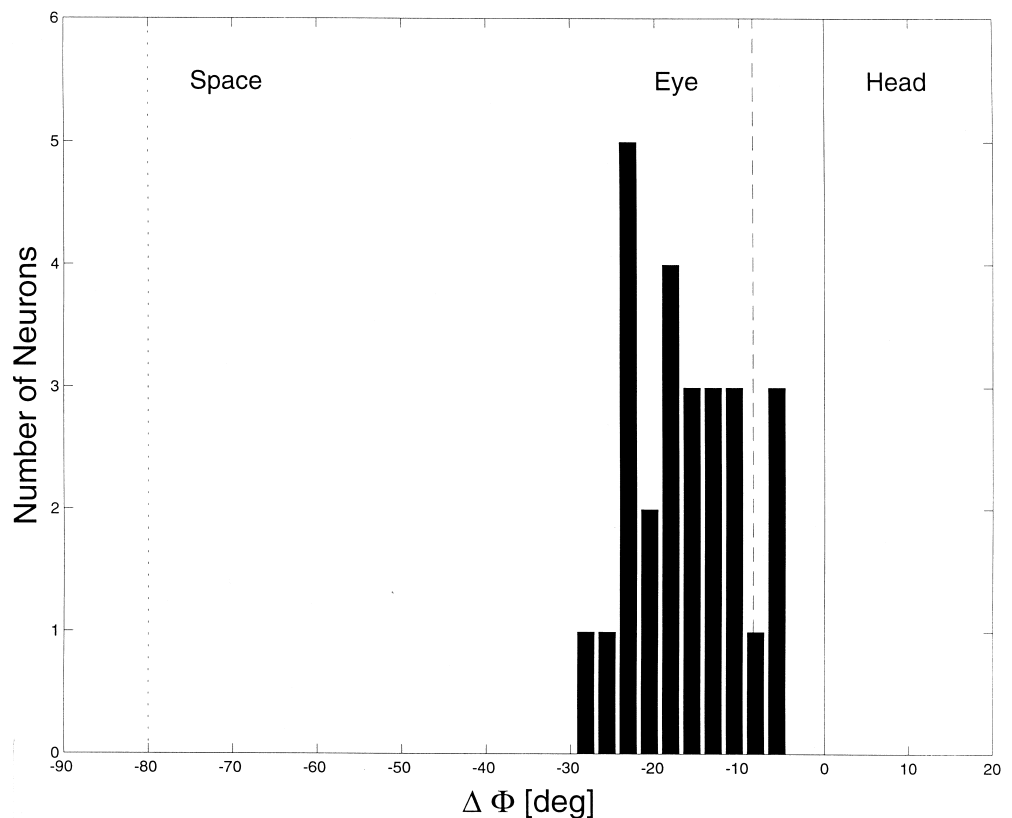
**Table 1** Summary of the microstimulation data. For all monkeys the number of stimulation sites ( $N$ ) and the amplitude of the head roll (in degrees) are given, together with the recorded shift in saccade direction (mean  $\pm$  SD) and ocular counterroll (OCR) difference. Note the differences in the amount of head roll. In all monkeys except Ca the shift in saccade direction exceeded the OCR difference significantly

Monkey	N	Head roll amplitude (deg)	Direction shift (deg)		Mean OCR (deg)	
			Mean	SD	Mean	SD
DE	6	90	-18.2	2.3	-11.1	1.0
YU	3	120	-23.2	3.9	-12.5	1.3
BR	2	25	-13.1	5.7	-6.4	1.2
CA	2	55	-15.3	4.9	-10.9	2.1

The shift in direction of the electrically evoked saccades is shown in Fig. 7. As an example we show the trajectories of the saccades evoked in Y.U. in two roll positions in Fig. 7A. Note that although the direction of the evoked saccade varies at different eye positions, throughout the oculomotor range the direction of the electrically evoked saccades is changed as a result of head roll. This change is systematically opposite to the direction of the head roll.

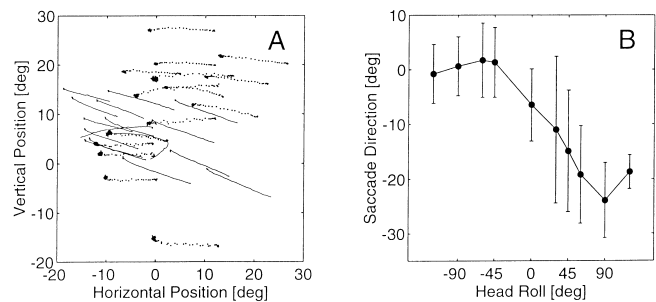
Figure 7B shows the means of the change of saccade directions as a function of head roll in the same monkey. The roughly sinusoidal relation between head roll and saccade direction has a peak-to-peak amplitude of more

**Fig. 5** Histograms of orientation shifts. Distribution of  $\Delta\Phi_0$  (see text), which resulted from rolling the monkeys. Predictions from a purely craniocentric (solid line,  $0^\circ$ ), oculocentric (dashed line, mean OCR difference between the right- and left-ear-down positions is  $-8.1^\circ$ ), and space-fixed coordinate system (dotted line, head roll difference is  $80^\circ$ ) have been added. The distribution of orientation shifts scatters around a value between the oculocentric and the space-fixed coordinate system



**Fig. 6A, B** Relation between saccade metrics and directional changes. The value of  $\Delta\Phi_0$  of each unit, plotted as a function of its preferred saccade amplitude (A) and direction (B). No significant relations were found with amplitude ( $r = 0.06$ ;  $P > 0.05$ ) and direction ( $r = -0.2$ ;  $P > 0.05$ )

than  $25^\circ$ , while the maximum OCR difference was only  $12.1^\circ$ . The mean changes in saccade direction and OCR for all monkeys are summarized in Table 1. In all monkeys but Ca, the OCR difference was significantly smaller than the shift in saccade direction ( $P < 0.05$ ). As in the recordings, no systematic differences were found as a function of evoked saccade metrics. Rotating monkey Yu about the pitch axis to static positions ranging from  $-90^\circ$  to  $90^\circ$  did not result in a significant ( $P > 0.05$ ) change of saccade direction (not shown).



**Fig. 7A, B** Relation between head roll and electrical saccade direction – Monkey Yu. A Trajectories of electrically evoked saccades of monkey Yu in two roll positions (dashed trajectories  $90^\circ$  left-ear-down; drawn trajectories  $90^\circ$  right-ear-down). B Saccade orientation change (mean  $\pm$  SD) as a function of head roll, for the complete set of positions measured in this monkey. Note that the peak-to-peak effect is more than  $25^\circ$ , considerably exceeding the amount of counterroll

## Discussion

In this paper we addressed the question of the nature of the reference frame in which the mSC is operating. As was pointed out in the Introduction, the output of the individual saccade-related burst neurons, as well as of the collicular population, are considered to represent a two-dimensional eye-displacement command map, organized in Listing's plane. By rotating monkeys about the roll axis that was roughly perpendicular to the Listing's plane, we

could study the changes in the relation between collicular activity and the resulting saccade vector.

At a behavioral level, head roll causes virtually no observable change in the saccadic output. The static torsion offset that is added to the eye position as a result of OCR is preserved throughout the saccades. Thus, at each head orientation, saccadic displacement vectors remain essentially two-dimensional (Fig. 2). In all head orientations, the eye saccades were equally straight and had similar kinematic properties (Fig. 3).

From both single-unit recordings and electrical stimulation, we found that single units as well as the collicular population reorient their preferred direction with respect to a craniotopic reference frame. Of the three reference frames that were considered in the Introduction, the data most closely resemble an oculocentric code. The orientation shift was in the same direction as the OCR, although it exceeded the amount of OCR that was measured roughly by a factor of 1.5–2.0 (Figs. 5, 7). However, the collicular reorientation was substantially less than the shift predicted by a space-centered reference frame.

A possible complicating factor in the analysis of single-unit recordings may be that some units in the mSC have large “gain fields” (Van Opstal et al. 1995). This means that the firing rate of a unit not only depends on the metrics of the saccade but also on the position of the eye in the orbit. In order to average out such phenomena, we stimulated the monkeys to make saccades throughout the oculomotor range. Although the distribution of eye positions did not always match perfectly for all head orientations (probably due to the visual environment in the laboratory), the distributions always largely overlapped (see Fig. 2). Furthermore, gain fields do not seem to cause a different preferred direction in different eye positions (Fig. 3 of Van Opstal et al. 1995), and would not predict our systematic changes, as they are randomly oriented. Therefore we are convinced that our findings cannot be explained by different sets of eye positions in the various head roll positions.

Similarly, as can be seen from Fig. 7A, saccades that are evoked by microstimulation with similar initial eye positions, but with different head-roll orientations, have substantially different directions.

### Possible mechanisms

We have measured a consistent and robust roll-dependent change of the directional tuning of the collicular output relative to the ensuing motor response. This change may be due to either passive changes in the plant, to neural control signals (“bias”), which are added downstream of the mSC, or both.

Simulation of the geometry of the extraocular muscle paths, based on anatomy and reasonable assumptions on muscle orientations in the orbit, and the orientation of Listing’s plane in stereotaxic coordinates (Suzuki et al. 1994) allows an estimation of the change in muscle-pulling direction during OCR. Since the mSC output is paral-

lel to Listing’s plane, only changes of the effective horizontal and vertical pulling directions are important. These appear to be smaller than or equal to the amount of OCR. The estimate found for eye positions that range  $\pm 20^\circ$  horizontally and vertically from primary position, is about two-thirds of the OCR, fairly independent of the choice of muscle paths and of other anatomical uncertainties.

Thus, if one assumes that the output of the mSC, with its retinotopic movement fields, follows OCR, then only about half of the observed directional change can be explained by mechanical properties of the plant.

We therefore conjecture that a neural bias-signal is responsible for the remaining shift. Bias signals that enter the oculomotor pathway downstream of the colliculus and change the oculomotor signal have been found before by other authors. It has been shown that, when the relation between retinal input and saccadic output of a monkey is changed as a result of the so-called short-term adaptation paradigm, the same saccade-related burst neurons were active for a (in both situations metrically different!) saccade toward the same visual stimulus (FitzGibbon and Goldberg 1986; Frens and Van Opstal 1997). One can therefore conclude, that during an “adapted” saccade, another signal is added to the collicular output.

Furthermore, it was shown that the systematic “upward bias” that is observed when monkeys make saccades to remembered targets (Gnadt et al. 1991; White et al. 1993) is not present in the collicular signal (Stanford and Sparks 1994). Thus, also this bias must result from signals that are added to the collicular motor signal.

The bias signal that we propose is probably gravity-related. It seems likely that its source is, either directly or indirectly, the otoliths, although we cannot exclude a somatosensory influence. To our knowledge no direct projections from the otoliths to the saccadic burst generators have been demonstrated. One possible indirect pathway may include the neural integrator, which integrates eye displacement commands to eye position commands. The nucleus of Cajal, which is part of the vertical/torsion integrator is known to receive extensive vestibular inputs (Crawford et al. 1991; Fukushima et al. 1992). Alternatively, the cerebellum, which receives input from the mSC through the nucleus reticularis tegmenti pontis (NRTP) and vestibular signals from the vestibular nuclei may play a role.

The most economical, functional explanation for the roll-dependent change in the directional tuning of the mSC is that the mSC output is coded in an oculocentric map, which rotates relative to the head during OCR. The additional bias toward the direction of gravity can be explained by assuming that the central visual input to the mSC is biased toward gravity (Sauvan and Peterhans 1995). Such an interpretation predicts a corresponding shift in the tuning curves of neurons in the cortical oculomotor areas, such as the lateral intraparietal areas (LIP) and the frontal eye fields (FEF).

Another explanation may be that during static roll the monkey would have made a different eye-head saccade, if the head had been free, and that this suppressed motor command is still present on the level of the mSC (Cowie

and Robinson 1994). Thus, the bias signal serves to transform the mSC command into a pure eye movement. In this respect it is noteworthy that the bias was not correlated to the encoded amplitude of an saccade-related burst neurons (Fig. 5), whereas a head component is expected to be more prominent in larger gaze shifts. Furthermore it has been suggested recently that the mSC controls the gaze (eye in space displacement), rather than being involved in the coordination between eye and head (Freedman et al. 1996). Thus an altered relation in the relative contributions of eye and head would not be reflected in the mSC. We suggest that the investigations of combined eye-head saccades should be extended to head positions tilted relative to gravity.

In conclusion, our experiments show that, in the alert monkey, gravity-related signals influence sensorimotor transformations at the level of the midbrain and the brainstem in a systematic way.

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