

## VI. INVITED LECTURES

### CORTICAL EFFECTS ON VESTIBULAR NUCLEUS NEURONS

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Higher levels of the nervous system exert effects that may be facilitatory and/or inhibitory on neurons in the vestibular nuclei and on vestibular reflexes. Previous work suggests that one source of this modulation is the cerebral cortex. Our goal was to study the potential substrate of corticovestibular effects in the cat (V. Wilson, P. Zarzecki, N. Isu, P. K. Rose, H. Sato, R. H. Schor, D. B. Thomson and T. Umezaki, *Soc. Neurosci., Abstr.* **23**: p. 752, 1997). Unilateral injections of WGA-HRP into Deiters' nucleus and the rostral descending nucleus showed that in the cat, as demonstrated earlier in the monkey, there are direct projections from several cortical areas to these nuclei: in the part of the cortex we searched, there were bilateral colonies of retrogradely filled neurons in cortical areas 6, 2, and 3a (mean number of neurons per colony about 60). Physiological experiments were performed on cats anaesthetized with chloralose-urethane, in which we stimulated in areas 2 and 3a while recording from ipsilateral vestibular nucleus neurons. These spontaneously firing neurons were tested for the presence of antidromic responses to stimulation of the upper cervical cord, and characterized by their responses to sinusoidal tilts. In response to cortical stimulation, a majority of neurons showed facilitation, inhibition, or a mixture of the two, with stimulation in area 2 more effective than stimulation in area 3a. The properties of these effects suggest that they were evoked by polysynaptic pathways. This conclusion is consistent with the anatomical evidence which shows that direct cortico-vestibular neurons form a very small percentage of the output neurons in the stimulated cortical regions and thus presumably play a proportionately minor role in the responses we observed. Cortical effects were distributed among vestibular neurons regardless of whether they received vertical canal, otolith, or no vertical vestibular input. Vestibulospinal tract neurons were much more likely to be affected by cortical stimulation than neurons not responding antidromically to the upper cervical stimulus, but there was no significant difference between effects on lateral and medial vestibulospinal tract neurons. This suggests that the areas we stimulated can influence a broad spectrum of vestibulospinal reflexes. Because areas 2 and 3a are known to receive vestibular input, this raises the possibility of a loop whereby this input interacts with a somatosensory one, producing a signal which is then fed back to influence activity in the vestibular nuclei. In any case, by their influence on vestibulospinal neurons, neurons in areas 2 and 3a should be able to modulate, in behaving animals, vestibular reflexes acting on the neck, trunk and limbs.

## CHANGES IN THE DIRECTIONAL PROPERTY OF THE VESTIBULOSPINAL REFLEX INDUCED BY PROPRIOCEPTIVE NECK SIGNALS: A CEREBELLAR MECHANISM

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The directional property of the vestibulospinal reflex (VSR) acting on the forelimb extensor triceps brachii (TB) can be modified by proprioceptive neck signals resulting from body-to-head displacement. In this way the vestibular input, which depends upon changes in head position with respect to space, may lead to muscle responses that preserve balance and body stability. In decerebrate cats, with the animal body kept straight with respect to the head, the response vector of the TB to labyrinth stimulation evaluated during wobble of the whole animal (at 0.156 Hz, 10°) was nearly orthogonal to the longitudinal axis, pointing to the side-down animal displacement. We have recently shown that 15°-30° of body displacement around a vertical axis passing through C1-C2, while keeping the head still, shifted the response vector of the TB by the same angle and in the same direction of body rotation, while remaining approximately perpendicular to the body axis (Manzoni et al., *J. Vest. Res.*, 7: 7-20, 1997). Thus, the proprioceptive neck input, which results from changing the body position with respect to the head, is able to modify the pattern of the VSR which appears to be organized in a body-centered reference frame.

Since inactivation of the cerebellar anterior vermis following local microinjection of the GABA-A against muscimol, reduced or suppressed the rotation of the triceps response vector induced by body-to-head displacement, we performed experiments in decerebrate cats to investigate how the cerebellum contributes to the sensorimotor transformation that adapts the spatial property of the VSR to the requirements of body stability. In particular, the activity of units, namely of Purkinje cells, located in the cerebellar anterior vermis was tested during wobble of the whole animal (at 0.156 Hz, 5°), leading to stimulation of labyrinth receptors. Most of these units responded to both clockwise and counterclockwise rotation. Some of these units (37%), which showed responses of similar amplitude to these stimuli (narrowly tuned cells), were characterized by a single vector (S max), whose preferred direction corresponded to the direction of stimulation giving rise to the maximal response. The majority of the units (63 %), however, responding with different amplitude to these rotations (broadly tuned cells), were characterized by two spatially and temporally orthogonal vectors (S max and S min), suggesting that labyrinthine signals with different spatial and temporal properties converged on them. Displacement of the body by 15°-30° in the horizontal plane induced changes in both the orientation and amplitude of the S max vector, which were to some extent related to the direction and amplitude of body displacement. Changes in gain and temporal phase of these unit response vectors were also observed following body-to-head rotation.

Since Purkinje cells of the cerebellar anterior vermis receive spatially oriented labyrinthine signals and affect the motor output by means of their efferent projec-

tions to the vestibulospinal neurons, we propose that the proprioceptive neck input regulates the convergence on these corticocerebellar units of labyrinthine signals with different spatial and temporal properties, thus adapting the spatial organization of the VSR to the requirements of body stability.

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