Effects of galvanic vestibular stimulation during human walking

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1. To identify vestibular influences on human walking, galvanic vestibular stimulation was applied to normal adult subjects as they walked to a previously seen target. A transmastoidal step stimulus commenced as subjects started walking. With the eyes shut, the galvanic stimulus caused large turns towards the side with the anodal current.

2. Ability to perceive the trajectory of gait without visual cues was measured by guiding blindfolded subjects from one arbitrary point to another, either walking or seated in a wheelchair. On reaching a destination position and removing the blindfold, subjects pointed to indicate the starting position. Subjects made considerable errors in estimating the trajectory, but were equally accurate whether in the wheelchair or walking.

3. To determine the effects of vestibular stimulation on the perception of trajectory, the galvanic stimulus was applied to blindfolded subjects as they were guided from one point to another in the wheelchair. The vestibular stimulus produced an illusory shift in the trajectory travelled. This shift was towards the side with the cathode, i.e. in the opposite direction to the turn produced by the stimulus during walking.

4. We conclude that galvanic vestibular stimulation during walking causes subjects to turn from their planned trajectory. In part, this altered course may compensate for an altered perception of trajectory produced by the stimulus. However, altered perception of the vertical or the base of support, or direct vestibulo-fugal influences on the leg muscles could contribute to the changes in gait.

When we walk towards a destination it is neither necessary nor common for us to keep our vision continuously fixed on the target. Once a target has been seen, it is possible to shut the eyes and walk directly to it if it is not too distant. In this situation, proprioceptive sensory inputs from the limbs and the vestibular organs provide information about the trajectory and stability of the body. Proprioceptive input from muscles and joints of the pelvis and hips can contribute to the sensation of the trajectory walked (Gordon *et al.* 1995). The vestibular organs provide signals about both the linear and angular acceleration of the head in space, and could also contribute to a sensation of trajectory if the frequency and acceleration of normal walking are appropriate. Patients who suffer pathological vestibular disorders commonly stagger and turn to one side. This is likely to arise from an inability to maintain vertical balance as shown by their similar problem when standing. However, an altered perception of trajectory might also contribute to this deviation from the intended path.

Human standing is thought to depend on a combined reflex response to proprioceptive, visual and vestibular sensory inputs. Vestibular input is not necessary to provide postural responses to correct the natural sway and perturbations of standing (Fitzpatrick *et al.* 1992) and does not contribute to the perception of sway during standing (Fitzpatrick & McCloskey, 1994). However, when vestibular input is inappropriate because of vestibular pathology or vestibular stimulation, stable standing is compromised.

In standing human subjects, galvanic vestibular stimulation evokes a prolonged 'galvanic body sway' (Coates, 1973) and transient electromyographic (EMG) responses in the leg muscles (Nashner & Wolfson, 1974; Britton *et al.* 1993). When a stimulus current is passed between the mastoid processes so that the current is anodal on one side and cathodal on the other, subjects sway towards the direction of the anode. If the head is facing forward subjects sway laterally, but if the head is turned to face the side, sway is in the antero-posterior plane. In part, this body sway might be a reaction to a perception of sway in the opposite direction that can be evoked by galvanic vestibular stimulation (Fitzpatrick *et al.* 1994). Other studies using galvanic vestibular stimulation in standing subjects suggest that the vestibular system establishes an internal vertical reference (Inglis *et al.* 1995), or is organized to keep the centre of mass of the body within safe limits relative to the area of foot contact with the ground (Day *et al.* 1997).

Like standing, human walking is a state of unstable equilibrium in which the body is balanced over a limited area of support. Standing approximates a state of static equilibrium with the centre of mass of the body kept above the area of the feet. Although walking represents a more complex dynamic equilibrium, it is analogous to standing in imposing restrictions on the position, velocity and acceleration of the body in relation to the moving base of support of the feet.

The present experiments investigate in normal subjects: (i) the effects of galvanic vestibular stimulation during walking, and (ii) the vestibular and proprioceptive contributions to the perceptions of a walked trajectory. The results show that at ordinary walking speeds, the perception of trajectory can be based on vestibular input, and that the availability of proprioceptive input related to walking does not further improve the accuracy of the perception of trajectory. During walking galvanic vestibular stimulation causes subjects to turn from a planned trajectory. Altered perception could contribute to this deviation.

METHODS

The initial experiment was designed to look for responses evoked by galvanic vestibular stimulation in walking subjects. Stimulus-specific changes in the trajectory of gait were observed. The second experiment, initiated after the observations made in the first, was a psychophysical study designed to determine whether vestibular stimulation altered the perception of trajectory during walking, and if so, whether this could account for the change in trajectory produced by vestibular stimulation. Nine healthy adults (25–38 years, 5 female) provided written informed consent to participate in these experiments that had been approved by the institute's human ethics committee. Seven subjects participated in each experiment, with five subjects, including one of the authors, participating in both.

Experiment 1

Stimulus. Electrodes (2 cm^2 AgCl) were attached over each mastoid process and were stabilized by an elastic headband. A battery-powered current source was used to pass a long step impulse lasting several seconds between the electrodes. One of four different stimuli was used for each trial. Stimulus intensity was either 0·5 or 1·0 mA, and the direction of the stimulus current was either anode-right or anode-left. Subjects could perceive the currents as weak cutaneous shocks on both sides and were told in advance whether a stimulus would be presented in the next trial.

Task. Subjects stood on a carpeted floor at the centre of one end of a marked rectangular area (5 m × 4 m), and viewed a target marker on the floor 4 m directly in front of them (Fig. 1*A*). They were instructed to shut their eyes and, when told to go, walk directly to the target. Subjects started with the right foot and paced the steps to a metronome that was set at either 52 steps min^{-1} or 104 steps min^{-1} for different trials. A countdown sequence ('three, two, one, shut, go') was provided so that there was approximately 1 s between shutting the eyes and starting the walk. The galvanic stimulus current commenced simultaneously with the 'go' command and persisted for the duration of the walk (~8 steps). Subjects were told to stop before they hit the distant wall and then, with their eyes still shut, were escorted back to the start by a circuitous path. The order of the four different stimuli (0·5 or 1 mA,

anode left or right) was randomized, but a control trial in which subjects walked at the same cadence but without a stimulus was alternated with the stimulus trials. This ensured a long period between stimuli to minimize possible residual effects of the stimuli. Thus, each subject made 16 walks, 8 with a vestibular stimulus (4 stimuli × 2 cadences) and 8 without a stimulus. One trial was performed in which the subject walked towards the target with the eyes open with a 1 mA stimulus, anode right.

Additional trials were performed in a smaller number of subjects. Three subjects walked with the head or trunk turned towards the side so that the head was facing in a direction perpendicular to the direction of gait, either to the left or right. In other trials, two subjects walked backwards.

Measurement. A video camera was positioned behind and above the subject and each walk was recorded on tape. Optical markers were placed at the back of each shoe, just above the point of floor contact. Markers were also placed at 1 m intervals on the floor to calibrate the walk area. After the experiments, the video was captured at 25 Hz as individual frames. The location of the foot placements was digitized manually (1280 × 1024 resolution) at the first frame following each heel strike during the walk.

Experiment 2

In this experiment blindfolded subjects were guided from a starting position (actual start, Fig. 1*B*) along one of four arcs to an end position. On reaching the end position, subjects removed the blindfold and pointed to indicate to the experimenter where they thought the start position was (perceived start). In some trials subjects walked and in other trials they were pushed in a wheelchair. In the wheelchair, vestibular input is likely to provide the most reliable sensory information about trajectory, although wheelchair accelerations could provide sensory input through changes in skin pressure. However, proprioceptive input associated with gait is also available from the legs when walking. In some trials when subjects were pushed in the wheelchair, galvanic stimuli were applied to disturb vestibular sensation.

Task. Subjects sat blindfolded in a wheelchair, and were pushed slowly about a large, level carpeted room (10·5 m × 7·3 m) in a random tortuous path, the curvature of which was frequently changed between clockwise and counter-clockwise to avoid a directional habituation. Subjects wore earmuffs and the room was silenced to minimize the use of any auditory cues for spatial localization. After approximately 2 min, a period that disorients subjects so that they no longer know their position in the room, the wheelchair was stopped and the subject told 'this is the start'. After a 10 s pause with the subject stationary, the experimenter pushed the subject along one of four predetermined arcs at approximately 52 steps min^{-1}, the slow walking speed of Experiment 1. When the chair was stopped the subject removed the blindfold and, while still seated, directed an experimenter to the precise location of the perceived start position. The distance and direction, in room co-ordinates, from the actual start to the end, and from the actual start to the perceived start, were measured. While these measurements were made, the subject was again blindfolded and pushed around the room in preparation for the next trial. Trials in which the subject walked were conducted in the same way, but to indicate the direction of turn, the experimenter intermittently touched the top of the subject's shoulders as a guide. In this way, subjects walked a smooth trajectory similar to that travelled in the wheelchair.

Stimulus and path. Electrodes were attached as described above and step stimuli of 1·0 mA intensity, either anode-right or anode-

left, were delivered to coincide with the start of movement of the wheelchair and end as the wheelchair stopped. In other trials, no stimulus was delivered. Subjects were not told in advance whether a stimulus would be presented in the next trial. To prevent subjects using the alignment of the wheelchair and the elapsed time to estimate the starting position, subjects were pushed in curved paths. The curvature was randomized from trial to trial to prevent subjects benefiting from any clues about past performance. Four paths were used, either clockwise or counter-clockwise, and with a radius of either ∼4·5 m or ∼9 m. Each subject performed six trials with the anode-right stimulus, six trials with anode-left, and six trials with no stimulus. The combinations of stimuli and path were presented in a random order. No stimuli were given during the eight walking trials that were carried out in a block after the completion of the trials in the wheelchair.

Measurement. During the experiment, measurements were recorded in room co-ordinates. From those data, an 'end to perceived start' vector was calculated relative to the 'end to start' vector for each trial.

RESULTS

Experiment 1

Without the vestibular stimulus, subjects had no difficulty in walking straight to the previously seen target with their eyes closed. They usually stepped on or over the target and never passed more than 25 cm from it. When the galvanic vestibular stimulus was applied at the start of the walk, subjects had no difficulty in walking to the target if their eyes were open, although several subjects reported that they felt some unsteadiness. Without vision, the vestibular stimulus caused subjects initially to deviate to the right with the anode at the right mastoid, and deviate to the left with the anode at the left mastoid. This was so for every trial and for every subject. Typical results from two subjects are shown in Fig. 2. Two patterns of response were observed. The more common pattern was for subjects to turn to the side determined by the stimulus, and then to continue to walk in that direction (Fig. 2*A*). Other subjects initially turned towards the anode for the first three or four steps, and then turned back towards the target, as if they had become aware that they had turned and were no longer facing the target (Fig. 2*B*). An experience reported by some subjects was that as they stepped they were surprised at the position of their foot after it hit the ground because it had landed too far to the side or crossed in front of the other foot. This was particularly so with the larger stimulus intensity and the lower cadence.

The effect of the galvanic stimulus on the angular deviation and stride length for each step in the walk is shown in Fig. 3. The distance for each step was measured as the
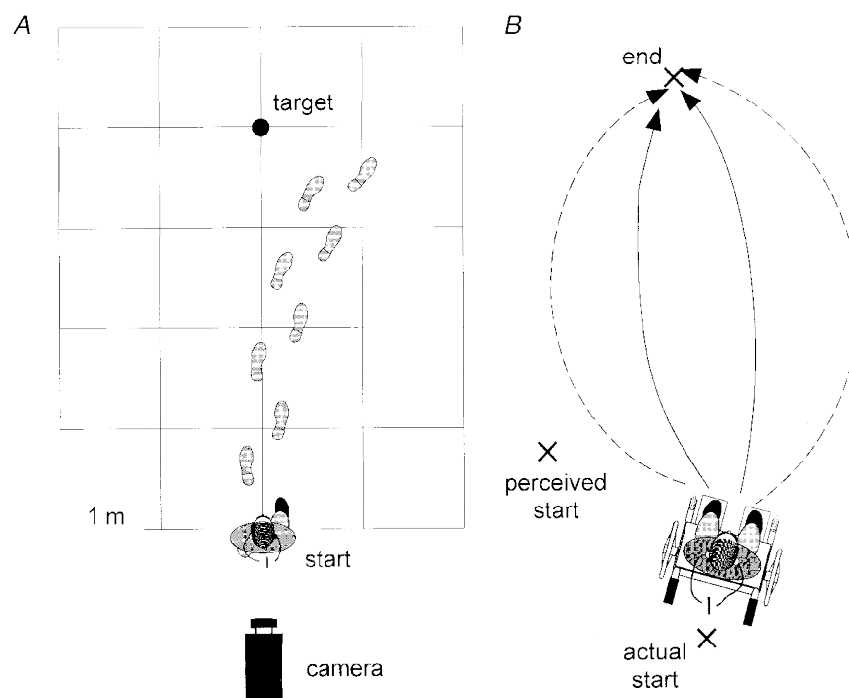

Figure 1. Experimental set-up

A, Experiment 1. Subjects stood and viewed a target 4 m ahead, and after shutting the eyes, walked straight ahead towards the target. A step current of different intensities and polarities was passed between the mastoid processes, commencing as the subject began to walk. Trajectory of gait was measured using a camera positioned above and behind the subject. *B*, Experiment 2. Subjects sat in a wheelchair, blindfolded and wearing earmuffs. The experimenter pushed them at walking pace from a start to an end position along a curved trajectory. As they started to move, a step current was passed between the mastoid processes. On reaching the end point, subjects removed the blindfold and indicated the perceived start point of the trajectory.

change between the position of the foot in its stance phase and the position of the same foot after the next swing phase and heel strike. The angle for each step was measured relative to the direction of the previous step of the same foot. Consequently, this removes the cumulative error of each step seen with the actual position of foot placements in Fig. 2. With no vestibular stimulus, there were only small deviations in direction with each step (Fig. 3).

Analysis of variance of the turn with subject, cadence, stimulus intensity and step as factors did not show an effect of stimulus intensity but did indicate a significant effect of step number ($F_{7,256} = 48 \cdot 9$, $P < 0 \cdot 001$) and an interaction of step and cadence ($F_{7,256} = 2 \cdot 3$, $P < 0 \cdot 05$). When the vestibular stimulus started at the beginning of the first step, that step was unaffected by the stimulus (Fig. 3). For steps 2, 3 and 4, there was a turn in the direction of the anode that was maximal for step 3 where it was greater when subjects walked at the slower pace ($26 \cdot 3 \pm 17 \cdot 0$ deg at 52 steps min^{-1}, $19 \cdot 0 \pm 10 \cdot 3$ deg at 104 steps min^{-1}; mean $\pm$ s.d., $P < 0 \cdot 05$). Subjects stepped as much as 44 cm to the side in a single pace. In step 5 subjects tended to turn back towards the target and later steps showed no significant turn. When the trials with vestibular stimulation were compared with the matched control trials, subjects turned significantly towards the anode in steps 2 and 3 at 52 steps min^{-1} but in steps 2, 3 and 4 at the faster pace ($P < 0 \cdot 05$, Student's *t* test with

Bonferroni correction). The turn back towards the target (step 5) was only significant at 52 steps min^{-1}.

When subjects attempted to walk backward along a straight path with the galvanic stimulus, they again turned towards the anode, the same direction as for forward gait. That is, they would walk backward along the same trajectory as a forward walk with the same stimulus. When subjects walked with the head turned to face over either the left or right shoulder, the galvanic stimuli did not produce any deviation in trajectory. This was so regardless of whether the head rotation arose through turn of the neck or of the trunk.

Experiment 2

Subjects were guided from one position in the room to another with the eyes shut and without any galvanic vestibular stimulus. The perceived start positions for all subjects and trials are shown in Fig. 4, with the paths offset to the same end position E. Subjects started from within the shaded region S and were pushed to the end position E along a curved path. Subjects then indicated the points P as their perceived start positions.

When subjects were walked from one position in the room to another with their eyes shut, the direction of the perceived start position was not significantly different ($-1 \cdot 7 \pm 18 \cdot 3$ deg) from the actual start position when averaged over all trials (Figs 4*A* and 5). For individual trials,

A

0.5mA
52/min

1.0mA
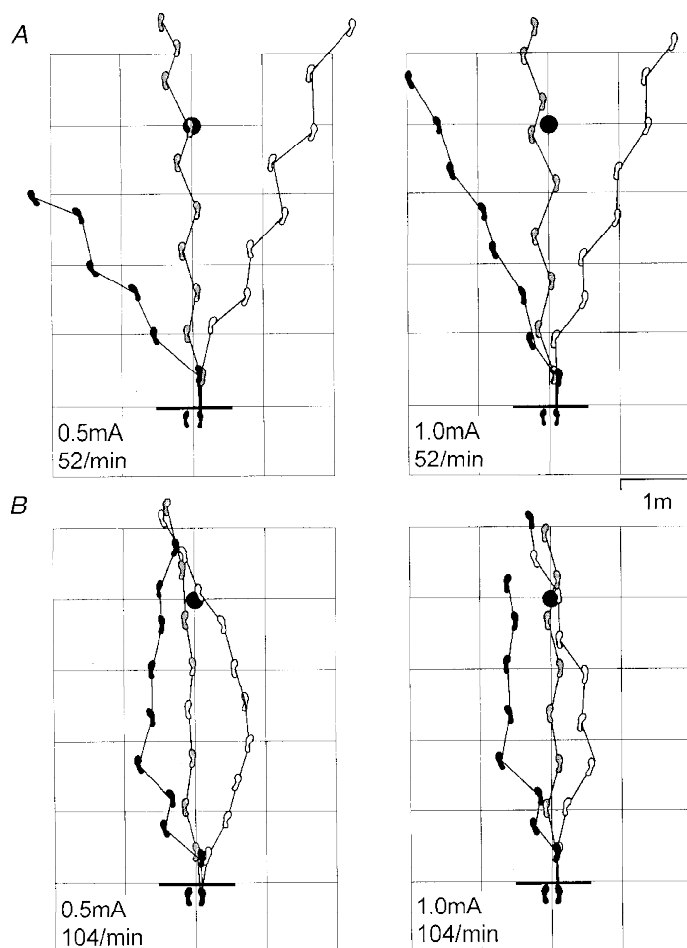52/min

1m

B

0.5mA
104/min

1.0mA
104/min

Figure 2. Walking trajectories

Results are shown for two different subjects (*A* and *B*). Subjects walked from the starting line attempting to reach the target circle. Without a vestibular stimulus, subjects walked straight to the target (shaded footsteps). With an anode-right stimulus, subjects initially veered to the right (open footsteps) and with an anode-left stimulus, they veered to the left (black footsteps). Both subjects turned during the first 4 steps. After that, subject *A* continued to walk away from the target whereas subject *B* turned back towards the target.
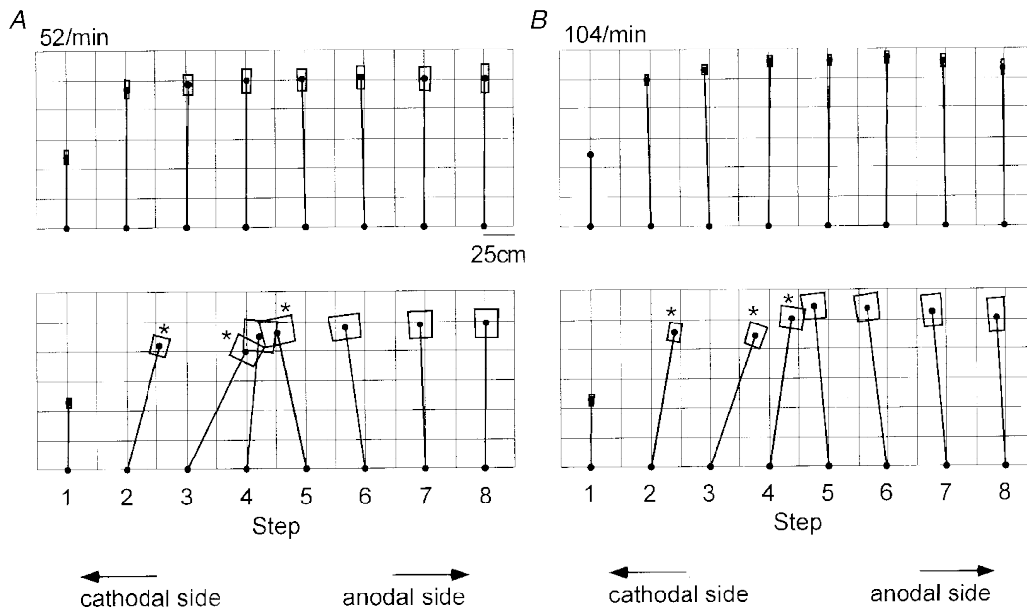
Figure 3. Turn during individual steps

Stride length and trajectory are shown for individual steps for the 1 mA galvanic stimulus (mean ± s.e.m., 25 cm grid). The distance and direction of each foot relative to the previous position and direction of that foot are plotted for steps 1–8. Subjects start with the right foot (step 1) and therefore it is the length of only half a stride. With no vestibular stimulus the steps are uniform (top panel). The vestibular stimulus does not affect the first step, but in the following 3 steps it changes the direction of the step towards the anodal side, with turn greater for the cadence of 52 steps min^{-1} (bottom left panel) than for 104 steps min^{-1} (bottom right panel). During the following steps (5 and 6) there is some turn back towards the target before straightening in the last steps. Asterisks indicate a significant turn compared with control steps ($P < 0.05$).

Figure 4. Perceptions of trajectories

Subjects were guided from a start position within the shaded region (S) to an end position (offset to the common point E). From position E, they indicated the filled points (P) as the perceived start positions. Subjects made considerable errors in direction and distance in estimating the start positions, but were equally accurate when they walked (A) and when they were pushed in the wheelchair (B). Galvanic vestibular stimulation shifted the perceived starts to the right (from the subject's view) with the anode right (C), and to the left with the anode left (D). The vestibular stimuli caused a greater variance in the estimate of the start directions.
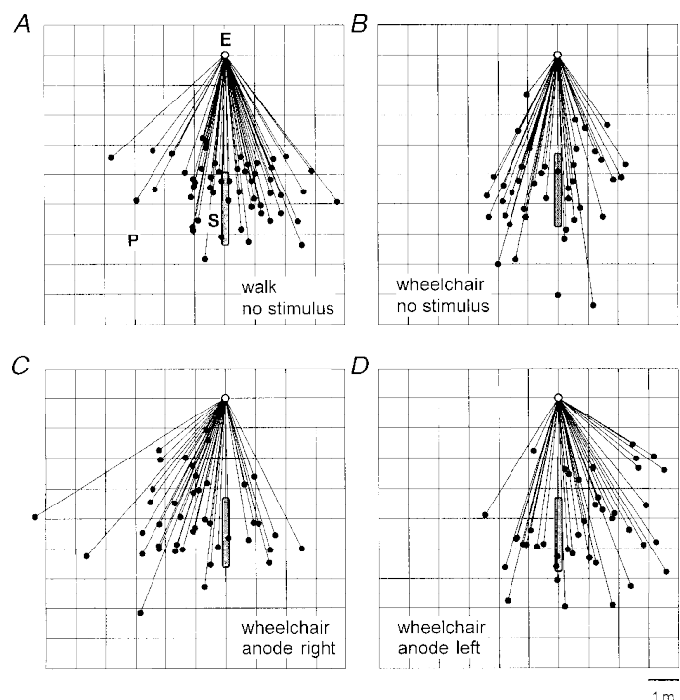
subjects made errors in direction of up to ±48 deg (mean absolute error 15·1 ± 10·3 deg). On average, subjects underestimated the distance to the start position by 16·4 ± 16·1 % ($P < 0.05$). These distance errors were often relatively large for individual trials, up to one-half of the actual distance.

When subjects were pushed in a wheelchair from one position in the room to another with their eyes shut, the mean perceived start position was again not significantly different (−2·4 ± 18·1 deg) in direction from the actual start position (Figs 4*B* and 5). For individual trials, subjects' errors in identifying the direction of the start position were up to ±38 deg (mean absolute error 15·3 ± 9·7 deg), and comparison of variances showed that this was not significantly different from when they walked ($F_{41,55} = 1.03$, $P = 0.47$). In the wheelchair, subjects again tended to underestimate the distance travelled (−6·0 ± 28·0 %) but this was not statistically significant.

A vestibular stimulus was applied while subjects were pushed in the wheelchair from one position to another. The vestibular stimulus altered subjects' perceptions of the direction of the start position (compare Fig. 4*C* and *D* with *B* and also with Fig. 5). For the anode-right stimulus the start position was perceived to be 17·3 ± 22·8 deg to the right, and for the anode-left stimulus the start position was perceived 12·2 ± 23·3 deg to the left (*t* test, $P < 0.005$, Bonferroni corrected). There was also a greater variance in the perceived direction of the start position when the vestibular stimulus was applied (anode-right, $F_{41,41} = 1.58$, anode-left $F_{41,41} = 1.65$; $P < 0.05$). The subjects' estimates of the distance to the start position were significantly less than the actual distance in these trials (14·1 ± 29·3 %, $P < 0.05$). However, there was no difference between the estimates with the vestibular stimulus and those without the vestibular stimulus.

DISCUSSION

The present study describes the effects of galvanic vestibular stimulation during human walking. Normal subjects had no difficulty walking straight ahead without visual cues, but bipolar galvanic vestibular stimulation applied during the walk caused subjects initially to deviate systematically towards the side of the anodal current. When subjects were pushed in a wheelchair the vestibular stimulus could not affect the trajectory. In this situation, galvanic stimulation caused a shift in the subjects' perceived trajectories in the direction opposite to that in which they turned while walking.

The way in which vestibular input is used during walking is unclear. Patients with bilateral vestibular lesions can walk in a straight line to a target without vision. However, they tend to be unstable laterally, to walk more slowly and to have increased head movement compared with normal subjects (Glasauer *et al.* 1994). Patients with an acute unilateral vestibular loss lean to the side of the lesion during standing, and veer to the side of the lesion, often violently, during walking (Halmagyi & Baloh, 1996; Böhmer, 1996). Transmastoidal galvanic stimulation is thought to act on the afferent fibres in the vestibular nerve, and in monkeys, to decrease firing rates in vestibular afferents on the side with anodal current (Goldberg *et al.* 1982; Courjon *et al.* 1987). Our finding that vestibular stimulation causes human subjects to turn towards the anode during walking is consistent with decreased input from the vestibular afferents affected by the anodal current.

Subjects turned from their path with relatively low levels of stimulation without vision but were not affected when they had their eyes open. Caloric vestibular stimulation has been used to disturb gait in subjects walking in place or on a treadmill with their eyes open (Kubo *et al.* 1997). With a deficit sufficient to cause dizziness and nystagmus, subjects
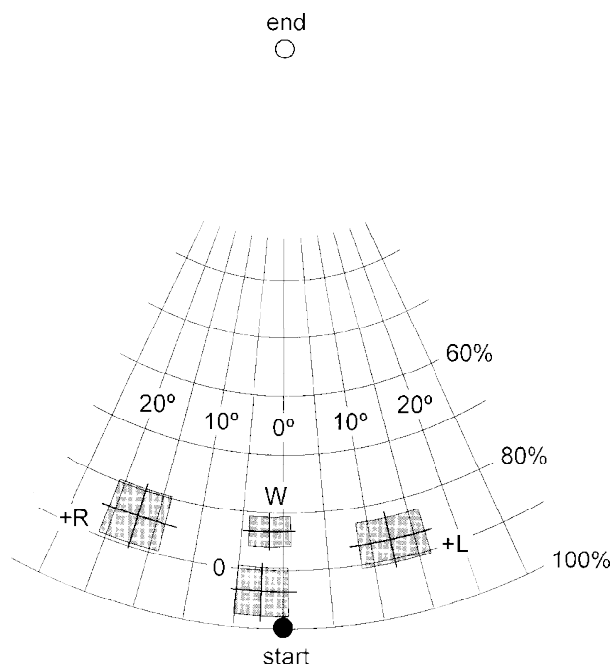

Figure 5. Mean perception of trajectory

Trajectories are normalized to a common start (●) and end (○) position. The mean perceived start positions (± 2 s.e.m. of direction and distance) are indicated by the shaded regions for walking (W) and wheelchair (O) without a vestibular stimulus, and for the wheelchair for the stimulus with the anode right (+R) and the anode left (+L). In all situations, subjects underestimated the distance travelled. The vestibular stimuli caused significant deviations in the perception of trajectory. Note that the smaller s.e.m. for walking arises because of a greater number of trials (56 *vs.* 42) rather than a smaller variance.

showed increased lateral movements at the hip but not at the foot, neck or head. Thus, when visual input is available it overrides even strong vestibular disturbances so that direction and balance during walking are maintained.

The direction and timing of the subjects' deviations from a straight path are consistent with the sway previously reported in subjects who were standing still. Vestibular stimuli of 0·5 and 1·0 mA can cause standing subjects to sway towards the anode. The large component of this sway reaction has a long latency (> 200 ms) and a long duration of many seconds (Britton *et al.* 1993). Similarly in the present experiment, there was no turn until the second step, and the period of initial turn (up to 3 steps) lasted for 2·3–3·5 s. This response was large. In individual steps subjects turned through angles of more than 30 deg (Fig. 3). However, the larger 1 mA stimulus did not produce a bigger response than the 0·5 mA stimulus, suggesting a saturated response at these relatively low currents. After the first three to four steps subjects differed in behaviour. It is likely that by this time some subjects were aware of their altered course. Subjects who were determined to arrive at the target and were aware they were off target tried to turn back towards it whereas those who were attempting to walk a straight path or were unaware they were off target continued to walk straight after the initial turn.

Subjects were very accurate in walking to the previously seen target but were quite inaccurate in indicating the starting position of a walk completed without vision although input from the same afferents was available in both tasks (Fig. 4*A*). This apparent inconsistency suggests a different use of sensory information during the two tasks. When subjects walk to a previously seen target, it is likely that they have a pre-planned strategy or motor program. During the walk, sensory input could be compared with the expected input and adjustments made to ensure that they arrive at the target. Subjects turned more while walking slowly than while walking quickly, suggesting that the vestibular signal was more important during the slower steps. Thus, during fast walking or running the accuracy of the trajectory may depend more on the correctness of the motor program and less on sensory input. In the same way, proprioceptive feedback during ballistic limb movements has a lesser role in determining accuracy.

If subjects walk from one point to another without a pre-formed plan, they must rely on sensory input alone to calculate the path travelled. In the absence of vision, both proprioceptive input from the legs (Gordon *et al.* 1995; Weber *et al.* 1998) and vestibular input from the semicircular canals and otoliths (Ivanenko *et al.* 1997) can contribute to the perception of travelled trajectories. In our studies, blindfolded subjects were just as good at indicating their starting position when they travelled in the wheelchair as when they walked, guided by the experimenter. The availability of proprioceptive input from the legs related to gait did not improve performance over that with vestibular input alone. However it should be noted that in the wheelchair somatosensory input about movement may arise from changes in skin pressure and joint forces produced by acceleration. A previous report which found that subjects were more accurate when walking than when pushed in a wheelchair differed from our study in that subjects made two large turns rather than moving through a continuous path, and remained blindfolded while they indicated the starting position (Montgomery, 1986). Our subjects were allowed vision when indicating the start, although there were no visual cues to its location. This may indicate that proprioceptive input from the legs and feet gives information additional to that available from the vestibular system during the pointing task but is redundant in the calculation of trajectories of travel.

The vestibular stimulus altered the subjects' perceptions of the trajectory travelled when they were pushed in a wheelchair without vision. With the anodal current at the right, subjects' indications of the starting point of the trajectory were consistent with perceiving a turn to the left. During an attempt to walk in a straight line, the perceptual consequences of the vestibular stimulation should lead to a compensatory movement in the direction opposite to the perceived turn. This was the direction of the observed effect. The vestibular stimulus with the anode on the right caused subjects to turn to the right as they attempted to walk straight ahead. Thus, in part, the deviation in the trajectory of gait produced by vestibular stimulation may be associated with an altered perception of trajectory.

In addition to the altered perception of trajectory, a sway reaction analogous to that evoked during standing could alter the direction of gait. During walking, balance is maintained by keeping the centre of mass of the body medial to the stance foot (MacKinnon & Winter, 1993) so that the body falls towards the lifted foot until it is stopped by placement of that foot. Unlike standing, maintaining the correct position of the centre of mass can be accomplished by altering the position of the feet rather than just the position of the body. Bipolar galvanic vestibular stimulation causes a perception that the body leans away from the anodal side (Fitzpatrick *et al.* 1994) or a perception that the direction of gravity leans towards the anodal side (Inglis *et al.* 1995). These perceptions should cause subjects to allow the body to fall more to the anode side and less to the cathode side during the gait cycle and thereby move sideways by more lateral foot placements with successive steps. This would explain a lateral or 'crablike' movement when walking and may be a mechanism that contributes to the turning observed in these experiments.

When standing, galvanic vestibular stimulation evokes larger sway reactions if the feet are positioned close together and smaller reactions when they are further apart. Thus, Day *et al.* (1997) suggested that the CNS interprets the vestibular signal in terms of the current base of support and organizes the response to stabilize the body by keeping the centre of mass within safe limits. The leaning and bending reactions of the body evoked by vestibular stimulation

indicate that, in conjunction with proprioceptive input from the body, the disturbed vestibular signal may be interpreted as a tilt of the support surface. In our study this would mean subjects perceived the foot on the anodal side to be 'uphill'. To stop walking 'downhill' they would need to push harder with the foot on the cathode side and less with the foot on the anode side. In doing so, they would turn in the direction of the anode if the floor was truly level.

During walking, the base of support alters throughout the step cycle. Only in the double-stance phase, when both feet are on the ground, must the centre of mass be within the static base of support for stability. Therefore it seems likely that interactions between the base of support and the vestibular signal might vary throughout the gait cycle. For example, the interpretation of the disturbed vestibular signal may be relatively unconstrained by the interaction with proprioceptive information while subjects are on one foot, but then interact with proprioceptive signalling of the base of support when the second foot touches the ground. Subjects' observations that the feet landed in the wrong positions as they walked would be consistent with such an intermittent or varying influence of proprioceptive input.

During standing galvanic vestibular stimulation can evoke relatively short-latency transient responses (70–120 ms) in the leg muscles as well as changes lasting for many seconds that are associated with the large sway response and illusions of body tilt (Britton *et al.* 1993; Fitzpatrick *et al.* 1994). The short-latency response might arise through a more direct influence on the leg muscles. The stimulus necessary to evoke the short-latency response (>1 mA) is greater than that required to evoke a sway response during standing, and greater than that required to produce the turning response seen here during walking. Thus, the short-latency response may not be very important during walking. Furthermore, the short latency (<130 ms) suggests that the effect could have been expected during the first step, but this was not observed.

During standing, the effects of galvanic stimulation on sway are relatively small and variable, even when the head is turned to the side so that sway is in the sagittal plane. Subjects typically sway about 1 deg at the ankles (e.g. Coates, 1973; Nashner & Wolfson, 1974; Smetanin *et al.* 1988; Britton *et al.* 1993; Fitzpatrick *et al.* 1994; Inglis *et al.* 1995). In contrast, the turn evoked by galvanic vestibular stimulation during walking is large and consistent enough to be observed by casual visual inspection in every trial. This large response to disturbed vestibular input may reflect a greater reliance on vestibular input during walking than during standing. A similar effect may be seen in standing subjects performing voluntary movements, where there is an independent movement-related vestibular response that is not evident in quietly standing subjects (Severac Cauquil & Day, 1998). The galvanic body sway reaction can be used as a test of peripheral vestibular function (Cass *et al.* 1996).

Thus, the turning reaction described here for walking may provide a more sensitive and more easily applied measure of vestibular postural function.

In conclusion, vestibular signals can provide information about the trajectory travelled at walking speed and this is not improved by the availability of proprioceptive input from the legs in the present experimental protocol. In the absence of vision, disturbances of vestibular input disturb perception of the direction of travel and subjects are unable to walk in a straight line. In part, the deviation from a straight path may compensate for the altered perception of trajectory but altered perception of the vertical, base of support or direct vestibulo-fugal influences on the leg muscles could also contribute.

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