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SENSORY PROCESSING IN THE VESTIBULAR NUCLEI DURING ACTIVE HEAD MOVEMENTS

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INTRODUCTION

The sensory epithelium of the vestibular system is a head-referenced system located within the bony labyrinths whose 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 (44, 23, 42), but these signals need to be modified during active head on trunk movements. During self-generated head movements the reflex movements of the back, limbs and neck, produced by vestibulospinal pathways must be suppressed or cancelled (39, 40, 19, 29). Similarly, the sensory reafferent vestibular inputs related to self-generated head movements must be distinguished in order to use vestibular signals to estimate movement of the body in space (29, 28).

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 (16, 21, 10). However, it is more likely that the distinction between active and passive 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 (31, 12, 24, 25, 4, 43), the cerebral cortex (1, 2, 20, 13), reticulo-spinal collaterals (17, 18), and the spinal cord (34, 37, 38) that could modify sensory processing during passive or self-generated head on trunk movements. The latter inputs usually reduce the vestibular nucleus unit responses to head on trunk rotation (8, 3, 14, 41).

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 (26, 11, 27) and during the vestibulo-collic reflex (15). Specifically, we found that many units in the vestibular nuclei had signals that were better related to trunk velocity in space than to head velocity in space during whole body rotation (15) and that many units were insensitive to head movements generated during gaze saccades. Although most vestibular nucleus units receive neck proprioceptive inputs that reduced their sensitivity to head on trunk movements, these inputs were not usually strong enough to render units insensitive to active head movements. Consequently, we concluded that additional signals, namely head

movements efference copy signals, were used to cancel or suppress self-generated vestibular signals.

One question that arises is whether the same efference copy signal that is used to transform vestibular signals from head movement coordinates to body coordinates during whole body rotation is also used during gaze saccades or smooth pursuit head movements to produce insensitivity to active head movements. If the premotor pathways that produce each type of head movement are different, the construction of an internal estimate of the active head movement motor command might also be different. More importantly, the functional utility of suppressing vestibular signals might vary as the functional goal of the head movement changes. The head movements produced by the vestibulo-collic reflex (VCR) are designed to stabilize the position of the head in space while the head movements produced during gaze saccades or smooth tracking are designed to change the position of the head in space. The vestibular reafferent signals produced by these different types of head movements could be utilized in different ways by the brain.

In this paper, we present evidence that the vestibular reafferent signals related to active, self-generated, head movements vary depending on the behavioral goal of the head movement. We will focus in particular on secondary vestibular units that were antidromically activated following electrical stimulation of the ventromedial funiculi of the cervical spinal cord that were presumably involved in producing the VCR.

METHODS

Single unit recordings were obtained from 107 horizontal canal related vestibular nucleus units in alert squirrel monkeys that were free to move their head in the yaw plane. The details of experimental methods are described elsewhere (15, 27). Eye and head movements were recorded with the magnetic search coil technique. Stimulating electrodes (250 μm Teflon-coated Ag-AgCl wires) were implanted bilaterally in the middle ear and in the ventromedial funiculi of the spinal cord at C1 (75 μm Teflon-coated platinum wires bared about 1 mm from their tips) to allow orthodromic and antidromic identification of secondary vestibulo-spinal units, respectively. The monkeys were seated in a plexiglass chair on a vestibular turntable and were permitted to make angular head movements ($\pm$ 40°) that were restricted to the plane of the horizontal semicircular canals. Other head movements were prevented by attaching their head to a rod that rotated within 5 mm of the C1-C2 axis of rotation. All head movements could be restricted by locking the rod in place. Changes in the body posture were minimized by the shape of the chair and by placing a harness over the animal's shoulders.

Active and Passive head, neck, and body rotation

Responses during whole body rotation were recorded at two frequencies (0.5 Hz, 40 °/s; 2.3 Hz, 20 °/s) while the head was fixed with respect to the vestibular turntable. Unit responses were recorded both in the presence and absence of an earth stationary visual target. The responses of most units were also recorded during cancellation of the vestibulo-ocular reflex produced by moving the turntable and target in tandem. Neck proprioceptive inputs were assayed by fixing the head in space during turntable rotation. Passive head on trunk rotations were produced by rotating the rod attached to the animal's head either manually or with a ceiling-mounted motor.

Unit responses were recorded while the monkey generated spontaneous gaze saccades (combined eye and head movements) in the absence of a visual target or while the monkey tracked sinusoidal moving visual targets (0.5 Hz, 40 °/s) with smooth head movements.

Combinations of active and passive head movements

Unit responses during whole body rotation were recorded at two frequencies (0.5 Hz, 40 °/s; 2.3 Hz, 20 °/s) while the head was free to move, in the absence of a visual target. In some units responses were recorded while the monkey fixated on an earth-stationary visual target while the whole body was rotated (0.5 Hz, 40 /s). The stimulus evoked compensatory head movements with respect to the table motion and tended to stabilize the head in space.

Data analysis

The response to sinusoidal stimuli was averaged with respect to the stimulus frequency, and the unit sensitivity (gain and phase) was assessed by fitting a sinewave function (fixed frequency, least squares fit) to the average. 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-free 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 50-150 °/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 whole body rotation with the head restrained.

RESULTS

Single unit recordings were obtained from 107 vestibular neurons in three squirrel monkeys whose head was free to move in the plane of the horizontal semicircular canal. Half (54/107) of the units encountered in the vestibular nuclei were not sensitive to eye movements. The results reported are based on the responses generated by these non-eye-movement (NEM) units. Most (27/34 tested) NEM units were orthodromically activated following electrical stimulation of the vestibular nerve at a latencies that were considered to be monosynaptic (1.3 ms). The secondary NEM units included nine cells that were antidromically activated following electrical stimulation of the C1 segment of the spinal cord.

Coordinate transformations during head-free whole body rotation

The vestibulocollic reflex (VCR) evoked during by whole body rotation in the head-free condition produced counter-rotating or compensatory head movements that tended to stabilize the head in space. On average, the gain of the VCR (head position/on trunk position) was 0.3, and therefore the reflex reduced the vestibular input sensed by the semicircular canals by approximately 30%. Different vestibular units responded to the VCR head on trunk movement in different ways. Figure 1 shows the firing behavior of a secondary vestibulospinal unit whose sensitivity to head velocity in space remained the same, i.e. the cell signaled the absolute head

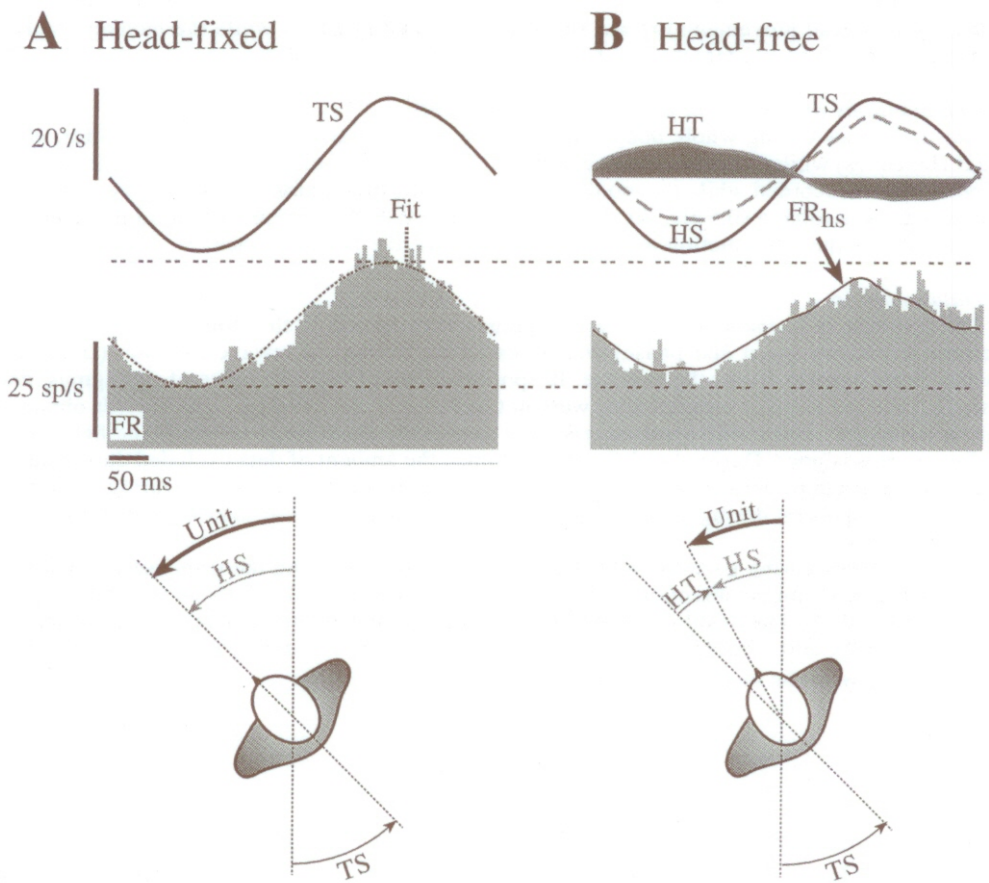

Fig. 1. - *A secondary vestibulospinal unit whose response to whole body rotation decreased during head on trunk movements produced by the VCR during whole body rotation.*

Shown are the averaged response during several cycles of (*A*) head-fixed and (*B*) head-free whole body rotation. The horizontal and dashed lines show the change in response modulation during with respect to the head-free head-fixed condition. The graphic illustration shown below each figure panel represents describes the head movement during each condition. In the head-fixed condition, head on trunk movements were eliminated (HT = 0) and the velocity of the head in space (HS) was the same as the turntable or trunk velocity (TS). In the head-free condition, a compensatory head on trunk movement (HT) was evoked by during turntable rotation (TS), which reduced the head velocity in space (HS, in this case TS plus HT). The model superimposed on the unit's firing rate (FR_{hs}) during the head-free condition is the vector product of the unit sensitivity during the head-fixed condition (dashed line labeled *fit*) and the head velocity in space during the head-free condition (HS).

velocity in space during head-fixed condition and during execution of the VCR. When the head was restrained from moving during whole body rotation (Fig. 1A) the unit's firing rate modulated in phase with ipsilateral turntable velocity (trunk in space, TS) with a sensitivity of 1.2 sp/s/°/s (fit; superimposed dashed line in Figure 1A).

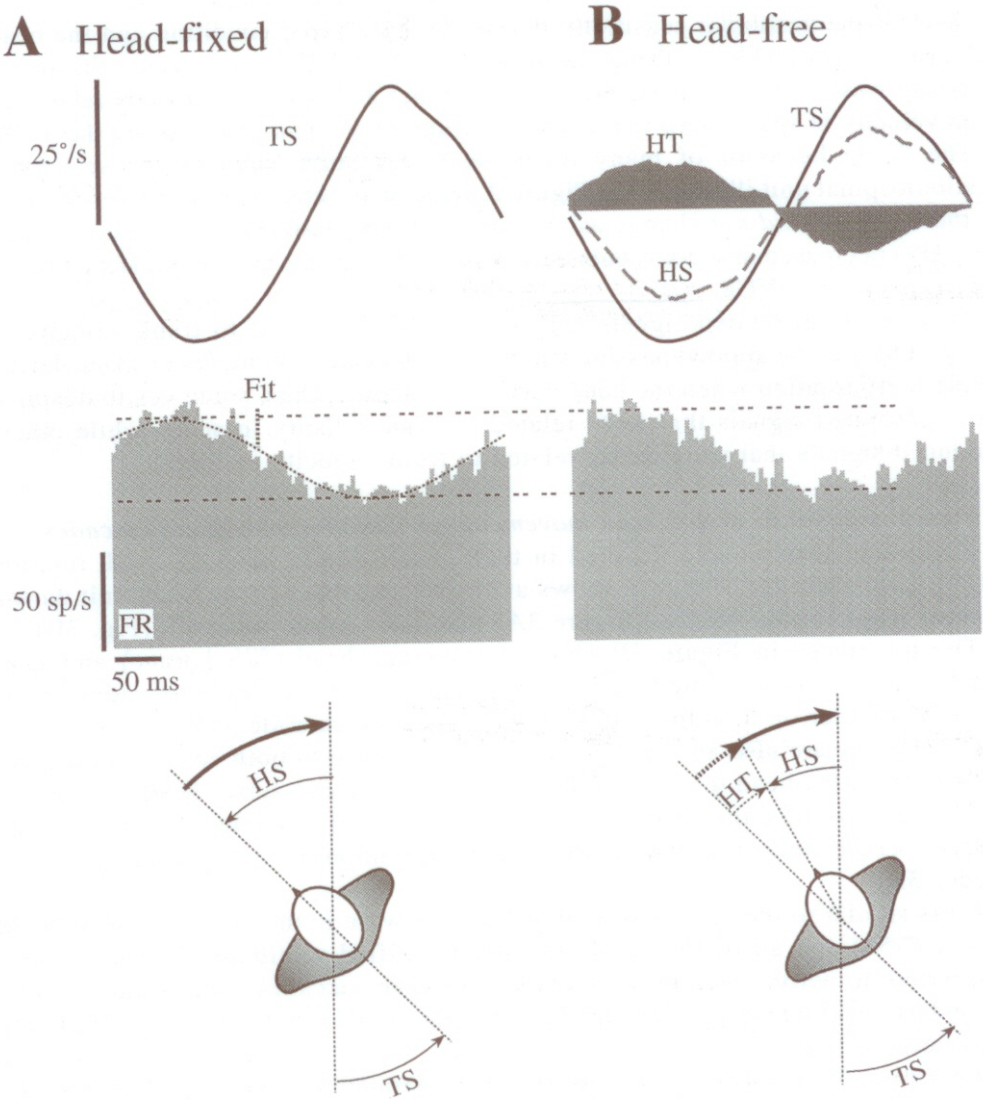

Fig. 2. - *The response of a different secondary vestibulospinal unit whose response did not change during head on trunk movements produced during whole body rotation.*

Shown are the averaged response during several cycles of (A) head-fixed and (B) head-free whole body rotation. Figure format is identical to Figure 1.

When the head was free to move, the head movements produced by the VCR (head on trunk, HT; Figure 1B) reduced the velocity of the head in space (HS, dashed trace) by 38% and the unit's firing rate modulation decreased proportionally (see horizontal lines crossing the histograms in panels A and B in Figure 1).

The model superimposed on the unit's firing rate was computed as the vector product of the vestibular sensitivity during the head-fixed condition and the head velocity in space (FR_{hs}) during the head-free condition. In this case, the unit's response was closely approximated by the model and it carried signals related to head velocity in space, despite the head on trunk movement produced by the VCR.

The firing behavior of many other vestibular units, such as the secondary vestibulospinal unit illustrated in Figure 2, were unaffected by the counter-rotation of the VCR and *did not* change as amplitude of head movement in space (dashed line, HS) decreased as a consequence of the head on trunk movement (filled trace, HT) produced by VCR.

These units generated signals that were to better related to trunk velocity in space (TS), i.e. the applied passive stimulus, than head movements in space during whole body rotation when the head was free to move. Thus, some vestibulospinal units generated signals that were related to head velocity in space while others produced signals that were better related to trunk velocity in space.

Signals related to active head movements produced during gaze saccades

Vestibular neurons also differed in their sensitivity to head on trunk rotation during gaze saccades. Figure 3 shows averaged responses of an NEM unit during passive whole body rotation (Figure 3A) and during gaze saccades (Fig. 3B).

The top traces in Figure 3B show the average head (filled trace) and gaze (dashed trace) velocity produced during by several active gaze saccades in the unit's vestibular on direction. Spike rasters for each saccade and the unit's averaged response are also shown. This unit was sensitive to both active and passive movement of the head in space, although its sensitivity to active head movements was somewhat less than would have been predicted from its response during passive whole body rotation (dotted trace superimposed on unit firing rate in Figure 3B).

Units similar to the one illustrated in Figure 3 were in the minority. Most NEM units (37/54) and all of the antidromically identified vestibulospinal units were insensitive to active head movements during gaze saccades. The responses of a secondary vestibulospinal unit during saccades in its vestibular on direction are illustrated in Figure 4.

The unit in Figure 4 is the same as the one illustrated in Figure 2 and its response to passive whole body rotation is shown in Figure 2A. The unit's insensitivity to active head movements, shown in Figure 4, presumably reflects the contribution of input related to head on trunk movement that effectively canceled inputs from the vestibular nerve. The majority of the NEM units in the vestibular nuclei, and most eye-movement related units, were similarly insensitive to active head movements during gaze saccades.

Most of the cells with canceled vestibular signals remain sensitive to passive perturbations of the head during saccades, even when the perturbations produced head on trunk movements. Consequently, it seems likely that the inputs that cancel vestibular signals are usually not dependent on proprioceptive reafferent sensory information alone, but rather an internal estimate of active head movement.

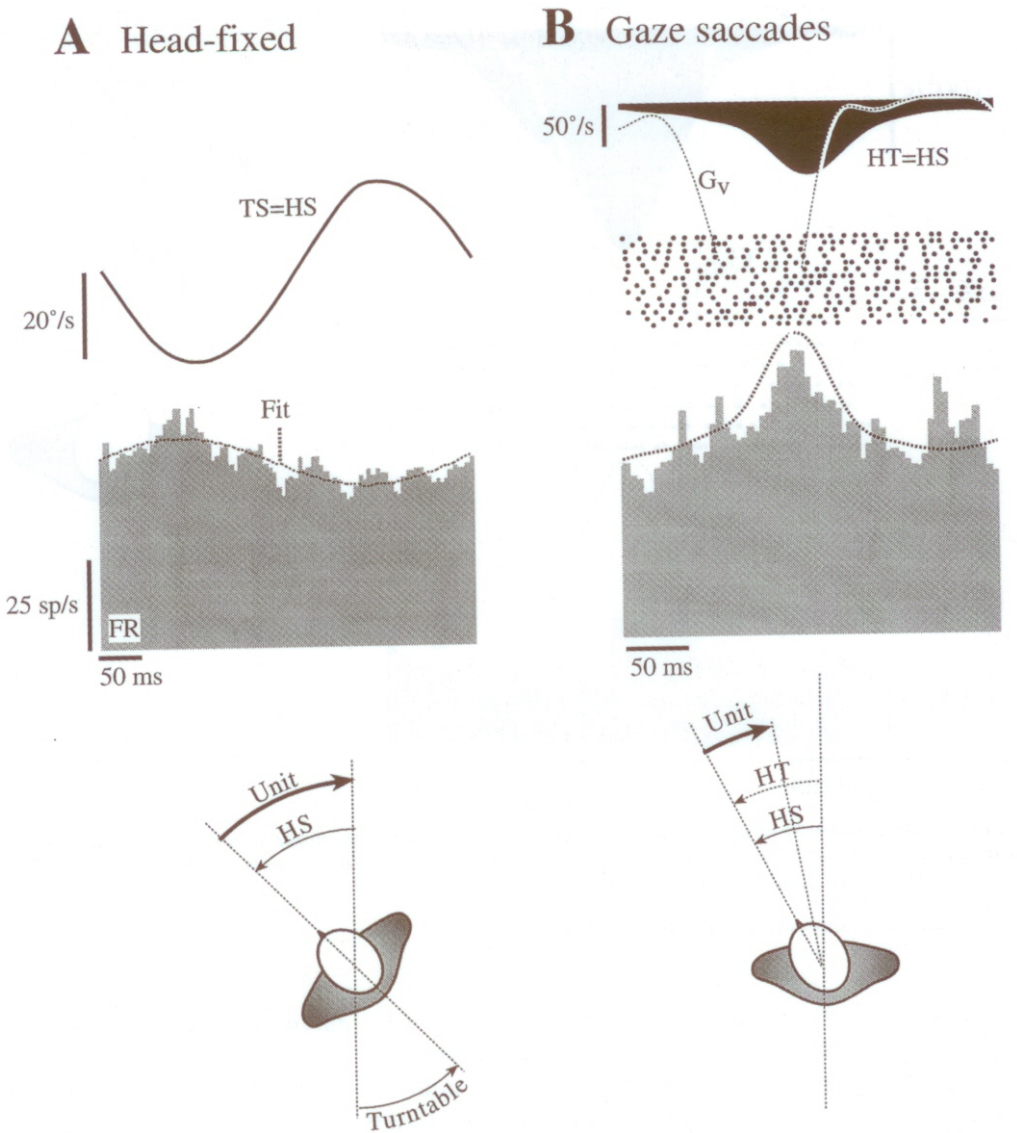

Fig. 3. - *The responses of a NEM unit (not identified as a vestibulospinal neuron) during voluntary head movements in the unit's vestibular on-direction (B) were attenuated with respect to the unit's sensitivity during whole body rotation (A).*

The graphic illustration shown below each figure describes the head movement during each condition. During spontaneous gaze saccades, the head on trunk movement produced an equivalent movement of the head in space (HS = HT). Traces shown in *B* include averaged head velocity (HS), gaze velocity (G_v) and unit firing rate (FR). A spike raster for each saccade included in the average is shown. The model superimposed on the unit's firing rate (FR_{hs}) during the gaze saccade is the vector product of the unit sensitivity during the head-fixed condition (dashed line labeled *fit*) and the head velocity in space produced during the saccade (HS).

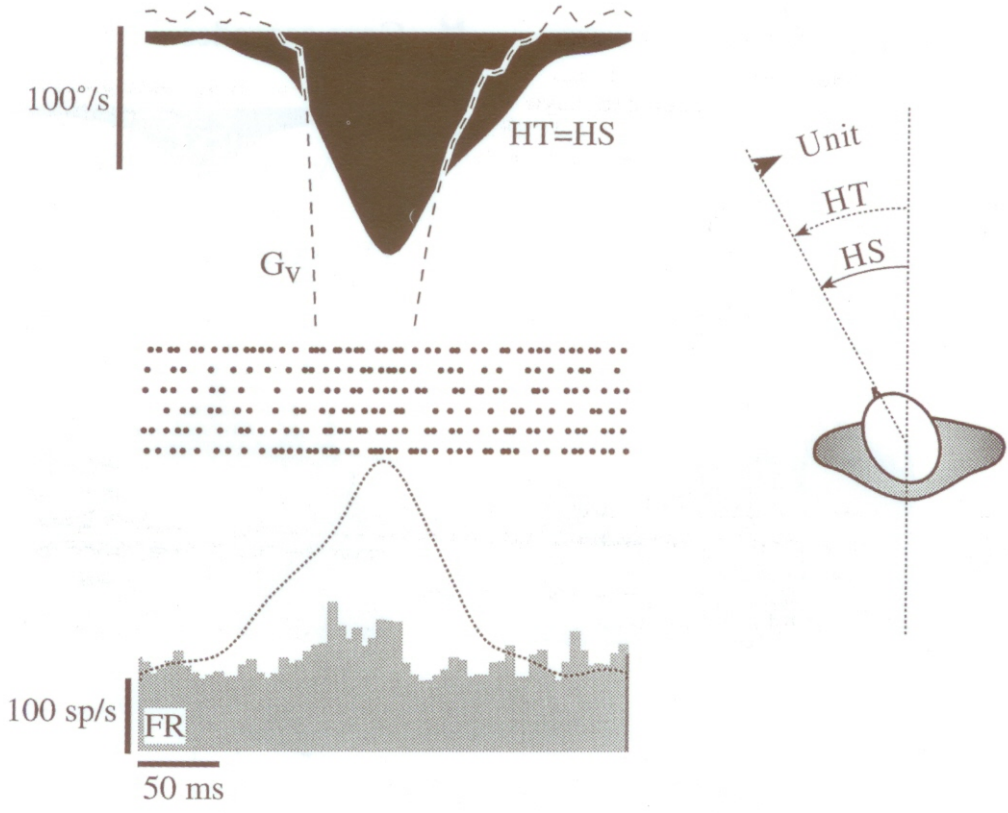

Fig. 4. - *The responses of a secondary vestibulospinal unit during spontaneous gaze saccades in the unit's vestibular on-direction whose responses were canceled with respect to the unit's sensitivity during whole body rotation (Fig. 2A).*

Format and abbreviations are identical to Figure 3.

Are the effects of head on trunk movements similar during compensatory reflexive head movements and voluntary gaze shifts?

The data presented above show that some neurons in the vestibular nuclei code head movement in space and others generate signals that are best correlated with trunk movement in space during whole body rotation. In addition, some vestibular neurons code both active and passive head movements, but most cells in the vestibular nuclei encountered in this study distinguish between head movements that are voluntarily produced and those that are produced by external forces. In each case, different units apparently receive inputs related to head on trunk rotation that add destructively with vestibular signals. When the sensitivity to head on trunk movements is large enough, it can override the reduction in vestibular input produced by the VCR during passive whole body rotation and produce a signal that is an internal estimate of trunk velocity in space and an accurate representation of the continuous external force. During saccades, the head on trunk signal can cancel

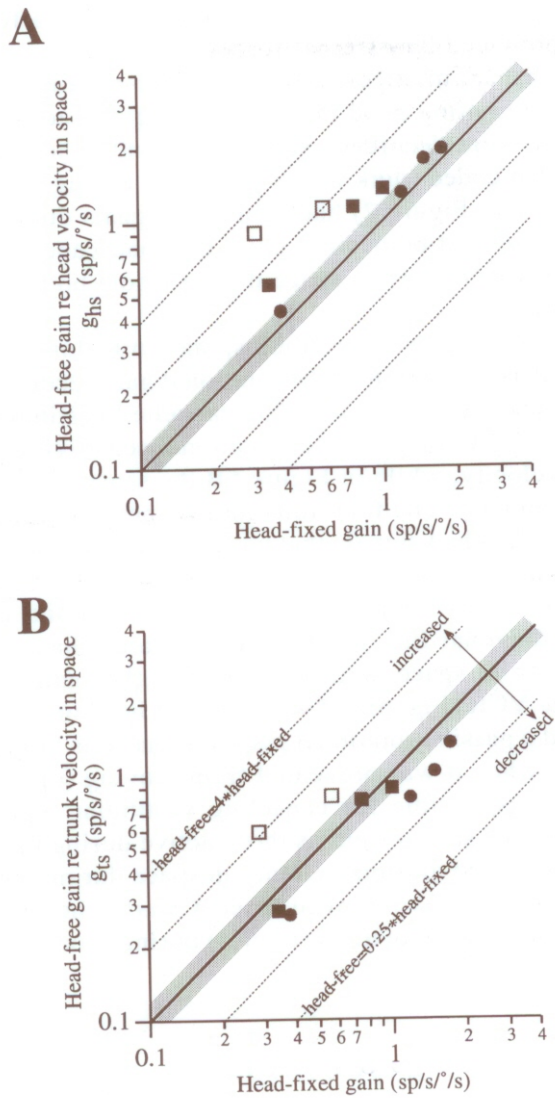

Fig. 5. - *A comparison of the unit sensitivity of secondary vestibulospinal units during head-free and head-fixed whole body rotation.*

Two computations of the same response are given, one with respect to the actual head in space measure (turntable velocity ± head on trunk velocity) and the other with respect to the actual passive stimulus (turntable velocity only). *A*. Unit sensitivity computed with respect to the head velocity in space during the head-free condition is plotted as a function of the sensitivity during the head-fixed condition. Units plotted near the center diagonal line (filled circles in shaded region) had responses that decreased proportionally with changes in head velocity in space and were similar to the unit illustrated in Figure 1. *B*. Unit sensitivity computed with respect to the trunk velocity in space during the head-free condition plotted as a function of the sensitivity during the head-fixed condition. Units plotted near the center diagonal line (filled squares near shaded region) had responses that were similar during the head-free and head-fixed conditions and an example is given similar to the unit illustrated in Figure 2. The units shown represented as open squares had larger responses during the head-free condition. All units shown had canceled responses during voluntary head movements.

vestibular signals related to active head movements without affecting sensitivity to head movements produced by external forces.

Are the same units that are unaffected by the counter-rotating action of the VCR also insensitive to the orienting head movements of gaze saccades? For the vestibulospinal units that were recorded, some were and others were not. Some vestibulospinal units that coded trunk velocity in space during whole body rotation (e.g., the unit illustrated in Figure 2) had canceled signals during gaze saccades. On the other hand, some vestibulospinal units that had canceled signals during gaze saccades coded head velocity in space during whole body rotation (e.g., the unit illustrated in Figure 1).

In Figure 5, the rotational gain of vestibulospinal units during head-free whole body rotation is plotted as a function of the rotational gain recorded when the head was fixed. As noted above, all of the units had cancelled vestibular signals during gaze saccades. In Figure 5A, the head-free rotational sensitivities were computed with respect to head velocity, while in Figure 5B the sensitivities were computed with respect to trunk velocity. The four units located near the center diagonal line in Figure 5A (filled circles) had signals that were related to head velocity in space during whole body rotation, and thus had a proportionally lower gain re trunk in space during execution of the VCR (Fig. 5B). The three units whose responses were near the center diagonal line in 5B (filled squares) had signals that were related to trunk velocity in space, and thus had a higher gain re head in space during execution of the VCR (Fig. 5B). Two units had head on trunk inputs during the VCR that produced a passive rotational response that was larger when the head was free to move than when it was prevented from moving (open squares). If the head on trunk signals responsible for canceling vestibular input to these units during saccades were of the same origin as those active during the VCR, all of the units should have been related to trunk velocity in space during the VCR and none should have been related to head velocity in space. Clearly, the strength of the head on trunk input was stronger in some units (circles) during saccades than during the VCR.

DISCUSSION

Powerful interactions between head on trunk rotation and vestibular nerve inputs to secondary vestibular neurons have been previously demonstrated in the elegant studies carried out in the laboratories of Pompeiano and Wilson (e.g., 8, 9, 45). The results of this study confirm that these neck movement inputs strongly affect the firing behavior of secondary vestibulospinal pathways during actual head movements made either reflexively in response to passive whole body rotation or voluntarily during orienting gaze saccades. However, the vestibular signals were not always modified in the same way by head on trunk rotations during the execution of these different behaviors. The sensory signals related to active head movements were effectively canceled in all of the vestibulospinal neurons that were identified, but only a fraction of these cells were affected by the head on trunk

movements produced by the VCR. A similar lack of correspondence between sensitivity to reflexive head movements and saccade related head movements was observed in many other vestibular units.

The results imply that the source of head on trunk input related to the VCR is different from the source of such inputs during saccades. In part, these inputs arise from pathways that carry neck proprioceptive signals, e.g., spino-vestibular pathways (32, 35, 30, 7, 45). But the signals related to reflexive and voluntary head on trunk movements could also arise from direct or indirect collateral inputs from pathways that are involved in producing these movements or from cerebellar (4, 5, 6, 33, 36, 43) or cortical pathways (1, 20, 13) that are involved in programming or modifying them. These neck motor efference copy signals could modify the sensitivity of vestibulospinal pathways to sensory reafferent signals as head on trunk movements are being generated. The use of an efference copy signal as opposed to a proprioceptive reafference signal as an estimate of the head on trunk movement would also allow the vestibulospinal pathways to play a role in compensating for passive, unintended perturbations of the head or changes in the inertial load of the head.

The lack of uniformity in the responses of the vestibulospinal units during the VCR may reflect a functional heterogeneity in the vestibulospinal pathways. Different classes of medial vestibulospinal neurons terminate in different laminae of the cervical spinal cord (22), and thus different cells may have different functions in maintaining neck posture. Neurons that are involved in producing the vestibulo-collic reflex might be expected to carry signals that are related to head velocity in space, since the reflex is functionally complementary to the vestibulo-ocular reflex in stabilizing gaze. Both reflexes produce compensatory movements that tend to stabilize the position of the eyes in space, but the VCR has a larger working range. Other, vestibulospinal pathways may function primarily in stabilizing the posture of the head on the shoulders or play a role in postural adjustments of the back and limbs. It is reasonable to expect that the latter functions require a vestibular signal that has been transformed into trunk coordinates by the addition of inputs related to head on trunk movement. The pathways related to maintaining head-on-shoulders posture might even be expected to have signals that are more strongly related to head on trunk movement during whole body rotation than to the head velocity in space. We have observed all three types of responses in our small sample of vestibulospinal units. The question that remains is whether the different types of interactions that were observed actually reflect the different functional roles of the vestibulospinal pathways.

SUMMARY

Many secondary vestibular neurons are sensitive to head on trunk rotation during reflex-induced and voluntary head movements. During passive whole body rotation the interaction of head on trunk signals related to the vestibulo-collic reflex with vestibular signals increases the rotational gain of many secondary

vestibular neurons, including many that project to the spinal cord. In some units, the sensitivity to head on trunk and vestibular input is matched and the resulting interaction produces an output that is related to the trunk velocity in space. In other units the head on trunk inputs are stronger and the resulting interaction produces an output that is larger during the reflex. During voluntary head movements, inputs related to head on trunk movement combine destructively with vestibular signals, and often cancel the sensory reafferent consequences of self-generated movements. Cancellation of sensory vestibular signals was observed in all of the antidromically identified secondary vestibulospinal units, even though many of these units were not significantly affected by reflexive head on trunk movements. The results imply that the inputs to vestibular neurons related to head on trunk rotation during reflexive and voluntary movements arise from different sources. We suggest that the relative strength of reflexive head on trunk input to different vestibular neurons might reflect the different functional roles they have in controlling the posture of the neck and body.

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