

Vestibular Reafference Shapes Voluntary Movement

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Summary

The vestibular organs in the inner ear are commonly thought of as sensors that serve balance, gaze control, and higher spatial functions such as navigation. Here, we investigate their role in the online control of voluntary movements. The central nervous system uses sensory feedback information during movement to detect and correct errors as they develop [1]. Vestibular organs signal three-dimensional head rotations and translations and so could provide error information for body movements that transport the head in space [2]. To test this, we electrically stimulated human vestibular nerves during a goal-directed voluntary tilt of the trunk. The stimulating current waveform was made identical to the angular velocity profile of the head in the roll plane. With this, we could proportionally increase or decrease the rate of vestibular nerve firing, as if the head were rotating faster or slower than it actually was [3]. In comparison to movements performed without stimulation, subjects tilted their trunk faster and further or slower and less far, depending upon the polarity of the stimulus. The response was negligible when identical stimulus waveforms were replayed to stationary subjects. We conclude that the brain uses vestibular information for online error correction of planned body-movement trajectories.

Results and Discussion

We reasoned that if online movement corrections are made on the basis of vestibular error signals, it should be possible to evoke corrective responses by artificially distorting vestibular feedback during a movement. We distorted vestibular information noninvasively in our subjects, without affecting other sensory systems, by passing a small current between electrodes placed behind the ears. This technique of galvanic vestibular stimulation (GVS) has the effect of increasing the spike frequency in vestibular nerves on the side of the cathodal electrode and decreasing it on the side of the anode [4–7]. Theoretical considerations [3] and empirical data [8–11] suggest that GVS produces a pattern of firing in the vestibular nerves that mimics a natural rotation of the head approximately in its roll plane. The movement

we chose to study, therefore, was one that contained a component of head rotation in this same plane. The movement, performed without vision at a moderate speed, was a rightward, sideways tilt of the trunk through a set angle (Figure 1). The movement was performed from a seated position to minimize any confounding balance responses produced by GVS [12].

The stimulation was tightly coupled to the movement by directly recording the angular velocity of the head and using this signal to determine the momentary stimulating current (Figure 1). When the head was stationary, no current flowed. When the head rotated in the roll plane, current would flow in one direction with clockwise movement and in the opposite direction with anticlockwise movement, the magnitude of the current being directly proportional to the head angular velocity. In animal studies, recordings from individual axons in the vestibular nerve have shown that there is summation at the neuronal level of vestibular signals evoked by movement and those evoked by galvanic stimuli [4]. Through this summation, our method of stimulation must therefore act to distort the natural pattern of vestibular firing, but only during movement. The galvanic stimulus in human subjects produces a pattern of vestibular nerve firing that mimics a constant velocity rotation of the head in roll [8–11]. Thus, with the change in the vestibular afferent signal proportional to the stimulating current, which in turn is proportional to the head angular velocity, the speed of the stimulus-evoked “virtual” head rotation will also be proportional to head angular velocity. Through summation, the net effect should be a pattern of vestibular firing similar to that produced by the head rotating slower or faster (depending upon stimulus polarity) than it actually is. If vestibular signals are used for online control of trunk movement trajectory, we predict that our stimulus will act to speed up the movement with one polarity and slow it down with the reversed polarity.

Figure 2A shows averaged movement traces obtained from one subject. In no-stimulus control trials (black traces), the movement was performed smoothly and took about 1.5 s to complete. The head tilted slightly more than the trunk, indicating a small amount of neck movement, even though subjects wore a foam surgical neck brace to discourage this. We coupled GVS to the movement in occasional ($p = 0.25$) and randomly selected trials. In half the trials with stimulation, the relationship between head direction and current direction was such that the rightward movement caused current to flow from the right (anode) to the left (cathode) electrode. With this polarity, we expected the net vestibular input to signal that the movement was progressing slower than intended and, therefore, to cause a speeding up. This is exactly what we observed. As shown in Figure 2A (red traces), the initial part of the trajectory was identical to that of the unstimulated movement. At around 400 ms into the movement, the traces started to deviate, and the movement velocity increased. In the other half of the stimulation trials, the relationship between head direction and current direc-

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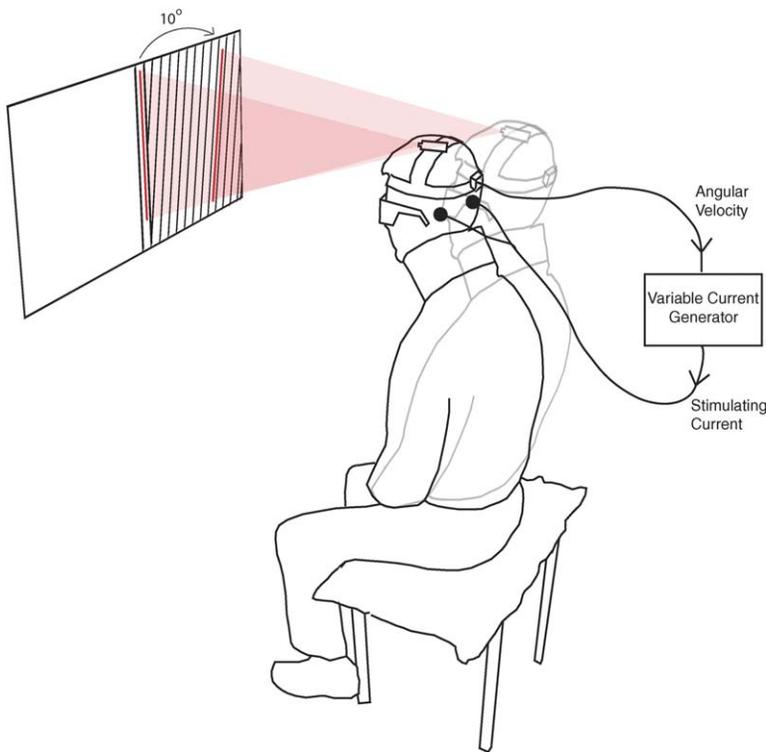


Figure 1. Galvanic Vestibular Stimulation during Goal-Directed Trunk Tilts

Seated subjects attempted to tilt their trunk through a set 10° angle in the roll plane without vision. A neck brace encouraged the head and trunk to move en bloc. Head angular velocity was transduced by a gyroscopic sensor, and the signal was simultaneously used to determine the current magnitude between two electrodes placed behind the mastoid processes. A head-mounted laser pointer provided initial and terminal visual feedback of head orientation. Vision was occluded during movement with LCD spectacles.

tion was reversed. As expected, this had the opposite effect and produced a slowing of the movement (Figure 2A, green traces).

For this particular subject, it is clear that when the stimulus polarity produced an overshoot (Figure 2A, red traces), there was some additional late compensation that brought the body back to the control tilt level. This compensation appeared to be asymmetrical because it was not evident with the opposite polarity that produced an undershoot (Figure 2A, green traces). However, these late effects were very variable between our subjects. Some showed the opposite behavior, in which there was little recovery from an overshoot but perfect recovery from an undershoot. Others produced symmetrical behavior, in which overshoots and undershoots were compensated equally. These idiosyncratic late effects probably arise from nonvestibular sensory signals indicating position error.

The effects of GVS on the dynamic phase of the movement suggest that vestibular feedback during the movement was used online to control the trajectory. However, a major objection could be that this was simply due to the stimulating current evoking a trunk movement that summed with the voluntary movement. Such a trunk movement, for example, could be produced by the balance control system. To test for this possibility, we replayed identical stimulus waveforms back to the subjects while they sat still without making any voluntary movements. Apart from the absence of voluntary movement, the procedure was the same as before. As expected from previous work [12], the stimulus presented under these conditions produced only very small and relatively insignificant body movements, as shown

for the same subject in Figure 2B. To quantify the effect, we computed mean difference traces (mean stimulated trials minus mean unstimulated trials) for trunk tilt, head tilt, and head angular velocity. From these we measured the peak difference and the time that it occurred for the movement condition. Then we measured the equivalent difference at the same point in time for the stationary condition. The group behavior (Figure 2C) was the same as described for the single subject above. A two-factor (*polarity, action*) repeated measures ANOVA (general linear model; SPSS) on these data showed for each measure a strong effect of *polarity* (trunk tilt: $F_{1,5} = 78.8$, $p < 0.001$; head tilt: $F_{1,5} = 50.7$, $p = 0.001$; head velocity: $F_{1,5} = 53.0$, $p = 0.001$) and a highly significant *polarity* X *action* interaction (trunk tilt: $F_{1,5} = 79.0$, $p < 0.001$; head tilt: $F_{1,5} = 51.8$, $p = 0.001$; head velocity: $F_{1,5} = 62.2$, $p = 0.001$). There were no significant differences in the magnitude of this effect between the first and last trial with GVS, suggesting that no adaptation had occurred.

The most parsimonious explanation for these results is that the vestibular signal generated by the movement itself (reafference) is inspected and compared to the signal that is expected. The expected sensory signal could arise either from a memory trace or from the operation of an internal model [13, 14]. Deviation from the expected feedback signal indicates movement error and so initiates a corrective maneuver. The alternative explanation, that the “extra” vestibular signal is interpreted as arising from an external agent (exafference), is less plausible given the lack of response to the same signal when subjects were sitting still. Therefore, our results can be distinguished from those that have shown

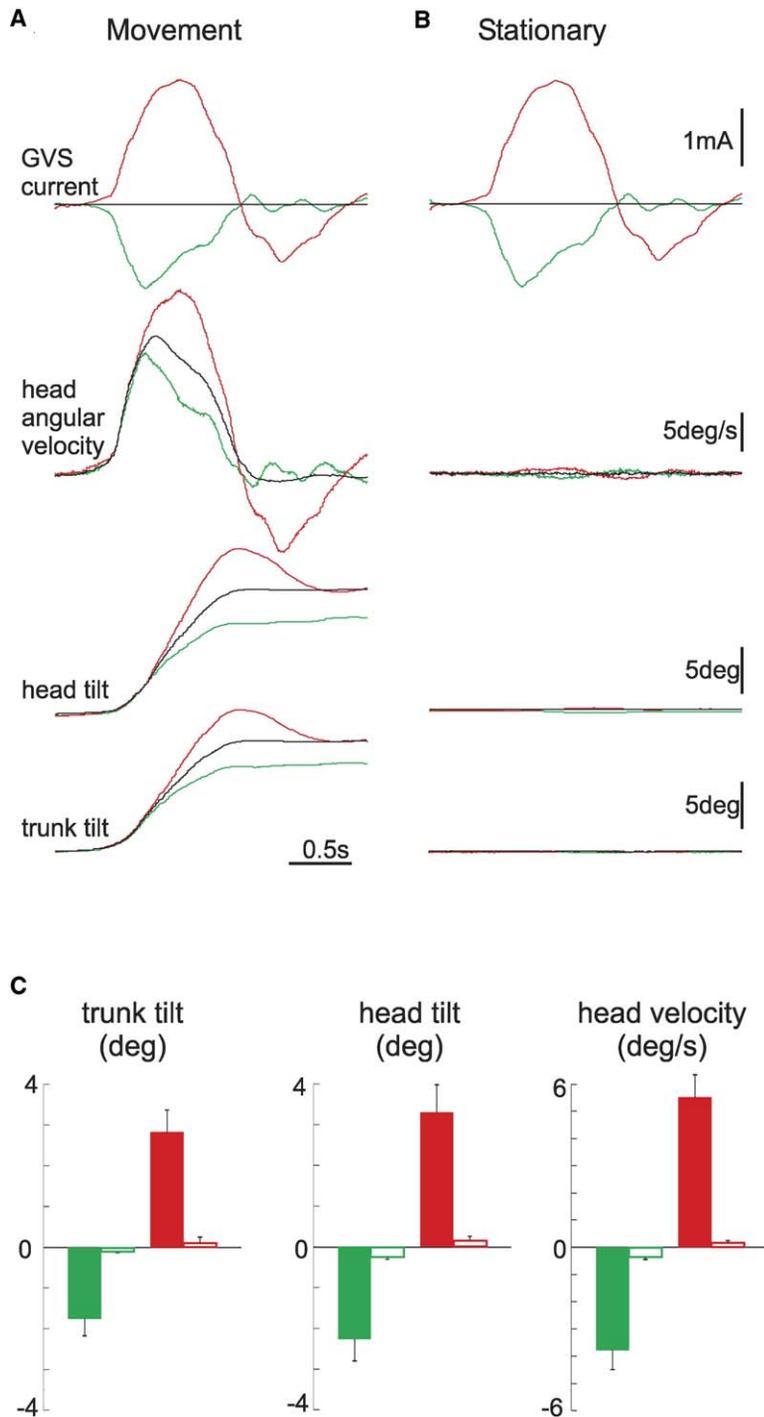


Figure 2. Kinematic Responses to Vestibular Stimulation

(A) Mean traces from a single subject during the movement task. During stimulation trials, rightward trunk movement resulted in the anodal electrode being behind the right ear (red traces) in 50% of trials and behind the left ear (green traces) in the other 50%. Black traces represent control trials (no stimulus). From the top, traces show stimulating current, head angular velocity, head tilt, and trunk tilt trajectories.

(B) Equivalent traces from the same subject when the identical mean current recorded during the movement task was subsequently applied during the sit-still task.

(C) Group mean responses to vestibular stimulation given by the peak difference between stimulation and control trials. Filled bars show responses during the movement task, and open bars show responses during the sit-still task. Color coding is as for above. Error bars denote 1 SEM.

online adjustments to arm reaching movements while the body is rotated in a motorized chair to stimulate vestibular exafference [15]. In that case, the vestibular contribution to the limb adjustment would be in redefining the new body position in relation to the target rather than monitoring the intrinsic accuracy of the movement.

Previous studies have investigated the interaction between GVS and different types of movement [2, 16–18]. The consensus has been that the stimulus generally produces an augmented response when com-

bined with a body movement. However, in most of these studies, the results have not been viewed in terms of online vestibular control of movement trajectory. The exception was the study of Séverac Cauquil and Day [2], who suggested that such a mechanism could explain their results. The difficulty they faced, though, was the coexistence of a confounding GVS-evoked balance response that was present as a result of the mode of stimulation and the motor task they employed. The present design circumvents this problem

by (1) studying subjects in a seated posture in which vestibular-evoked balance responses are inherently very small and (2) using a dynamic stimulus that is directly coupled to the instantaneous state of movement, thus reinforcing the illusion of the artificial signal having arisen from erroneous reafference.

In conclusion, we have provided compelling evidence that the vestibular system plays an important role in the online control of whole-body voluntary movements. This can be added to the growing list of vestibular functions that include self-motion perception [19], navigation [20, 21], and spatial orientation [22–24], as well as the classical oculomotor and balance functions. The vestibular sensorimotor loop presumably acts together with other loops, such as those fed by vision and proprioception, to keep movement on-track. It may be especially valuable when other senses become less reliable, such as in the dark, or for complex, high-precision whole-body movements, such as those of the gymnast or circus performer.

Experimental Procedures

Six subjects performed trunk rotations in the roll plane while seated upon a foam-covered stool (Figure 1). A foam neck brace minimized neck movement. A laser light attached to a plastic helmet projected a 44 cm vertical line on a 100 × 50 cm board placed 150 cm away at eye level. This provided visual feedback of body orientation. The subject initially aligned the laser between two central vertical lines and then initiated a trial with a button press. At this point, vision was occluded (Plato LCD spectacles, Translucent Technologies), and the subject attempted a 10° rightward trunk tilt. After 3.5 s after button press, which gave enough time for the movement to be completed, vision was restored for 2 s. This allowed the subject to compare the angle of laser orientation with a series of 10° parallel lines on the board (line thickness = 2.5 mm, 13 mm separation). Vision was again occluded, and the subject returned to the start position in response to a brief tone. Vision was then restored, and the next trial started. Thus, terminal visual feedback allowed subjects to improve tilt accuracy on a trial-by-trial basis.

Thirty training trials were given to promote consistent movement duration and accuracy. GVS was then applied in 25% of 96 randomly selected trials by applying a current between two 3 cm² electrodes placed over the mastoid processes. Terminal visual feedback was not allowed for the GVS trials. The signal from a head-mounted gyroscopic angular velocity sensor (model CRS02, Silicon Sensing Systems) was used to determine the instantaneous stimulating current. Thus, GVS was time-locked to movement, with current magnitude (≤ 2 mA) being directly proportional to head angular velocity in the roll plane. Current polarity was reversed in half of the randomly selected GVS trials. In a second session, we recorded the effect of GVS on trunk and head position when subjects were not performing a voluntary movement. The procedure was identical to that of the first session but with subjects being instructed to sit still. The stimulating current waveform applied during these sit-still trials was the mean waveform generated during the movement trials; it was computed for each subject and polarity separately.

In addition to recording head angular velocity and GVS current profile, we also recorded trunk and head tilt angle from markers fixed on both shoulders and on either side of the helmet. The trajectories of the markers were recorded in three dimensions with a motion-capture system (Coda mpx30, Charnwood Dynamics). All signals were sampled at 200 Hz. Trials within each condition were averaged after alignment with respect to movement onset. Measurements were made on difference traces computed from the mean no-stimulus control trials subtracted from the mean GVS trials. We measured the peak difference during the movement condition and the difference in the stationary condition at the same point

in time in relation to the onset of stimulation. A two-factor repeated-measures ANOVA was applied to the data, with *current polarity* and *action* (moving/stationary) as factors.

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