Signal Processing of Semicircular Canal and Otolith Signals in the Vestibular Nuclei during Passive and Active Head Movements

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Abstract: The vestibular nerve sends signals to the brain that code the movement and position of the head in space. These signals are used by the brain for a variety of functions, including the control of reflex and voluntary movements and the construction of a sense of self-motion. If many of these functions are to be carried out, a distinction must be made between sensory vestibular signals related to active head movements and those related to passive head movements. Current evidence is that the distinction occurs at an early stage of sensory processing in the brain, and the results are evident in the firing behavior of neurons in the vestibular nuclei that receive direct inputs from the vestibular nerve. Several specific examples of how sensory information related to passive and active head movements is transformed in the vestibular nuclei are discussed.

Keywords: vestibular nuclei; otolith; vestibulo-ocular reflex; head movements

INTRODUCTION

The vestibular sensory receptors are located within the bony labyrinths embedded in the petrous temporal bone of the head. Their function is to detect the position and motion of the head in space. The signals produced by the vestibular nerve are important for spatial perception and for producing a variety of reflexes that help maintain balance and equilibrium. An essential feature of the central processing required of this head movement sensory system, like all sensory systems, is the ability to distinguish between sensory experiences that are due to self-stimulation and those that are produced by passive, external forces.

The distinction between passive and active head movements is important for constructing an internal estimate of self-motion as well as producing coordinated responses to head perturbations. When the head is moved by passive, external forces, the vestibular system, together with other sensory systems, such as visual and proprioceptive systems, construct an internal estimate of head motion.[1–3] The estimate is

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used to produce a variety of postural reflex movements of the trunk, limbs, neck, and eyes, movements that help stabilize gaze and the orientation of the body and limbs. The estimate of passive head movement allows subsequent estimates of the motion of the body and limbs, and by comparison the relative motion of objects in the external world.[4]

The process of distinguishing between vestibular signals related to self-generated head movements and passive head movements in space could begin as early as the vestibular sensory epithelium by way of efferent vestibular pathways.[5,6] However, it is more likely that the distinction between passive and active head movements is carried out centrally by structures that receive these sensory signals. The main recipient of vestibular afferent information, the vestibular nucleus, receives inputs from the cerebellum, cerebral cortex, reticulospinal collaterals, and spinal cord that could modify sensory processing during passive or self-generated head on trunk movements.[7] The latter inputs usually reduce the vestibular nucleus unit responses to head-on-trunk rotation.[8]

The results of our recent studies suggest that the signals carried by secondary vestibular neurons in the vestibular nuclei are different during passive and active head movements[9,10] and during the vestibulocollic reflex (VCR).[11,12] The vestibular nuclei are not homogeneous. The region gives rise to several important descending and ascending pathways.[13] In this paper, we summarize how sensory signals related to active, self-generated head movements vary in different classes of vestibular nucleus neurons that have been examined to date.

METHODS

Recording Techniques

Single-unit recordings were done in alert squirrel monkeys that were free to move their head in the yaw plane while seated on a vestibular rotator. The monkeys wore a tightly fitting jacket and were perched on a Plexiglas foot rest on a vestibular turntable. They were allowed to grasp a handrail that surrounded them at chest height. The head was attached to a rod that permitted angular head movements in the plane of the horizontal semicircular canals. The axis of head motion was placed either in line with the interaural plane (“on-axis” rotation) or 5–8 cm forward of the interaural plane. The latter “off-axis” head movements stimulated both otolith and semicircular canal afferents. Head and body movements were restrained by attaching the monkey’s jacket to the turntable and the monkey’s head to a rod that allowed free head movements in the yaw plane.

Eye and head movements were recorded with the magnetic search-coil technique. Stimulating electrodes were implanted bilaterally in the middle ear to allow orthodromic identification of neurons that receive synaptic inputs from the vestibular nerve and to allow verification of the location of recording sites in the vestibular nuclei using evoked field potential analysis. In some animals, stimulating electrodes were implanted in the ventromedial funiculi of the spinal cord at C1 or the thalamus to allow antidromic identification of neurons that project to the thalamus or the spinal cord.

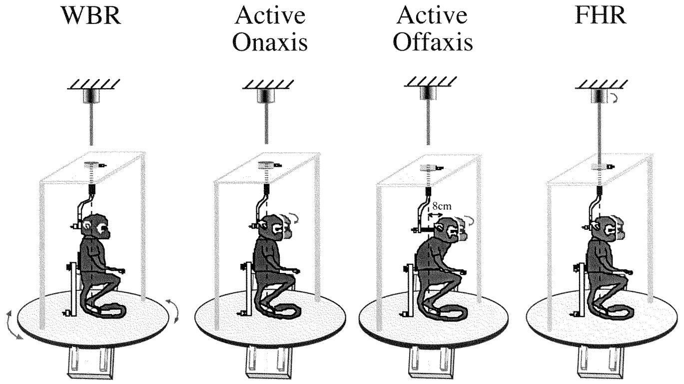


FIGURE 1. Experimental setups used for comparing passive and active head movement signals in squirrel monkeys: passive whole-body rotation or translation with head fixed to vestibular turntable; active on-axis (self-generated saccadic, VCR, or pursuit head movements allowed in the plane of the horizontal semicircular canal); axis of head rotation intersects interaural axis; active off-axis (self-generated head movements allowed in the plane of the horizontal semicircular canal). Axis of head rotation passes 5–8 cm behind the interaural plane. FHR: Forced, passive head-on-trunk rotation by attaching head to ceiling motor.

Experimental Protocols: Passive and Active Head, Neck, and Body Rotation

FIGURE 1 illustrates the methods used to compare single-unit responses to passive and active head movements. Single-unit responses were studied during passive whole-body rotation (WBR) at two stimulus frequencies (0.5 Hz, 40°/s; 2.3 Hz, 20°/s) either with the head fixed with respect to the vestibular turntable or with the head free to move in the yaw plane. The axis of head-on-trunk rotation was positioned so that it either intersected the interaural axis (on-axis position), allowing head-on-trunk movements that minimized stimulation of otolith receptors, or in an off-axis position that allowed head-on-trunk movements that stimulated both the semicircular canals and otoliths. The responses of some units were also studied during passive sinusoidal translation produced by a linear sled mounted on top of the turntable. Forced, passive head-on-trunk rotations (FHRs) were produced by rotating the rod attached to the animal's head either manually or with a ceiling-mounted motor. In some cases, a recording of active head movements was made that was then used to produce similar passive head-on-trunk rotations (HTRs) with the ceiling motor. Neck proprioceptive inputs to vestibular neurons were studied by holding the head stationary in space while passively rotating the turntable.

Three types of active, self-generated head movements were studied: (1) vestibulocollic reflex head movements evoked by passive WBR, (2) spontaneous gaze saccades, and (3) smooth tracking head movements of sinusoidal moving visual targets.

Data Analysis

Neural sensitivity to passive and active head movements was estimated using multiple linear regression analysis. The factors contributing to fitting functions included variables related to eye movement, neck rotation, as well as movement of the head in space. Estimates of neuronal sensitivity to neck rotation alone were based on parametric analysis of responses evoked when the head was kept stationary in space while the body was passively rotated by the turntable. Responses related to quick phases of nystagmus, and periods when the monkey was not alert, were not included in the averages. The records obtained during paradigms that used visual targets were also excluded from averages if the behavioral performance was poor. During head-fixed paradigms, the amount of data excluded during quick phases of nystagmus was based on the response during ocular saccades. During head-unrestrained paradigms, responses during quick phases of head-nystagmus were also excluded from the rotational analysis.

Unit responses during gaze saccades were evaluated by averaging the response to groups of saccades that had similar direction and peak head velocities. Head velocities typically ranged between 50° and 150°/s. The vestibular sensitivity during active head movements was compared to an estimate of the unit's head velocity and acceleration sensitivities during high-frequency WBR with the head restrained.

RESULTS

Vestibular nerve fibers generate similar responses to head movements during passive and active head movements. FIGURE 2 shows the response of a primary vestibular afferent fiber during simultaneous passive and active head movements. The monkey generated a series of active head movements while its body was passively

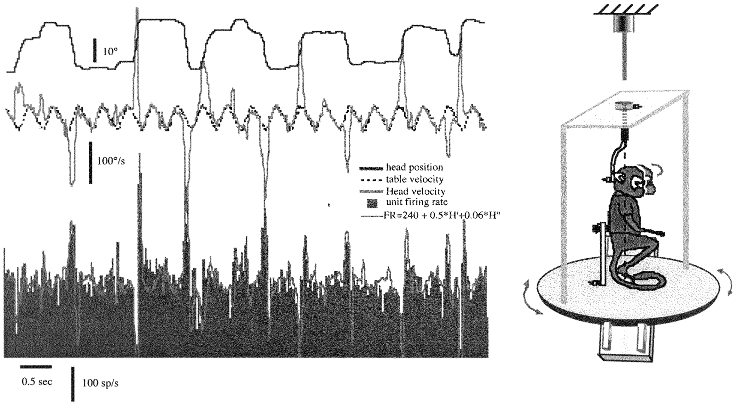


FIGURE 2. Primary vestibular nerve afferent generates similar responses during passive and active head movements. Vestibular turntable was rotated sinusoidally at 2.3 Hz while the head was free to move. Consequently, movement of the head in space was a combination of passive and active head movements. *Top trace* is head position with respect to the turntable. *Middle traces* are angular head velocity in space (*solid trace*) and passive angular head velocity in space (*dashed trace*). The solid trace superimposed on the firing-rate histogram on the bottom is a model of the unit's firing rate based on its response to passive rotation alone.

rotated by the vestibular turntable. The top trace is a record of the monkey's head movement with respect to the turntable. The middle traces show the passive head velocity in space generated by turntable rotation (dotted middle trace) and the velocity of combined passive and active head movements (solid middle trace). The bottom histogram is the firing rate of the vestibular nerve afferent. The trace superimposed on the firing rate histogram is the response expected if the afferent were equally sensitive to passive and active head movements.

Vestibular Nucleus Neurons Sensitive to Both Passive and Active Head Movements

The firing behavior of over 160 vestibular nucleus neurons that were sensitive to rotation of the head in the plane of the horizontal semicircular canal and/or to inter-

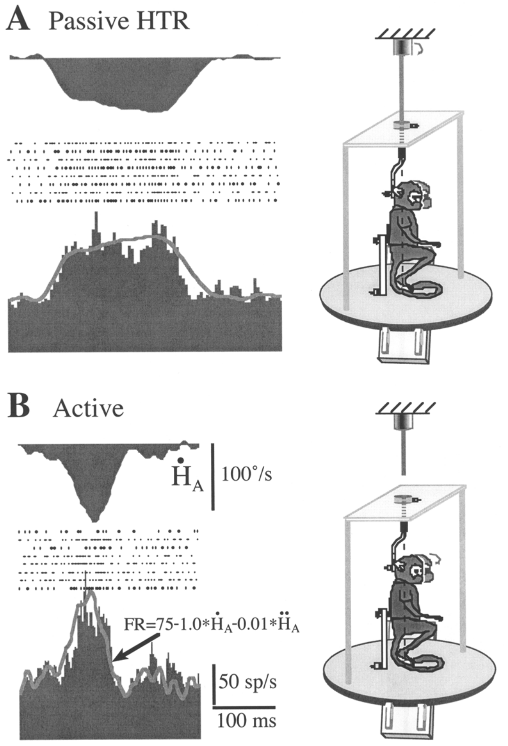
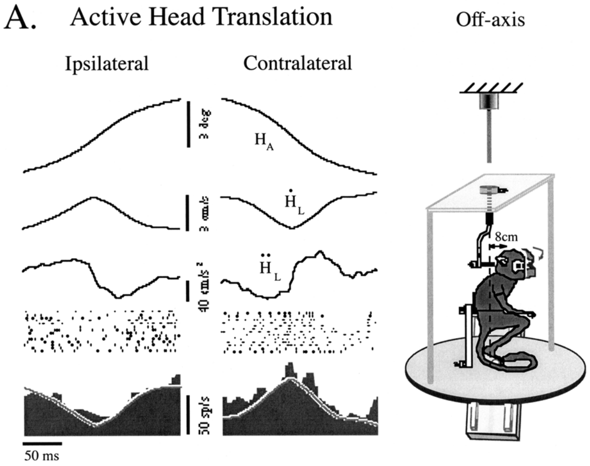


FIGURE 3. Horizontal-canal-related vestibular nucleus neuron sensitive to both passive and active head rotation. (**A**) Passive head-on-trunk rotation (average of eight steps in head velocity in the cell's excitatory on-direction). The *filled trace* at the top shows the average angular head velocity. The *middle traces* show spike rasters from individual trials. The *bottom trace* shows unit firing rate. (**B**) Responses during active head movements generated during gaze saccades. The traces superimposed on the firing-rate histograms are the responses expected on the basis of the cell's response to sinusoidal WBR at 2.3 Hz. The neuron's firing rate was not related to eye movements.

aural translation have been studied during passive and active head movements. Some vestibular nucleus neurons also generated responses to passive and active head movements that were similar. Many neurons in the vestibular nuclei are sensitive to eye movements, and most cells of this type are presumed to be related to producing or controlling the vestibulo-ocular reflex (VOR). These neurons are located primarily in the rostral parts of the vestibular nuclei. Vestibular nucleus non-eye-movement-related (NEM) neurons are located throughout the vestibular nuclei. NEM neurons project to many regions of the thalamus, brainstem, cerebellum, and spinal cord, and thus are related to a wide variety of functions. FIGURE 3 shows the firing behavior of a horizontal-canal-related NEM vestibular nucleus neuron that was sensitive to both passive and active head movements. The records in FIGURE 3A are averages of eight rapid step changes in angular head velocity produced by attaching the monkey's head to a ceiling motor. The head rotation was in the plane of the semicircular canal, and the axis of rotation was centered on the monkey's head intersecting the interaural plane. The step in head velocity produced an increase in firing rate that was proportional to head velocity (1.0 spikes/s/°/s). The comparable averaged response recorded during self-generated active angular head rotations produced during gaze saccades is shown in FIGURE 3B. The step changes in head velocity were more transient during active head movements, but the values for peak acceleration and velocity of the movements were comparable. The solid traces superimposed on the firing-rate histograms are the responses predicted on the basis of the cell's response to passive WBR (equation in FIGURE 3B). For active head movements in this cell's "on" direction (ipsilateral), the sensitivity to head rotation during active head movements was similar.

The responses of central vestibular neurons to active head translation were studied by allowing the monkey to generate head movements in the horizontal plane with the axis of head rotation moved 5–8 cm behind the center of the head. In this posture, head rotations produced a combination of linear translation and angular rotation. FIGURE 4 illustrates the response of a central otolith neuron to both passive and active head translation during off-axis head rotation. The neuron was not sensitive to angular head rotation with the head centered on the axis of rotation of the turntable. Its firing rate was modulated in phase with linear head velocity (18.7 spikes/s/cm/s) during sinusoidal linear translation at 2.0 Hz. In FIGURE 4A, the neuron's averaged response during head saccades generated with the head restrained in an off-axis position (diagram on the right) is illustrated. The spike rasters for individual saccades are illustrated. The cell was inhibited when the head was actively translated in the ipsilateral direction (left traces) and excited during contralateral head translations (right traces). The solid traces superimposed on the firing-rate histograms are the responses predicted from the cell's sensitivity to whole-body linear translation. These active head movements were stored on a computer and used to program a similar sequence of passive forced head movements using the ceiling motor (FIG. 4B). The passive head movements evoked in this manner were similar, but not identical, to the active head movements due to flexibility in the coupling of the motor to the head and to changes in resistance to movement produced by the monkey. The profiles of inhibition by ipsilateral translation, and excitation by contralateral translation, were similar to those generated during active head movements, and roughly predictable from the cell's response to passive whole-body linear translation (solid traces superimposed on firing-rate histograms in FIG. 4B).

A. Active Head Translation



B. Passive Forced Translation

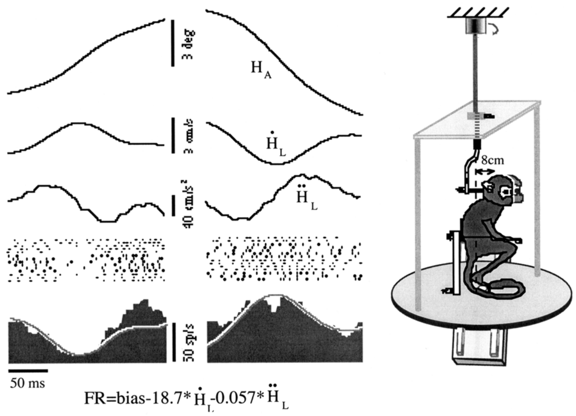


FIGURE 4. Otolith-related vestibular nucleus neuron sensitive to both passive and active head translation. (**A**) Active head-on-trunk off-axis rotations (average of 14 ipsilateral and contralateral head movements). The *top traces* show the average change in angular head position, linear head velocity, and linear head acceleration. The *middle traces* show spike rasters from individual trials. The *bottom trace* shows unit firing rate. (**B**) Responses during passive, forced head movements similar to active head movements. The traces superimposed on the firing rate histograms show the responses expected on the basis of the cell's response to sinusoidal whole body translation at 2.0 Hz. The neuron's firing rate was not related to eye movements.

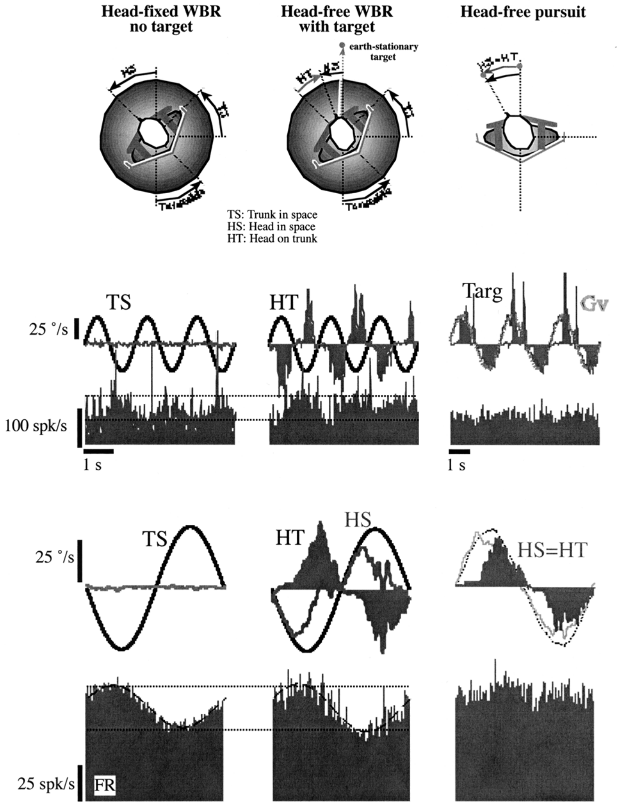


FIGURE 5. Non-eye-movement-related vestibular nucleus neuron that was differentially sensitive to passive head movements. Top pictures illustrate three different paradigms used during recording. Records in the *left column* show the cell's response to passive WBR. The *center column* illustrates the lack of a change in the neuron's response (*dashed lines* between left and center columns) when active head-on-trunk movements (HT) reduced head velocity in space (HS). The *righthand column* shows the cell's lack of a response during active head-on-trunk movements generated while tracking a visual target that was moving in space. A combination of saccades and smooth tracking head movements was produced.

Vestibular Nucleus Neurons Preferentially Sensitive to Passive Head Movements

Most vestibular nucleus neurons were unlike the cells illustrated in FIGURES 2–4, and generated dramatically different responses during passive and active head movements. The most dramatic changes were an insensitivity to active head movements. FIGURE 5 illustrates recordings obtained from a secondary horizontal-canal-related NEM neuron in the vestibular nuclei that was insensitive to active head movements. Records from three different conditions are illustrated. The records on the left were obtained during passive WBR at 0.5 Hz while the monkey's head was restrained from moving. In this condition, the movement of the trunk in space (TS) was the same as the movement of the head in space (HS). Records obtained during three representative cycles of WBR are shown as well as the average response over many cycles (bottom traces).

The center column of records was also recorded during passive WBR at 0.5 Hz, but the monkey's head was free to move, and it was encouraged to maintain its head stable in space by fixating on an earth-stationary target. In this condition, active movements of the head on the trunk (filled traces) were generated that were opposite in direction to movements of the body in space (solid sinusoidal traces). The effect was to dramatically reduce the movement of the head in space (HS trace in bottom averaged records). In spite of a reduction of head velocity in space in this condition, the modulation in the neuron's firing rate by turntable rotation was nearly the same as when the head was fixed to the turntable (dashed lines superimposed on the spike histograms).

The records in the righthand column of FIGURE 5 show responses of the same neuron when the monkey pursued a moving visual target with a combination of eye and head movements. Only a fraction of the pursuit was generated by saccadic or smooth-following head-on-trunk movements (filled traces), but the average peak head velocity in space (HS) was similar to that generated during WBR. In this condition, active head movements generated all of the head movement in space, and movement of the head in space did not modulate the neuron's firing rate. In sum, this secondary vestibular neuron was differentially sensitive to passive, non-self-generated head movements. In these contexts, its firing rate was better related to movement of the trunk in space than to movement of the head in space. The latter observation obtained for the majority of non-eye-movement-related neurons in the vestibular nuclei.[11]

Firing Behavior of Eye-Movement-Related Neurons during Active Head Movements

The majority of NEM neurons in the vestibular nuclei were differentially sensitive to passive head movements.[10] Most eye-movement-related neurons also were differentially sensitive to passive head movements, although their responses were more complex. FIGURE 6 illustrates the firing behavior of four different types of eye-movement-related vestibular nucleus neurons during gaze saccades that included a significant active head movement component. The records are averages of many gaze saccades, with spike rasters shown for individual saccades. The traces superimposed on firing-rate histograms are the responses that would be expected if the neuron's generated head-movement-related signals during both passive and active head movements. The eye-movement signals generated by eye-movement-related cells also affected their firing behavior during gaze saccades. The firing behavior of the position-vestibular-pause (PVP) and position-vestibular I and II (PVI and PVII) neurons was related to eye position. PVP and eye-head-vestibular (EHV) vestibular neurons were sensitive to eye velocity during smooth pursuit eye movements. PVP neurons characteristically paused during gaze saccades. There is considerable evidence that PVP, PVI, and EHV neurons contribute to the VOR. PVII neurons responded to contralateral head rotations, and receive direct inputs from the vestibular nerve. Many neurons, including the neuron illustrated in FIGURE 6, receive inputs from the otolith afferents and may contribute to otolith ocular reflexes.

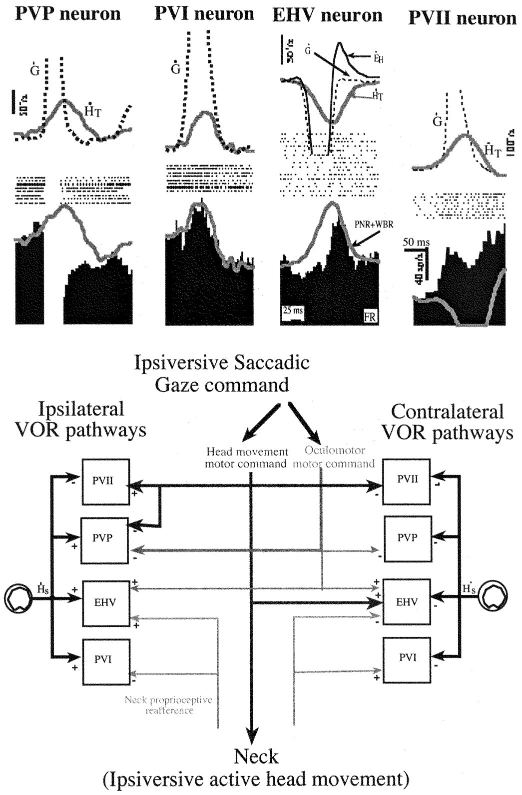


FIGURE 6. Firing behavior of four types of eye-movement-related vestibular neurons during active head movements. The *top traces* in each of the upper panels show averaged head-on-trunk velocity (*solid traces*) and average gaze velocity for several ipsiversive gaze saccades. The middle traces show spike rasters from individual saccades. The traces superimposed on firing-rate histograms are the responses expected on the basis of the cell's sensitivity to passive WBR and passive neck rotation. The diagram at the bottom of the figure summarizes oculomotor efference copy, head movement efference copy, and neck sensory reafferent inputs to different classes of VOR interneurons in the vestibular nuclei. The thickness of the lines indicates strength of inputs.

In squirrel monkeys, the head movements associated with saccadic gaze shifts typically begin at the same time as, or slightly before the initiation of saccadic eye movements and last 100 ms or more after the gaze shift is completed. Consequently, head-movement-related signals generated by these VOR-related neurons could be divided into two components: firing behavior during the combined active eye-head gaze shift, and firing behavior during the VOR eye movements that occurred immediately after the gaze shift was completed. Different types of eye-movement-related neurons generated different responses during gaze saccades and gaze-saccade-related VOR eye movements. PVP, EHV, and PVII neurons were insensitive to active head movements during active gaze shifts. PVP neurons stopped firing altogether.

EHV neurons either generated bursts of spikes related to ocular saccades or were insensitive to the active gaze shift like the cell illustrated in FIGURE 6, but they were not sensitive to active head movements until just before the end of the gaze shift when the VOR began to stabilize gaze. PVII neurons were similar to the cell illustrated in FIGURE 5, and were insensitive to active head movements related to gaze saccades. PVI neurons were exceptional, in that they were sensitive to active head movements during saccadic gaze shifts and to head movements related to VOR eye movements immediately after gaze shifts.

Contribution of Neck Proprioceptive and Efference Copy Signals to Differential Sensitivity of Vestibular Nucleus Neurons to Active Head Movements

The complex signal processing that occurs in different constituents of central VOR pathways during gaze saccades is summarized in the diagram at the bottom of FIGURE 6, which summarizes the results of several recent studies.[10,12,14] A variety of signals contributes to shaping the responses of different classes of secondary VOR neurons. Saccade-related oculomotor efference copy signals modify signal processing in PVP and, to a lesser extent, EHV neurons during active head movements. Head movement efference copy signals modify signal processing in

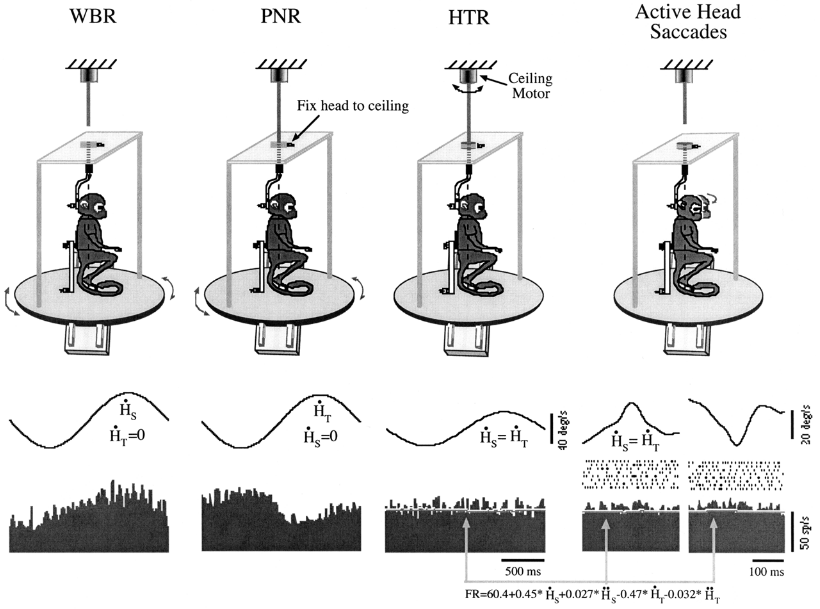


FIGURE 7. Neck sensory reafferent inputs cancel vestibular signals on a non-eye-movement-related vestibular nucleus neuron. The neuron's responses during passive WBR and passive neck rotation (PNR) were roughly equivalent and canceled each other during passive and active head-on-trunk rotation (HTR). Traces superimposed on firing-rate histograms are the responses expected on the basis of the cell's sensitivity to passive WBR and PNR.

PVII, PVP, and EHV neurons. Finally, neck proprioceptive reafferent signals modestly affect signal processing in PVI and EHV neurons.

Neck proprioceptive inputs dramatically affect signal processing in some non-eye-movement-related vestibular neurons, and effectively cause them to generate signals that are better related to movement of the trunk in space than to movement of the head in space, regardless of whether head-on-trunk movements are active or passive. The firing behavior of one such neuron is illustrated in FIGURE 7. During passive WBR, this cell's firing rate was primarily related to ipsilateral angular head velocity. Its response did not change during off-axis rotation, which suggests that it received little input from otolith vestibular receptors. On the other hand, it received a strong input from neck proprioceptors. During passive neck rotation (PNR experiment), the cell's firing rate was related to contralateral angular head-on-trunk velocity. When the head was passively rotated on the trunk with the ceiling motor (HTR condition), the neck and vestibular inputs to the neuron canceled each other. Head velocity in space was equal to head-on-trunk velocity, and the neuron's firing rate was essentially unmodulated. A similar lack of modulation was observed during active, self-generated head movements in both the ipsilateral and contralateral directions. The traces superimposed on the firing-rate histograms are the responses predicted from its responses during passive WBR and passive neck rotation (equation at the bottom of the figure).

Many vestibular neurons that were insensitive to active head movements were also insensitive to passive neck rotation and remained sensitive to passive head-on-trunk rotation. The insensitivity of these cells to active head movements was thus probably due to the addition of a head movement efference copy signal. An example of such a neuron is shown in FIGURE 8. This particular cell received direct inputs

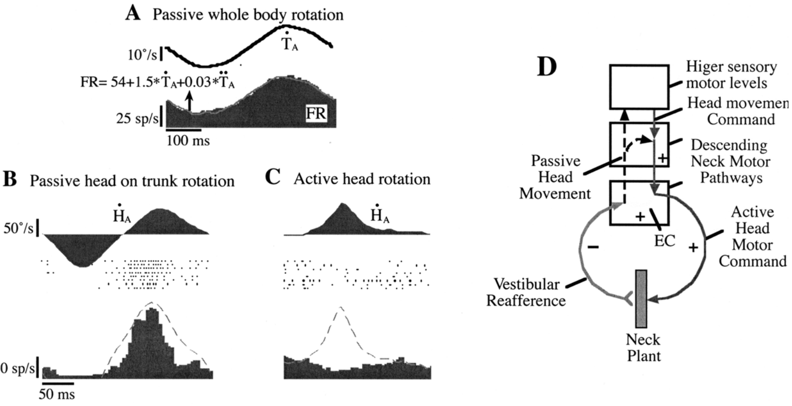


FIGURE 8. Head movement efference copy signals canceling vestibular signals on a vestibulo-spinal tract neuron. (**A**) Response to sinusoidal passive WBR at 2.3 Hz. (**B**) Response during HTR oscillations that were similar in peak velocity and acceleration to active head rotations in **C**. Traces superimposed on firing rate histograms are the responses expected on the basis of the cell's sensitivity to passive WBR. (**D**) Schematic adapted from von Holst and Mittelstaedt.[15] See text for further discussion.

from the vestibular nerve and was antidromically activated following electrical stimulation of the spinal cord. Its firing rate was strongly modulated in phase with head velocity during passive WBR (FIG. 8A) and during passive head-on-trunk rotation (FIG. 8B). The cell was not excited during comparable active head movements, which suggests that a central efference copy of head-on-trunk movements was responsible for cancellation of vestibular signals on this neuron rather than neck proprioceptive inputs. The diagram in FIGURE 8D is modified from the classic paper by von Holst and Mittelstaedt[15] on the reafference principle. Their thesis was that efference copy signals often cancel sensory reafferent signals produced by active motor commands. They argued that this cancellation probably occurred at segmental levels of central processing rather than higher centers. The scheme allowed segmental reflex motor programs to be executed without taking into account sensory reafferent consequences of ongoing intended movements. In the case of the vestibulocollic-reflex-related neuron illustrated in this figure, the sensory reafferent signal produced by active head movement commands is a vestibular signal. Neurons of this type may project directly to neck motor neurons and produce head-on-trunk stabilizing reflex head movements when the head is passively perturbed or loaded. This reflex would work against the motor programs that produce active head movements were it not canceled. The evidence from our studies suggests that the addition of a head movement efference copy signal to vestibular signals in the vestibular nuclei may perform this function.

DISCUSSION

The vestibular nerve sends sensory signals to the brain that code the position and movement of the head in gravitoinertial space. The sensory information is used not only to construct an internal estimate of self-motion, but also to provide a reference frame for calculating the relative coordinates of motor control systems. The vestibular nuclei constitute the first place in the central nervous system that these sensory signals can be modified. What we have learned over the last 30 years is that sensory vestibular signals are profoundly modified and transformed in the vestibular nuclei. The dynamic characteristics of vestibular signals are modified. The spatial tuning of vestibular signals is transformed by convergence of information from different vestibular end organs from both labyrinths. Visual and proprioceptive estimates of self-motion are added to vestibular estimates. Finally, motor signals related to eye, head, and limb movements profoundly modify the responses of vestibular neurons. The modifications produced by these various influences produce a remarkable variety in the signals produced by individual vestibular nucleus neurons.

We have only begun to understand how and where these different signals are constructed and distributed to other sensory-motor integrative centers in the spinal cord, brainstem, cerebellum, and cerebral cortex. The approach to understanding how the vestibular system in general and the vestibular nuclei in particular contribute to the maintenance of visual stability, postural control, and sensory estimates of self-motion will have to include the use of appropriate behavioral techniques in combination with neurophysiological studies of anatomically identified central pathways in animals demonstrating alert behavior.

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REFERENCES

1. Zacharias, G.L. & L.R. Young. 1981. Influence of combined visual and vestibular cues on human perception and control of horizontal rotation. Exp. Brain Res. **41:** 159–171.
2. Mergner, T. & W. Becker. 1990. Perception of horizontal self-rotation: multisensory and cognitive aspects. *In* Perception and Control of Self-Motion. R. Warren & A.H. Wertheim, Eds.: 219–263. Lawrence Erbaum. Hillsdale, NJ.
3. Mergner, T. 2002. The matryoshka dolls principle in human dynamic behavior in space: a theory of linked references for multisensory perception and control of action. Curr. Psychol. Cogn. **21:** 129–212.
4. Mergner, T., C. Maurer & R.J. Peterka. 2003. A multisensory posture control model of human upright stance. Prog. Brain Res. **142:** 189–201.
5. Goldberg, J.M., A.M Brichta & P.A. Wackym. 2000. Efferent vestibular system: anatomy, physiology, and neurochemistry. *In* Neurochemistry of the Vestibular System. A.J. Beitz & J.H. Anderson, Eds.: Chapt. 4: 61–84. CRC Press. Boca Raton, FL.
6. Purcell, I.M. & A.A. Perachio. 1997. Three-dimensional analysis of vestibular efferent neurons innervating semicircular canals of the gerbil. J. Neurophysiol. **78:** 3234–3248.
7. Büttner-Ennever, J.A. 1988. Anatomy of the oculomotor system. *In* Reviews of Oculomotor Research. J.A. Büttner-Ennever, Ed.: 119–176. Elsevier. Amsterdam.
8. Wilson, V.J. 1991. Vestibulospinal and neck reflexes: interaction in the vestibular nuclei. Arch. Ital. Biol. **129:** 43–52.
9. McCrea, R.A., G.T. Gdowski, R. Boyle & T. Belton. 1999. Firing behavior of vestibular neurons during active and passive head movements: vestibulo-spinal and other non-eye-movement related neurons. J. Neurophysiol. **82:** 416–428.
10. McCrea, R.A. & G.T. Gdowski. 2003. Firing behaviour of squirrel monkey eye movement-related vestibular nucleus neurons during gaze saccades. J. Physiol. **546:** 207–224.
11. Gdowski, G.T. & R.A. McCrea. 1999. Integration of vestibular and head movement signals in the vestibular nuclei during whole-body rotation. J. Neurophysiol. **82:** 436–449.
12. Gdowski, G.T. & R.A. McCrea. 2000. Neck proprioceptive inputs to primate vestibular nucleus neurons. Exp Brain Res. **135:** 511–526.
13. Highstein, S.M. & R.A. McCrea. 1988. The anatomy of the vestibular nuclei. *In* Reviews of Oculomotor Research. J.A. Büttner-Ennever, Ed.: 177–202. Elsevier. Amsterdam.
14. Gdowski, G.T., T. Belton & R.A. McCrea. 2001. The neurophysiological substrate for the cervico-ocular reflex in the squirrel monkey. Exp Brain Res. **140:** 253–264.
15. Von Holst, E. & H. Mittelstaedt. 1950. Das Reafferenzprincip (Wechselwirkungen zwischen Zentralnedrvensystem und Peripherie). Naturwissenschaften. **37:** 464–476.