Trunk Position Influences Vestibular Responses of Fastigial Nucleus Neurons in the Alert Monkey

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Kleine, J. F., Y. Guan, E. Kipiani, L. Glonti, M. Hoshi, and U. Büttner. Trunk position influences vestibular responses of fastigial nucleus neurons in the alert monkey. J Neurophysiol 91: 2090–2100, 2004; 10.1152/jn.00849.2003. Vestibulospinal reflexes play an important role for body stabilization during locomotion and for postural control. For an appropriate distribution of vestibular signals to spinal motoneurons, the orientation of the body relative to the head needs to be taken into account. For different trunk positions, identical vestibular stimuli must activate different sets of muscles to ensure body stabilization. Because the cerebellar vermis and the underlying fastigial nucleus (FN) might be involved in this task, vestibular neurons in the rostral FN of alert rhesus monkeys were recorded during sinusoidal vestibular stimulation (0.1–1.0 Hz) in the roll and pitch planes at different trunk-re-head positions (center and ±45°). From the sensitivity and phase values measured in these planes, the response properties in the intermediate planes and the stimulus orientation eliciting the optimal response [response vector orientation (RVO)] were calculated. In most neurons, the RVOS rotated systematically with respect to the head, when trunk-re-head position was altered, so that they tended to maintain their orientation with respect to the trunk. Sensitivity and phase at the RVO were not affected. This pattern was the same for neurons in the right and left FN and independent of stimulus frequency. The average sensitivity of this partially compensatory RVO shift in response to trunk-re-head displacements, evaluated by linear regression analyses, was 0.59°/° (n = 73 neurons). These data show that FN neurons may encode vestibular information in a coordinate system that is closer to a trunk-centered than to a head-centered reference frame. They indicate an important role of this nucleus in motor programs related to posture and gait control.

INTRODUCTION

The vestibular system plays an important role in the control of the spinal motor system, eye movements, and perception. Vestibular signals that involve vestibulospinal mechanisms have to be fused with a number of body-related signals to generate appropriate reflexory motor responses during motion and for postural control. This is probably most obvious for head-trunk interaction. For example, any perturbing force that leads to vestibular stimulation with the head pointing forward will induce a vestibulospinal response in a specific set of trunk and/or limb muscles to prevent the body from falling. However, if the head is turned 90° to the side, an identical vestibular stimulus must activate quite a different set of muscles to ensure body stabilization. Hence, vestibulospinal reflex mechanisms need to take into account the relative positions of head and trunk to adequately distribute reflex activity to trunk and limb muscles, the effectors organs of the vestibulospinal reflex arc.

It has been shown experimentally that such redistribution of vestibulospinal reflex activity in response to changes of head-on-trunk position does indeed occur. For instance, using transmastoidal galvanic vestibular stimulation, Hlavacka and Njokiktijen (1985) and Fransson et al. (2000) showed that the plane of the induced refectorory body sway rotated systematically to remain approximately aligned with the interaural line, when the head was turned from the straight-ahead position to the side. Similarly, systematic changes in vestibularly evoked electromyographic responses in leg muscles were demonstrated after changes in head-on-trunk position (Kennedy and Inglis 2002; Tokita et al. 1989, 1991).

Little is known about the neuronal basis of this fundamental mechanism. There is plenty of evidence that neck-related information is processed in the vestibular nuclei. This was, for instance, demonstrated by single unit recordings, performed in immobilized (Anastasopoulos and Mergner 1982) or decerebrate cats (Boyle and Pompeiano 1981; Wilson et al. 1990) and also in alert monkeys (Gdowski and McCrea 2000), although there may be important species-related differences among primates as regards the presence or absence of proprioceptive neck inputs to specific subgroups of vestibular nuclei neurons (Roy and Cullen 2002). Reticulo-spinal neurons in the medul- lary reticular formation have also been shown to carry converging vestibular and neck information (Pompeiano et al. 1984). However, these studies investigated dynamic vestibularnneck interaction, mostly in the same plane, but not the fundamental problem raised above.

Another structure that receives considerable vestibular input is the cerebellum, specifically the anterior vermis as part of the spinocerebellum (Kotchabhakdi and Walberg 1978; Precht et al. 1977). Lesions here lead to disorders of gait and postural control (Ito 1984; Wilson and Melvill Jones 1979). A high percentage of Purkinje cells (PCs) also respond to natural vestibular stimulation, reflecting semicircular canal and otolith input (Pompeiano et al. 1997). Manzoni et al. (1999) subjected decerebrate cats to combined vestibular pitch and roll stimulation (wobble stimulus) at different trunk-re-head positions. These conditions are directly related to the situation described above. Recording from the anterior vermis, these authors showed that for most PCs the vestibular response characteristics changed with different trunk positions.

Purkinje cells of the vermis project to the vestibular nuclei (Voogd 1989) and to the fastigial nucleus (FN) (Armstrong and
Schild 1978), the most medial deep cerebellar nucleus. In the alert, behaving monkey, neurons in the FN respond to natural vestibular stimulation (Büttner et al. 1991; Gardner and Fuchs 1975; Siebold et al. 1999). These neurons, which are mainly located in the rostral FN, are not related to individual eye movements and have therefore previously been labeled “vestibular only” neurons. In contrast, neurons in the caudal FN are modulated during individual eye movements (saccades, smooth pursuit eye movements) (Robinson and Fuchs 2001). Accordingly, the caudal FN is also called the fastigial oculomotor region (FOR) (Noda et al. 1990).

A previous study on “vestibular only” neurons in the rostral FN that applied vestibular stimulation in vertical planes (Siebold et al. 1997) indicated that the responses were often “cosine-tuned” with respect to stimulus orientation; with cosine tuning, the sensitivity of the vestibular response is a function of the cosine of the angle between the orientation where the response is maximal [response vector orientation (RVO)], and the response phase is constant, except for a phase reversal at the orientations orthogonal to the RVO (minimum orientation), where sensitivity is zero. When investigated at different frequencies, however, it turned out that the vast majority of FN neurons was actually capable to generate more complex response patterns, with variable degrees of modulation at the minimum orientation (sensitivity > 0), and gradual changes of the response phase with stimulus orientation (Kleine et al. 1999; Siebold et al. 1999, 2001). Such patterns, which are also encountered in the vestibular nuclei (e.g., Angelaki et al. 1993; Baker et al. 1984) require input signals that differ in both their spatial properties and their phase behavior and have therefore been labeled as indicating “spatio-temporal convergence” (STC) (e.g., Angelaki 1993). STC responses may arise, for instance, due to the convergence of signals from semicircular canal and otolith afferents, which has been shown to be common in FN neurons (Siebold et al. 2001; Zhou et al. 2001). Quantitative analyses of STC responses in FN neurons showed that the vast majority of these complex response patterns could mathematically be accurately described as the simple linear sum of cosine-tuned input signals (Kleine et al. 1999), a property we called “linear STC.”

In this study, we used an economic paradigm, based on linear STC, to investigate the influence of trunk-re-head position on the spatio-temporal response properties of FN neurons at different stimulus frequencies. It will be shown that the RVO of FN neurons generally changes systematically with head-on-trunk position. These changes are partially compensatory, indicating that the FN encodes vestibular information in a coordinate system that is closer to a trunk-centered than to a head-centered reference frame.

METHODS

All experimental and surgical procedures were in accord with the APS’s guiding principles in the care and use of animals and approved by the responsible governmental institution. Two monkeys (Macaca mulatta) were prepared for chronic single-unit recordings. Prior to surgery, they were accustomed to sit in a primate chair and to wear an individually molded chest corselet, which allowed to control the position of the trunk. Under general anesthesia and aseptic conditions, a chamber for single-unit recording was implanted. Bolts were attached to the skull to maintain a stable head position during the experiments (for details, see Boyle et al. 1985). Single-unit activity was recorded with varnished tungsten microelectrodes (impedance, 2.5–4 MΩ) and eye position with the search-coil method (for techniques and calibration procedures, see Bartl et al. 1996). During the experiments, the monkey sat in the primate chair with its head immobilized by a head holder in a normal, upright position, in which the horizontal semicircular canals are tilted approximately 15° upward from the earth horizontal. The padded chest corselet was attached to a rotatable platform inside the primate chair, the axis of which passed through the dens of the atlantoaxial joint, allowing to manipulate and control the position of the trunk relative to the head in a painless and comfortable manner, with a small possible error (≤ 5°) due to the flexibility of the corselet and of the plastic parts that connected it to the platform.

Vestibular stimulation

For vertical vestibular stimulation, the monkey was rotated sinusoidally around an earth horizontal axis at frequencies between 0.1 and 1.0 Hz (Siebold et al. 1997, 1999). Amplitudes ranged from ± 10° (1.0 Hz) to ± 15° and velocities ranged from 9.5 to 75.4°/s. The standard stimulus was 0.6 Hz (± 15°). Neurons were tested and recorded at two orthogonal stimulus orientations (roll and pitch), which allows calculation of the neuronal responses at all intermediate stimulus orientations (Kleine et al. 1999; see next section). At each stimulus orientation, trunk position was altered (45° left, center, 45° right) relative to the head (Fig. 1). Thus there were three different tonic trunk-re-head positions during the application of dynamic vestibular stimulation in roll or pitch.

Analysis

All data (neuronal activity, vestibular stimulus) were digitized (20-μs temporal resolution for neuronal discharges, 200-Hz sampling rate for vestibular stimulus signal) and stored with the information on head and trunk position for off-line analysis. For each of the six stimulus conditions (2 stimulus-re-head orientations at 3 trunk-re-head positions), 7–30 cycles, depending on frequency, were recorded. Neuronal activity was averaged across stimulus cycles and quantified by calculating spike histograms (32 bins/stimulus cycle) and fitting these with a least-squares best sine function. Silencing of neurons (cutoff) during part of the stimulus cycle was accounted for by considering only those spike histogram bins for the fit which were neighbored by at least one nonzero bin (Kleine et al. 1999). Sensitivity (imp/s•deg) and phase are expressed relative to head position, with positive phase values indicating phase leads.

In a previous study, we had investigated the spatio-temporal properties of vestibular FN neurons by subjecting monkeys to vestibular stimulation in an earth-fixed vertical plane while they were slowly rotated about their yaw axis, allowing to measure neuronal response properties in the full range of (vertical) stimulus orientations at different frequencies (Kleine et al. 1999). We showed that the vast

FIG. 1. Stimulus conditions. Panels show a schematic top view of the monkey. Larger ellipse represents the trunk; smaller ellipse represents the head. Black lines inside the head indicate orientation of the left vertical semicircular canals. Dotted lines correspond to the vestibular stimulation axes.
majority of responses could be accurately quantified on the basis of a mathematical framework that assumes linear summation of (an arbitrary number of) cosine tuned input signals (“linear STC”). As a consequence of linear STC, each response can be split up and reduced to the vectorial components of two arbitrarily chosen, linear independent reference vectors for mathematical description. A practically relevant corollary is that, in our case of vertical vestibular stimulation, the spatio-temporal behavior of a linear STC neuron is completely determined by its responses at any two stimulus orientations, as long as these are linearly independent (e.g., orthogonal). Accordingly, for this study, responses were measured in two orthogonal orientations (roll and pitch) and the response parameters for the intermediate stimulus orientations, the stimulus orientation eliciting the maximal response (response vector orientation, RVO), and the corresponding gain and phase values were calculated from these measurements for each trunk position (left, center, right; Figs. 2 and 3) (cf. Kleine et al. 1999). This approach was chosen because further measurements at multiple stimulus orientations would have been excessively time consuming and impractical for the present experiments. Although the assumption of linear STC was not explicitly retested, there is no indication that the present and our previous samples of FN neurons would be substantially different in this respect (Kleine et al. 1999; Siebold et al. 1999, 2001), because the general response properties were very similar (see RESULTS). Furthermore, the repeated measurements at different trunk-re-head positions and different stimulus conditions performed in this study provide an implicit control that strongly supports the validity of our experimental approach: neither the qualitatively uniform dependency of the RVO on trunk position nor the general stability of the calculated RVO gain and phase (see RESULTS and Figs. 4–6) are compatible with the substantial random error in these measures that would follow from major violations of the linear STC assumption in the present data set.

In the following, the RVO is expressed in degrees and related to the head for a full 360° range of stimulus-re-head positions, in which stimulation in roll corresponds to 0 or 180°, in the left anterior–right posterior canal plane (LARP) to 45 or 225°, in pitch to 90 or 270°, and in the right anterior–left posterior canal plane (RALP) to 135 or 315°. Response phases at the RVO were arranged so that they fall into the range between −45 and 135° at the reference condition (trunk center, 0.6-Hz stimulus frequency), allowing us to classify units as either velocity-related (phase 45° to 135°) or roughly head velocity–related (phase 45° to 135°). With the conventions used for the stimulus orientations and the sign convention used for the phase angles, an RVO in roll (0°) with an RVO phase of 0°, for instance, corresponds to a maximal, position-related response at left–ear-down, and an RVO in pitch (90°) with an RVO phase of 90° to a maximal, velocity-related response during nose down movement.

Recording sites

Tracer substances (Di I) (Snodderly and Gur 1995) were placed at selected recording sites to aid histological reconstruction. At the end of all experiments, one monkey (monkey T) was deeply anesthetized with barbiturate and perfused transcardially with 10% formalin. The brain was removed and blocked in the stereotaxic plane. Coronal sections, taken every 50 μm, were processed for the tract tracing substance and counterstained with cresyl violet. The histological reconstructions confirmed that the recording sites were confined to the rostral part of the fastigial nucleus. Because the second monkey (monkey C) was still alive during the preparation of the manuscript, a detailed histological reconstruction of the recording sites was not yet possible. However, based on the basis of our previous, extensive experience with recordings from the rostral part of the fastigial nucleus (Büttner et al. 1991; Kleine et al. 1999; Siebold et al. 1997, 1999, 2001) and caudal (Helmchen et al. 1994; Kleine et al. 2003) FN, we believe that these neurons were also recorded in FN.

RESULTS

General characteristics

Results are based on the analysis of 104 vestibular neurons (monkey T, n = 42; monkey C, n = 62) recorded in the left or right FN. All neurons were spontaneously active with an irregular activity (Gardner and Fuchs 1975; Siebold et al. 1997). The criteria for identifying neurons in FN were similar to those described previously (Siebold et al. 1999). Activity related to saccades allowed a functional separation of the caudal FN (Helmchen et al. 1994) from the rostral FN, where the vestibular neurons described here were recorded. There was no recognizable correlation between the stereotaxic location of the vestibular units and any of the response properties described in the following sections.

The RVO at the standard frequency of 0.6 Hz with the trunk in center position was determined for 89 of 104 neurons, for which measurements were available in both roll and pitch at this frequency. The RVOs were distributed across the entire range, with a relative paucity of RVOs close (+22.5°) to the pitch plane (nose up pitch, n = 3; nose down pitch, n = 8) and a slight predominance of RVOs close to the planes of the ipsilateral anterior and posterior semicircular canals (iAC, n = 12; iPC, n = 24) or close to ipsilateral ear down roll (n = 7). The RVOs of 11.6, and 18 neurons were close to contralateral roll, the cPC, and the cAC, respectively. The response phase at the RVO was closer to head velocity than to trunk position for the majority of units [velocity-related (45° < RVO phase ≤ 135°), n = 57; position-related (−45° < RVO phase ≤ 45°), n = 32]. The calculated sensitivity at the RVO ranged from 0.79 to 4.92 imp/s° [1.94 ± 0.82 (SD) imp/s°]. These values are similar to those observed in our earlier studies (Kleine et al. 1999; Siebold et al. 1997, 1999).

Influence of trunk-re-head position

The RVO for different trunk positions at 0.6 Hz could be determined for 88 neurons. Data at all three positions (trunk left, center and trunk right) were obtained for 77 of these neurons. Figure 2 shows a typical example.

The trunk is turned to the left by 45° in Fig. 2 (left column). During stimulation in roll, the neuron is almost not modulated; however, it shows clear modulation during pitch stimulation. Accordingly, the sensitivity is high during pitch, but low during roll stimulation. The phase in both stimulus conditions is close to head velocity. According to these data, the calculated RVO is close to pitch (82°), indicating that the best neuronal response occurs with nose-down stimulation. With the trunk rotated to the right (right column), there is very good modulation during roll, but no modulation during pitch stimulation. Accordingly, the calculated RVO is close to roll (178°). The RVO (145°) is intermediate and close to RALP with the trunk in center position (middle column).

Because the RVO is expressed in relation to the head, it obviously does not remain stable with respect to the head when the trunk-re-head position is passively altered. Effectively, the RVO rotates (re head) to remain approximately aligned with a specific orientation of the trunk. In this particular sample, the RVO rotated by about 95° (re head) for the imposed 90° trunk displacement (RVO at 177.5° with trunk right vs. 82.4° with trunk left) to remain approximately aligned with the “RALP-
plane" of the trunk (the plane that is parallel to RALP with the trunk in the center position). This is illustrated in Fig. 2D, which shows, for each trunk-re-head position, the relative orientation between stimulation axis (dotted lines) and head and trunk that would elicit the maximal response: while the angle between head and stimulation axis changes, the angle between trunk and stimulation axis remains approximately constant for all trunk-re-head orientations. In functional terms,
one may say that the induced RVO rotation is fully compensatory ($\sim 90^\circ$) for the imposed trunk-re-head displacement. Thus the vestibular response of this neuron can be considered as organized in a trunk-centered rather than a head-centered reference frame. For comparison, Fig. 3 displays, in identical layout, data from a neuron operating in a reference frame that was approximately head-centered: the respective responses in roll and pitch were similar for all trunk-re-head orientations, yielding RVOs that were approximately constant with respect to the head, but rotated with respect to the trunk (Fig. 3, C and D).

The influence of trunk-re-head displacement on response properties was evaluated by linear regression analyses performed on those units for which the RVO could be determined at all three trunk positions at at least one stimulus frequency. This applied for 80 neurons, including 77 neurons for which these data were available at the standard frequency of 0.6 Hz. From the obtained 185 data sets that yielded $185 \times 3$ regression lines (for the 3 parameters RVO, RVO phase, and RVO gain), outliers were removed by eliminating those ($n = 10$) for which the slope of the regression line for RVO versus trunk position and/or RVO phase

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**FIG. 3.** Sample neuron exhibiting “head-centered” vestibular responses. Panel layout as in Fig. 2. The “best-response” orientation (re stimulation axis) changes for the trunk but remains approximately constant for the head.
versus trunk position fell below the 2nd or above the 98th percentile of the respective distribution of slopes. The analysis of the remaining 175 data sets from 73 neurons is summarized in Fig. 4.

Figure 4 displays a synopsis of the relations between trunk position and RVO (top), RVO phase (middle), and RVO gain, respectively, obtained at the standard frequency of 0.6 Hz. Evidently, in the vast majority of cases, there was a systematic dependency of the RVO on trunk position that was qualitatively similar and had the same direction as that exhibited by the sample neuron displayed in Fig. 2. For monkey C, but not for monkey T, there was a notable asymmetry in the RVO shifts, which were often larger for trunk right than for trunk left displacements. The reason for this asymmetry is not clear, but it might be due to idiosyncrasies in the assumed posture of the lower trunk and/or extremities at trunk left versus trunk right position of this monkey. Overall, however, the relation between trunk-re-head position and RVO was approximately linear, and therefore quantitatively evaluated by linear regression across all three trunk positions, as a reasonable estimate of the magnitude of the RVO shift in each individual data set. The resulting distribution of the slopes of the regression lines was basically monomodal for each stimulus frequency as well as for the entire sample of 175 data sets obtained at different frequencies (Fig. 4B), with an overall average of $0.59 \pm 0.33^{\circ/\circ}$ (SD) that was, of course, significantly different from zero ($P < 10^{-15}$, t-test). The responses at different frequencies analysis yielded distributions with similar shapes and mean slopes ranging from 0.52 to 0.85$^{\circ/\circ}$ (Fig. 3C), which were, for each frequency, significantly different from zero ($P < 10^{-5}$). Thus although the induced RVO shifts were close to fully compensatory for only a minority of cells (30 units exhibited slopes $>0.8^{\circ/\circ}$ at least 1 frequency), changes in trunk-re-head position had a robust and systematic effect on the RVO of most neurons, and the spatial organization of the vestibular responses was closer to a trunk-centered than to a head centered reference frame in the majority of units.

In contrast, gain and phase at the RVO were not systematically affected by changes in trunk-re-head position. Although seemingly erratic changes in RVO gain or phase occurred in a small number of measurements, these parameters remained stable in the vast majority of cases (Fig. 4A, middle and bottom). The slopes of the corresponding regression lines (for the entire sample) were randomly and narrowly distributed.
about zero (Fig. 3B, mean slopes were $-0.019 \pm 0.22^\circ/\circ$ for RVO phase and $0.0002 \pm 0.0066$ (imp/s/°)/° for RVO gain, respectively). Neither the overall averages nor any of the means obtained at individual frequencies (Fig. 4C) were significantly different from zero ($t$-test).

**Responses at different frequencies**

For 16 units that were tested at five or six different frequencies, a complete data set was available at each frequency with measurements in both roll and pitch at all three trunk positions, allowing to evaluate possible frequency-dependent changes of the RVO and of the response properties at the RVO for different trunk positions. Figure 5 displays a synopsis of these data by plotting RVOs, and gain and phase at the RVO for all 16 neurons, with the data obtained at different trunk positions placed into separate columns as indicated. In Fig. 6, the results from four sample neurons, selected from Fig. 5, are displayed in separate panels to allow direct comparison of the data obtained at different trunk positions for individual units.

Again, the influence of trunk position on the RVO is clearly apparent in Figs. 5 and 6, with a systematic and roughly parallel upward shift of the RVO-versus-frequency lines for the trunk right compared with the trunk left positions (Figs. 5 and 6, RVO panels). In contrast, stimulus frequency generally had no systematic influence on the RVOs, which remained fairly stable across frequencies in the majority of units (Fig. 5). As previously described (Siebold et al. 1999), there was an approximately threefold systematic increase of the RVO gain across the decade of frequencies (0.1–1.0 Hz) investigated, while RVO phase remained stable with increasing stimulus frequency for the majority of neurons (Fig. 5, gain and phase panels, respectively). Although RVOs and RVO phases were typically stable across the frequency range investigated, a small minority of units exhibited considerable RVO fluctuations and a somewhat larger number showed considerable phase drifts. For instance, with the trunk in center position, 1 of the 16 neurons (6%) investigated at 5 frequencies exhibited RVO changes in excess of $90^\circ$ for frequencies between 0.1 and 1.0 Hz, and 2 of 16 exhibited phase changes of more than $90^\circ$ (13%). For the overall 27 neurons tested at three or more frequencies, the corresponding numbers were 3 (11%) and 5 (19%), respectively. However, for the majority of these as well as for the “RVO-stable” and “phase-stable” neurons, the RVO and RVO phase curves obtained at different trunk positions were very similar, taking a roughly parallel course (RVO, e.g., Fig. 6, neuron 2) or being quite accurately superimposed on each other (phase, e.g., Fig. 6, neuron 4). Also, the gain curves obtained for different trunk positions showed similar frequency-dependent changes across frequencies for the majority of individual units (Fig. 6).
Spatio-temporal response properties

In a previous study, investigation of vestibular FN neurons at different frequencies revealed the presence of converging spatially and temporally diverse input signals (STC) in the majority of units (Kleine et al. 1999). STC properties of individual units often changed considerably between different measurements: for instance, tuning ratios (TR, the ratio of the gain at the stimulus orientation eliciting the minimum response to the gain at the RVO that allows a quantitative assessment of STC) (e.g., Angelaki 1993) could be negligibly small at one stimulus frequency (approximately 0.1), indicating a close to cosine-tuned response, and become considerably high when the same cell was recorded at a neighboring frequency, revealing STC (Kleine et al. 1999). Similar effects were observed in this study. For instance, 25 of 27 neurons, in which TRs were obtained for at least three stimulus frequencies exhibited one or more TRs >0.2, and in 23 of these 27 neurons, the TRs differed by more than 0.3 in different stimulus conditions. TRs often changed between frequencies and between different trunk positions at the same stimulus frequency, without any readily identifiable systematic correlation or pattern. However, the presence of STC was no prerequisite for the trunk-position-dependent changes of the RVO to occur. This is illustrated by the sample neuron of Fig. 2, which exhibited close to cosine tuned responses at all trunk positions at this frequency (TRs close to 0), but showed a fully compensatory RVO shift for the imposed trunk displacement. Overall, the slopes of the regression lines for the RVO versus trunk position relations were not correlated with the corresponding average tuning ratios of the responses ($r = -0.01, P = 0.89$).

**DISCUSSION**

**Responses to trunk displacement**

Our data show that the spatial properties of vestibular FN neurons are profoundly modified by changes in trunk-re-head position. When trunk-re-head position was altered, the RVO of most neurons shifted systematically. Gain and phase at the RVO, in contrast, were typically not affected. The observed RVO shifts were qualitatively homogeneous for the neuronal sample, and they were functionally expedient, because they tended to keep the RVO constant with respect to the trunk. However, although the RVO changes were, in this sense, fully compensatory for the imposed trunk displacement for a certain
percentage of neurons (slopes for RVO vs. trunk position of \(\sim 1^\circ\)), the compensation was only partial in most instances (Fig. 4), and the distribution of slopes was symmetrical about an average value of \(0.59^\circ\).

Strictly speaking, this average value does not necessarily reflect accurately the trunk displacement sensitivity of the FN population or of possible functionally related subpopulations of neurons, because the effective RVO of converging cells also depends on the sensitivities and phases of the individual signals. Although it is certainly unrealistic that all the diverse signals of the FN population would eventually converge into some global FN output that is uniformly conveyed to all different effector muscles, it is therefore interesting to note that the hypothetical trunk displacement sensitivity of the present neuronal sample, when correctly calculated from the vectorial (i.e., the complex number) representations of the gains and phases of all measured responses in roll and pitch, was \(0.85^\circ\) and thus somewhat larger than the arithmetic mean of the distribution of slopes (\(0.59^\circ\)). However, it seems irrefutable that the vestibular signals in the FN generally compensate only partially for changes in trunk-re-head position. Several factors might contribute to this finding. First, although the position of the upper part of the trunk was reasonably well controlled at \(\pm 45^\circ\) by the applied chest corset, the lumbar spine and the extremities were free to move, and hence, other proprioceptive inputs that may have additional impact on FN signals were not controlled. Second, the passive support of the head and trunk by the experimental apparatus might have alleviated the need for precise stabilizing vestibulospinal reflexes and thus have influenced the recorded FN signals. Third, although a fully compensatory shift of the RVO for any imposed trunk displacement seems desirable for the effector muscles of the vestibulospinal reflex arc, there is, to our knowledge, no definite evidence to prove that they do indeed behave in this ideal way. The above-mentioned studies that examined the influence of trunk displacement on vestibularly evoked body sway or EMG responses in leg muscles (Fransson et al. 2000; Hlavacka and Njiokiktjien 1985; Kennedy and Inglis 2002; Tokita et al. 1989, 1991), are, in this respect, qualitative in nature. A fully compensatory RVO shift was described for trunk displacements of \(\pm 30^\circ\) in the triceps muscle in decerebrate cats (Manzoni et al. 1998). However, it seems possible that the relation between RVO and trunk-re-head position might get increasingly nonlinear with increasing angles of trunk displacement, leading to attenuation of the trunk-displacement sensitivity of the effector muscles. Fourth, the central compensation for trunk displacements might be distributed across different vestibular areas in cerebellum and brain stem, and the FN output signal may have to fuse with trunk-displacement sensitive vestibular signals originating elsewhere to achieve full compensation.

Irrespective of the overall consistency of the data, there were a few instances in which the calculated responses deviated from the “typical” pattern (e.g., by exhibiting nonmonotonous (“triangular”) relations between RVO and trunk position or larger RVO phase or RVO gain alterations in response to trunk displacements; Fig. 4A). However, it must be considered that the computation of neuronal response properties from measurements obtained at only two stimulus orientations relies on the indispensable minimum of information for such calculations. Irrespective of the general validity of this approach (see Methods), the obtained results are therefore clearly more vulnerable to random noise than if they were based on data sets with more implicit redundancy. Conceivably, therefore at least some of these “atypical” patterns may reflect random effects rather than distinct physiological properties of the respective neurons. Consequently, both these relatively rare “atypical” responses and the broadness of the distribution of slopes for RVO versus trunk position, which ranged from “no compensation” (slopes of \(\sim 0^\circ\)) to “overcompensation” (slopes \(>1^\circ\)), likely reflect the limitations of the experimental paradigm and physiological variability rather than the presence of separate classes of neurons with distinct response properties. The symmetry and monomodality of the slope distribution (Fig. 4B, RVO panel) are also in favor of this view.

Related studies

Although the experimental paradigm is close to natural conditions, there seems to be no report on equivalent recordings made in the vestibular nuclei. The only study (Manzoni et al. 1999) that applied comparable stimulus conditions investigated PCs in the anterior vermis of decerebrate cats, i.e., a structure known to project to the rostral FN. A comparison of our findings with these results indicates that responses in the anterior vermis are more variable. Only about one-third of the recorded PCs showed compensatory responses, whereas the remaining neurons showed anticompensatory or “triangular” responses (Manzoni et al. 1999). Many PCs (about 30%) were not affected by trunk displacement, and some were no longer modulated after trunk displacement; an effect we did not observe in our FN neurons. This larger variability of PC responses could reflect convergence of a larger number of PCs on a smaller number of FN neurons and further signal processing that serves to provide a more direct and suitable cerebellar output signal. It must also be considered that we applied a trunk displacement of \(\pm 45^\circ\), whereas Manzoni et al. (1999) used a maximal displacement of only \(\pm 30^\circ\), with presumably smaller signal-to-noise ratios. As in our experimental paradigm, Manzoni et al. applied vestibular stimuli in only two orthogonal planes, which were, in their case, delivered simultaneously by means of two \(90^\circ\) phase-shifted signals (“wobble” stimulus), making their computed response parameters at least equally vulnerable to influences of random noise. Of course, the differences between PCs and FN neurons could also relate to species differences or the type of preparation (decerebrate cats).

Variability of FN signals

In an earlier study (Siebold et al. 1999), we observed that the RVO shifted with stimulus frequency (\(<3.0\) to \(\geq 1.0\) Hz) by more than 90° in a substantial minority (17%) of vestibular FN neurons. In addition, 29% of neurons exhibited RVO phase changes of more than 90° across the frequency range investigated. In this study, RVOs and RVO phases appeared to be somewhat more stable (see Results). This is remarkable, because the lack of redundancy in the present experimental paradigm would predict an increase rather than a decrease in variability of the calculated response parameters. Consequently, some of the response variability observed in our previous study can possibly be attributed to uncontrolled changes in trunk-re-head position. On the other hand, the present data show that this cannot be the only relevant factor, because comparable changes in RVO and RVO phase still occurred. Indeed, the generally accurate correspondence, or the
parallel course, of the RVO phase versus frequency and the RVO versus frequency-curves obtained at different trunk positions even in units exhibiting larger fluctuations of these parameters with frequency (Fig. 6, neurons 2 and 4) is evidence against the general validity of this explanation. In addition, the sometimes surprising consistency in these data, which were collected in periods that easily exceeded 30 min in which the monkey’s posture and orientation in space were repeatedly manipulated, argue strongly against random influences as the source of these seemingly unsystematic fluctuations in response properties. It also seems unlikely that stimulus frequency alone is the sole determinant of these effects. Rather, we feel that they reflect the influence of additional, still uncontrolled confounding variables that need to be identified by future experiments.

**Input signals**

It is probable that the information about trunk-re-head position derives from neck proprioception, presumably muscle spindle receptors. Such information is conveyed directly to the vestibular nuclei and the cerebellum as well as the central cervical nucleus in the spinal cord and the external cuneate nucleus and the lateral reticular nucleus in the brain stem. Whereas the central cervical nucleus projects to the cerebellum with collaterals to the vestibular nuclei (Sato et al. 1997), the external cuneate nucleus seems to project only to the cerebellum (Jasmin and Courville 1987). Thus this latter connection could provide neck information that bypasses the vestibular nuclei. Neurons in the external cuneate nucleus encode phasic and tonic neck displacements. Some neurons additionally show a weak vestibular sensitivity (Anastasopoulos et al. 1991). Neurons in the central cervical nucleus also respond to sinusoidal neck rotation, and a majority of neurons also to natural vestibular stimulation (Thomson et al. 1996). The gain of the vestibular response is generally lower. Convergence of neck and vestibular inputs is also a common finding for neurons in the lateral reticular neurons (Kubin et al. 1981).

Vestibular information from the vestibular nuclei reaches the FN by direct projections and indirectly via the anterior vermis (Armstrong and Schild 1978; Kotchabhakdi and Walberg 1978). In addition, there also seems to be some vestibular input from primary vestibular afferents (Bäurle et al. 1998; Korte and Mugnaini 1979).

**Functional considerations**

The present data confirm the previously observed, almost ubiquitous presence of STC in FN neurons (cf. Kleine et al. 1999). Obviously, spatial diversity of the vestibular input signals to FN neurons that is reflected in STC responses is a prerequisite for the observed trunk position-dependent RVO shifts. One might speculate that these effects also depend on their temporal diversity. However, the present data contradict this assumption. Even fully compensatory RVO shifts occurred in responses that were close to cosine tuned at each trunk position (e.g., Fig. 2), and TRs and trunk position sensitivities were not correlated. Indeed, calculations show that fully compensatory RVO shifts can be realized by a relatively simple neuronal model, consisting of two orthogonal, cosine-tuned vestibular input signals with identical phase behavior, the gain of each of which is modulated by either one of two tonic signals encoding trunk position, which are likewise orthogonal and cosine-tuned (Kleine and Büttner, unpublished results).

Accordingly, the trunk position–dependent change of the vestibular response properties of FN neurons can be considered as due to the interaction of “gain-modulated” input signals or as a representation of interacting spatially diverse signals with “gain field” characteristics. The concept of gain fields has first been used to describe the eye-position dependence of visual responses in the parietal cortex (Andersen et al. 1985) and characterizes a general computational principle by which neuronal networks may produce coordinate transformations, e.g., from retinotopic to head centered coordinates as in the parietal lobe for the visuomotor system (Andersen et al. 1985), or from head centered toward trunk centered coordinates as in the present example for the vestibulospinal system. It is interesting to note that the brain might employ similar computational principles for distinct sensory modalities in the cerebellum as in the parietal lobe. However, the ubiquitous presence of STC in FN neurons adds additional complexity. Its functional relevance needs to be clarified by future theoretical or experimental studies.

One might argue that the trunk position–dependent RVO shifts observed in vermal PCs and FN are not necessarily functionally important, but could also reflect neuronal processing that already occurred elsewhere, e.g., in the vestibular nuclei (VN). Indeed, the firing behavior of many VN units was found to be more closely related to trunk than to head velocity during passive whole body rotation in head-unrestrained squirrel monkeys, a finding that can also be interpreted in terms of a coordinate transformation (Gdowski and McCrea 1999). However, this study, as well as other related studies that focused on VN signal changes for self-generated versus passively applied head and body movements (e.g., McCrea et al. 1999; Roy and Cullen 2002), investigated dynamic response changes during head and/or trunk movements that both took place in the horizontal plane and hence cannot be directly compared with this study, which demonstrates changes in the spatial tuning of FN neurons to vertical vestibular stimulation after changes in tonic trunk-re-head position in the horizontal plane.

Irrespective of the resultant need for experiments that examine VN neurons under comparable stimulus conditions, however, there is strong direct evidence indicating the functional importance of these cerebellar signals. Manzoni et al. (1998) showed in decerebrate cats that the rotations of the RVO of the triceps muscle induced by trunk displacements, which were fully compensatory in control conditions for trunk displacements ≤30°, was strongly attenuated or abolished, when the ipsilateral anterior vermis was inactivated by muscimol injection. In addition, the relative uniformity and fair consistency in the responses of FN neurons, which contrasts with the more variable behavior of vermal PCs (Manzoni et al. 1999), indicates that the FN serves as a processing stage and not as a mere passive relay station for signals transmitted from the vermal cortex. These findings show that the cerebellum plays an indispensable and active role in the coordinate transformations from head-centered toward trunk-centered coordinates that are required for an appropriate functioning of vestibulospinal reflex mechanisms.