

VESTIBULOSPINAL AND NECK REFLEXES: INTERACTION IN THE VESTIBULAR NUCLEI

V. J. WILSON

The Rockefeller University, 1230 York Ave, New York, NY 10021, U.S.A.

INTRODUCTION

The labyrinth and vestibular nuclei together constitute an important sensory system whose activation or malfunction can have profound motor, and other, consequences. The system is of intrinsic interest, and has also provided a valuable model for the study of sensorimotor transformation. The vestibular nuclei and their motor outputs, vestibulo-ocular and vestibulospinal reflexes, have been investigated extensively in numerous laboratories for the last three decades. It is no exaggeration to say that the foundation for the great progress that has been achieved was provided by the work of Alf Brodal, his colleagues, and students, first summarized in "The Vestibular Nuclei and their Connections, Anatomy and Functional Correlations" (11). These anatomical experiments were the starting point for my work, which has dealt with the physiology of the vestibular nuclei, and with the influence that they exert on the spinal cord *via* vestibulospinal reflexes. These reflexes, however, cannot be thought of in isolation, as it has been clear for many years that they form a functional unit together with reflexes originating in receptors in the neck. Interaction between neck- and vestibular-evoked activity has been observed and studied in detail at cervical and lumbar interneurons presumably involved in vestibulospinal and neck reflex pathways (10, 40, 42). However, the first site in the central nervous system where convergence between vestibular and neck afferent input takes place is in the vestibular nuclei. In this paper I will review some recent work on this convergence in decerebrate cats, and then consider the relevance of these findings to what is known about interaction of vestibulospinal and neck reflexes.

NECK-VESTIBULAR CONVERGENCE IN THE VESTIBULAR NUCLEI.

Experiments utilizing electric and natural stimulation have shown that neck and vestibular afferents can activate the same neurons in the vestibular nuclei, and that some of these neurons project to the extraocular nuclei, others to the spinal cord (1, 6, 7, 8, 9, 24). Boyle and Pompeiano (6, 7) have conducted detailed experiments on this convergence, using sinusoidal roll tilt of the whole animal to stimulate vestibular receptors, of the body with the head fixed in space to

stimulate neck receptors, of the head to activate the two sets of receptors simultaneously. Their studies concentrated on vestibulospinal and unidentified neurons in Deiters' nucleus; the latter presumably included vestibulo-ocular neurons (22, 23). Vestibulospinal neurons were identified by antidromic stimulation only at C3-C4: the spinal level to which their axons projected was therefore not known. Neurons recorded rostroventrally or dorsocaudally in the nucleus are more likely to project to cervical or lumbar regions of the spinal cord, respectively (32), but the blurred somatotopic organization of Deiters' nucleus means that location cannot be used to identify the projection of any one neuron (see ref 43). The neurons in the population were described as having otolith input, but there is uncertainty in this classification because Boyle and Pompeiano's standard vestibular stimulus, 0.026 Hz, 5-10 deg in amplitude, can activate neurons having otolith, canal, or otolith plus canal input (see Figures 1 and 2 in ref 25). An important result of Boyle and Pompeiano's experiments was that more than half of the neurons influenced by vestibular stimulation were also influenced by neck rotation. In about two thirds of the neurons with convergence, roll tilt evoked vestibular and neck actions of apposite polarity, as defined by being out of phase by more than 90 deg. When produced simultaneously by head rotation, such opposing actions added linearly, sometimes to the point of cancellation. In the remaining third of the neurons, neck and vestibular responses had phase differences smaller than 90 deg and were considered parallel. Anastasopoulos and Mergner (1) studied neurons influenced by horizontal rotation, using trapezoids instead of sinusoidal stimuli. A little more than a quarter of their neurons with vestibular input had strong neck input, which had phasic and tonic components. The dynamic components could be synergistic or antagonistic with vestibular-evoked activity.

We have recently extended the experiments of Boyle and Pompeiano (25, 26). Like them, we stimulated labyrinth and neck receptors separately, or together, by means of sinusoidal rotations. The sample consisted of neurons in Deiters' nucleus and in the rostral part of the descending nucleus; some neurons were vestibulospinal, again identified only by antidromic stimulation at C4, others unidentified. Our experiments differed from Boyle and Pompeiano's in two ways. First, we used a stimulus that combined roll and pitch (39). This stimulus, which activated the utricle and vertical canals but not the horizontal canal, enabled us to determine the vertical plane that was most effective for activating each neuron, i.e. the neuron's response vector orientation. This orientation was usually measured at at least two frequencies, 0.05 and 0.2 Hz, and remained stable in a large majority of neurons, implying that all the receptors influencing such neurons are spatially aligned, even though their dynamics may differ. Others have shown that for some neurons there is evidence of misalignment: at some frequencies of stimulation the neuron may respond equally well to all planes of stimulation (neurons with spatio-temporal convergence, on STC neurons, ref 2). There were few such neurons in our sample. Second, we were able to study the dynamics of the neuron's response by delivering sinusoidal stimuli in or near the orientation of the response vector, at frequencies of 0.02-1 Hz. Together, these procedures made possible classification

of a neuron as receiving input from a single canal (canal dynamics, vector orientation near the plane of the ipsilateral anterior or posterior canal), two canals (canal dynamics, vector orientation more than 25 deg from either canal plane), otoliths, or otoliths plus canal. The criteria separating the last two categories were based on response dynamics. In Deiters' nucleus most otolith or otolith plus canal neurons had response vectors in the roll quadrants (within 45 deg of roll) rather than in the pitch quadrants, and there were almost no vectors very near pitch, confirming previous work (38,39; but see 12,13). In contrast, neurons with vectors in the roll and pitch quadrants were evenly distributed in the rostral part of the descending nucleus. Figure 1 summarizes the distribution of response types and vector orientations in the two nuclei.

The effects of neck rotation were tested on the population described above (26). Presence of a response to the neck stimulus was related to two variables. First, neck input was most prevalent in neurons with activation from more than one receptor region (otolith plus canal, 7/9; canal plus canal, 7/8), although it was also observed frequently in neurons with otolith input only (12/25); it was found least often in neurons activated from a single canal (6/29). Second, neck input was also usually found in neurons whose vestibular response vectors were in the roll quadrants: 36/66 "roll" neurons had neck input (21/22 with vectors within 15 deg of roll), only 4/15 "pitch" neurons. The two variables were related, as neurons with convergent input typically had vectors near roll: perhaps vector orientation rather than the origin of the vestibular response is the primary factor determining whether a neuron responds to neck rotation.

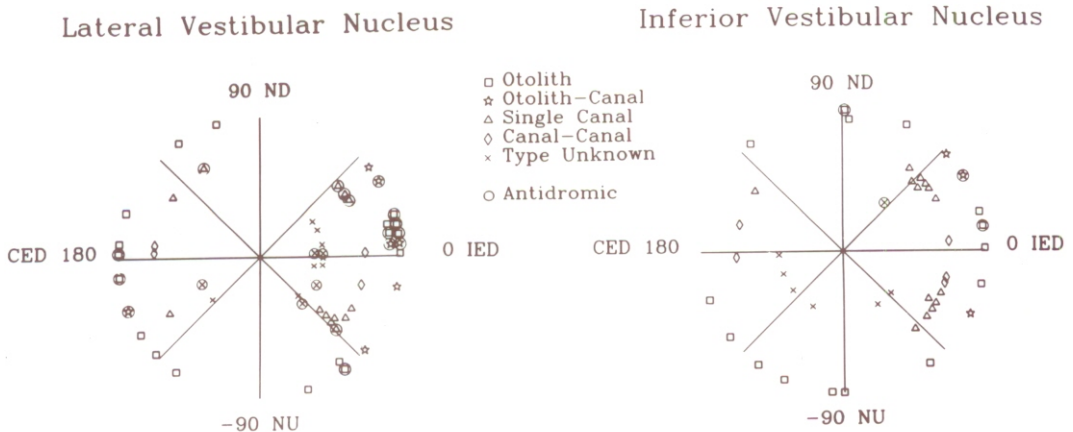


Fig. 1. - Polar diagrams of the vestibular vector orientations of neurons located in the lateral (Deiters') and inferior (descending) vestibular nuclei. Orientations were determined using stimuli combining roll and pitch, usually at 0.05 Hz. Key shows symbols denoting each type of predominant vestibular afferent input. Antidromically driven vestibulospinal neurons are circled. Neurons that respond maximally to roll rotations have vector orientations at 0 deg or 180 deg, i.e. when the ipsi or contralateral ear is tilted down (IED and CED), whereas neurons with the best response to nose up (NU) and nose down (ND) pitch rotation are plotted at -90 deg or 90 deg respectively. From Kasper et al. (25).

How do the properties of the vestibular and neck input converging on a given neuron compare? Neck and vestibular response vector orientations were nearly opposite for many (18/26) neurons, differing by close to 180 deg (i.e. vectors in the same plane, but pointing in opposite directions). Few vectors differed by less than 150 deg, and none by as little as 90 deg. Considering only orientation, therefore, we saw nothing similar to the parallel responses of Boyle and Pompeiano. In addition to orientation, we also compared gain and phase. Mean gain and phase advance (with respect to position) of the responses of all neurons to neck stimulation were 1.4 spikes/sec/deg and 32 deg at 0.02 Hz, both gain and phase advance increasing with frequency. At 0.02 Hz mean vestibular gain and phase were very similar, for both otolith (1.2 spikes/sec/deg, 20 deg) and otolith plus canal (1.2 spikes/sec/deg, 35 deg) neurons. With increasing frequency *mean* neck and vestibular values diverged somewhat, but for individual neurons they often remained surprisingly similar. Taking into account orientation, gain and phase and assuming neck and vestibular inputs add linearly, we can predict that there will be little or no response to head rotation for a substantial fraction of otolith and otolith plus canal neurons over a broad frequency range, and this is precisely what happens (Figure 2A, B). In the case of neurons with canal input, there were often greater differences between

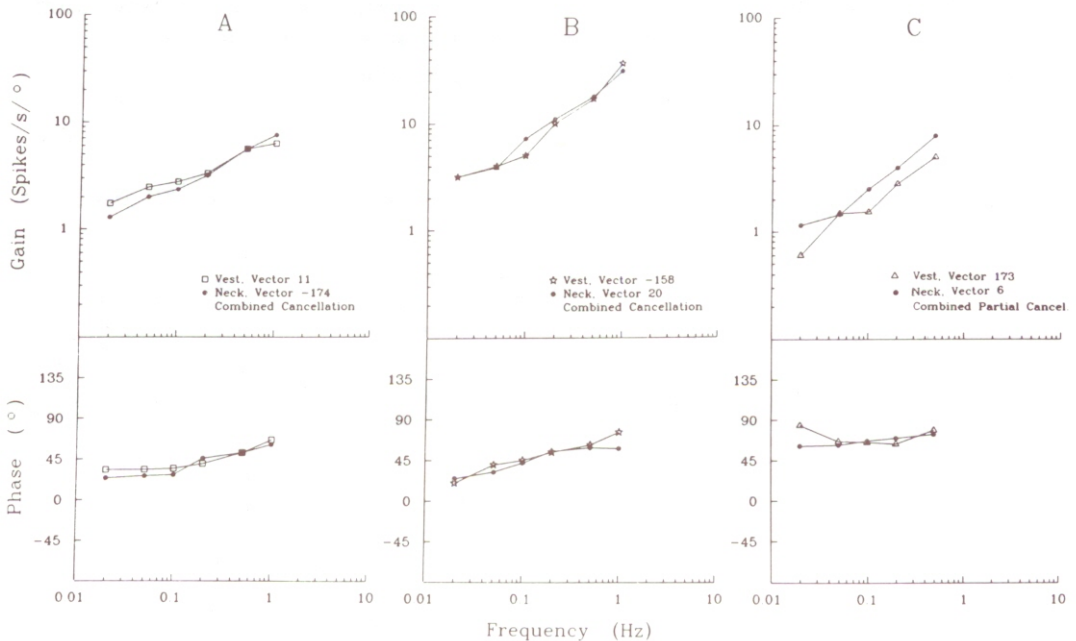


Fig. 2. - Dynamics of vestibular and neck responses in three neurons. Vestibular and neck vector orientations are almost opposite in all three examples. The vestibular response type in A was classified as predominantly otolith, B as otolith plus canal, and C as canal plus canal. In A and B the vestibular and neck responses have almost identical gain and phase at all tested frequencies, resulting in complete cancellation during combined stimulation. In C, cancellation was seen at 0.05 Hz, but a small response to combined stimulation was present at other frequencies. From Kasper et al. (26).

neck and vestibular gain and phase than there were with neurons receiving otolith or otolith plus canal input, but cancellation could nevertheless be observed at some frequencies of head rotation (Figure 2C). In some canal neurons, phases of neck and vestibular responses were very different. Head rotation resulted in a response with flat gain and phase close to position over the whole frequency range, apparently coding head position in space.

The question remains, what is the source of the signal evoked in the vestibular nuclei by neck rotation? The activity of spindles in neck muscles, particularly perivertebral muscles, is modulated by the same stimuli that modulate the activity of vestibular neurons, with roughly comparable dynamics (14,27). It seems likely that the signal originates at least in part from these spindles, but this remains to be demonstrated directly.

REFLEXES OF NECK AND VESTIBULAR ORIGIN.

Vestibulospinal reflexes acting on the limbs interact with the tonic neck reflex; the vestibular reflex acting on the neck (vestibulocollic reflex) interacts with the cervicocollic reflex, which originates in neck receptors. A detailed consideration of the properties and neural circuitry of these reflexes is beyond the scope of this brief review. I will concentrate mainly on those aspects of the reflexes related to their spatial organization, and to neck-vestibular interaction.

Reflexes acting on the limbs. — Recent work on vestibulospinal and tonic neck reflexes has been conducted almost entirely on the forelimb. The evidence shows that with static roll, or with low frequency sinusoidal roll tilt, the two reflexes are antagonistic in elbow extensor muscles and may cancel (21, 28, 30). As expected from such observations, with low frequency stimuli not only are gain and phase of the two reflexes similar, but their response vector orientations are approximately opposite (20, 21, 37, 44). Vestibular and neck vectors of elbow extensor muscles are both close to roll; for shoulder muscles vestibular vectors are also close to roll, whereas neck vectors have a significant nose-up pitch component (44). The weakness of the vestibular response to pitch that was observed in elbow muscles in these experiments is in contrast to the textbook description of vestibulospinal reflexes (35; see ref 44 for further discussion).

Although it is functionally meaningful that in response to slow head movements neck and vestibular reflexes may cancel, thereby minimizing any changes in body position, the cat's head movements have an important content of frequencies in the range of 2.5-7 Hz (15, 41; D.G.D. Watt and M.C. Wetzel, personal communication). What kind of interaction can we expect between the two reflexes during rapid head movements, i.e. as stimulus frequency increases? The orientations of the response vectors of both vestibular and neck reflexes in elbow and shoulder extensor muscles are quite stable over a wide frequency range, so that the role of spatial organization remains unchanged. However, gain and phase of tonic

neck and vestibulospinal reflexes diverge as frequency increases (20). The difference arises because vestibulospinal reflexes, having their origin in both otoliths and canals, have a greater sensitivity to head velocity than do tonic neck reflexes. Because of this difference in dynamics, and because neck and vestibular response vector orientations differ in some muscles, experiments to study the properties of the motor output in response to head rotation, i.e. to combined stimulation of neck and vestibular receptors, need to be done with stimuli that cover a broad frequency range and that contain more than one direction of head rotation. From the data that are available it can be predicted that, even when low frequency gain and phase are well matched, there will be only partial cancellation of the two reflexes in shoulder and elbow extensors above the mid-frequency range, and that because of vector orientation differences there may be a net response in shoulder muscles even at low frequencies.

The lateral vestibulospinal tract, which is the main pathway for vestibular signals to the spinal segments controlling limb musculature, originates almost entirely in Deiters' nucleus (32; see ref 43). It is therefore of interest to compare properties of vestibulospinal and tonic neck reflexes acting on the forelimbs with the properties, described in the previous section, of neurons in this nucleus. As already indicated, in most experiments with natural stimulation Deiters' vestibulospinal neurons were identified antidromically only from the C4 segment, and the spinal level at which their axons terminated was not known. Nevertheless, we can conclude that many Deiters' neurons have properties that match closely those of reflexes acting on the forelimbs. The distribution of vestibular and neck response vector orientations, mainly in the roll quadrants, is consistent with the spatial properties of both vestibular and neck reflexes. For many neurons, response vector orientations remain stable as stimulus frequency changes, a behavior again similar to that of the reflexes. Finally, with two-dimensional stimuli, many otolith and otolith plus canal neurons show the cancellation of neck and vestibular responses that is observed at the reflex level. Many canal neurons do not have neck input: they may account for the dominance of vestibular reflexes expected during high frequency head movements.

Reflexes acting on the neck. — The vestibulocollic reflex, evoked by stimulation of both otolith organs and semicircular canals, differs from vestibular reflexes acting on the limbs not only in its dynamics, with a phase advance that approaches acceleration at higher frequencies of stimulation (see ref 36), but also in its spatial organization. First, it has a robust response to a pitch stimulus (3, 17). Second, it exhibits spatio-temporal convergence: at low stimulus frequencies canal-otolith convergence may produce activity whose amplitude varies little with stimulus plane (3); muscle response vector orientations can often be determined only at stimulus frequencies equal to or exceeding 0.5 Hz, when canal-evoked activity becomes dominant. At frequencies where response vector orientations can be determined, those of the vestibulocollic reflex and of the cervicocollic reflex, evoked by muscle stretch and activation of spindle receptors (31), are quite similar for individual

muscles (4). Dynamics of the vestibulocollic reflex, especially the vertical reflex which has an otolith component, and of the cervicocollic reflex are also very much alike (16, 31). Interaction between these two reflexes, which appears to be linear over a wide frequency range, has different results depending on the stimulus paradigm. When the head moves on a fixed body, both reflexes act to restore head position, and add (16, 17, 18, 31). When the whole body moves and the head is free to counter-rotate, the reflexes oppose each other: the vestibulocollic reflex acts to maintain the head fixed in space (i.e. to restore the original head position), but the resulting head movement, and muscle stretch, evoke a cervicocollic reflex which tries to keep the head fixed on the body (31).

Until recently there have been no studies of identified vestibular nucleus neurons projecting to the neck segments of the spinal cord (vestibulocollic neurons) with natural stimulation. Such neurons are present in the medial and descending nuclei, as well as in Deiters' nucleus (34). For participation in the vertical vestibulocollic reflex the STC neurons of Baker et al. (2), of unknown location and projection, are good candidates, although reflex STC behavior could be constructed by convergence, at motoneurons or premotor interneurons, of vestibulocollic neurons carrying signals with different dynamics and spatial orientation. As far as neck-vestibular interaction is concerned, there is some difference between results obtained with stimulation in horizontal and vertical planes. As indicated above, in response to horizontal trapezoids Anastasopoulos and Mergner (1), who sampled in all three of the relevant nuclei, did see neurons where neck and vestibular inputs summed, others where they subtracted. Neurons with strong neck input were found particularly in the region where the medial, descending and Deiters' nuclei border on each other, as well as in the caudal medial and descending nuclei. In contrast, Kasper et al. (26) using sinusoidal stimuli in vertical planes, saw almost no neurons that had the summation of neck and vestibular inputs that would be expected during head rotation; instead, there was typically some degree of subtraction. A few neurons with canal input showed some addition at a low stimulus frequency (e.g. Fig. 5 in ref 26). Kasper et al. (26) did not record in the rostral medial nucleus, or caudally in the vestibular nuclei, and additive interaction may occur at cells in these locations. It seems more likely that functionally meaningful neck-vestibular interaction, additive in some reflex patterns and subtractive in others, takes place at the spinal level. Appropriate candidates for vestibulocollic neurons, therefore, could be cells receiving little or no neck input (26): such neurons invariably make up a substantial part of the sample in all experiments (1, 6, 7, 26). Recent experiments with stimulation in vertical planes, however, have shown that neck-vestibular interaction is similar for vestibulocollic neurons and the earlier largely unidentified sample of Kasper et al. (26): about 3/4 of vestibulocollic neurons receive neck input, and in most cases neck and vestibular inputs oppose each other (V.J. Wilson, Y. Yamagata, B.J. Yates, R.H. Schor and S. Nonaka, manuscript in preparation). Further studies are required before we understand the neural basis of the interaction of vestibulocollic and cervicocollic reflexes.

CONCLUSIONS

It is becoming possible to speculate about how vestibular nucleus neurons with different patterns of vestibular and neck input may participate in various reflexes evoked by activation of receptors in labyrinth and neck. As already indicated, many specific questions remain. A more general one also needs to be addressed: what, if any, unique role(s) do vestibulospinal neurons play in the reflexes? They are not necessary for tonic neck reflexes, which can be elicited, although not necessarily unchanged, in an animal with the spinal cord transected at C1 (29). Even vestibulocollic reflexes are still present after interruption of the most direct connections between vestibular neurons and neck motoneurons. For example the horizontal vestibulocollic reflex survives interruption of the medial vestibulospinal tract, which contains all the axons of horizontal canal-driven second order vestibulocollic neurons (5, 19). Deeper lesions interrupting reticulospinal fibers do affect the gain of the reflex (5). Clearly reticulospinal fibers, known to receive vestibular and neck input (e.g. 33) are involved in vestibulospinal reflexes under normal conditions, and probably in neck-evoked reflexes as well. The precise role played in the reflexes by fibers originating in vestibular nuclei and reticular formation remains to be determined.

Acknowledgement. — Work in the author's laboratory was supported by grants from NIH (NS02619) and NASA (NSG2380).

REFERENCES

1. ANASTASOPOULOS, D. and MERGNER, T. Canal-neck interaction in vestibular nucleus neurons of the cat. *Exp. Brain Res.*, **46**: 269-280, 1982.
2. BAKER, J., GOLDBERG, J., HERMANN G. and PETERSON, B.W. Spatial and temporal response properties of secondary neurons that receive convergent input in vestibular nuclei of alert cats. *Brain Res.*, **294**: 138-143, 1984.
3. BAKER, J., GOLDBERG, J. and PETERSON, B.W. Spatial and temporal response properties of the vestibulocollic reflex in decerebrate cats. *J. Neurophysiol.*, **54**: 735-756, 1985.
4. BANOVETZ, J.M., RUDE, S.A., PERLMUTTER, S.I., PETERSON, B.W. and BAKER, J.F. A comparison of neck reflexes in alert and decerebrate cats. *Neurosci. Abstr.*, **13**: 1312, 1987.
5. BILOTTO, G., GOLDBERG, J., PETERSON, B.W. and WILSON, V.J. Dynamic properties of vestibular reflexes in the decerebrate cat. *Exp. Brain Res.*, **47**: 343-352, 1982.
6. BOYLE, R. and POMPEIANO, O., Convergence and interaction of neck and macular vestibular inputs of vestibulospinal neurons. *J. Neurophysiol.*, **45**: 852-868, 1981.
7. BOYLE, R. and POMPEIANO, O. Responses of vestibulospinal neurons to neck and macular vestibular inputs in the presence or absence of the paleocerebellum. *Ann. N.Y. Acad. Sci.*, **374**: 373-394, 1981.
8. BRINK, E.E., HIRAI, N. and WILSON, V.J. Influence of neck afferents on vestibulospinal neurons. *Exp. Brain Res.*, **38**: 285-292, 1980.
9. BRINK, E.E., JINNAI, K., HIRAI, N. and WILSON, V.J. Cervical input to vestibulocollic neurons. *Brain Res.*, **217**: 13-21, 1981.
10. BRINK, E.E., SUZUKI, I., TIMERICK, S.J.B. and WILSON, V.J. Tonic neck reflex of

- the decerebrate cat: A role for propriospinal neurons. *J. Neurophysiol.*, **54**: 978-987, 1985.
11. BRODAL, A., POMPEIANO, O. and WALBERG, F. *The Vestibular Nuclei and their Connections, Anatomy and Functional Correlations* Edinburgh: Oliver and Boyd, 1962.
 12. CHAN, Y.S., CHEUNG, Y.M. and HWANG, J.C. Effect of tilt on the response of neuronal activity within the cat vestibular nuclei during slow and constant velocity rotation. *Brain Res.*, **345**: 271-278, 1985.
 13. CHAN, Y.S., CHEUNG, Y.M. and HWANG, J.C. Response characteristics of neurons in the cat vestibular nuclei during slow and constant velocity off-vertical axis rotations in the clockwise and counterclockwise rotations. *Brain Res.*, **406**: 294-301, 1987.
 14. CHAN, Y.S., KASPER, J. and WILSON, V.J. Dynamics and directional sensitivity of neck muscle spindle responses to head rotation. *J. Neurophysiol.*, **57**: 1716-1729, 1987.
 15. DONAGHY, M. The cat's vestibulo-ocular reflex. *J. Physiol.*, **300**: 337-351, 1980.
 16. DUTIA, M.B. Interaction between vestibulocollic and cervicocollic reflexes: automatic compensation of reflex gain by muscle afferents. *Progr. Brain Res.*, **76**: 173-180, 1988.
 17. DUTIA, M.B. and HUNTER, M.J. The sagittal vestibulocollic reflex and its interaction with neck proprioceptive afferents in the decerebrate cat. *J. Physiol. Lond.*, **359**: 17-29, 1985.
 18. DUTIA, M.B. and PRICE, R.F. Interaction between the vestibulocollic reflex and the cervicocollic stretch reflex in the decerebrate cat. *J. Physiol. Lond.*, **387**: 19-30, 1987.
 19. EZURE, K., SASAKI, S., UCHINO, Y. and WILSON, V.J. Frequency-response analysis of vestibular-induced neck reflex in cat. II. Functional significance of cervical afferents and polysynaptic descending pathways. *J. Neurophysiol.*, **41**: 459-471, 1978.
 20. EZURE, K. and WILSON, V.J. Dynamic of neck-to-forelimb reflexes in the decerebrate cat. *J. Neurophysiol.* **50**: 688-695, 1983.
 21. EZURE, K. and WILSON, V.J. Interaction of tonic neck and vestibular reflexes in the forelimb of the decerebrate cat. *Exp. Brain Res.*, **54**: 289-292, 1984.
 22. GACEK, R.R. Anatomical demonstration of the vestibulo-ocular projections in the cat. *Acta Oto-Laryngol.*, suppl., 293, 1971.
 23. HIGHSTEIN, S.M. and REISINE, H. The ascending tract of Deiters' and horizontal gaze. *Ann. N.Y. Acad. Sci.*, **374**: 102-111, 1981.
 24. HIKOSAKA, O. and MAEDA, M. Cervical effects on abducens motoneurons and their interaction with vestibulo-ocular reflex. *Exp. Brain Res.*, **18**: 512-530, 1973.
 25. KASPER, J., SCHOR, R.H. and WILSON, V.J. Response of vestibular neurons to head rotations in vertical planes. I. Response to vestibular stimulation. *J. Neurophysiol.*, **60**: 1753-1764, 1988.
 26. KASPER, J., SCHOR, R.H. and WILSON, V.J. Response of vestibular neurons to head rotations in vertical planes. II. Response to neck stimulation and vestibular-neck interaction. *J. Neurophysiol.*, **60**: 1765-1778, 1988.
 27. KASPER, J., SCHOR, R.H., YATES, B.J. and WILSON, V.J. Three dimensional sensitivity and caudal projection of neck spinal afferents. *J. Neurophysiol.*, **59**: 1497-1509, 1988.
 28. LINDSAY, K.W., ROBERTS, T.D.M. and ROSENBERG, J.R. Asymmetric tonic labyrinth reflexes and their interaction with neck reflexes in the decerebrate cat. *J. Physiol. Lond.*, **261**: 583-601, 1976.
 29. MAGNUS, R. Welche Teile des Zentralnervensystems müssen für das Zustandekommen der tonischen Hals und Labyrinthreflexe auf die Körpermuskulatur vorhanden sein? *Pfluegers Arch.*, **159**: 224-250, 1914.
 30. MANZONI, D., POMPEIANO, O., SRIVASTAVA, U.C. and STAMPACCHIA, G. Responses of forelimb extensors to sinusoidal stimulation of macular labyrinth and neck receptors. *Arch. Ital. Biol.*, **121**: 205-214, 1983.
 31. PETERSON, B.W., GOLDBERG, J., BILOTTO, G. and FULLER, J.H. Cervicocollic reflex: its dynamic properties and interaction with vestibular reflexes. *J. Neurophysiol.*, **54**: 90-109, 1985.

32. POMPEIANO, O. and BRODAL, A. The origin of vestibulospinal fibres in the cat. An experimental-anatomical study, with comments on the descending medial longitudinal fasciculus. *Arch. Ital. Biol.*, **95**: 166-195, 1957.
33. POMPEIANO, O., MANZONI, D., SRIVASTAVA, U.C. and STAMPACCHIA, G. Convergence and interaction of neck and macular vestibular inputs on reticulospinal neurons. *Neuroscience*, **12**: 111-128, 1984.
34. RAPOPORT, S., SUSSWEIN, A., UCHINO, Y. and WILSON, V.J. Properties of vestibular neurones projecting to neck segments of the cat spinal cord. *J. Physiol. Lond.*, **268**: 493-510, 1977.
35. ROBERTS, T.D.M. *Neurophysiology of Postular Mechanisms* (2nd ed). London: Butterworths, 1978.
36. SCHOR, R.H., KEARNEY, R.E. and DIERINGER, N. Reflex stabilization of the head. Pp 141-166 in Peterson, B.W. and Richmond, F.J. (Eds.), *Control of Head Movement*, New York: Oxford University Press, 1988.
37. SCHOR, R.H. and MILLER, A.D. Vestibular reflexes in neck and forelimb muscles evoked by roll tilt. *J. Neurophysiol.*, **46**: 167-178, 1981.
38. SCHOR, R.H., MILLER, A.D., TIMERICK, S.J.B. and TOMKO, D.L. Responses to head tilt in cat central vestibular neurons. II. Frequency dependence of neural response vectors. *J. Neurophysiol.*, **53**: 1444-1452, 1985.
39. SCHOR, R.H., MILLER, A.D. and TOMKO, D.L. Responses to head tilt in cat central vestibular neurons. I. Direction of maximum sensitivity. *J. Neurophysiol.*, **51**: 136-146, 1984.
40. SUZUKI, I., TIMERICK, S.J.B. and WILSON, V.J. Body position with respect to the head or body position in space is coded by lumbar interneurons. *J. Neurophysiol.*, **54**: 123-133, 1985.
41. WATT, D.G.D. and WETZEL, M.C. Linear head movement of walking and trotting cats. *Neurosci. Abstr.*, **3**: 280, 1977.
42. WILSON, V.J., EZURE, K. and TIMERICK, S.J.B. Tonic neck reflex of the decerebrate cat: Response of spinal interneurons to natural stimulation of neck and vestibular receptors. *J. Neurophysiol.*, **51**: 567-577, 1984.
43. WILSON, V.J. and MELVILL JONES, G. *Mammalian Vestibular Physiology*, New York: Plenum, 1979.
44. WILSON, V.J., SUZUKI, I., SCHOR, R.H. and PARK, B.R. Spatial organization of neck and vestibular reflexes acting on the forelimbs of the decerebrate cat. *J. Neurophysiol.*, **55**: 514-526, 1986.