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# EFFECTS OF TRUNK-TO-HEAD ROTATION ON THE LABYRINTHINE RESPONSES OF RAT RETICULAR NEURONS

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**Abstract—Vestibulospinal reflexes elicited by head displacement become appropriate for body stabilization owing to the integration of neck input by the cerebellar anterior vermis. Due to this integration, the preferred direction of spinal motoneurons' responses to animal tilt rotates by the same angle and by the same direction as the head over the body, which makes it dependent on the direction of body displacement rather than on head displacement. It is known that the cerebellar control of spinal motoneurons involves the reticular formation. Since the preferred directions of corticocerebellar units' responses to animal tilt are tuned by neck rotation, as occuring in spinal motoneurons, we investigated whether a similar tuning can be observed also in the intermediate station of reticular formation. In anaesthetized rats, the activity of neurons in the medullary reticular formation was recorded during wobble of the whole animal at 0.156 Hz, a stimulus that tilted the animal's head by a constant amplitude (5°), in a direction rotating clockwise or counter clockwise over the horizontal plane. The response gain and the direction of tilt eliciting the maximal activity were evaluated with the head and body axes aligned and during a maintained body-to-head displacement of 5–20° over the horizontal plane, in either direction. We found that the neck displacement modified the response gain and/or the average activity of most of the responsive neurons. Rotation of the response direction was observed only in a minor percentage of the recorded neurons. The modifications of reticular neurons' responses were different from those observed in the P-cells of the cerebellar anterior vermis, which rarely showed gain and activity changes and often exhibited a rotation of their response directions. In conclusion, reticular neurons take part in the neck tuning of vestibulospinal reflexes by transforming a head-driven sensory input into a body-centred postural response. The present findings prompt re-evaluation of the role played by the reticular neurons and the cerebellum in vestibulospinal reflexes.**

**Key words: vestibulospinal reflexes, neck input, cerebellum, reticular formation.**

## INTRODUCTION

Vestibular information elicited by head displacement in space exerts a prominent role in the control of posture (Magnus, 1928; Roberts, 1978), particularly after reduction of visual and proprioceptive information or when the base of the support is unstable (Igarashi et al., 1970; Lackner et al., 1999; Welgampola and Colebatch, 2001; Cenciarini and Peterka, 2006). Labyrinthine signals elicit vestibulospinal (VS) reflexes that are spatially organized, each muscle being maximally activated for a particular (preferred) direction of head displacement (Wilson et al., 1986). For instance, in the decerebrate cat, the maximal activation of the forelimb extensor triceps brachii takes place during a roll tilt in the frontal plane directed towards the recording side. However, vestibular signals must be integrated with proprioceptive neck signals related to the body-to-head position (von Holst and Mittelstaedt, 1950; Roberts, 1978) in order to stabilize the body position. This process has two different aspects: one is that the vestibular and neck reflexes elicited by coplanar head and neck rotation interact in order to modify the postural tone only when the position of the trunk in space changes, as pointed out by von Holst and Mittelstaedt (1950) and Roberts (1978). It is well established that this interaction of VS and cervicospinal reflexes is nearly linear (Lindsay et al., 1976; Ezure and Wilson, 1983; Manzoni et al., 1983). This mechanism, which has been documented in decerebrate preparations, also underlies the perception of body motion in healthy humans (Mergner et al., 1991, 1997).

The other aspect, which is addressed in the present study, is that a maintained head-to-body orientation, which elicits a tonic neck input, allows one to infer body motion from labyrinthine signals, leading to substantial changes in the pattern of VS reflexes. As shown in Fig. 1, the same labyrinthine signals are elicited by body sway (black arrow) in the sagittal plane, when subjects have their head directed forwards (Fig. 1A) and in the frontal plane, when the head is rotated by 90° towards a shoulder, in the same direction as the body sway (see Fig. 1B). However, the two illustrated conditions require

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*Abbreviations:* BF, base frequency; CCW, counter clockwise; CW, clockwise; D, direction; ND, nose-down; NU, nose-up; RF, reticular formation; SD, side-down; $S_{max}$, maximal sensitivity vector; $S_{min}$, minimal sensitivity vector; SN, signal-to-noise; SPDH, sequential pulse density histogram; STC, spatiotemporal convergence; SU, side-up; VS, vestibulospinal.

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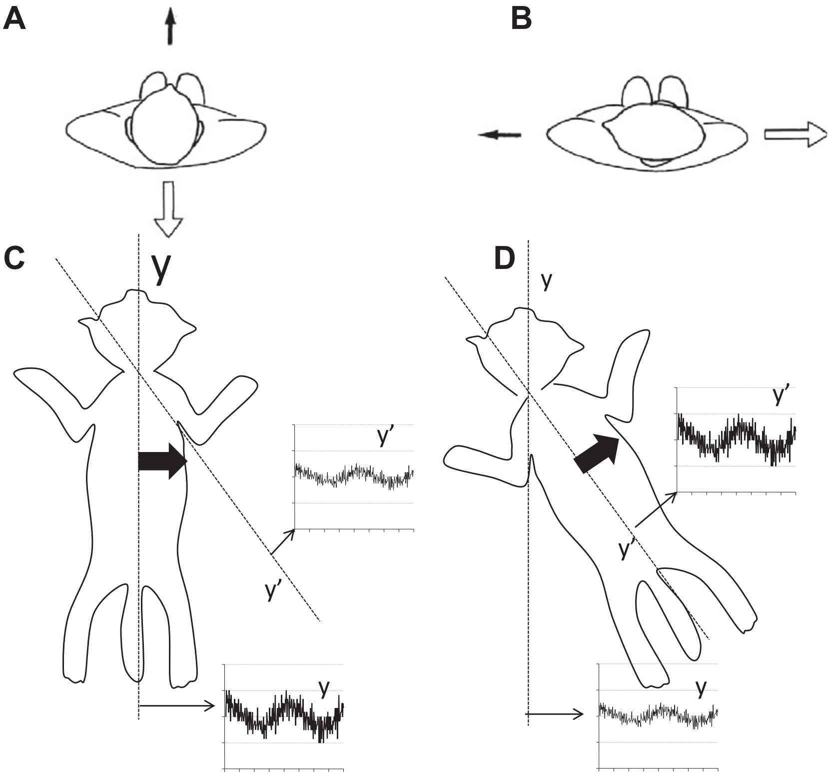

**Fig. 1.** Neck tuning of VS reflexes. (A, B) The relative position of the head with respect to the body changes the coupling between the vestibular input elicited by body sway (black arrows) and the postural response (white arrows). Note that in both (A) and (B) the direction of head displacement (and of the elicited vestibular input) is identical but the postural responses must be different in order to maintain balance. (C, D) Effect of a change in body-to-head position on the preferred direction of the triceps brachii response to tilts in vertical planes. In (C), when the head-and body longitudinal axes are aligned, the maximal EMG response is obtained for a roll tilt in the frontal plane (indicated by the thick, black arrow), around the longitudinal head–body axis (*y*). Tilt around an obliqual axis (*y*′) elicit a smaller EMG response. In (D) the body was rotated with respect to the head, so that its axis was parallel to *y*′. In this position, the maximal response was obtained for a tilt around the *y*′ axis, while the response to tilt around the *y* axis gets smaller, so that the preferred response direction (thick, black arrow) remained perpendicular to the longitudinal body axis. The insets represent the modulations of EMG activity observed during tilt around *y* and *y*′.

different postural reflexes (white arrows) in order to maintain balance. This non-linear interaction of vestibular and neck signals, which is expected when the head and neck rotation are not coplanar (Mergner et al., 1997), can be appreciated when galvanic vestibular stimulation is delivered with the head oriented in different positions with respect to the body (Lund and Broberg, 1983; Britton et al., 1993; Fitzpatrick et al., 1994). In this instance the central nervous system interprets the stimulus as a sway in the direction of the stimulated labyrinth and generates a postural response in the opposite direction. Both the perceived and the elicited body sway rotate by the same angle as the head over the body. The neurophysiological mechanism of this transformation has been addressed in the decerebrate cat, where it has been shown that body-to-head rotation modifies by the same angle the preferred response direction of the forelimb extensor muscles response to animal tilt (Manzoni et al., 1998). In this way the pattern of VS reflexes changes by changing the position of the head with respect to the body, so that a given muscle results maximally activated for a particular direction of the body rather than head displacement (see Fig. 1C, D). This obviously makes the reflex appropriate for maintaining body stability. It has been documented in decerebrate cat (Manzoni et al., 1998), as well as humans (Kammermeier et al., 2009) that the tuning exerted on VS reflexes by neck rotation is abolished by inactivation (Manzoni et al., 1998) and pathology (Kammermeier et al., 2009) of the cerebellar vermis, respectively: this means that without the cerebellum there is a loss of the neck–vestibular integration allowing to transform information about head motion into a postural response appropriate to counteract body sway.

It is of interest that, in decerebrate cat body-to-head displacement modifies the labyrinthine responses of the P-cells of cerebellar anterior vermis, similar to what was observed in the spinal motoneuron: on the average the preferred response direction of P-cells rotates in the same direction and by the same amplitude as the body with respect to the head (Manzoni et al., 1999). Thus, given the lack of neck tuning on motoneuronal responses to labyrinthine input which occurs following cerebellar inactivation, it was proposed that directional modifications of P-cells may induce similar changes in the vestibular responses of their target neurons located within the fastigial and the vestibular nuclei and, as a consequence, in spinal motoneurons (Manzoni et al., 1999). Indeed, following changes in the body-to-head