

VESTIBULAR CONTRIBUTIONS TO TARGET-DIRECTED REACHING
MOVEMENTS

by

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Abstract

Through the use of galvanic vestibular stimulation (GVS), vestibular input has been implicated in the online control of goal-directed actions. Deviations of hand trajectory towards the anode electrode have been observed when stimulation is delivered during movement (Bresciani et al., 2002a; Bresciani et al., 2002b; Mars et al., 2003). The purpose of this experiment was to investigate the role of vestibular information in the planning and execution of target-directed reaching movements. Ten participants sat in a chair fixed to a rotating platform and pointed to an illuminated target when an auditory tone sounded. On all trials, participants were moved from an initial reclined position to a final upright posture and vision of the scene was removed at the auditory tone. Target position could either be cued or uncued. On stimulation trials, a 2 mA, 1000 ms pulse of bipolar, binaural GVS was delivered at the start of the reaction time (RT) interval. Pointing movements were analyzed at the start of the movement, the time of target plane acquisition, and the trial end. Neither GVS nor cue type had an influence on initial pointing direction. At the target plane, anode left trajectories were significantly above and to the left of the no GVS and the anode right trajectories. By trial end, however, clear lateral deviations were present with anode left and anode right trajectories significantly to the left and to the right of the no GVS condition, respectively. These findings suggest that GVS may have little impact on action planning when there is a high degree of whole-body stability. On the other hand, once sufficient time has passed for online control processes to mediate the ongoing action, and a movement transition is imminent, there is an increased weighting of vestibular input.

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Introduction

Vestibular contributions to human movement have been extensively investigated using bilateral, bipolar galvanic vestibular stimulation (GVS) (Fitzpatrick & Day, 2004). This technique involves placing electrodes behind the ears, over the mastoid processes, and applying a small current percutaneously. GVS affects the primary irregular afferents of the vestibular nerve, with a cathodal stimulus causing an increase in firing rate, and an anodal stimulus causing a decrease in firing rate (Minor & Goldberg, 1991).¹ The virtual head motion signal that subsequently arises does not equate to any naturally produced sensation, but has been described in a vector-based model that separately examines the effects of GVS on the semicircular canals and the otolith organs (Fitzpatrick & Day, 2004). This model predicts that binaural, bipolar GVS will induce an afferent signal with components akin to that of a large roll and a small yaw towards the cathode.² Regardless of the fact that galvanic and kinetic stimuli cannot be equated, given that GVS generates a pure vestibular perturbation, it remains a valuable research tool for determining the role of the vestibular system in a variety of motor control tasks (Fitzpatrick & Day, 2004).

Responses to GVS have been characterized in postural, oculomotor, and locomotor tasks.³ The most notable reaction of a subject is the observable whole-body sway towards the anode electrode (Day, Severac Cauquil, Bartolomei, Pastor, & Lyon, 1997). This is presumably due to the interpretation that the GVS-evoked signal was a result of real motion. The eyes respond in a similar manner. When GVS is applied, there is a pre-dominant torsional oculomotor response whereby the top of the eyes rotate

¹ For more information on GVS, see Appendix A: Galvanic Vestibular Stimulation

² For more information on Fitzpatrick & Day's (2004) GVS Vector Model, see Appendix A: GVS Vector Model

³ For more information on responses to GVS, see Appendix A: Responses to GVS, and Vestibular Contributions to Human Movement

continuously toward the anode until the offset of stimulation (Severac Cauquil, Faldon, Popov, Day, & Bronstein, 2003). During forward walking, participants' trajectories also deviate towards the anode electrode (Bent, Inglis, & McFadyen, 2004; Bent, McFadyen, & Inglis, 2004; Bent, McFadyen, Merkley, Kennedy, & Inglis, 2000; Carlsen et al., 2005; Fitzpatrick, Wardman, & Taylor, 1999; Kennedy et al., 2003). Furthermore, GVS has permitted detailed analyses of the vestibular contributions to gait, focused on upper and lower body control during gait initiation and steady-state walking (Bent, Inglis et al., 2004; Bent, McFadyen et al., 2004) as well as visual – vestibular interactions during walking (Bent, McFadyen, & Inglis, 2002; Bent, McFadyen et al., 2004; Carlsen et al., 2005; Fitzpatrick et al., 1999; Kennedy et al., 2003).

Despite the in-depth investigations that have been undertaken to explore the role of vestibular input during postural and locomotor tasks, very little is known about vestibular contributions to goal-directed arm movements. Presumably, since vestibular signals inform the central nervous system about the location of the head in space, they are critical in constructing an internal representation of the spatial environment between the subject and the target of the goal-directed action. Thus, it would be expected that vestibular information would be used to plan and execute reaching movements. Relatively few studies have addressed this issue, with only a portion of these using the technique of GVS. In addition, hand position analyses have focused on lateral trajectory deviations in the transverse plane. Bresciani, Blouin, Popov, Bourdin et al. (2002) had participants stand with their head fixed and point to remembered targets. In half of the trials, bilateral, bipolar GVS was randomly delivered at movement onset. Results showed that small, but significant, deviations of pointing trajectories towards the anode

electrode occurred 240 ms after stimulation. Similar results were reported when participants performed the same task in a seated position; however, deviations occurred 70 ms later, at 310 ms after movement onset (Bresciani, Blouin, Popov, Sarlegna et al., 2002). Mars, Archambault, and Feldman (2003) also demonstrated modifications of pointing trajectories towards the anode when GVS was delivered concurrent with the movement 'go' signal. Though participants were free to move their head and trunk while pointing, trunk motion only accounted for 60% of lateral and sagittal hand endpoint deviation. GVS has also been shown to affect the control of arm movements during more continuous tasks such as drawing (Guerraz, Blouin, & Vercher, 2003). When participants had to reproduce a geometric shape with the tip of their index finger, simultaneous GVS induced significant deviations of the drawings to the side of the anode.

This ensemble of studies clearly suggests that vestibular input is involved in the online control of goal-directed arm movements. It has been hypothesized that this online vestibular control could rely on either a sensorimotor compensation, or an updating of visual space (Bresciani, Blouin, Sarlegna et al., 2002a; Bresciani, Gauthier, Vercher, & Blouin, 2005). Participants make minimal errors when pointing to remembered targets while being concurrently rotated (Bresciani, Blouin, Sarlegna et al., 2002a). In contrast, when pointing is initiated after rotation is complete, large errors are observed. Similarly, there was no difference in reaching accuracy between pre- and post-test trials, if participants were subjected to an updating adaptation (Bresciani et al., 2005). A sensorimotor adaptation, on the other hand, had significant effects on reaching accuracy in post-test trials. This evidence suggests that there is an underlying sensorimotor

mechanism that is involved in the vestibular control of goal-directed arm movements which serves to continuously counteract rotation-induced effects.

Many questions regarding the role of vestibular input during goal-directed arm movements remain. Primarily, it is still unknown how incoming vestibular input contributes to the planning of goal-directed arm actions. Since it has been shown that vestibular information can be used online during a reaching task, it would be expected that vestibular information would also be used in the preparation of an appropriate pointing response after the imperative stimulus is given. Furthermore, the response to GVS is multi-dimensional in nature (Fitzpatrick & Day, 2004). Only analyzing responses in terms of lateral deviations in the transverse plane provides limited insight into the true form of the reaction. Instead, by arranging targets and analyzing movements in the frontal plane, a more complete understanding of the vestibular influence on goal-directed actions can be obtained.

The following experiment attempted to address these issues by examining participants' ability to point to a remembered target during a dynamic task. Target information was either provided in advance (cued), or at the "go" signal (uncued). Also, on some trials, GVS was delivered during both reaction time (RT) and movement time (MT) to induce a vestibular perturbation. Overall, it was hypothesized that GVS would affect participants' pointing movements such that they would deviate in the direction opposite the evoked vestibular sensation. Based on the predictions of Fitzpatrick and Day's (2004) model, participants were expected to point downwards and to the side of the anode in order to compensate for this perceived motion. More specifically, it was predicted that vestibular input would be involved in planning the aiming movements.

Therefore, measures of movement initiation were expected to reflect deviations towards the anode electrode. Furthermore, these deviations were expected to be most prevalent in the uncued target condition (since planning had to occur during the RT interval), and small or absent in the cued target condition (where movements could be planned in advance). Finally, based on the results of both Bresciani et al. (2002; 2002b) and Mars et al. (2003), deviations at movement endpoint were hypothesized to be greater in magnitude than those at movement initiation due to the involvement of online processes that would act to compensate for the ongoing vestibular disturbance.

Materials and Methods

Participants

Ten right-handed university students (2 males and 8 females, aged 21-31) with no history of motion sickness, epilepsy, neurological or musculo-skeletal problems were recruited to take part in this study. All participants had normal or corrected-to-normal visual acuity. Participants provided informed consent prior to their participation. The study was conducted in accordance with the ethical guidelines set by the University of British Columbia.

Apparatus

Participants were seated in a high-backed chair with armrests. The head was oriented such that the orbito-meatal plane was parallel to the floor when sitting upright. The head was secured to the chair using two L-shaped side braces that were connected with a forehead strap. Participants' right wrists were also stabilized using an orthopaedic brace

designed to restrict wrist motion. The forearms were placed palm-down on the chair's armrests. In this position, the right forearm depressed a switch attached to the right armrest. Release of the switch was used to signal movement onset.

The chair itself was fixed to a custom-built rotating platform. Rotation occurred on all trials and consisted of moving participants from an initial reclined position to a final upright posture. The goal of including whole-body rotation during the aiming trials was to activate the vestibular system and increase the weighting of incoming vestibular input.

Bipolar, binaural galvanic vestibular stimulation was delivered using two 9-cm² carbon-rubber electrodes coated with electrode gel and placed behind the participants' ears, over the mastoid processes. Two different electrode polarity configurations were used: anode behind the right ear, cathode behind the left ear (hereafter referred to as 'anode right') and anode behind the left ear, cathode behind the right ear (hereafter referred to as 'anode left'). The stimulus consisted of a 2 mA, 1000 ms square-wave pulse delivered from an A/D converter (Micro 1401, Cambridge Electronic Design Ltd., Cambridge, UK) through a constant-current stimulus isolation unit (A-M Systems 2200, A-M Systems Inc., Carlsberg, USA). A fixed level of stimulation was used across participants, as opposed to the determination of individual threshold values (e.g. Bent et al., 2000) because of the disparity between the threshold environment and the experimental environment. Typically, threshold determination is based on a definitive visible observation of sway while standing with the eyes closed. The context of the experimental task in this study, however, required participants to be seated, with their head fixed. Furthermore, stimulation occurred during forward whole-body rocking (a

condition expected to increase weighting of vestibular information), not quiet stance. Though the determination of a seated GVS threshold would have been a better match, it would still have failed to mimic the testing environment. Therefore, a fixed value was deemed just as appropriate as a threshold value. This approach is consistent with other GVS-pointing studies which have also selected a single, consistent magnitude of stimulation for GVS trials (Bresciani, Blouin, Popov, Bourdin et al., 2002; Bresciani, Blouin, Popov, Sarlegna et al., 2002; Mars et al., 2003).

Liquid crystal display (LCD) occlusion goggles (Translucent Technologies Inc., Toronto, Ontario) were used to selectively block participants' vision of the target array during the RT and MT phases of every trial. This restricted any illusory target motion that may have occurred as a result of GVS.

A computer equipped with Spike2 v5.13 software (Cambridge Electronic Design Ltd., Cambridge, UK) was used to run the experiment. The program controlled chair motion, target presentation, GVS delivery, "go" tone sounding and motion analysis recordings.

Stimulus Display

During each trial, participants were presented with one of four possible targets. The target array was constructed from red light-emitting diodes (LEDs) inserted into a clear acrylic plastic sheet that was hinge-mounted onto a moveable stand (Figure 1). All four targets were positioned in the same frontal plane and were equally spaced along an arc (radius = 16 cm), with the uppermost target 33 cm superior to the level of the chair armrests, and at the midline. In the antero-posterior direction, the targets were placed

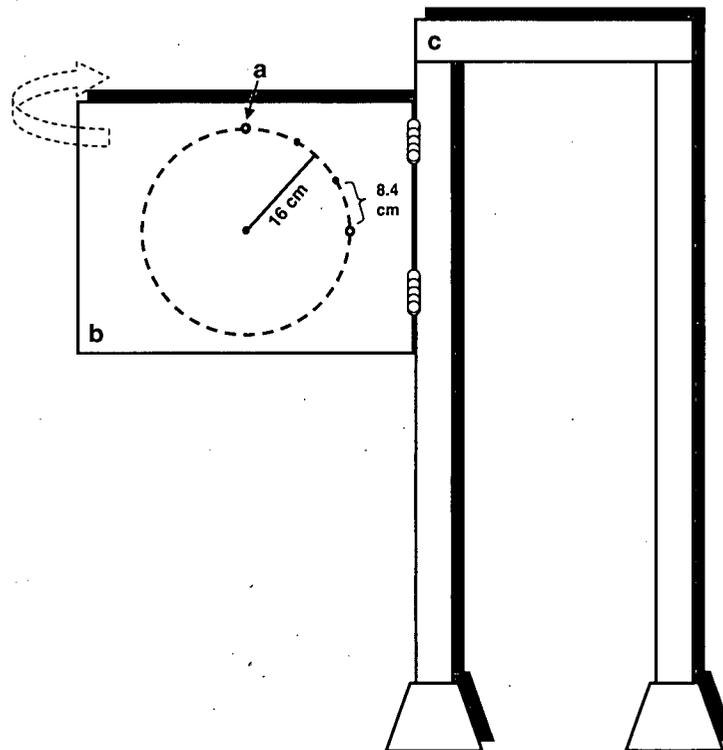


Figure 1. Stimulus display with (a) red LEDs inserted into (b) a clear acrylic plastic sheet that was hinge-mounted onto a (c) moveable stand. *Circled LEDs*, filler targets (T1 and T4); *un-circled LEDs*, experimental targets (T2 and T3).

such that they were comfortably acquirable as soon as the auditory “go” signal was given. To determine this location, the chair was placed in the rotational position corresponding to that which occurred in each trial when the “go” tone sounded. Then, each participant was asked to extend their right arm forwards in a pointing fashion, with their index finger outstretched. The targets were adjusted to be at the limit of each participant’s individual reach. During each trial, after participants’ vision had been occluded, the target array was manually swung away so that it could not be contacted during the aiming movement. The two targets forming the endpoints of the arc served only as “filler” targets. The goal of the filler targets was to reduce target predictability, thereby decreasing the likelihood that participants would completely pre-program their actions.

Motion Analysis

Infrared-emitting diode (iRED) markers were placed on the head, the trunk and the right limb in order to record both body and hand trajectories in 3-dimensions. One three-marker cluster was placed in the middle of the forehead, while a second cluster was affixed to the middle of the trunk, at the level of the clavicles. These head and trunk markers were in place to ensure that there were no resulting postural adjustments during any of the GVS trials. Trials that displayed postural deviations were excluded from the analysis. (In the end, no trials had to be removed based on this stipulation). Eight markers were positioned on the right limb. Two three-marker clusters were positioned on the lateral aspect of the upper arm (neutral orientation), and the lateral aspect of the forearm (pronated orientation); two single markers were also placed on the lateral epicondyle of the humerus and at the end of the index finger, respectively. During each

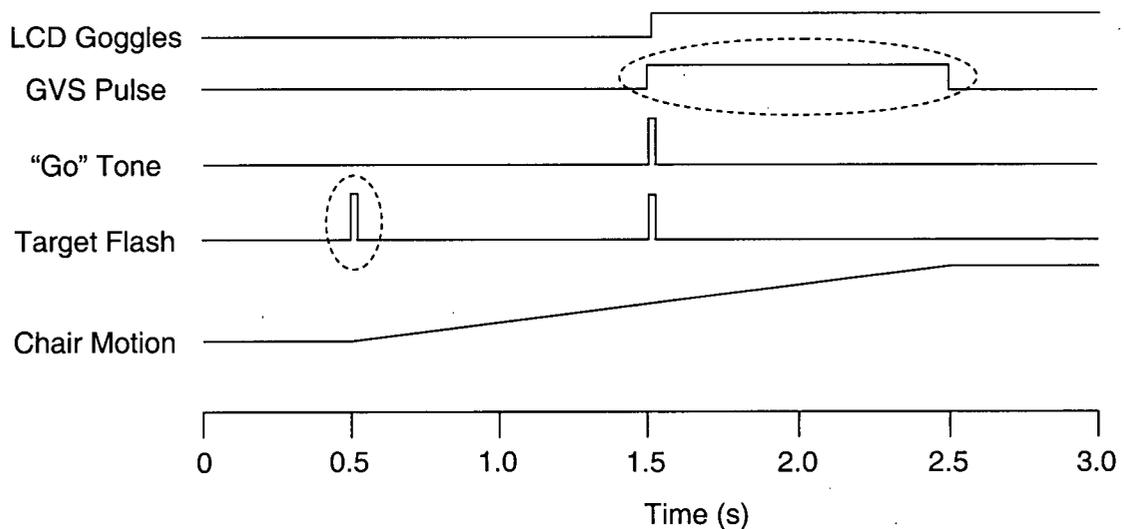


Figure 2. Trial timeline. *Dotted line* encompasses events that did not occur on every trial. First target flash was specific to cued trials. GVS pulse was specific to stimulation trials and could also be negative.

trial, the 3-D position of the iRED markers was monitored by an Optotrak Certus motion analysis system (Northern Digital Inc., Waterloo, Ontario) sampling at 200 Hz.

Experimental Task

The experimental task consisted of pointing to the indicated target from a seated position while being rotated forward. Participants were instructed to point to the target as quickly and accurately as possible when the “go” tone sounded. As shown in Figure 2, the onset of chair motion indicated the start of a 1000 ms foreperiod interval, following which an auditory “go” tone (1000 Hz, 80dB, 50 ms) signaled the participant to execute their movement to the designated target. Once chair motion stopped and the participant completed his/her pointing movement, the platform was re-set for the next trial. The chair moved at a constant velocity ($\sim 6^\circ/\text{s}$) from the onset of the trial.

Target presentation occurred at one of two points in time. In the ‘uncued’ target condition, the target flashed (25 ms) coincident with the onset of the auditory “go” tone. In this situation, the participant became aware of the required pointing movement only at the start of the RT interval. In the ‘cued’ target condition, on the other hand, the target flashed at the start of the foreperiod interval and again later, when the “go” tone sounded, providing the participant with advance information about the target to which they had to point.

On GVS trials, pulse delivery always occurred concurrent with the “go” tone and lasted 1000 ms. This meant that vestibular stimulation was present throughout the RT interval, and allowed us to investigate whether vestibular information (in this case,

erroneous information) was used during the preparation of target-directed pointing movements.

In all conditions, vision was eliminated 25 ms into the RT interval by closing the LCD goggles. Vision remained extinguished until the chair and platform had been re-set for the next trial.

Design

Each participant attended a single experimental session lasting approximately 2 hours. The session began with a block of 56 practice trials (14 trials per target; 7 cued, 7 uncued) to ensure that participants were comfortable with the task and could successfully coordinate their pointing action with the chair motion. No GVS was delivered during these trials.

Next, participants completed two blocks of experimental trials. Each block contained a unique mode of target presentation (cued vs. uncued). Block order was counter-balanced across participants. Each condition consisted of 96 trials: 80 trials to the experimental targets and 16 trials to the filler targets. The experimental target trials were made-up of 40 trials with stimulation (2 targets x 2 GVS polarities x 10 trials) and 40 trials without stimulation (2 targets x 20 trials). The filler target trials consisted of 8 trials with stimulation (2 targets x 2 GVS polarities x 2 trials) and 8 trials without stimulation (2 targets x 4 trials). Within each block, the trials were pseudo-randomized into two equivalent subsets of 48, where there were never more than three successive stimulation trials. Participants were provided with rest between trials and blocks as required.

Data Analysis and Statistics

Pointing trials were analyzed in terms of time-based performance measures and trajectory-based positional measures. Mean RTs and MTs were calculated for each unique condition (as defined by cue type, target position, and GVS type). RT was computed as the difference between the time at release of the armrest switch and the time at the “go” signal. MT was computed as the difference between the time at which the index finger crossed the frontal target plane, and the time at release of the switch.

Raw Optotrak data were converted into 3-D coordinates in order to provide position data and path trajectories for the head and trunk markers, as well as for the index finger marker. These data were filtered with a 2nd order, dual-pass, low pass Butterworth filter at a 10 Hz cut-off frequency. Head and trunk marker trajectories were qualitatively analyzed in the frontal plane to ensure that there were no postural deviations time-locked to the onset of GVS. Since chair motion continued throughout the trial and vision was removed during the pointing action, all participants carried their pointing movements past the location of the targets. Therefore, pointing movements were analyzed at three distinct points in time: the start of the movement, the time of target plane acquisition (target plane), and the time at which both chair motion and GVS ceased (trial end). Mean 2-dimensional spatial path trajectories were calculated in the transverse plane for each condition (Cressman, Franks, Enns, & Chua, 2006). The plane was defined such that it encompassed the entire movement trajectory from the starting position to the trial end position, in the forwards and horizontal directions. Next, for every 5 mm of forward progression, a mean spatial position was computed. If an individual trajectory did not

have a position value at one of the pre-defined spatial locations, linear interpolation from the closest data points was used.

At the start of the movement, the mean spatial trajectories were used to compute the average initial heading over the first 5 cm of forward displacement. For each 5 mm increase in forward progression, a vector was calculated with respect to the starting point of that mean path. The average direction of these vectors, described as the angle formed with respect to the horizontal, was taken as a representation of the initial heading of participants' pointing movements.

At the target plane, finger trajectory position in the frontal plane was determined for each trial. Mean horizontal and vertical position, as well as horizontal and vertical constant error (CE) with respect to the target, were computed. Variability of the horizontal and vertical positions within each condition was also assessed. Variable error (VE) was calculated as the standard deviation of the finger position values for each respective direction. For ease of comparison, some graphically displayed values have been normalized to the no GVS condition as the effect of GVS on the pointing trajectories is of primary interest.

A similar analysis was carried out at the trial end. Mean horizontal and vertical position of the index finger, as well as the variability about these means, were calculated. Once again, values normalized to the no GVS condition have been displayed.

All dependent measures were subjected to a 2 cue (cued, uncued) x 2 target (T2, T3) x 3 GVS (no GVS, anode left, anode right) repeated measures ANOVA. The alpha level for all analyses was set at $p = .05$. Tukey's HSD was used for all post hoc comparisons.

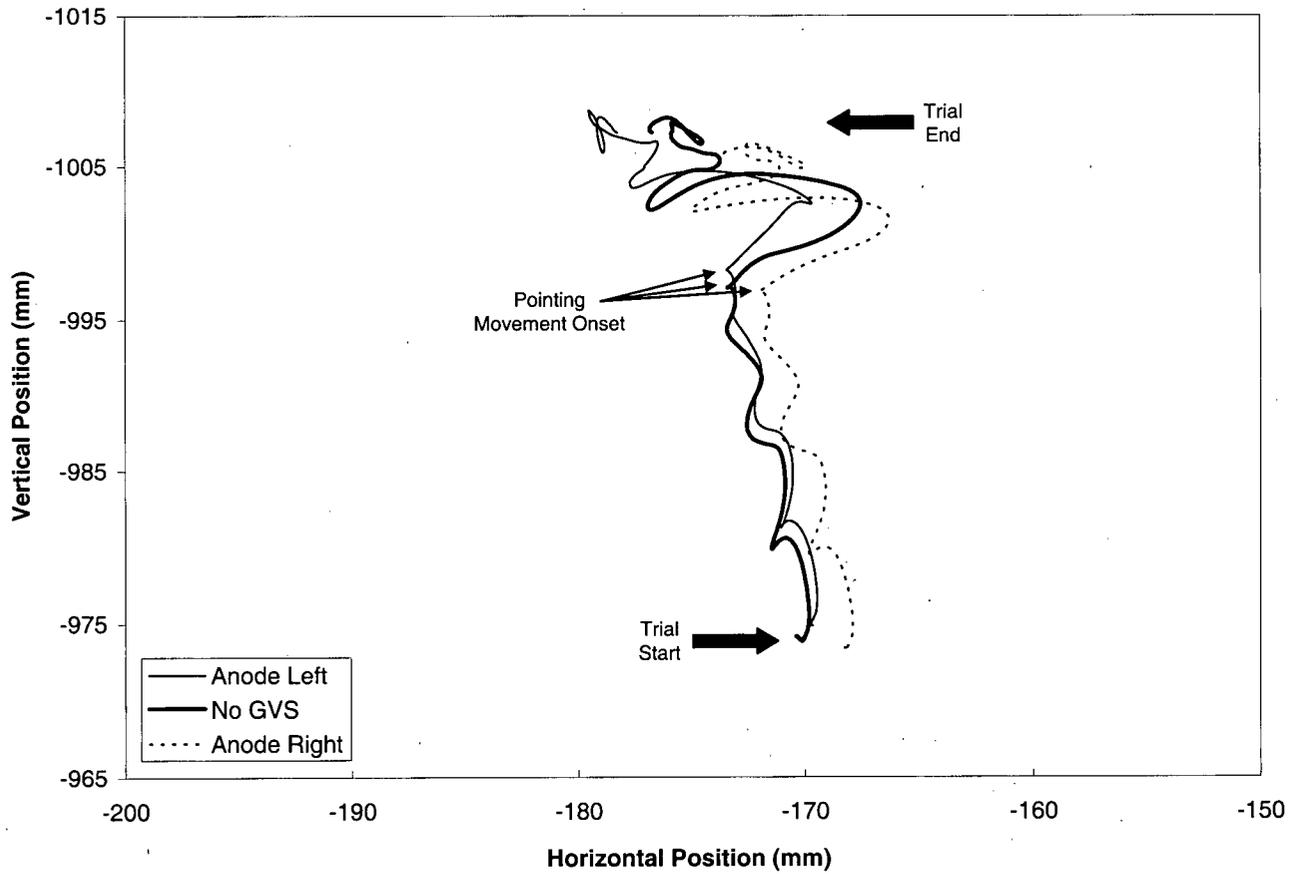


Figure 3. Head marker trajectory in the frontal plane for individual anode left, no GVS, and anode right trials in a representative participant. *Thick solid line*, no GVS condition; *thin solid line*, anode left condition; *dotted line*, anode right condition. Note that the largest horizontal motion of the marker is coincident with pointing movement onset, and that no characteristic GVS-related deviations can be seen.

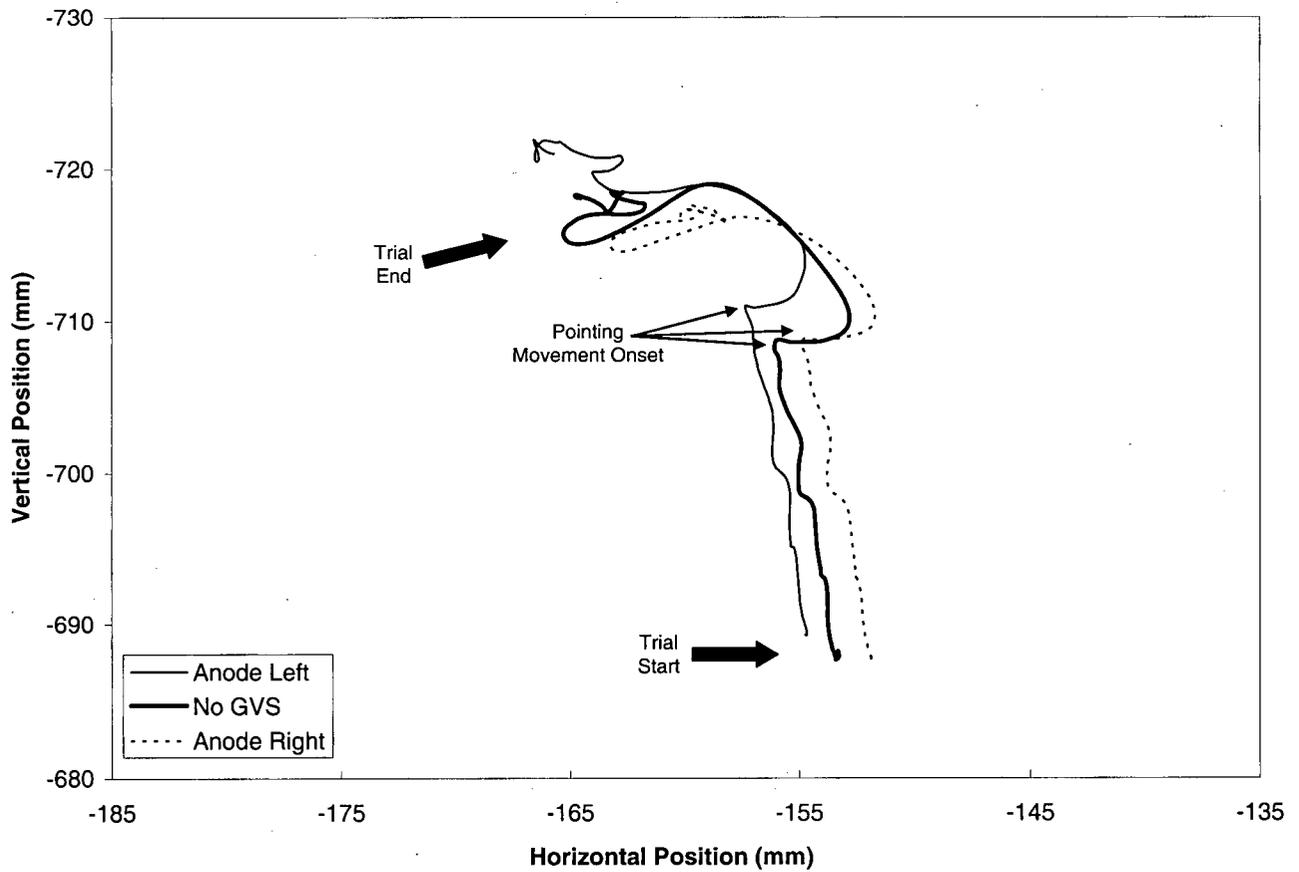


Figure 4. Trunk marker trajectory in the frontal plane for individual anode left, no GVS and anode right trials in a representative participant. *Thick solid line*, no GVS condition; *thin solid line*, anode left condition; *dotted line*, anode right condition. Note that the largest horizontal motion of the marker is coincident with pointing movement onset, and that no characteristic GVS-related deviations can be seen.

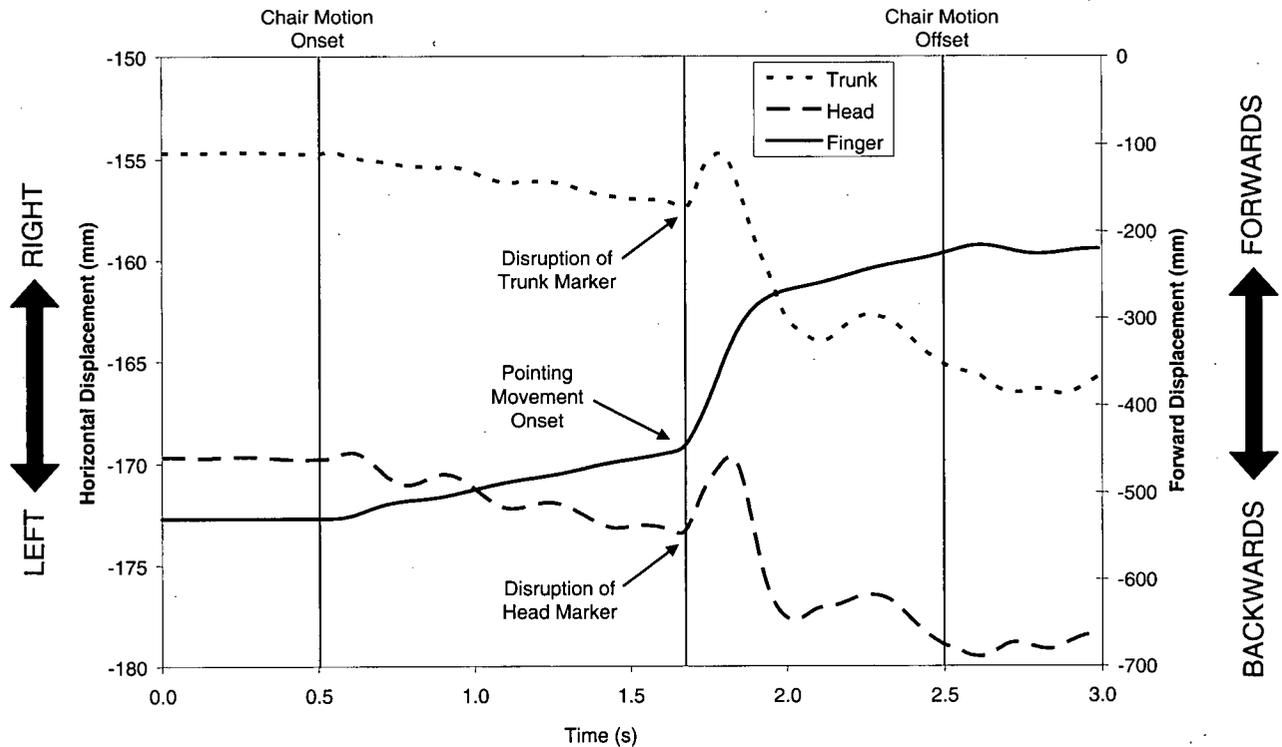


Figure 5. Head and trunk horizontal displacement and finger forward displacement over the course of an individual anode left trial in a representative participant. *Solid line*, finger trajectory; *small-dashed line*, trunk trajectory; *large-dashed line*, head trajectory. *Solid vertical lines* represent events of interest including chair motion onset and offset, and pointing movement onset. For both the head and the trunk marker there is an alteration in horizontal position that is time-locked to the start of the pointing movement. The gradual leftward progression of the markers that can be observed occurred because the plane of chair motion was not parallel to the defined depth axis.

Any trials where participants reacted before the “go” tone, or accidentally contacted the stimulus display were removed from the analysis. The data sets of two participants were also excluded due to a high percentage of early reactions in the cued condition, and experimental error between the anode and cathode electrodes, respectively.

Results

Postural Deviations

As expected, participants did not sway consistently towards the anode electrode during stimulation trials. As is shown in Figures 3 and 4, there were no clear GVS-induced differences between the head and trunk marker trajectories for the no GVS, anode left or anode right trials, in a representative participant. The deviation that can be observed is an artifact of the plane of chair motion and the pointing movement itself. Chair motion occurred in a plane that was not parallel to the defined depth axis. A horizontal deviation was thus generated as the chair and the participant traveled across this fixed plane during forward rotation. This characteristic leftward displacement was seen in all trials for all participants. The onset of the pointing movements, as well as the rapid ascent to peak velocity, also disrupted the horizontal position of the head and trunk markers. Figure 5 displays the forward displacement of the finger aligned in time with the horizontal motion of the head and trunk. The wobble of both the head and trunk markers is time-locked to the onset and progression of the pointing movement. Note that GVS onset commenced on average 200 ms before the onset of the pointing movement. A typical

postural response to GVS occurs approximately 150-180 ms after stimulus onset (Britton et al., 1993). No trials displayed any observable sway towards the anode electrode at this point in time.

Reaction Time and Movement Time

Mean RTs and MTs are displayed in Table 1. For RT, there was a main effect of cue, $F_{(1,7)} = 42.401$, $p < 0.001$ and a main effect of GVS, $F_{(2,14)} = 8.058$, $p = 0.005$. Participants effectively used the advance information in the cued condition to prepare their pointing movements, reacting more quickly (192 ± 22 ms) than in the uncued condition (236 ± 23 ms). Furthermore, participants also reacted faster on trials in which they received GVS (anode left = 210 ± 32 ms, anode right = 211 ± 29 ms), versus non-stimulation trials (221 ± 32 ms). This decrease in RT could be attributed to intersensory facilitation, whereby participants tend to respond more quickly when the primary stimulus is accompanied by an accessory stimulus (Nickerson, 1973). Terao et al. (1997) found that simple RT for a wrist extension movement was decreased when the visual “go” stimulus occurred simultaneously with subthreshold transcranial magnetic stimulation. In the present study, it is possible that on stimulation trials, GVS acted as an accessory stimulus facilitating the response to the concurrently presented target flash and auditory “go” tone.

Not surprisingly, there was a main effect of target, $F_{(1,7)} = 15.983$, $p = 0.005$, for MT. It took longer for participants to reach T2 (242 ± 54 ms) than T3 (225 ± 46 ms) since they had to cover a greater distance and were reaching more towards the midline. There was also a weak cue x GVS interaction, $F_{(2,14)} = 3.786$, $p = 0.049$, whereby cued,

Table 1. Mean reaction times (RT) and movement times (MT), along with their respective standard deviations (SD), for all conditions. RT was defined as the difference between the time at release of the armrest switch and the time at the “go” signal. MT was defined as the difference between the time at which the index finger crossed the frontal target plane, and the time at release of the switch.

			RT (ms)	SD (ms)	MT (ms)	SD (ms)
CUED	T2	NO GVS	197	25	243	57
		AL	188	23	251	67
		AR	188	19	242	56
	T3	NO GVS	202	28	227	50
		AL	185	16	235	53
		AR	193	19	228	51
UNCUED	T2	NO GVS	238	19	242	54
		AL	235	27	239	49
		AR	231	23	237	55
	T3	NO GVS	247	23	221	44
		AL	231	23	219	49
		AR	233	25	219	45

Table 2. Horizontal (horiz) and vertical (vert) constant errors (CE) (with respect to target position) and standard deviations (SD) at target plane acquisition for all conditions. Horizontally, negative values indicate errors made to the left of the target, and positive values indicate errors made to the right of the target. Vertically, negative values indicate errors made below the target and positive values indicate errors made above the target.

			CE Horiz (mm)	SD (mm)	CE Vert (mm)	SD (mm)
CUED	T2	NO GVS	32.5	21.1	-27.4	57.5
		AL	28.3	24.1	-20.2	66.1
		AR	33.7	19.4	-21.2	52.9
	T3	NO GVS	30.6	17.3	-23.9	47.4
		AL	25.2	14.7	-11.5	49.1
		AR	32.8	18.4	-22.6	44.2
UNCUED	T2	NO GVS	28.8	22.2	-26.5	53.0
		AL	26.5	24.1	-25.2	51.5
		AR	29.5	22.1	-25.5	52.8
	T3	NO GVS	29.5	25.7	-23.5	43.7
		AL	28.5	26.0	-18.0	39.3
		AR	28.9	22.2	-24.4	45.1

anode left movements were significantly slower (242 ± 58 ms) than other trial types.

Start of Movement

There were no significant main effects of cue ($F_{(1,7)} < 1$), target ($F_{(1,7)} = 3.086$, $p = 0.122$), or GVS ($F_{(2,14)} < 1$) on the initial heading of the pointing trajectories. All interactions also failed to reach significance (cue x GVS, $F_{(2,14)} = 1.183$, $p = 0.335$; all other interactions, $F < 1$). Participants were not influenced to immediately deviate in the direction of the anode electrode during stimulation trials. This seems to suggest that the erroneous vestibular input was not incorporated into the planned action. Rather, the participants began to execute their pointing movements in the same manner as when they were not receiving erroneous vestibular signals.

Target Plane

The mean horizontal and vertical positions achieved at the target plane with respect to the target, and with respect to the no GVS condition are presented in Figures 6 and 7, respectively. Generally, when participants reached the target plane, their trajectories were below and to the right of the target (Table 2). Chair motion altered participants' vertical position by moving their finger downwards with respect to its starting point. Since feedback about terminal finger position was not provided, chair motion may have contributed to the overall negative vertical CE. Analysis of CE showed a main effect of GVS in both the horizontal, $F_{(2,14)} = 8.458$, $p = 0.004$, and vertical, $F_{(2,14)} = 10.152$, $p = 0.002$, directions. There was also a target x GVS interaction for vertical CE, $F_{(2,14)} = 4.389$, $p = 0.033$. Looking beyond basic accuracy, these data illustrate that anode left

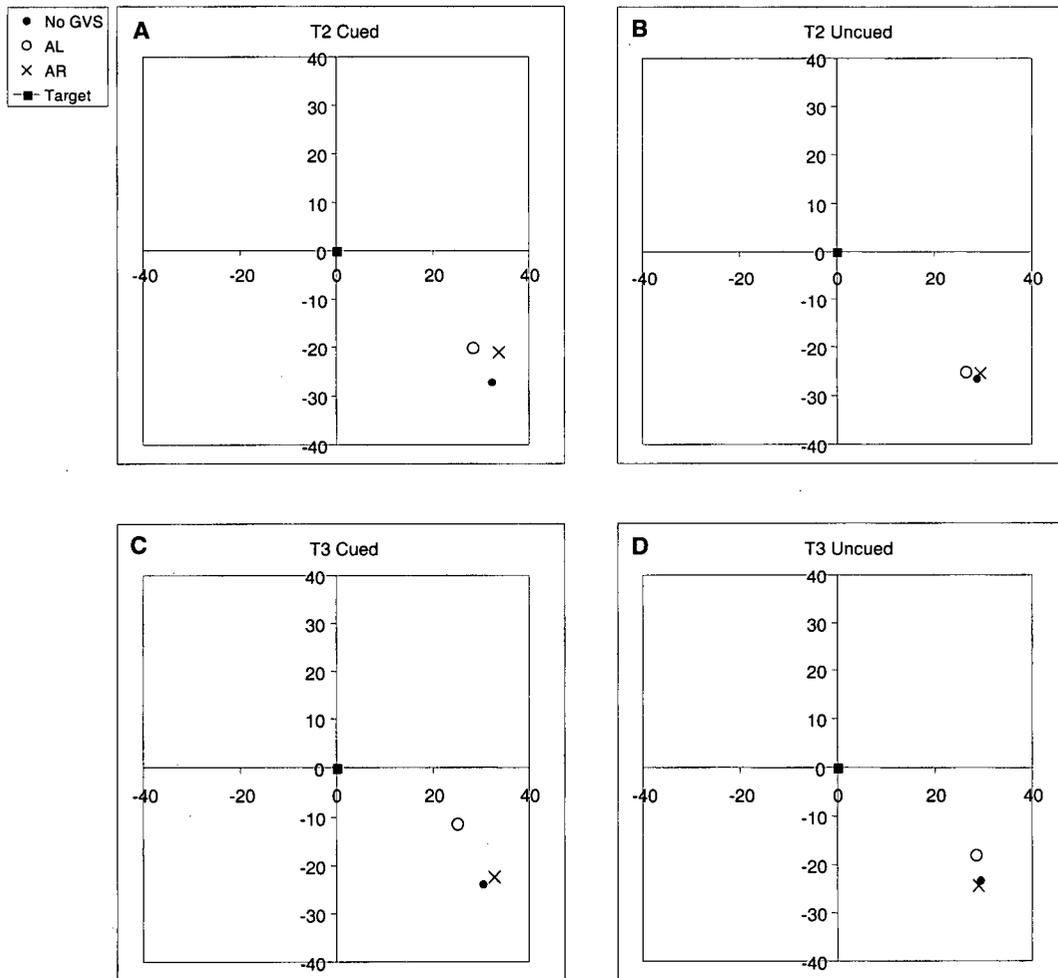


Figure 6. Mean position achieved in the frontal plane (with respect to the target) at target plane acquisition for the (A) target 2 cued, (B) target 2 uncued, (C) target 3 cued and (D) target 3 uncued conditions. All units are in millimeters. *Filled circles*, no GVS condition; *open circles*, anode left condition; *crosses*, anode right condition; *filled squares*, target.

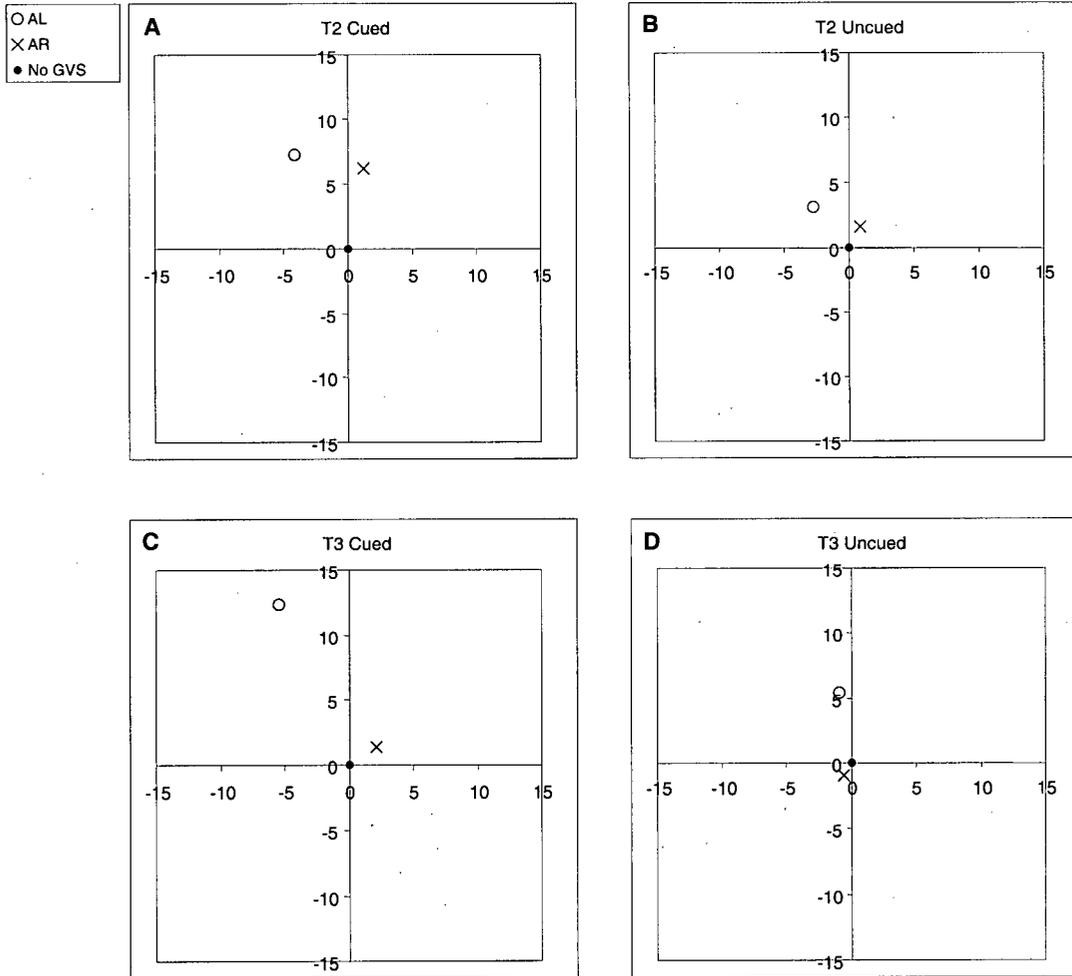


Figure 7. Mean position achieved in the frontal plane (with respect to the no GVS condition) at target plane acquisition for the (A) target 2 cued, (B) target 2 uncued, (C) target 3 cued and (D) target 3 uncued conditions. All units are in millimeters. *Filled circles*, no GVS condition; *open circles*, anode left condition; *crosses*, anode right condition.

trajectories were significantly to the left of, and above, both the no GVS and the anode right trajectories. This horizontal deviation is in line with previously observed trajectory deviations occurring during anode left stimulation (Bresciani, Blouin, Popov, Bourdin et al., 2002; Bresciani, Blouin, Popov, Sarlegna et al., 2002; Bresciani et al., 2005; Mars et al., 2003). There were no differences, however, between the no GVS and anode right conditions.

Variability of position at the target plane was also analyzed (Table 3). There was a main effect of GVS, $F_{(2,14)} = 6.841$, $p = 0.008$, for horizontal VE. Anode left trials were significantly less variable (11.6 ± 3.2 mm) than anode right (13.1 ± 4.1 mm) or no GVS (13.9 ± 3.8 mm) trials. No significant differences for vertical VE were found.

Trial End

Though small differences between stimulation and non-stimulation trials were observed as participants reached the target location, this distinction became much more apparent at the trial end (Figures 8 and 9). At this point in time participants were still aiming for the two separate targets with trajectories towards T2 remaining above ($F_{(1,7)} = 496.537$, $p < 0.001$) and to the left ($F_{(1,7)} = 496.537$, $p < 0.001$) of those directed at T3. Most importantly, however, there was a main effect of GVS, $F_{(2,14)} = 88.764$, $p < 0.001$, for horizontal position. All three GVS conditions were significantly different from one another. With respect to the no GVS condition, anode left trajectories deviated significantly to the left, while anode right trajectories showed the opposite response, deviating significantly to the right. Similar to the differences seen at the target plane, at

Table 3. Horizontal (horiz) and vertical (vert) variable errors (VE) and standard deviations (SD) at target plane acquisition for all conditions.

			VE Horiz (mm)	SD (mm)	VE Vert (mm)	SD (mm)
CUED	T2	NO GVS	12.4	2.6	17.9	3.6
		AL	12.5	4.0	20.9	7.1
		AR	12.9	5.3	21.2	9.3
	T3	NO GVS	12.2	3.9	21.6	5.7
		AL	9.8	3.1	20.7	6.1
		AR	14.2	2.4	18.3	7.7
UNCUED	T2	NO GVS	14.8	3.5	20.5	4.8
		AL	13.3	2.7	25.3	4.9
		AR	14.7	4.0	19.6	5.0
	T3	NO GVS	16.1	4.1	21.4	3.8
		AL	10.7	1.8	24.2	7.1
		AR	10.7	3.6	21.9	5.7

Table 4. Horizontal (horiz) and vertical (vert) variable errors (VE) and standard deviations (SD) at the trial end for all conditions.

			VE Horiz (mm)	SD (mm)	VE Vert (mm)	SD (mm)
CUED	T2	NO GVS	12.0	3.6	15.8	3.5
		AL	12.9	4.3	13.7	3.5
		AR	11.3	2.8	15.8	5.4
	T3	NO GVS	11.6	2.0	16.8	5.7
		AL	14.2	2.9	15.9	6.2
		AR	11.0	1.9	16.3	5.6
UNCUED	T2	NO GVS	14.6	6.7	15.3	3.2
		AL	15.9	5.0	15.8	7.0
		AR	12.9	5.3	14.1	4.9
	T3	NO GVS	15.0	4.6	17.6	5.7
		AL	15.5	7.2	16.5	5.0
		AR	13.1	5.5	16.6	8.2

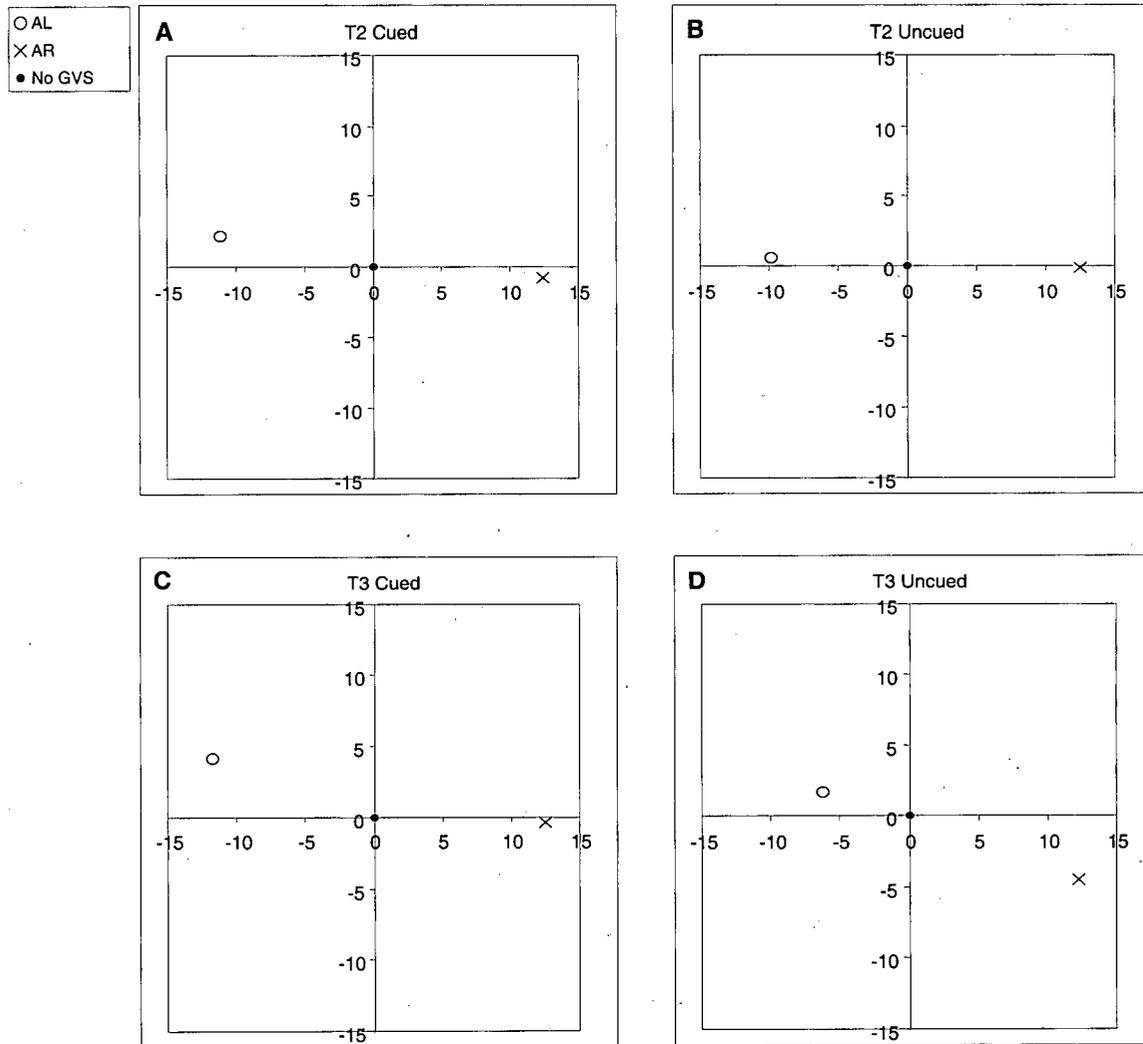


Figure 8. Mean position achieved in the frontal plane (with respect to the no GVS condition) at the trial end for the (A) target 2 cued, (B) target 2 uncued, (C) target 3 cued and (D) target 3 uncued conditions. All units are in millimeters. *Filled circles*, no GVS condition; *open circles*, anode left condition; *crosses*, anode right condition.

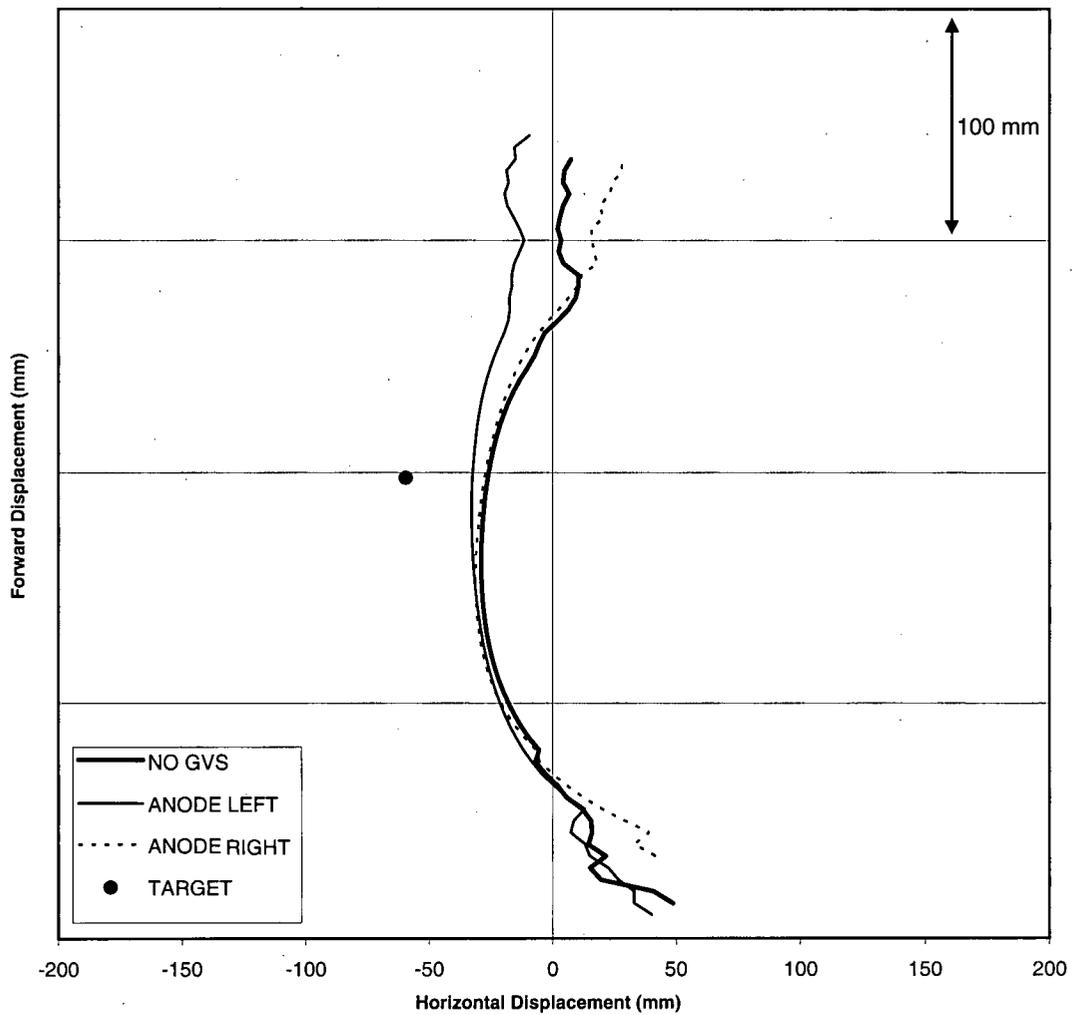


Figure 9. Mean 2-dimensional spatial path trajectories in the transverse plane for all T2, uncued trials in a representative participant. *Thick solid line*, no GVS condition; *thin solid line*, anode left condition; *dashed line*, anode right condition; *filled black circle*, target 2.

the trial end there was also a main effect of GVS, $F_{(2,14)} = 4.408$, $p = 0.033$, for vertical position. Once again, anode left trajectories were positioned significantly above anode right trajectories.

Horizontal and vertical position VE is shown in Table 4. There was a main effect of GVS, $F_{(2,14)} = 4.642$, $p = 0.028$, for horizontal VE only, with anode left positions being significantly more variable than anode right positions.

Discussion

The present experiment sought to examine the vestibular contributions to the preparation and execution of goal-directed aiming movements during a dynamic task. For the duration of the experiment, participants were seated in a chair fixed to a rotating platform. On each trial, the chair rotated through an 11.5° range at a constant velocity, moving participants from an initial reclined position to a final upright posture. The purpose of this whole-body motion was to stimulate the vestibular system and increase reliance upon vestibular sensory input. Concurrent with this motion, participants were instructed to point as quickly and accurately as possible to the indicated target when an auditory “go” tone sounded. Target presentation was either cued, so that participants had advance knowledge of the goal target, or uncued, so that the goal target was only known at the “go” tone. Also, on some trials, GVS was triggered coincident with the “go” signal, resulting in the provision of erroneous vestibular information during the RT and MT intervals of the aiming movement.

Before proceeding to interpret the effects of these artificial vestibular perturbations on participants' actions, it was necessary to ensure that participants were in

fact able to successfully complete the task. First, analyses of the raw position data indicated that participants were pointing to significantly different locations in space depending on whether it was a T2 or T3 trial. T2-directed trials had trajectories that were significantly higher and to the left of T3-directed trajectories. The CE analyses showed that participants generally pointed below and to the right of the targets, with errors in a range of 2-4 cm both horizontally and vertically. Arguably, the fact that vision was selectively removed during RT and MT, and that participants were in motion throughout each trial, made this task more challenging than a basic goal-directed pointing action. Taking this into consideration, the magnitude of the errors made with respect to the targets seems relatively small. The values for the horizontal and vertical VE at the target plane further strengthen the case that participants were able to point to the remembered targets. In either direction, VE never exceeded 2.5 cm. Also, between-subject standard deviations for VE were quite low, suggesting that this was a homogeneous result across participants. As a whole, these results indicate that participants were able to effectively execute the task they were asked to do.

As has been demonstrated previously, this study confirmed that GVS can have an effect on the trajectories of goal-directed aiming movements (Bresciani, Blouin, Popov, Bourdin et al., 2002; Bresciani, Blouin, Popov, Sarlegna et al., 2002; Bresciani et al., 2005; Mars et al., 2003). Consistent with past investigations, lateral deviations in the direction of the anode electrode were observed at the endpoint of the pointing trials, suggesting that in some capacity participants were affected and compensated for the induced vestibular disturbances. However, in contrast with these previous experiments, the present study aimed to specifically examine the impact of vestibular input on the

planning phase of these actions. Therefore, galvanic stimuli were introduced during the RT interval (the period during which a motor plan for the upcoming movement is constructed) and the initial direction of pointing was analyzed. It was hypothesized that, during GVS trials, if vestibular information was used to prepare the ensuing pointing action, participants would begin to deviate downwards and to the side of the anode electrode immediately after movement onset. This hypothesis was not supported. Not only did participants show no differences in initial pointing direction based on different galvanic stimuli, but there was also a lack of differences based on cue type. Different types of target cueing were included to provide participants with two distinct planning-related scenarios. With a cued target, the entire motor plan could be formulated before GVS was triggered, leaving only the command to initiate action unsent. An uncued target, on the other hand, meant that participants had no choice but to plan their action while under the influence of GVS. By offering an opportunity to examine pre-planned versus un-planned movements, it was hoped that this protocol would further delve into the effects of GVS on the planning of a goal-directed arm action.

Reaction time results show that participants responded significantly faster to cued versus uncued targets. The presence of this traditional pre-cueing effect suggests that in the cued condition, participants were able to program the indicated parameters in advance (Rosenbaum, 1980). Since differences in planning did occur, but no associated differences in the average initial heading were observed under the influence of GVS, it may be that given this particular set-up, vestibular information was not taken into account when planning an aiming movement to a remembered target.

Pointing trajectories were also analyzed at two other points in time: target plane acquisition, and trial end. Unlike the initial phase of the movement discussed above, the results observed at these two time points cannot necessarily be viewed as purely representative of pre-planned parameters. Instead, online sensorimotor processes may have already been in effect. The implication of this possibility will be discussed in subsequent paragraphs.

At the target plane, there were also very few differences seen between the no GVS, anode left and anode right trials. Anode left trajectories were significantly above and to the left of the no GVS and the anode right trajectories. Though this difference is certainly in the expected direction, the strength of results in GVS studies generally lies in the opposite effects observed with anode left and anode right electrode configurations. Because the anode left configuration was the only one to alter participants' trajectories (with respect to the no GVS condition), it is difficult to comment on the extent to which vestibular information was being relied upon.

At the end of the trial, however, clear lateral deviations were present. At the point of GVS and chair motion cessation, participants' trajectories were significantly to the left and to the right of the no GVS condition with anode left and anode right stimulation, respectively.

Taken together, this series of results shows that vestibular input (as inferred through the effects of GVS) was used during the goal-directed aiming task, but that it was not weighted equally throughout. Specifically, it seems that the vestibular system may play a limited role in the planning of upper limb pointing actions, while its contributions increase during online control.

Though this outcome was unanticipated, it is not inexplicable. The primary role of the vestibular system is to inform the central nervous system of the motion and orientation of the head in space through the detection of linear and angular accelerations. This information, in conjunction with neck afferent signals, is then interpreted as changes in whole-body motion, or in motion of the head with respect to the trunk. The need for vestibular input in motor control has been shown to be both task- and environment-dependent. Generally, increasing body stability decreases reliance on the vestibular system (Welgampola & Colebatch, 2001). For example, providing participants with external support, or an increased stance width attenuates reflexive responses to GVS in the soleus muscle. Conversely, decreasing stability by having participants stand on a compliant foam surface augments these responses (Welgampola & Colebatch, 2001). During GVS, an increased base of support also causes reductions in horizontal translations of the head and center of pressure (Day et al., 1997). The use of vestibular input can be further regulated depending on the availability, dominance, necessity and reliability of other sensory sources (Carlsen et al., 2005; Kennedy et al., 2003). Even within a single task, such as locomotion, phase-dependent modulation of vestibular information has been reported (Bent, Inglis et al., 2004).

This past evidence indicates that it is not uncommon for the role of incoming vestibular information to vary amongst different aspects of human motor control. In the current study, it may be that the variations observed between the effects of GVS during the different phases of the movement represent yet another such case. Perhaps, given the experimental protocol and the nature of goal-directed arm actions, vestibular input was considered inconsequential to planning and thus GVS failed to affect any planned

parameters. First, the experimental apparatus provided a high level of whole-body stability. Participants were seated in a chair that fully supported their thighs, as well as their back. The chair back also provided support for the head which was further restrained by side braces and a forehead strap. Participants could rest their arms on the chair's armrests and their feet firmly on the wooden platform below the chair. Second, given this stable posture, participants were aware, at some level, that a forward pointing action would do little to alter their head and body position. Third, chair motion was consistent and predictable in nature. During the block of practice trials, participants had the opportunity to become familiar with the timing and sensation of this repeated movement. Furthermore, at the time of the "go" signal, a constant chair velocity had been achieved. Taking this sensory set into consideration, participants may have had no reason to spend time or energy processing information from the vestibular system while creating their action plan. Since changes in linear and angular motion were highly predictable, and whole-body stability was not threatened by movement onset, vestibular input may have been down-regulated during the planning phase.

However, it could also be argued that experimental factors may have hindered the emergence of GVS effects in the initial stages of participants' aiming movements. Primarily, it is possible that there was insufficient time in the RT interval for vestibular input to be incorporated into the motor plan. In their investigation of the online effects of GVS on reaching movements, Bresciani, Blouin, Popov, Bourdin et al. (2002) argue that it was most likely transcortically-mediated processes that led to the observed deviations in arm trajectories. The time-course for online corrections was 240 ms and 310 ms after stimulus onset during standing and seated reaching tasks, respectively (Bresciani, Blouin,

Popov, Bourdin et al., 2002; Bresciani, Blouin, Popov, Sarlegna et al., 2002). They propose that if direct pathways from vestibular input to motoneurons were involved (e.g. vestibulospinal pathway), much earlier responses would be present. For example, during a free-standing task, Britton et al. (1993) showed detectable electromyographic responses in the soleus between 50 and 60 ms after galvanic stimulation, with body sway onset at a latency of 150 to 180 ms. If the same neural pathways that mediate online arm trajectory changes are assumed to be responsible for the involvement of vestibular input in motor planning, then it is possible that the reaction time interval was not long enough for such effects to manifest. Mean reaction time was 192 ms in the cued condition and 236 ms in the uncued condition. Both of these values fall short of the minimum necessary 240 ms found by Bresciani, Blouin, Popov, Bourdin et al. (2002). Previous GVS studies have also found that, based on the nature of the task, sometimes stimulation occurs too late to have an effect (Bent, McFadyen et al., 2004). When participants were stimulated at the onset of the anticipatory postural adjustment during gait initiation, foot placement in the first step was not significantly altered. It was proposed that the galvanic stimuli were presented too late to interfere with gait initiation.

As stated previously, GVS-related differences began to emerge at the target plane and were very clear by the trial end. Since GVS continued throughout the movement until the trial end, it is difficult to say whether these effects were a result of pre-programmed parameters, or whether they reflect online use of the perturbed vestibular information. Certainly at the target plane one could argue that an online influence was not possible. The movement times (220-250 ms) to the target plane may have been too short for participants to use any sensory feedback to alter their pointing trajectories. In

terms of visual and kinesthetic feedback, the time required to detect an error, determine a correction, and initiate this correction in the ongoing movement has been found to be a minimum of 150-200 ms (Schmidt & Lee, 2005). Furthermore, online compensation for a vestibular disturbance has been shown to be even longer, ranging from 240 – 310 ms, depending on whole-body posture (Bresciani, Blouin, Popov, Bourdin et al., 2002; Bresciani, Blouin, Popov, Sarlegna et al., 2002). Therefore, considering these processing times, as well as the lack of vision during both the planning and execution phases of the movement, it seems plausible that this initial component of the action was pre-programmed in nature. Seeing as there were no observable effects of GVS on the initial pointing direction, which was also assumed to represent a pre-programmed parameter, such an interpretation can be easily accommodated.

On the other hand, time from movement onset to trial end was much longer (grand mean = 786 ms) and clearly provided adequate time for online control processes to become active. Due to the lack of vision available to participants, it may seem unreasonable to assume that online control was even used at all, and that instead movements were completely pre-programmed. However, other studies that have had participants point in complete darkness to remembered targets have shown online corrections in response to GVS (Bresciani, Blouin, Popov, Bourdin et al., 2002; Bresciani, Blouin, Popov, Sarlegna et al., 2002). These results support the view that a vestibular online control component is possible even when visual information about the scene is not accessible. The GVS-induced deviations seen in the current study also maintain that online compensation for sensed body motion can occur during an aiming movement.

Beyond allowing sufficient time for online control to take effect, the trial end was also unique in another way: it was a definitive, detectable termination point. Based on instructions, participants knew that the end of the trial was signified by a cessation of chair motion in the forward direction, and a re-setting of the apparatus for the subsequent trial. Moreover, they were experienced with the timing of this sequence. What is not clear is whether participants also regarded this “trial end” as the end of their pointing movement, or if they considered their movement complete after target plane acquisition. The former seems to have greater potential given that participants were executing their movements in a no vision condition and could never be certain when they had acquired the target location. If participants were considering the termination of chair motion as an indicator of the end of their pointing movements, it can then be viewed as a pertinent transition point. Because of this, participants may have also aimed to slow down and stop their movements at this time and would have been “homing in” on the target position to achieve the most accurate final posture. Therefore, on the whole, the trial end was most likely a transition that required a higher degree of control than the rest of the movement.

It has been suggested in the past that vestibular information may have a greater importance in slower paced dynamic tasks (Bent et al., 2000). This encompasses transitions, which generally involve a decrease of movement velocity in order to reach the desired state. In their investigation of the magnitude effects of GVS on human gait, Bent et al. (2000) also discuss some pilot work where they had participants run under the influence of GVS. They observed that GVS had very little impact on running trajectory. Namely, the typical deviations seen during walking did not occur. But, when participants

began to slow down, and were transitioning to come to a stop, they were suddenly affected by the galvanic stimuli. Kennedy, Cressman, Carlsen and Chua (2005) also demonstrated that when participants were preparing for a change in walking direction, they increased the weighting of vestibular input. Thus, in the current study, it seems that the largest trajectory deviations were observed at trial end not only because online processes were capable of operating, but more importantly because participants were at a movement transition point that required an increased dependence on incoming vestibular information.

A final point that needs to be addressed is a lack of congruence between the vertical deviations predicted by Fitzpatrick and Day's (2004) GVS vector model and those observed. According to the model, bipolar, binaural GVS causes the perception of a large roll and small yaw towards the cathode electrode. In order to compensate for this perceived motion, it was expected that participants would not only deviate laterally to the side of anode electrode, but would also deviate downwards on the same side. Based on this rationale, finger position was analyzed in the frontal plane. The predicted results did not occur. Rather, very few differences in vertical position were observed. At the target plane, anode left trajectories were slightly above anode right and no GVS trajectories. But, at the trial end, where the greatest lateral deviations were observed, there were no differences in vertical position. There is no obvious explanation for these results. Perhaps the downward displacement caused by the chair motion was too great to allow for the identification of independent finger motion in this direction. Future studies should continue to investigate whether the predictions of this model apply to goal-directed arm actions using more specific experimental manipulations. For example, Day and

Fitzpatrick (2005) have shown that head-pitch angle affects the perception of illusory whole-body rotation generated by GVS. This result matches predictions made by the model. Therefore, an interesting manipulation may be to have participants point to a target with different head-pitch angles while being stimulated with GVS. If different illusory motions are sensed, different hand trajectory deviations would be expected.

Concluding Remarks

In summary, this study provides further evidence that the use of incoming vestibular input can be modulated based upon specific task events. Specifically, during goal-directed arm actions from a seated position, GVS was found to have little impact on action planning, while a greater influence emerged online, particularly at movement end. These results suggest that if there is a high degree of whole-body stability and little potential for the upcoming movement to disrupt this state, participants do not use vestibular information to plan their pointing movement. On the other hand, once sufficient time has passed for online control processes to mediate the ongoing action, and a movement transition is imminent, there is an increased weighting of vestibular input. This leads to clear lateral trajectory deviations towards the anode electrode, suggesting that participants are compensating for the artificial vestibular signals they are being given.

Future Directions

The results of this experiment prompt several questions which lay the foundation for future investigations. Though this study provided insight into the role of vestibular input

in the planning of upper limb pointing movements within the context of a particular experimental set-up, a more general idea of the extent to which this sensory information can influence action planning has yet to be established. Here, body stability was high and there was no acceleration of the head during the planning phase. Furthermore, the direction, amplitude, and velocity of the ensuing pointing action were unlikely to alter the whole-body postural state. Therefore, carrying out a pointing action where these parameters are specifically and methodically manipulated may be informative. For example, chair motion could be altered such that the reaction time interval occurs during a period of acceleration. Or, pointing could be observed in the absence of imposed motion but in a less posturally stable environment. Such protocol alterations could allude to whether the planning of goal-directed actions is ever susceptible to a vestibular influence.

In terms of galvanic stimuli, it would be beneficial to isolate GVS to RT or MT. This way, one could be sure that stimulation was only being provided during the planning phase or the online phase of the movement. In the current study, it had to be inferred which period of stimulation was producing the observed effects.

The role of vestibular input during movement transitions was another theoretical aspect illustrated by the trajectory deviations seen at the trial end. In an effort to further examine this aspect of pointing movements, a task that involved a mid-action transition could be created. Participants could be required to point to a central target. En route, a right or left target could be illuminated towards which they subsequently had to direct their movement. GVS could be timed to occur at various places with respect to this transition in order to determine if vestibular weighting changed.

Finally, visual-vestibular interactions could be investigated. It is well-accepted that vision attenuates responses to galvanic stimuli. Thus, studying the role of vestibular input during goal-directed arm actions in the presence of vision may help us further understand the impact of this system in a more practical environment.

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APPENDIX A:
LITERATURE REVIEW

The Vestibular System

The vestibular system functions to provide information about the orientation of the head in space. It consists of two small apparatuses located in the right and left inner ears. Each apparatus is composed of a total of five sensory organs that are housed within the vestibular labyrinth. Both the semicircular canals and the otolith organs inform the central nervous system (CNS) about head position and head motion via signals derived through the mechanical perturbation of hair cells.

The anterior, posterior, and horizontal semicircular canals serve to detect angular acceleration. Each canal is formed by a tube interrupted by a penetration of hair cells. This tube is filled with an extracellular fluid called endolymph. During head motion, the vestibular labyrinth is displaced in conjunction with the head. The endolymph, however, is not; it lags behind, deflecting the cilia of the hair cells in the direction opposite movement. Such deflection alters the firing of the vestibular afferents and provides the CNS with signals regarding the detected head motion.

Within an apparatus, the canals are oriented approximately perpendicular to one another, permitting them each to sense angular changes in a unique plane of motion. There is redundancy, however, between the apparatuses. Therefore, each semicircular canal works in conjunction with a canal from the opposite ear. Each anterior canal is aligned, and thus paired with, the contralateral posterior semicircular canal, while the two horizontal canals work together. For any given movement, whilst one canal of the pair is generating a vestibular afferent signal with an increased discharge rate, the remaining canal is generating a signal with a decreased discharge rate. Based on this arrangement,

the semicircular canals can detect the direction and magnitude of any changes in head roll, pitch, or yaw.

The two otolith organs, the saccule and the utricle, detect linear accelerations of the head. The utricle detects lateral and sagittal linear acceleration, while the saccule detects vertical and sagittal acceleration. Both are constructed of a bundle of hair cells whose cilia are embedded into an otolithic membrane weighted with calcium carbonate crystals, or otoconia. During linear motion of the head, this mass lags behind. Consequently, the cilia deflect, causing an increase or decrease in the firing rate of the vestibular afferents. The orientation of the two otoliths and the spatial arrangement of their embedded hair cells differ. The utricle lies approximately in parallel with the base of the skull, while the saccule is oriented vertically. Importantly, both the saccular and the utricular surfaces are divided approximately in half by a striola. Just as the semicircular canals functioned in pairs that generated opposing signals, the otolithic hair cells are arranged so that any detected acceleration will increase the firing rate of cells on one side of the striola and decrease the firing rate of cells on the other side, thus allowing all directions of linear acceleration to be sensed (Fitzpatrick & Day, 2004).

The vestibular afferent input generated by these sensory organs travels via the eighth cranial nerve to the complex of four vestibular nuclei located in the brainstem at the junction of the pons and the medulla. From here, the incoming signals are sent to a variety of other neural structures including the oculomotor nuclei, the cerebellum, the thalamus, and the spinal cord so that vestibular output can be used to control eye, neck, trunk, and limb movements.

Vestibulo-ocular reflexes act to maintain eye position while the head is moving. Input from the semicircular canals initiates rotational vestibulo-ocular reflexes, which allow visual fixation while the head is turning to the left or right. The translational and counter-rolling vestibulo-ocular reflexes, both initiated by otolithic input, compensate for linear motion and vertical head tilt, respectively. Vestibular input also aids in the control of head movements through the vestibulo-colic reflex. This reflex is apparent in the event of any perturbation, and acts on the neck muscles to stabilize the head in space. Finally, the vestibular system plays an important role in mediating postural control. Vestibulo-spinal reflexes function in the automatic maintenance of postural stability.

Galvanic Vestibular Stimulation

Galvanic vestibular stimulation, otherwise known as GVS, is a simple laboratory technique that can be used to provide an artificial vestibular stimulus (Fitzpatrick & Day, 2004). In bilateral, bipolar GVS, electrodes are placed behind each ear over the two mastoid processes: one serving as the anode, the other as the cathode. This set-up allows a small current to be applied percutaneously. Consequently, GVS by-passes the mechanical transduction that normally occurs at the hair cells and directly affects the afferents composing the vestibular nerve. The primary irregular afferents are most affected by GVS, with a cathodal stimulus causing an increase in firing rate, and an anodal stimulus causing a decrease in firing rate (Minor & Goldberg, 1991). Furthermore, unlike actual dynamic motion, all of the irregular afferents are equally affected. This results in a virtual head motion signal that does not equate to any naturally produced sensation (Fitzpatrick & Day, 2004). Regardless, since GVS can be used to generate a

pure vestibular perturbation, it is a valuable research tool for investigating the influence of vestibular information on human motor control.

Responses to GVS

Based upon the neural connections of the vestibular system, GVS evokes detectable postural, reflexive, and oculomotor responses. The most notable reaction of a subject in response to GVS is the observable whole-body sway towards the anode electrode. This is presumably due to the interpretation that the GVS-evoked signal arose as a result of real motion. Day et al. (1997) provided the most complete description of this response, characterizing it as both a leaning and bending towards the anodal side. Participants began tilting towards the anode soon after GVS onset. The body, however, did not move as a rigid structure. Rather, the torso tilted with respect to the pelvis and the head tilted with respect to the torso. At stimulus offset, participants returned to their starting positions. This whole-body motion is not affected by advance knowledge of the timing of the upcoming vestibular perturbation, or by self-triggering of GVS (Guerraz & Day, 2005). The goal of this response has been contemplated by several researchers. Some studies suggest that GVS changes the internal representation of gravity, thus setting a new estimate of verticality (Hlavacka, Mergner, & Krizkova, 1996; Inglis, Shupert, Hlavacka, & Horak, 1995). By leaning, participants align themselves with this new reference. Since all body segments do not tilt to the same extent, others believe that postural responses to GVS function instead as a balance protection mechanism (Day et al., 1997). Under this hypothesis, whole-body tilt serves to keep the vertical projection of the center of mass within the boundaries of the base of support in order to prevent

toppling. The fact that increasing stance width and seating subjects both decrease the magnitude of the tilt response, lends support to this hypothesis (Day et al., 1997). Modulation of the whole-body response is also observed if GVS is applied coincident with a voluntary upper body movement (Severac Cauquil & Day, 1998).

Reflexive responses to GVS have been reported in muscles that are actively engaged in maintaining posture and balance (Britton et al., 1993). In standing subjects with their head turned to the side, a two-component electromyographic response is observed in the soleus muscle immediately after galvanic stimulation (Britton et al., 1993; Welgampola & Colebatch, 2001). The first component, occurring within 50-60 ms of stimulation, has a small amplitude and a short duration. The second component has a latency of approximately 120 ms. Its polarity is opposite that of the first component, and it is in the appropriate direction to produce the observed body sway. Similar responses can be seen in the arms if they are being used for postural support (Britton et al., 1993). Sensory feedback modulates reflexive responses such that any information that increases stability and decreases reliance on the vestibular system decreases the magnitude of the response (Welgampola & Colebatch, 2001). For example, providing participants with vision, external support, or an increased stance width attenuates reflexive responses to GVS in the soleus muscle. Conversely, decreasing stability by having participants stand on a compliant foam surface augments reflexive responses (Welgampola & Colebatch, 2001).

It has also been shown that the eyes respond to GVS in a manner similar to that of the whole-body postural response. When GVS is applied, there is a pre-dominant torsional oculomotor response that occurs with a latency of approximately 46 ms

(Severac Cauquil et al., 2003). The top of the eyes rotate continuously toward the anode until the offset of stimulation, at which time they rotate in the opposite direction. The effects of GVS on vertical and horizontal eye movements are much weaker. Stimulation causes a slight vertical deviation of both eyes in opposite directions. As with the torsional response, this effect is polarity-dependent and is reversed at GVS offset. Horizontally, GVS evokes a weak movement of the eyes in the direction of the anode which ceases at stimulation offset. Similar to the goal of the postural tilt, which stabilizes the body in response to stimulation, GVS-induced eye movements are thought to help stabilize the visual field based on incoming vestibular information.

GVS Vector Model

As stated previously, the sensations evoked by GVS cannot be equated to any real-life kinetic stimuli. However, it is clear that participants respond to GVS in a specific and consistent manner. Based on a large body of empirical evidence and detailed anatomical reports on the structure of the vestibular organs, Fitzpatrick and Day (2004) proposed a vector-based model describing the sensations associated with binaural, bipolar GVS. Following a stepwise approach, this model separately examines the effects of GVS on the semicircular canals and the otolith organs. A final vector summation determines the overall net effect of GVS on the human vestibular system.

First, consider a situation where the anode is located behind the right ear, and the cathode behind the left. Since all of the hair cells in a single semicircular canal respond to only one direction of angular acceleration, the sensations evoked by GVS can be resolved into three movement vectors described in terms of yaw, roll and pitch. On the

side of the cathode electrode, there is an increase in the firing rate of all afferents. Consequently, a leftward yaw is simulated in the horizontal canal. Both the anterior and posterior canals signal the same left ear-down roll, but opposing pitches, with the anterior canal signaling a nose-down tilt and the posterior canal a nose-up tilt. On the side of the anode electrode, there is a decrease in the firing rate of all afferents. This results in the generation of a leftward yaw signal in the right horizontal canal, and simulates a left ear-down roll in the anterior and posterior canals. Once again, opposing pitch signals are generated in the anterior and posterior canals. After considering the exact orientation of the canal structure within the head and canceling all opposing signals, the net effect of GVS on the semicircular canals is rotation about an axis in the sagittal plane that is directed backward and upward.

GVS evokes a small response in the utricle and the saccule. As stated previously, natural movements cause the populations of hair cells on either side of the striola to generate opposing signals that combine to provide the CNS with an accurate depiction of the linear acceleration of the head. Cathodal stimulation, however, increases the firing of the afferents on both sides of the striola. Thus, two signals indicating linear acceleration that is equal in magnitude, but opposite in direction, are produced. For the saccule, these signals cancel out because there are an equal number of hair cells on either side of the striola. Since this exact balance is not achieved in the utricle, a small net acceleration towards the cathode, or tilt towards the anode, is sensed. Anodal stimulation also affects all afferents equally, decreasing firing rates on both sides of the striola. Once again, the saccular signals cancel each other out, while the sensation of a small net acceleration towards the anode is generated in the utricle. As the signal of net acceleration towards

the anode is smaller than that towards the cathode, the overall signal generated by the otolith organs during binaural, bipolar GVS is that of a small acceleration towards the cathode, or tilt towards the anode.

Based on these analyses, Fitzpatrick and Day's (2004) model predicts that binaural, bipolar GVS will induce an afferent signal with components akin to that of a large roll and a small yaw towards the cathode, as well as a small linear acceleration towards the cathode or tilt towards the anode. This model clearly accounts for the observed whole-body sway towards the anode electrode, since GVS makes participants feel as though they are moving towards the cathode. The predicted utricular signal, however, is not behaviourally accounted for. Observed responses would seem to enhance this sensation rather than counteract it. But, if only one half of the utricular surface is considered, a large acceleration towards the anode, or tilt towards the cathode, is predicted. This prediction falls in line with observations. Therefore, Fitzpatrick and Day (2004) propose that the medial portion of the utricle is the only section that contributes to the balance response.

Vestibular Contributions to Human Movement

Locomotion

More recently, research using GVS has begun to extend beyond the description of basic responses to stimulation and modulating factors. Instead, GVS has been used as a tool to explore the vestibular contributions in a variety of tasks, as well as the interactions of the vestibular system with other sensory systems. Primarily, this research has focused on the components of human gait and the visual and vestibular interactions during locomotion.

Human locomotion involves the coordination of a complex series of movements that transport the body through space in an upright posture. Because of its dynamic nature and inherent periods of instability, the vestibular system most likely plays a role in informing the CNS during some, if not all, phases of the motion. During forward walking with the eyes closed, participants consistently deviate in the direction of the anode electrode (Bent, Inglis et al., 2004; Bent, McFadyen et al., 2004; Bent et al., 2000; Carlsen et al., 2005; Fitzpatrick et al., 1999; Kennedy et al., 2003). The magnitude of this deviation is dependent upon the intensity of stimulation, with greater intensities leading to increased lateral deviations (Bent et al., 2000). Different hypotheses for the cause of deviation have been proposed. Potentially, it is an altered perception of trajectory that leads participants astray (Fitzpatrick et al., 1999). Alternately, the deviation has been interpreted as signifying that participants were responding to information indicating their center of mass had moved in the cathodal direction. Therefore, they placed their limbs in such a way to prevent further deviation and re-align themselves 'vertically' (Bent et al., 2000).

More detailed analyses of the vestibular contributions to gait have also been made, looking specifically at upper and lower body vestibular control during gait initiation and steady-state walking (Bent, Inglis et al., 2004; Bent, McFadyen et al., 2004). During gait initiation, the top-down body roll response towards the anode occurs earlier and with greater magnitude as the task becomes increasingly dynamic (Bent, McFadyen et al., 2004). During steady-state walking, regulation of upper body control remains homogenous throughout the gait cycle (Bent, Inglis et al., 2004). In terms of lower body control, on the other hand, there is modulation of vestibular information

based on gait-specific events. During both initiation and steady-state gait, the greatest effects of GVS were observed when stimulation was delivered at heel contact (Bent, Inglis et al., 2004; Bent, McFadyen et al., 2004). This suggests a greater weighting of vestibular information during double support, which is considered to be a critical time for planning the next step. The use of GVS in these studies revealed the complex contributions of the vestibular system to upper and lower body control during locomotion.

GVS has also been used to elucidate visual – vestibular interactions during gait. Often studies require participants to perform GVS walking trials with their eyes both open and closed. Generally, trajectory deviations towards the anode are attenuated, and sometimes even eliminated, when subjects are allowed full vision (Fitzpatrick et al., 1999; Kennedy et al., 2003). Similarly, during step initiation, an attenuation of upper body roll and smaller changes in foot placement are seen when vision is available (Bent et al., 2002; Bent, McFadyen et al., 2004). These results suggest that visual information has the capacity to override vestibular information, especially in the case of a vestibular disturbance.

Visual and vestibular perturbations have also been combined during locomotion to explore the nature of the interaction between the two sensory systems. Kennedy et al. (2003) had participants walk forward towards a blank wall under 12 different conditions involving GVS and displacing prisms. In the GVS-only condition, participants deviated towards the anode, as expected. Surprisingly, when the displacing prisms were presented alone, they caused very little alteration of the walking trajectory. When the prisms and GVS signaled the same direction of perturbation, participants responded by deviating in

that direction. The magnitude of deviation, however, was no larger than that seen with GVS alone. When the prisms and GVS signaled opposite directions of perturbation, participants deviated in the direction indicated by the prisms. Kennedy et al. (2003) concluded that vestibular contributions are increased when visual input is unavailable or unnecessary for task completion. But, in a situation where both types of sensory input become undependable, vision regains its dominant role. This hypothesis was tested in a follow-up study involving targeted locomotion (Carlsen et al., 2005). The authors reasoned that targets would make both visual and vestibular information relevant for successful task performance. Therefore, it was expected that conditions combining GVS and displacing prisms would now show additive effects on trajectory deviations. This was, in fact, the case, suggesting that when both sensory systems are necessary for task completion, neither is down-regulated by the central nervous system.

APPENDIX B:
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