When is Vestibular Information Important During Walking?

Leah R. Bent, J. Timothy Inglis, and Bradford J. McFadyen

1School of Human Kinetics, The University of British Columbia, Vancouver, British Columbia V6T 1Z1; 2International Collaboration on Repair Discoveries, Vancouver, British Columbia V6T 1Z1; 3Department of Rehabilitation, Faculty of Medicine, Laval University, G1K 7P4 Quebec; 4Center for Interdisciplinary Research in Rehabilitation and Social Integration, Quebec Rehabilitation Institute, Quebec G1M 2S8, Canada

Submitted 23 December 2003; accepted in final form 20 April 2004

Bent, Leah R., J. Timothy Inglis, and Bradford J. McFadyen. When is vestibular information important during walking? J Neurophysiol 92: 1269–1275, 2004. First published April 21, 2004; 10.1152/jn.01260.2003. Locomotion relies on vision, somatosensory input, and vestibular information. Both vision and somatosensory signals have been shown to be phase dependently modulated during locomotion; however, the regulation of vestibular information has not been investigated in humans. By delivering galvanic vestibular stimulation (GVS) to subjects at either heel contact, mid-stance, or toe-off, it was possible to investigate when vestibular information was important during the gait cycle. The results indicated a difference in the vestibular regulation of upper versus lower body control. Upper body responses to GVS applied at different times did not differ in magnitude for the head (P = 0.2383), trunk (P = 0.1473), or pelvis (P = 0.1732) showing a similar dependence on vestibular information for upper body alignment across the gait cycle. In contrast, foot placement was dependent on the time when stimulation was delivered. Changes in foot placement were significantly larger at heel contact (during the double support phase) than when stimulation was delivered at mid-stance (in the single support phase of the gait cycle; P = 0.0193). These latter results demonstrate, for the first time, evidence of phase-dependent modulation of vestibular information during human walking.

INTRODUCTION

From our first years of life until old age, walking is our most important mode of transportation. Although successful locomotion is deceivingly simple-looking, it requires a complex coordination of the whole body, including information from vision, somatosensory inputs (such as from skin and muscle), and vestibular contributions. It has been demonstrated that both visual (Hollands and Marple Horvat 1996) and somatosensory (Zehr and Stein 1999) information exhibit phase-dependent influences on postural control during dynamic tasks such as walking. The role of the vestibular system during walking is not as well understood, however, largely due to the challenge of isolating this sensory system for manipulation.

Research from healthy subjects suggests that vestibular information contributes to head stabilization during dynamic tasks to enable successful gaze control (Pozzo et al. 1990) as well as to provide a stable reference frame from which to generate postural responses (Pozzo et al. 1995). In addition, studies have indicated vestibular involvement in navigational tasks, such as walking to a previously seen target, in the absence of vision (Fitzpatrick et al. 1999; Jahn et al. 2000). Vestibular contributions during dynamic postural tasks have also been proposed to play a role through “sensory reafference” (Inglis et al. 1995) in determining the appropriateness of triggered postural responses for balance control.

The study of chronic vestibular-deficient patients further indicates the importance of vestibular input in the successful completion of locomotor activities. Subjects with bilateral vestibular deficits, for example, are able to walk successfully over a short distance without vision (Cohen 2000; Glasauer et al. 1994; Tucker et al. 1998), although tending to walk slower and veering off the path earlier than healthy subjects. Furthermore, unilateral vestibular deficits result in significant lateral deviations toward the lesioned side when patients walk slowly (Brandt 2000; Brandt et al. 2001; Jahn et al. 2000).

Only very recently has the technique of galvanic vestibular stimulation (GVS) been used to study vestibular contributions to locomotion (Bent et al. 2000; Fitzpatrick et al. 1999; Jahn et al. 2000). By applying a current through the mastoid processes, the firing activity of the peripheral afferents of the eighth cranial nerve are increased on the side of the cathode electrode and decreased on the side of the anode electrode (Goldberg et al. 1984; Minor and Goldberg 1991). Use of the GVS technique provides the opportunity to perturb the vestibular system at discrete intervals to test the vestibular afferent sensitivity (weighting) during motor tasks. During walking, the application of GVS has been shown to cause path deviation toward the anode electrode (Bent et al. 2000; Fitzpatrick et al. 1999).

Although sensory information from vision and somatosensation are known to be used in a phase-dependent manner during human locomotion, no investigation to date has examined whether vestibular inputs are similarly modulated. One recent study in cats supports the theory of phase-dependent vestibular modulation (Matsuyama and Drew 2000). Vestibulospinal neurons (VSNs) with lumbar spinal connections in cats were observed to have increased firing at heel contact of the forelimb during treadmill locomotion. These data were interpreted as indicating increased vestibular contributions to facilitate antigravity activity and propulsion for the hindlimb during the stance phase of gait.

In the current study, the tool of GVS will provide an opportunity to investigate such phase contributions during locomotion in humans. The present research aims are to investigate the nature of the contribution of vestibular information on upper and lower body control during steady-state human walking. Two specific research questions were posed. First, are there phase-dependent responses to GVS during steady-state locomotion?
gait? Second, are these responses different for the upper and lower body? Some of these data have appeared in abstract form (Bent et al. 2003).

METHODS

Eight healthy subjects (5 male and 3 female) aged 25.5 ± 6.98 (SD) yr (height: 177.9 ± 6.2 cm; mass: 70.6 ± 11.9 kg) were recruited. Subjects were informed of the protocol and provided written consent to participate. All participants reported no previous history of motion sickness, epilepsy, or any neurological or musculoskeletal problems. Approval from the ethics committee of the Quebec Rehabilitation Institute was obtained prior to data collection. Studies have been performed according to the Declaration of Helsinki.

Equipment and subject preparation

An Optotak system (NDI, Model No. 3020; 2 position sensors) was used to collect three-dimensional kinematic data (digitally sampled at 100 Hz) to determine linear segmental positions and to estimate body center of mass (CoM) displacement. Three noncollinear infrared markers (IREDs) were placed on the subject’s medial forefoot, on the back of the trunk (2 at the level of T4 and 1 at the level of T12), on the posterior aspect of the pelvis (between the posterior superior iliac spines), and on each foot. During data analyses, a local axis system was first defined for the triad of markers on each segment. Then specific anatomical references and anthropometric measures for each segment were used to estimate the CoM and the principle axes of each segment as part of a software package for kinematic analyses (KinGait: MISCHAC). The local axis system was realigned along the principal axes. Finally, custom software was used to estimate a representative CoM position of the upper body (representing 2/3 of the body mass) for each data sample as the weighted sum of the CoM positions of the head, trunk, and pelvis. Segmental roll angles (in the frontal plane) of the head, trunk, and pelvis as well as foot placement on the floor were also calculated from the kinematic data. Segment roll (calculated as local angles, therefore representing true angles) and foot placement in the mediolateral direction (calculated in global space) were chosen as the main dependent variables based on previous research findings (Bent et al. 2002b; Day et al. 1997). In addition, foot placement in the mediolateral direction has been shown to be a primary means of altering path trajectory in response to GVS during walking (Bent et al. 2000; Fitzpatrick et al. 1999). Two AMTI force platforms (Advanced mechanical technology inc., model OR6-5) were staggered along the floor so that subjects walked across them during their steady-state progression (with their right and then left foot, respectively). Force data were sampled at 1,000 Hz.

Binaural, bipolar GVS was delivered from two carbon rubber electrodes that were 9 cm² in area and placed behind the ears. Stimulation was delivered by a Grass Stimulator (Model Grass S48) through a constant current stimulus isolation unit (AM Systems 2200). The intensity of the stimulation varied for each subject. As in previous experiments (Bent et al. 2000, 2002a), each subject’s individual threshold for GVS response during standing was determined prior to data collection. Briefly, subjects stood with their feet together (but not touching), and the stimulus intensity was gradually increased from 0.05 mA. Threshold was determined when upper body movement was observed toward the anode side in the frontal plane or subjects reported any sensations of dizziness or disorientation. The intensity of stimulation during the experiment was set at three times the individual anodal threshold with a minimum current of 1.0 mA (range: 1.0–1.5 mA).

Test procedures

Participants stood a distance of three steps from the first force platform. Practice (3–5 trials) was given before data collection to establish a comfortable, natural walking speed while walking with vision occluded. Instructions were given to initiate gait with their right lower limb and to walk forward until instructed to stop (≥4.3 m or ≥7–8 steps). Participants walked with their arms slightly flexed at the elbow to allow regular arm swing as well as the use of the upper limbs in postural strategies if desired during walking but primarily to prevent the blocking of IREDs. Vision was occluded with a pair of custom-made opaque goggles that enabled light to enter but prevented determination of edges or objects. Subjects were instructed to keep their eyes open inside the goggles.

GVS was triggered at three different events for the right limb during steady-state gait: heel contact (HC) triggered by an increase of 5 N in vertical ground reaction force; mid-stance (MS); which is also coincident with mid-swing of the contralateral limb) triggered by a change from a backward oriented to a forward oriented anterior posterior ground reaction force; and toe-off (TO) triggered by a decrease in vertical ground reaction force <5 N. Delivery of the GVS perturbation included three different configurations including the anode electrode placed over the left mastoid process (L), the right mastoid process (R), or no stimulation (control condition). The GVS perturbation continued for the duration of the trial (3–4 s). Five trials were collected for each of the six stimulation conditions (anode R/anode L/TO/MS/HC). In addition to these 30 stimulation trials, there were 9 trials collected with no stimulation.

Data reduction

All data in the GVS trials were adjusted to have zero amplitude at the specific gait event where stimulation occurred (HC, MS, TO). This was done by aligning the control and GVS trials at the stimulation event and subtracting out the control data. Due to limitations in camera placement, the head data were not always present at the point of first heel contact with the right limb (RHC1). As a result, the beginning of data analysis was set at left toe-off (LTO1; the next gait event ~100 ms later) for the HC trials. To verify that this decision did not result in removing any stimulation effects, an ANOVA was calculated for peak head roll at LTO1 and indicated no significant differences between stimulation and non stimulation conditions [F(2,14) = 2.506, P = 0.1174]. Throughout the results and discussion, data are reported as occurring after stimulation at HC.

All event-locked data, as described in the preceding text, were time normalized across 400% based on specific events in the gait cycle. The phases were comprised as follows: phase 1 (0–100%) from first left toe-off (LTO1) to right foot MS; phase 2 (100–200%) from MS to first right TO; phase 3 (200–300%) from right TO to second right heel contact (RHC2); and phase 4 (300–400%) from RHC2 to second right toe-off (RTO2). Normal movement variability was then removed by subtracting averaged non-GVS data from individual GVS trials using the same anchoring points. After this procedure, only the residual roll responses due to stimulation remained, which could then be assessed for peak roll angles in degrees. The onset of the roll response by the head, trunk, and pelvis was assessed based on the point in time when segment roll after stimulation surpassed the average roll in a control trial ±1 SD. These data were converted into units of time for each subject and then averaged across subjects for each GVS condition.

Mediolateral placements of the right and left feet were calculated at each step as the location of the toe at foot contact relative to left toe position at LTO1. Step 1 after GVS at HC and MS was taken with the left foot. In TO trials step 1 was performed with the right foot. Therefore to enable data averaging, foot-placement changes were presented in terms of steps 1 and 2 after stimulation and not with respect to right and left foot changes. Repeated-measures ANOVAs were used to test for significant effects between conditions. Post hoc analyses were run using Tukey’s honestly significant difference. For all statistical tests, significance was determined at P < 0.05.
RESULTS

Delivery of GVS resulted in roll of the head, trunk, and pelvis toward the anode electrode. Head roll was significantly earlier than the trunk \( [300 \text{ ms}; F(2,15) = 51.05, P < 0.0001] \) and was followed by the trunk and pelvis roll \( (700 \) and \( 800 \) ms), which occurred at similar latencies to each other, giving rise to a top-down response to the GVS perturbation as has been reported previously in the literature (Bent et al. 2002b; Day et al. 1997). Significant differences in the magnitude of peak roll were found during GVS trials for all subjects for head roll \( [2.34^\circ; F(1,7) = 262.872, P < 0.0001] \), trunk roll \( [2.79^\circ; F(1,7) = 137.588, P < 0.0001] \), and pelvis roll \( [2.70^\circ; F(1,7) = 178.324, P < 0.0001] \) relative to movement without stimulation. No significant differences were found for the magnitude of the peak roll response among the three events of GVS at HC, MS, and TO for the head \( [F(2,14) = 1.592, P = 0.2383] \), the trunk \( [F(2,14) = 2.203, P = 0.1473] \), or the pelvis \( [F(2,14) = 1.993, P = 0.1732, \text{ Fig. 1}] \).

For foot placement, no significant changes were found at step 1 after the delivery of GVS at any gait event (Fig. 2). However, significant alterations in foot placement were observed by step 2 \( [F(2,14) = 41.389, P < 0.0001] \) compared with trials with no stimulation. Significant interactions \( [F(4,28) = 10.822, P < 0.0001] \) followed by a post hoc Tukey’s test determined that significant changes to foot placement occurred when GVS was delivered at HC for both anode right \( (14.9 \text{ cm}) \) and left \( (-9.8 \text{ cm}) \) in comparison to no stimulation. In addition, significant differences were found for stimulation at TO with the anode to the right \( (9.8 \text{ cm}) \) compared with no-stimulation trials. Further assessment of foot-placement magnitude determined that there was a significant difference between event conditions \( [F(2,14) = 5.306, P = 0.0193] \). Averaged absolute foot-placement changes after stimulation to the right and left sides at HC \( (12.4 \text{ cm}) \) were shown to be significantly larger than after stimulation at MS \( (6.3 \text{ cm}; P < 0.05; \text{ Fig. 3A}) \). The foot-placement changes at HC were also larger than changes after stimulation at TO \( (9 \text{ cm}) \), although differences between these two events were not statistically significant.

CoM displacement changes were assessed at each step along with foot-placement changes. Significant differences in displacement were found by step two at the point when changes in foot placement were observed \( [F(4,28) = 12.036, P < 0.0001; \text{ Fig. 3B}] \). Post hoc analyses determined that CoM displacement in HC anode right, HC anode left, and TO anode right trials were all significantly different from CoM displacement in trials without stimulation \( (P < 0.05) \). In addition averaged CoM displacement in HC trials \( (8.5 \text{ cm}) \) was found to be significantly larger than in MS trials \( (4.2 \text{ cm}) \) and larger, although not significantly, than CoM displacement at TO \( (5.12 \text{ cm}) \).

DISCUSSION

To date, no research has studied whether vestibular contributions during human walking are phase regulated. In our study, we used GVS to probe whether the weighting of vestibular information was modulated differently during separate phases of steady-state gait in humans. Differences were found for vestibular regulation of the upper and lower body, suggesting independent upper and lower body control. Vestibular regulation of the timings and amplitudes of upper body roll responses were controlled in a similar manner as when maintaining upright standing (i.e., roll toward the anode electrode, beginning from the head down) and did not differ in magnitude across the walking cycle. In contrast, significant changes in foot-placement timing and magnitude were observed, which were found to be dependent on when the vestibular perturbation was introduced during the gait cycle. This latter finding shows phase-dependent alterations in vestibular contributions to lower limb control during locomotion; this parallels what is known for the regulation of information arising from other
sensory modalities such as from visual (Hollands and Marple-Horvat 1996), cutaneous (Eng et al. 1994; Wand et al. 1980; Zehr and Stein 1999), and muscle afferent (Dietz et al. 1990; Sinkjaer et al. 1996; Yang and Stein 1990; Zehr and Stein 1999) signals.

To successfully maintain steady-state locomotion, both appropriate propulsion and the maintenance of dynamic equilibrium must be achieved (Forssberg 1979; Winter 1987). Mediolateral placement of the feet during forward walking is the primary means of effectively altering CoM deviations in the frontal plane (MacKinnon and Winter 1993). By altering the foot placement and subsequently the forces applied on the ground, one can change the direction of the CoM acceleration to control both the progression of gait and dynamic equilibrium. In light of the current results indicating phase related vestibular modulation for the control of foot placement, vestibular information appears to play a critical role in the regulation of whole body dynamic stability that differs depending on the specific point during the gait cycle.

The largest change in foot placement was observed when the GVS was initiated at heel-contact and the smallest change when stimulation was applied at mid-swing. Although foot-placement measures do not occur at a fixed latency after stimulation (e.g., subsequent foot placement occurs sooner after GVS at TO than for GVS at HC), the observed effects by step 2 are not likely to be due to the duration of the perturbation. If duration of stimulation were the cause of the changes observed by step 2, one would also expect to observe changes by step 1, which also involves a longer stimulation duration after GVS at HC as compared with after GVS at TO. No trend was even observed in the magnitude of foot-placement changes among the three conditions by step 1. Therefore these results suggest that changes are due to phase-dependent vestibular modulation, with the largest vestibular contributions occurring during double support and the smallest during single support.

The observation that no response occurs until step 2 is also not due to a delay in stimulus processing. We have shown previously (Bent et al. 2004) that subjects are able to begin programming changes in foot placement within 100 ms. Stimulation at HC in this gait initiation study was shown to alter placement of the subsequent step even though programming for the step was complete by TO (Hollands and Marple-Horvat 1996), concluding that only 100 ms was necessary to complete the programming for the altered foot trajectory. Therefore we can be confident that the responses we observe at step 2 are related to the point at which the stimulus was delivered and not a subsequent point resulting from an inherent GVS delay.

Why might there be a greater vestibular weighting for the control of limb placement associated with HC? It has been suggested that a critical time for the programming of limb placement occurs during the double support phase. Hollands and Marple-Horvat (1996) demonstrated that, during locomotion, the planning of accurate foot placement to a previously seen target is accomplished during the last 100 ms of the stance phase (also related to the double support phase after contact of the contralateral limb). This critical period for visual sampling indicates that changes in length and width of the limb trajectory can be modified within one step cycle. These researchers concluded that programming for limb placement is complete by the time the foot leaves the ground at TO. Therefore the
A Foot Placement Changes (m)

B CoM Displacement (m)

double support period could present an opportunity for vestibular information to contribute to the alterations of the foot trajectory.

Vestibular upregulation at HC may also serve to provide “sensory reafference,” a term related to the use of sensory information to monitor the success of a voluntary movement or triggered postural response (Inglis et al. 1995; Séverac Cauquil and Day 1998). In the event of a slip or trip during locomotion, specific postural strategies to maintain dynamic stability are initiated (Figura et al. 1986; Nashner 1983). Work in both humans (Horak et al. 1994, 2001; Inglis et al. 1995) and cats (Inglis and MacPherson 1995) has shown that responses to perturbed standing posture from platform translations are triggered at very rapid onset latencies by somatosensory information and then proposed to be modulated based on sensory reafference from vestibular inputs (Inglis et al. 1995).

To generate an appropriate internal representation of the body in space, information from the vestibular system must be integrated with somatosensory inputs (Hlavacka et al. 1995; Lund and Broberg 1983). During double support with two feet on the ground, somatosensory information can relay a more reliable indication of body base of support than during the swing phase when one limb is in the air. Integration of vestibular information and somatosensory input during double support would indicate whether the movement of the body relative to the base of support would result in the desired end position during both perturbed and unperturbed walking. This would provide information to facilitate appropriate changes to foot placement. Recently evidence has also been presented which supports the importance of vestibular integration with load-related afferent feedback from the lower limbs (Marsden et al. 2003), suggesting an important role for somatosensory input in vestibular responses.
Finally, evidence of phase-dependent modulation has recently been supported through recordings of VSNs with connections to lumbar spinal regions in the walking cat (Matsumoto and Drew 2000). These researchers found that the largest percentage of recorded VSNs demonstrated an increased firing rate at the point of forelimb foot contact during walking on a treadmill. It was concluded that these projections have the greatest influence on extensor muscles of the hindlimbs and therefore act primarily to facilitate antigravity activity during the stance phase of locomotion. Although vestibular influences over lower limb control were phase dependent, the present results suggest that vestibular regulation is homogeneous across the gait cycle for upper body posture control. These results can be explained with respect to the role of vestibular signals to ensure alignment of the body segments in an appropriate geocentric orientation. Pozzo and colleagues (1990) have suggested that the head acts as a frame of reference during complex dynamic tasks because both the vestibular and visual systems are able to relay information regarding the head in space. To ensure that the information from these sensory systems is appropriate and that sensitivity to change is optimized, the head has been found to be stabilized in space in the pitch (Pozzo et al. 1990, 1991; Shupert and Horak 1996), yaw (Cromwell et al. 2001) and roll (Pozzo et al. 1995) planes, including evidence of anticipatory control of head acceleration in the pitch plane during forward locomotion (Prince et al. 1994). Pozzo and colleagues (1995) indicated that the perception of self in the environment is believed to result from the integration of vestibular and visual (when present) information, along with somatosensory inputs, to enable a transformation of the head based reference frame to the exocentric reference frame and therefore facilitate appropriate postural responses to maintain equilibrium. Stabilization of the head on the trunk through proprioceptive input has also been proposed to aid in the translation between reference frames (Pozzo et al. 1995) and is supported by additional research examining the role of integration in generating appropriate postural responses (Hlavacka et al. 1995; Horak et al. 1994, 2001; Lund and Broberg 1983). Furthermore, Prince and colleagues (1994) demonstrated stabilization of the head on the trunk via top down anticipatory control of the upper body during unperturbed walking, lending support to our current observations of a top down response and to the implications for the importance of stabilization of the head for successful locomotion. In light of these previous investigations and the current data, it is proposed that vestibular information plays a critical role in the maintenance of head stabilization in a gravitational reference frame across all phases of locomotion. When integrated with somatosensory input, vestibular control of the head in space is proposed to enable the successful completion of complex dynamic tasks.

To conclude, the present findings show, for the first time, a phase-dependent modulation of vestibular information during walking. The phase-dependent modulation, however, was only related to lower limb control. The observation that weighting of vestibular information was greatest for lower limb changes during the double support phase supports a role for vestibular information in the planning of foot placement for successful forward progression. Maintenance of a stabilized reference frame was also found to be important for successful locomotion. The homogenous upper body roll response across phases suggests that equal importance (regulation) was given to vestibular information to align the upper body, particularly the head, during locomotion. These results unveil a level of complex regulation underlying vestibular contributions for successful steady-state locomotion in relation to distinct upper versus lower body control.

**ACKNOWLEDGMENTS**

Special thanks to M.-C. Simard, F. Comeau, M. Gérin-Lajoie, and G. St-Vincent for contributions to this work. Present address of L. R. Bent: Prince of Wales Medical Research Institute, Randwick, NSW, Australia 2031

**GRANTS**

This work was supported by funding from the Natural Science and Engineering Council of Canada to L. R. Bent, B. J. McFadyen, and J. T. Inglis.

**REFERENCES**


