

Galvanic vestibular stimulation in humans produces online arm movement deviations when reaching towards memorized visual targets

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Abstract

Using galvanic vestibular stimulation (GVS), we tested whether a change in vestibular input at the onset of goal-directed arm movements induces deviations in arm trajectory. Eight head-fixed standing subjects were instructed to reach for memorized visual targets in complete darkness. In half of the trials, randomly-selected, a 3 mA bipolar binaural galvanic stimulation of randomly alternating polarity was triggered by the movement onset. Results revealed significant GVS-induced directional shifts of reaching movements towards the anode side. The earliest significant deviations of hand path occurred 240 ms after stimulation onset. The likely goal of these online deviations of arm trajectory was to compensate for a vestibular-evoked apparent change in the spatial relationship between the target and the hand. © 2002 Elsevier Science Ireland Ltd. All rights reserved.

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When reaching for a target with the hand, subjects first build a motor plan based on the spatial relationships between the target and the hand. The motor plan contains the specific features of the future movement, as direction and amplitude parameters, and is built taking into account the initial state of the motor apparatus. When arm movement unfolds without visual guidance, performance relies essentially on the accuracy of this motor planning. However, the planned motor commands may no longer be adequate if a change in the spatial relationship between the subject and the target occurs just prior to or during the reaching movement. This issue has been mostly investigated in reaching tasks that involved a change in the target position [5,20] or external forces applied to the arm during the movements [6,12]. Corrections in arm trajectory usually occur within less than 250 ms following the external perturbation, evidencing that the arm motor system can respond online to sensed events compromising the motor plan.

As the vestibular system is sensitive to head-in-space

accelerations, modifications in labyrinthine signals can be interpreted by the central nervous system as resulting from body motion. This is particularly the case when vestibular activation occurs without modification in the proprioceptive input from neck muscles [3,18]. Whereas the participation of vestibular signals in motor control has been evidenced in postural [19], locomotor [2], and oculomotor [8] studies, little is known about vestibular signal involvement in the control of goal-directed arm movements. Using a galvanic vestibular stimulation (GVS) technique, we tested whether online trajectory deviations take place when unexpected changes in vestibular input occur at the onset of reaching movements. Since GVS-evoked effective or illusory body motions are usually oriented in the frontal plane (i.e. orthogonal to the general orientation of the reaching movements), we mainly expected a GVS effect on the directional component of arm movements and little or no effect on amplitude.

Eight right-handed subjects, aged from 22 to 35 years (mean = 26) participated in the experiment. None of the subjects had a history of vestibular abnormalities or other neurological disorders. Fig. 1 presents a schematic representation of the experimental set-up. Subjects stood upright

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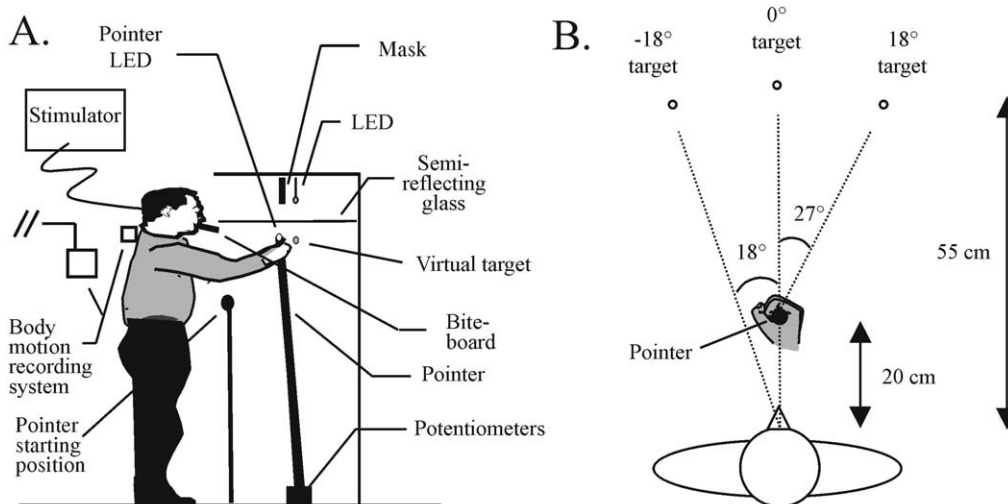


Fig. 1. Experimental set-up (A) and schematic upper view displaying direction and distance of the targets with respect to head and starting hand position (B).

in front of the apparatus in complete darkness. A bite-board was used to prevent possible GVS-induced head motion. In their right hand, subjects held a pointer at chest level, the tip of which was used to point. The pointer consisted of two telescoping light steel rods fitted together to allow pointing movements in the horizontal plane. A green light-emitting diode (LED) was fixed on the top of the pointer to provide visual feedback of hand position. A notch in a metallic horizontal bar situated near the subject's mid-trunk indicated the starting position of the pointer. The virtual images of three green LEDs (3 mm in diameter), seen through a semi-reflecting horizontal glass, were used as targets. These virtual targets were 35 cm distant from the hand starting position and located 18° on either side of body midline (27° with respect to the hand starting position) and straight ahead (see Fig. 1B). Two potentiometers located at the rod base were used to measure movements of the pointer in the sagittal (y co-ordinates) and frontal (x co-ordinates) planes. The potentiometers were sampled at 200 Hz using a 12-bit analogue/digital converter. GVS was delivered by a constant current stimulator and applied via two electrodes (3 cm in diameter) taped over the mastoid processes. The stimulation consisted of a 3 mA rectangular, unipolar binaural direct electric current. An electronic switch on the stimulator was used to change stimulation polarity. Any possible GVS-induced trunk motion was monitored, in spite of the use of a bite-board, with a Fastrak (Polhemus) system. The Fastrak sensor was fixed to the subject's back at the first thoracic vertebra level. These postural data were sampled at 60 Hz.

At the start of a trial, the pointer LED was lit for 2 s to refresh the calibration of the proprioceptive signal from the arm sensorimotor system [10]. One second after the extinction of the pointer LED, one of the three targets was flashed for 10 ms. Then, subjects reached for the target with the hand. Memorized targets were used to avoid any illusory

motion of stationary seen targets that could have resulted from possible oculomotor responses to the GVS.

Subjects performed 20 trials for each target position. In a randomly-selected half of these trials, the release of the electrical contact between the pointer and the starting position triggered GVS (five trials with the anode on the right mastoid, five trials with the anode on the left mastoid). When applied, GVS lasted until the end of the trial. Resting periods of 30 s followed each trial with GVS to allow the vestibular system to return to its normal resting state.

The direction (in degrees) and the amplitude (in cm) of reaching movements were analyzed to assess subjects' accuracy. To by-pass the constant errors that each subject was likely to produce during unseen reaching movements towards memorized visual targets, we normalized the directions and amplitudes of subjects' hand movements. Normalized directions were computed for each subject and each target position by subtracting the mean hand direction obtained in the condition without GVS (control condition) from the mean hand direction obtained in each GVS condition (anode on right and left mastoids, respectively). Negative and positive normalized directions, respectively represented left and right deviations from mean control trajectories. Normalized amplitudes were computed by subtracting the magnitude of reaching movements without GVS from the magnitude of reaching movements in each GVS condition. The direction and amplitude variability in final hand position were also estimated by computing the standard deviation of the within-subjects mean for each experimental condition. Movement offset was defined as the first time the velocity of the hand dropped under 2 cm/s. For each trial, values relative to trunk position and orientation 50 ms before movement onset were used as reference values. To quantify trunk motion resulting from arm movement execution, reference values were subtracted from the values recorded at movement offset. Four postural variables

were analyzed: lateral and antero-posterior translations of the trunk and trunk rotations about the roll and yaw axes. To assess the effect of GVS polarity on each postural variable, mean values obtained in the condition without GVS were subtracted from the mean values obtained in each GVS condition. This computation allowed a direct comparison of the postural effects of the two stimulation polarities (as we compared directly the effects of GVS polarity on hand direction).

A 2×3 (Stimulation polarity (anode left, anode right) \times Target (-18° , 0° , 18°)) analysis of variance (ANOVA) revealed a significant effect of GVS polarity on normalized endpoint directions ($F_{(1,7)} = 73.08$, $P < 0.0001$). On average, subjects pointed at -0.87 and 0.69° with respect to the control trials when the anode was on the left and on the right side, respectively. Therefore, the GVS induced a shift in movement endpoint towards the anode side. The normalized endpoint directions did not depend on the target position. Concerning direction variability, a 3×3 (Stimulation (anode left, anode right, control) \times Target (-18° , 0° , 18°)) ANOVA showed that this variable was unaffected by the GVS (global mean = 2.07°), but depended on target position ($F_{(2,14)} = 7.10$, $P < 0.01$). Post-hoc comparison (Newman–Keuls test, $P < 0.05$) revealed that final hand direction was less variable for movements directed towards the central target (mean = 1.67°) than for those directed towards eccentric targets (global mean = 2.24°). This result is consistent with previous studies suggesting that accuracy in encoding target positions tends to degrade as the eyes deviate from their central position [4].

Neither GVS polarity nor target position had a significant effect on movement time (on average, movement time was 745 ms). To determine when GVS polarity significantly affected arm trajectory, we compared the normalized directions of left and right anodes every 10 ms after movement onset (see Fig. 2A). A significant effect of GVS polarity on the normalized directions appeared 240 ms after movement onset ($F_{(1,7)} = 6.12$, $P < 0.05$). Each pointing movement (from movement onset to movement offset) was also normalized over time in order to compare the normalized directions at defined intervals during the movement: in steps of 5% from 5 to 100% of movement time (see Fig. 2B). A significant effect of GVS polarity on the normalized directions appeared at 30% of the movement time ($F_{(1,7)} = 5.86$, $P < 0.05$).

Both GVS polarities gave rise to slight overshoots in reaching movements (global mean = 0.56 mm), but these were non-significant (2×3 ANOVA; Stimulation polarity (anode left, anode right) \times Target (-18° , 0° , 18°)). A 3×3 (Stimulation (anode left, anode right, control) \times Target (-18° , 0° , 18°)) ANOVA indicated that neither the GVS nor the target factor significantly affected the variability in movement amplitude.

Each of the four postural variables was submitted to a 2×3 (Stimulation polarity (anode left, anode right) \times Target (-18° , 0° , 18°)) ANOVA. Trunk lateral translations

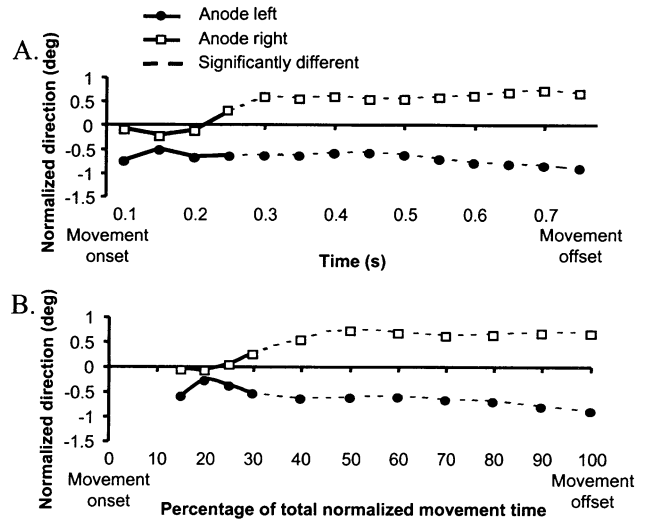


Fig. 2. Mean normalized directions measured every 50 ms during movement (A). Mean normalized directions measured at different intervals of the total normalized movement time (B). The first 100 ms (A) and the first 15% (B) of the movement do not appear on the graphs because the radius used for computing hand direction was extremely small in the initial portion of the movement resulting in misleadingly large and abrupt changes in movement direction. Dashed lines indicate the time at which normalized directions became significantly different.

($F_{(1,7)} = 13.56$, $P < 0.01$) and trunk rotations about the roll axis ($F_{(1,7)} = 38.02$, $P < 0.001$) turned out to be significantly affected by stimulation polarity. The average trunk movement was 1.8 mm to the right with a leftward roll of 0.58° in the anode left condition, and 2 mm to the left with a rightward roll of 0.17° in the anode right condition. Lateral trunk translations were also significantly affected by target position ($F_{(2,14)} = 4.56$, $P < 0.05$). A Newman–Keuls post-hoc test ($P < 0.05$) showed that the 0.8 mm trunk translation to the left induced by arm movements towards the left target significantly differed from the 1 mm trunk translation to the right evoked by arm movements towards the right target. Table 1 summarizes the results of statistical analyses.

The results of the present study showed a deviation of hand trajectory towards the anode side when a galvanic stimulation of the labyrinth was delivered at the onset of the reaching movement. Bipolar binaural GVS gives rise to a vestibular afferent pattern similar to that arising from head displacement towards the cathode side. In a head-free condition, movements of the head and/or body are usually observed towards the anode side [9]. These movements, which are delivered by the postural control system, would aim at bringing the head and/or body back to vertical after a (false) body displacement detection towards the cathode. In our experiment, the use of a bite-board prevented head movements and GVS elicited only minute lateral translations and roll tilt of the trunk. If changes in neck afferent signals accompanied vestibular stimulation, these would have been very small. The central nervous system is likely to have interpreted the stimulation as resulting from whole-

Table 1
Summary of the statistical analyses^a

Measured variables	Experimental factors	
	Stimulation	Target position
Normalized directions at movement offset (2 (anode left, anode right) × 3 (−18°, 0°, 18°))	$F_{(1,7)} = 73.08$; $P < 0.0001$	–
Direction variability at movement offset (3 (anode left, control, anode right) × 3 (−18°, 0°, 18°))	–	$F_{(2,14)} = 7.10$; $P < 0.01$
Normalized directions 240 ms after movement onset (2 (anode left, anode right) × 3 (−18°, 0°, 18°))	$F_{(1,7)} = 6.12$; $P < 0.05$	–
Normalized amplitudes at movement offset (2 (anode left, anode right) × 3 (−18°, 0°, 18°))	–	–
Amplitude variability at movement offset (3 (anode left, control, anode right) × 3 (−18°, 0°, 18°))	–	–
Trunk lateral displacements (2 (anode left, anode right) × 3 (−18°, 0°, 18°))	$F_{(1,7)} = 13.56$; $P < 0.01$	$F_{(2,14)} = 4.56$; $P < 0.05$
Trunk antero-posterior displacements (2 (anode left, anode right) × 3 (−18°, 0°, 18°))	–	–
Trunk rotation about the roll axis (2 (anode left, anode right) × 3 (−18°, 0°, 18°))	$F_{(1,7)} = 38.02$; $P < 0.001$	–
Trunk rotation about the yaw axis (2 (anode left, anode right) × 3 (−18°, 0°, 18°))	–	–

^a (–) Indicates that the effect is not significant.

body motion towards the cathode side rather than from head motion with respect to the trunk. As the slight GVS-evoked lateral translations of the trunk were directed towards the cathode side, the recorded hand deviations towards the anode side could not be induced by these translations. For these reasons, we conclude that the ‘corrections’ of arm trajectory towards the anode side result from a vestibularly-sensed whole-body motion. Thus, the present study demonstrates that reaching movements can be controlled online when a change in vestibular afferent signal occurs during arm movement.

The earliest significant effect of GVS on movement trajectory was observed 240 ms after stimulus onset. This delay is similar to the correction latencies reported when the change in the spatial relationship between the subject and the target is visually- or proprioceptively-detected [5,20]. The measured 240 ms delay is, however, much longer than several other vestibularly-induced motor responses. For instance, the fastest vestibularly-evoked electromyographic reaction recorded in free-standing subjects is about 65 ms for lower limb muscles [14] and 40 ms for the triceps brachii muscle [7], and body sway motion occurs 185 ms after GVS onset [19]. Vestibularly-induced neck muscle activation during head-free falls has a latency of 22 ms [15], and compensatory eye movements occur about 16 ms following vestibular stimulation [13,16]. These fast motor responses imply direct pathways from vestibular input to motoneurons (e.g. vestibulospinal, vestibulocollic and vestibuloocular pathways). Therefore, the delay necessary to bring about changes in arm trajectory following GVS suggests time-consuming transcortically-mediated processes requiring multisensorial input integration. These probably include those occurring in the posterior parietal cortex. This area responds to vestibular and somatosensory inputs and is involved in building up body-in-

space representations [1]. Individual cells of the posterior parietal cortex have been found to code the relative distance of a target from the hand [17]. Strong arguments for the participation of this area to the online correction of movement trajectories when a change in the hand-to-target position relationship occurs have also been presented in a recent study by Desmurget and colleagues [11] using a transcranial magnetic stimulation technique.

When GVS was delivered during reaching movements, the vestibular signal informed the central nervous system about body motion. Most of the other afferent signals (e.g. proprioception) provided information about body stability. Yet, GVS gave rise to reaching errors. The results of the present experiment therefore highlight the efficiency of the vestibular input to monitor body motion during reaching movements.

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