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Human body-segment tilts induced by galvanic stimulation: a vestibularly driven balance protection mechanism

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1. We have studied the effects of changes in posture on the motor response to galvanic vestibular stimulation (GVS). The purpose of the experiments was to investigate whether the function of the GVS-evoked response is to stabilize the body or the head in space. Subjects faced forwards with eyes closed standing with various stance widths and sitting. In all cases the GVS-evoked response consisted of a sway of the body towards the anodal ear.

2. In the first set of experiments the response was measured from changes in (i) electromyographic activity of hip and ankle muscles, (ii) the lateral ground reaction force, and (iii) lateral motion of the body at the level of the neck (C7). For all measurements the response became smaller as the feet were placed further apart.

3. In the second set of experiments we measured the GVS-evoked tilts of the head, torso and pelvis. The basic response consisted of a tilt in space (anodal ear down) of all three segments. The head tilted more than the trunk and the trunk tilted more than the pelvis producing a leaning and bending of the body towards the anodal ear. This change in posture was sustained for the duration of the stimulus.

4. The tilt of all three segments was reduced by increasing the stance width. This was due to a reduction in evoked tilt of the pelvis, the bending of the upper body remaining relatively unchanged. Changing from a standing to a sitting posture produced additional reductions in tilt by reducing the degree of upper body bending.

5. The results indicate that the response is organized to stabilize the body rather than the head in space. We suggest that GVS produces a vestibular input akin to that experienced on an inclined support surface and that the function of the response is to counter any threat to balance by keeping the centre of mass of the body within safe limits.

Passing a small current across the mastoid processes stimulates the vestibular system and in standing subjects evokes a sway of the body. This 'galvanic vestibular stimulation' (GVS) acts by modulating the spontaneous firing of vestibular afferents, increasing their firing frequency on the side of the cathode and decreasing it on the side of the anode (Lowenstein, 1955; Goldberg, Smith & Fernandez, 1984; Courjon, Precht & Sirkin, 1987). The stimulus probably produces an unnatural pattern of activity in the vestibular nerves (Minor & Goldberg, 1991). Nevertheless, the CNS appears to extract some meaning from the input since the motor response is well organized and highly adaptable. For example, the pattern and size of response is known to be shaped by the nature of the underlying motor task (Britton, Day, Brown, Rothwell, Thompson & Marsden, 1993; Fitzpatrick, Burke & Gandevia, 1994), the parts of the body involved in the task (Britton *et al.* 1993), the availability of other sensory inputs (Britton *et al.* 1993) and the direction in which the head is facing with respect to the feet (Nashner & Wolfson, 1974; Lund & Broberg, 1983; Pastor, Day & Marsden, 1993). In the present study we address two interrelated questions. What meaning does the CNS attach to the GVS-evoked input? Also, what is the function of the motor response?

Lund & Broberg (1983) proposed that GVS-evoked input acts as an error signal. This idea stems from the critical observation that the direction of the induced body-sway response is governed by the angular position of the head in the horizontal plane (yaw) relative to the feet (Nashner & Wolfson, 1974; Lund & Broberg, 1983; Pastor *et al.* 1993). The selection of muscles is such that the direction of the adjustment is always towards the anodal ear, irrespective of the degree of rotation of the head on the torso or of the torso on the legs (Lund & Broberg, 1983). For example, if the anode is placed behind the right ear and the subject faces forwards, the body sways to the right. If the subject faces to the left, the body sways forwards. This behaviour can be explained by the fact that the vestibular apparatus is fixed in the head and consequently signals motion in a head-referenced co-ordinate system. The variable pattern of muscle response is therefore consistent with the operation of an error-correcting mechanism in which the error is signalled by the vestibular system and the correction is performed by a whole-body adjustment. However, it is not clear exactly what is being controlled under these circumstances. One possibility is that the adjustment is organized to keep the body stabilized in an attempt to either maintain a posture or preserve balance. Alternatively, its function might be to stabilize the head in space. The importance of the vestibular system for head stabilization has been emphasized in a number of studies (Taguchi, Hirabayashi & Kikukawa, 1984; Guitton, Kearney, Wereley & Peterson, 1986; Gresty, 1987; Bronstein, 1988; Kanaya, Gresty, Bronstein, Buckwell & Day, 1995). It is also consistent with the observation that when a subject stands with feet together and eyes closed, the GVS-evoked response produces an almost constant trajectory of the head (in head-referenced co-ordinates) for a range of initial head yaw angles (Pastor *et al.* 1993).

We explore these possibilities by measuring how the laterally directed response in standing subjects is modified simply by altering the distance between the feet. We have focused on stance width because it is known to exert a powerful influence on the frontal plane control of balance. First, it increases the size of the base of support so that changes in the position of the body's centre of mass present less of a threat to balance. Second, the lower body structure becomes more stable in the frontal plane because hip joint muscles and proprioceptors are better able to co-operate with those of the ankle joints to control the structure (Day, Steiger, Thompson & Marsden, 1993). In addition to its influence on balance, stance width is also an interesting variable from the point of view of head motion. The change in geometry of the lower body structure leads to a change in the relationship between leg lateral motion and the resulting movement of the head in space (Day *et al.* 1993). From these considerations it might be expected that if the response to GVS is organized to stabilize the body or the head in space then alterations in stance width will influence the response in some way. In the first series of experiments we measure electromyographic activity, ground reaction forces and lateral body motion in subjects standing freely with various stance widths. In the second series of experiments we go on to study rotational components of the response by measuring the evoked tilt of each of three major segments of the body (the head, torso and pelvis) when standing with different stance widths and when sitting. Parts of these data have previously been reported in brief form (Day, Pastor & Marsden, 1992; Séverac Cauquil, Lyon & Day, 1995; Day, Pastor, Bartolomei & Bonato, 1995).

METHODS

A constant-current stimulator, designed and built in the Department, was used to produce the galvanic vestibular stimulation. The experiments were approved by the local ethics committee and the informed consent of each subject was sought. The stimulus was applied to the subject via two 3 cm diameter electrodes made of soft dental metal which were fixed to the mastoid processes using collodion glue and filled with electrode gel to ensure good electrical contact.

Effect of stance width on body translation

In this experiment seven healthy subjects were tested. Subjects stood on a force-plate (type 9281B; Kistler Instrumente AG, Winterthur, Switzerland), which registered ground reaction forces in three dimensions, and were submitted to galvanic stimuli of 0·5 mA intensity and 2 s duration. This intensity was chosen as it gave rise to a measurable and reproducible body-sway response but produced little or no cutaneous sensation. An infrared-emitting diode (IRED) was fixed to the skin overlying C7 using double-sided adhesive tape. The three-dimensional position in space of the IRED was measured using a motion detection system (Selspot II; Selcom AB, Partille, Sweden). The position data were digitally differentiated to give velocity of body motion in three dimensions. The speed (magnitude of the vector sum of the three components of velocity) of the body was also calculated. Position and force data were collected with a sampling frequency of 200 Hz. The signal-to-noise ratio was improved by averaging every four consecutive data points giving an effective sampling frequency of 50 Hz.

Lines were drawn on the force-plate to assist the subjects in standing with the specific stance widths (defined as the distance between the medial borders of the feet) of 0, 4, 8 and 16 cm. At the beginning of each trial subjects adopted the stance width specified by the experimenter. With their hands clasped in front of them, but otherwise relaxed, subjects were instructed to face straight ahead, close their eyes and keep as still as possible. A variable time later (2–6 s) the stimulus was applied. At the end of a trial subjects were asked to open their eyes and adjust their stance width ready for the next trial. The intertrial interval varied from 15 to 25 s. The eight conditions, four stance widths at two different polarities of stimulation (anode right or left), were varied in a pseudorandom fashion. Each subject underwent eighty trials consisting of ten trials per condition. Averaged responses were computed from the ten trials of each of the eight conditions.

Effect of stance width on leg EMG responses

In the second experiment EMG responses to the galvanic stimulus were measured from a number of muscles of the right and left legs in six healthy subjects. Pilot experiments indicated that EMG responses were conspicuous in hip abductor and ankle plantar flexor muscles and so recordings were made bilaterally using 9 mm diameter surface electrodes placed 4–5 cm apart on the skin overlying gluteus medius (Glut), tensor fasciae latae (TFL), soleus (Sol) and medial gastrocnemius (Gast). EMG signals were amplified (Digitimer D150), bandpass filtered (80–300 Hz) and rectified. EMG data were collected with a sampling frequency of 1000 Hz and means calculated on-line. The experimental procedure was similar to that of the first experiment. However, because the EMG response of an individual muscle was small compared with background noise levels, a larger number of trials ($n = 30$) was averaged for each condition to improve the signal-to-noise ratio. A second departure was that subjects adopted only three stance widths (0, 4 and 16 cm) and for each stance width stayed in position until the total number of trials had been completed. However, for each stance width the polarity of stimulation was varied in a pseudorandom fashion across trials and the order of presentation of stance widths was varied across subjects.

Effect of stance width on tilt of body segments

Ten healthy subjects were included in this study. Subjects stood or sat on a high stool on the force-plate. The position (with time) of the point of application of the resultant ground reaction force, or centre of pressure, was calculated. The angles in space (tilts) in the frontal (roll) plane of three major body segments (head, torso and pelvis) were calculated from measurements obtained with the Selspot system of the position of a pair of IREDs attached to each segment. Two IREDs were mounted on a rigid helmet worn by the subject to measure head tilt; two were stuck onto the skin at the level of the scapula to measure torso tilt; and two were mounted on a frame clamped to the iliac crests to measure the tilt of the pelvis (Fig. 1). The IREDs of each pair were mounted 25–35 cm apart. Initial work showed that small tilts of a rigid structure in one plane could reliably be measured using two IREDs placed this distance apart provided the motion was largely restricted to this plane. The tilt of each segment prior to stimulation was seldom zero because of small inaccuracies in the placement of the IREDs. Therefore, initial offsets were removed by subtracting the mean value of tilt over the first 1 s of each trial (prestimulus period) from each of the data points in that trial. In addition to angles in space, the relative tilts of the head on the torso and the torso on the pelvis were calculated by subtracting the tilt of the lower segment from that of the upper. This provided a measure of the change in angle (in the frontal plane) at the joint system between each of these pairs of segments.

Subjects were instructed to stand or sit still with their arms folded on their chest, their head facing forward and their eyes closed. Data collection lasted for 8 s and began after a variable delay following eye closure. The galvanic stimulus began 1 s into data collection and lasted for 4 s. The polarity of the stimulus (anode right or left) was randomized across trials. Data were collected at 400 Hz and every four consecutive data points were averaged to improve signal-to-noise ratio, giving an effective sampling frequency of 100 Hz.

Responses to GVS were measured under different conditions in order to study the effects of stance width and stimulus intensity when standing, and to compare sitting with standing. The following experiments were conducted.

Effect of stimulus intensity. Ten subjects standing with feet 16 cm apart were stimulated at five different intensities (currents): 0·1, 0·3, 0·5, 0·7 and 0·9 mA. Trials at each intensity were recorded in separate blocks. The order of the blocks was randomized across subjects.

Effect of stance width and sitting. Ten subjects standing with three different stance widths, feet together, feet 4 cm apart, feet 16 cm apart, and in a sitting position were stimulated at 0·7 mA. The stance width condition in the standing trials was randomized across trials but the sitting position trials were recorded as a separate block.

Effect of stance width at lower stimulus intensity. Six subjects standing with feet together and feet 16 cm apart were stimulated at 0·5 mA. The stance width condition was randomized across trials.

For each subject ten trials per condition were recorded and later averaged by computer. The maximum amplitude of mean tilt of each of the segments in each condition was then measured.

Statistical analysis

An analysis of variance with repeated measures was performed to test the effect of the different factors investigated. When appropriate, statistical differences between different levels within a factor (contrasts) were also evaluated. For each analysis, every subject contributed one value (mean response) to each level within a factor. Group means were calculated by summing the individual mean values and dividing by the number of subjects. The S.E.M. refers to the variability of the individual mean values.

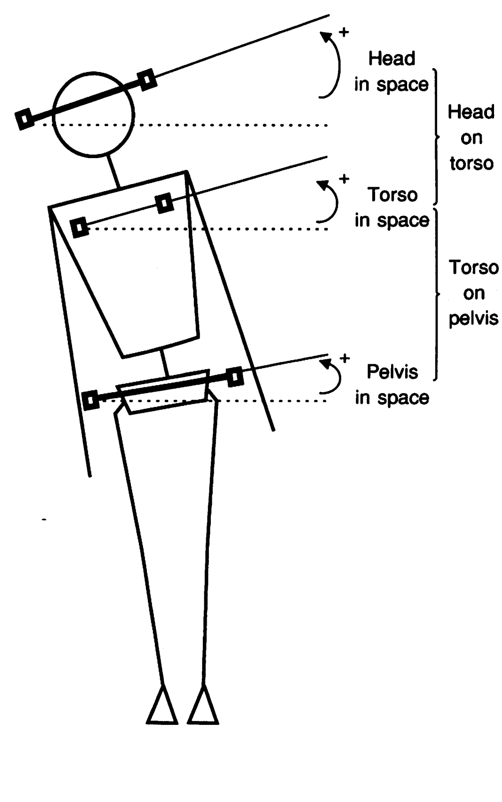

Figure 1. Measurement of tilt of head, torso and pelvis

Angles calculated from the position of two IREDs attached to each segment. Relative tilts (head on torso and torso on pelvis) are calculated by subtracting the tilt of the lower from that of the upper segment in each case.

RESULTS

Effect of stance width on ground reaction forces and translation of the body at C7

Figure 2*A* illustrates, for each of the four stance widths, the group mean position change in the horizontal plane of the marker placed over C7. The galvanic stimulus induced a movement of the body in a direction approximately to the right or left (towards the anode). The effect of increasing the stance width was to reduce dramatically the extent of this lateral movement. The magnitude of this effect was quantified by measuring the total distance travelled by the marker over the period of 0·25 to 1·25 s following the onset of stimulation. This measurement was made from the averaged traces of each subject for each condition. There were no significant effects of polarity on this measure although the effect of stance width was highly significant ($P < 0{\cdot}001$; Fig. 2*B*).

Figure 3*A* shows the time course of the group mean lateral ground reaction forces which acted to accelerate the mass of the body sideways. The ensuing body motion is indicated by the lateral component of velocity at the level of C7. Both records suggest that the complete time course of the response was attenuated by an increase in stance width. The effect was measured from the mean lateral velocity attained during the interval 0·75–1·0 s after onset of stimulation from averaged traces. Polarity had a powerful influence on the sign but no effect on the magnitude of this value. There was a highly significant effect of stance width ($P < 0{\cdot}001$; Fig. 3*B*).

The records at the bottom of Fig. 3*A* illustrate the group mean speed of body motion prior to and during the stimulation period. The speed of the body increased in response to the galvanic stimulus but the effect diminished as stance width increased. Mean response speed was measured over the interval 0·75–1·0 s following stimulus onset. There was a strong effect of stance width ($P < 0{\cdot}001$; Fig. 3*C*) on response speed but there were no significant effects involving polarity. As shown previously (Day *et al.* 1993), the mean baseline speed of spontaneous body sway in the prestimulus period, measured over the 0·25 s interval prior to stimulation, was also reduced by increasing stance width ($P < 0{\cdot}001$; Fig. 3*C*).

Effect of stance width on EMG responses in leg muscles

The averaged rectified EMG responses from hip abductor and ankle plantarflexor muscles are shown in Fig. 4. The EMG responses from individual muscles were generally of low amplitude and are best visualized by superimposing records obtained for the two polarities of stimulation. The initial lateral acceleration of the body was produced by a change in muscle activity that started approximately 120 ms after the onset of stimulation and lasted for around 300 ms. Responses during this 300 ms period were present in all eight muscles studied. The response in homonymous muscles of the right and left legs were of opposite sign and for any one muscle the sign reversed with polarity of stimulation. For example, with the anode on the right, which induced a rightward motion of the body, the left hip abductors and left ankle plantar flexors displayed an

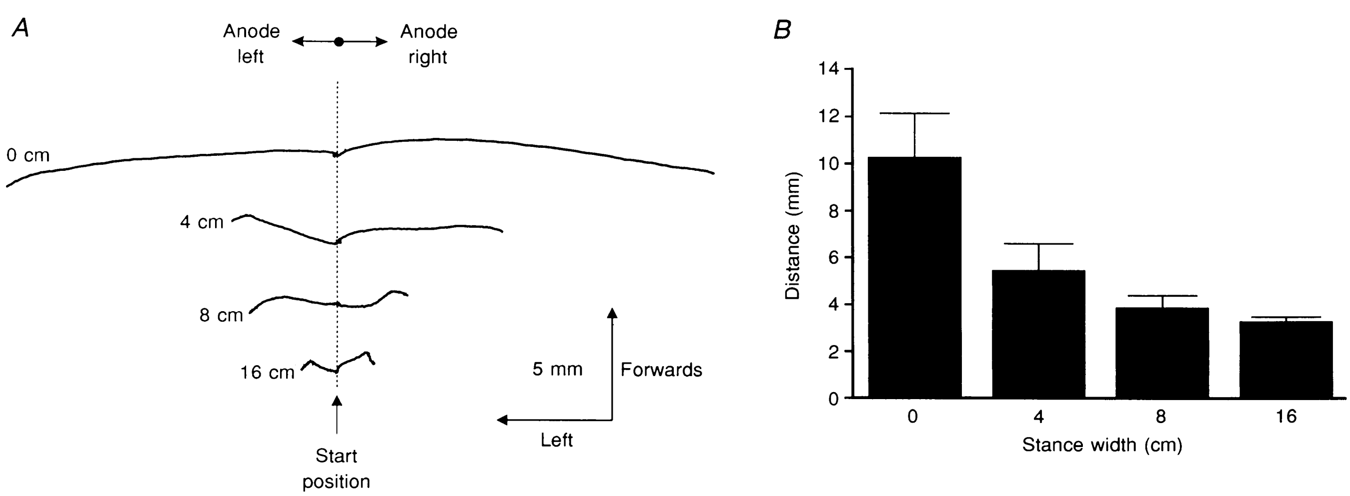

Figure 2. Group mean paths described by the IRED at C7 in the horizontal plane

Paths (viewed from above) during the interval 0·1–2·0 s after stimulus onset are shown in *A*. For each stance width (indicated to the left of the traces) the starting positions of the IRED for the two polarities of stimulation (anode right or left) have been aligned on the vertical dashed line. For clarity, each pair of traces have been separated in the anteroposterior direction. *B*, the group mean (+ S.E.M.) distance travelled by the IRED during the interval 0·25–1·25 s after stimulus onset. Values obtained with the two polarities have been combined in the final mean.

increase in muscle activity, whereas those muscles from the right leg showed a decrease in activity. After this initial 300 ms response, the muscle activities reversed in sign which generated ground reaction forces to decelerate the body and hold it at its new position. The size of the EMG response was substantially reduced by increasing the stance width. Even with a small increase of stance width to 4 cm the response in most muscles had virtually disappeared. At 16 cm no responses could be seen in these muscles.

Tilt of body segments

In general, GVS induced lateral tilts of the head, the torso and the pelvis in standing subjects. The polarity of the stimulus determined the direction of tilt (anodal ear down) but had no effect on response amplitude. For a given polarity the direction of tilt was the same for all segments. The body started to tilt shortly after stimulus onset. It remained tilted while the stimulus was held on and returned approximately to its starting position when the stimulus

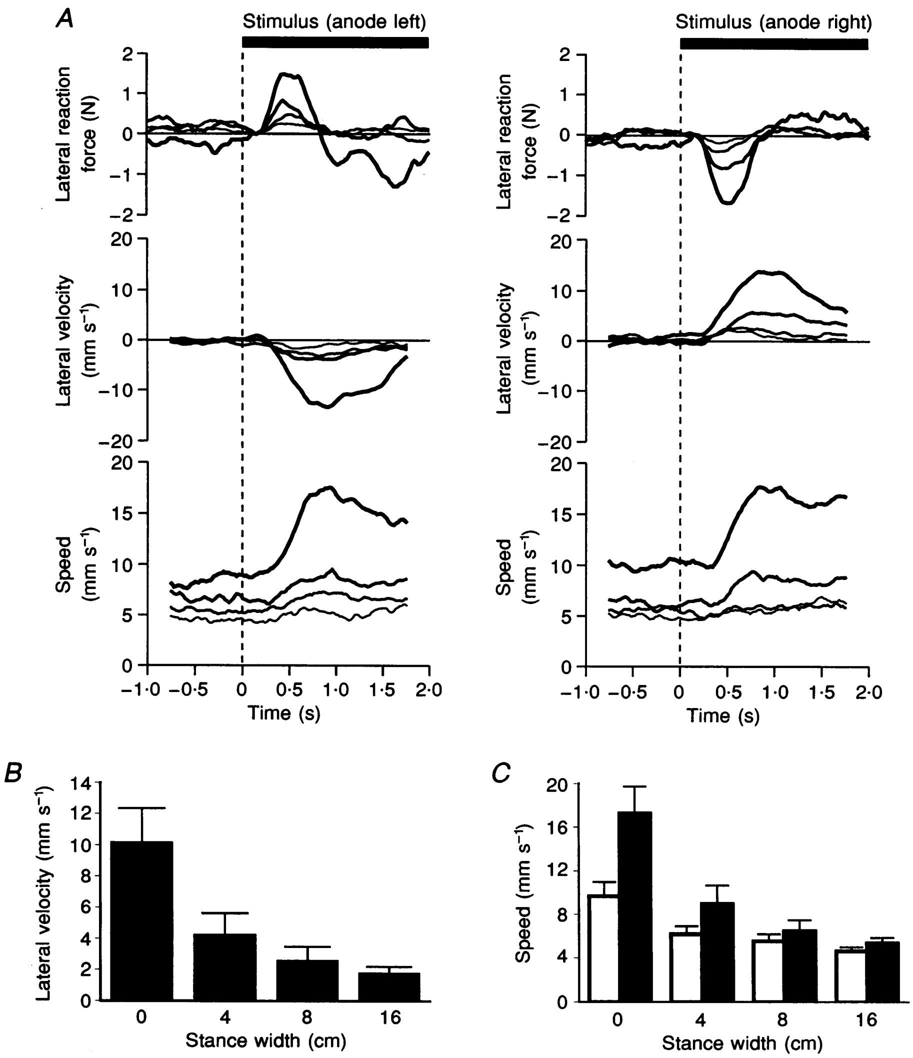

Figure 3. Effect of stance width on time course of responses

A, group mean traces of (from top): lateral ground reaction force, lateral component of velocity at C7, and speed at C7, with anode on the left (left panel) and anode on the right (right panel). The time of stimulus onset is indicated by the vertical dashed line. Stimulus duration is shown by the horizontal bar at the top. Responses obtained with the four stance widths have been superimposed and each given a different line thickness (the thicker the line the narrower the stance width). Positive values indicate a rightward direction for the lateral components of reaction force and velocity. Lateral reaction forces have been aligned to zero at 0·1 s after stimulus onset. *B*, the group mean (+S.E.M.) of the mean lateral velocity during the interval 0·75–1·0 s after stimulus onset is shown for each stance width. *C*, for each stance width the group mean (+S.E.M.) of the mean baseline speed obtained during the 0·25 s interval prior to stimulus onset (□) and the group mean (+S.E.M.) of the mean response speed obtained during the interval 0·75–1·0 s after stimulus onset (■) are shown. In *B* and *C* values obtained with the two polarities have been combined in the final mean.

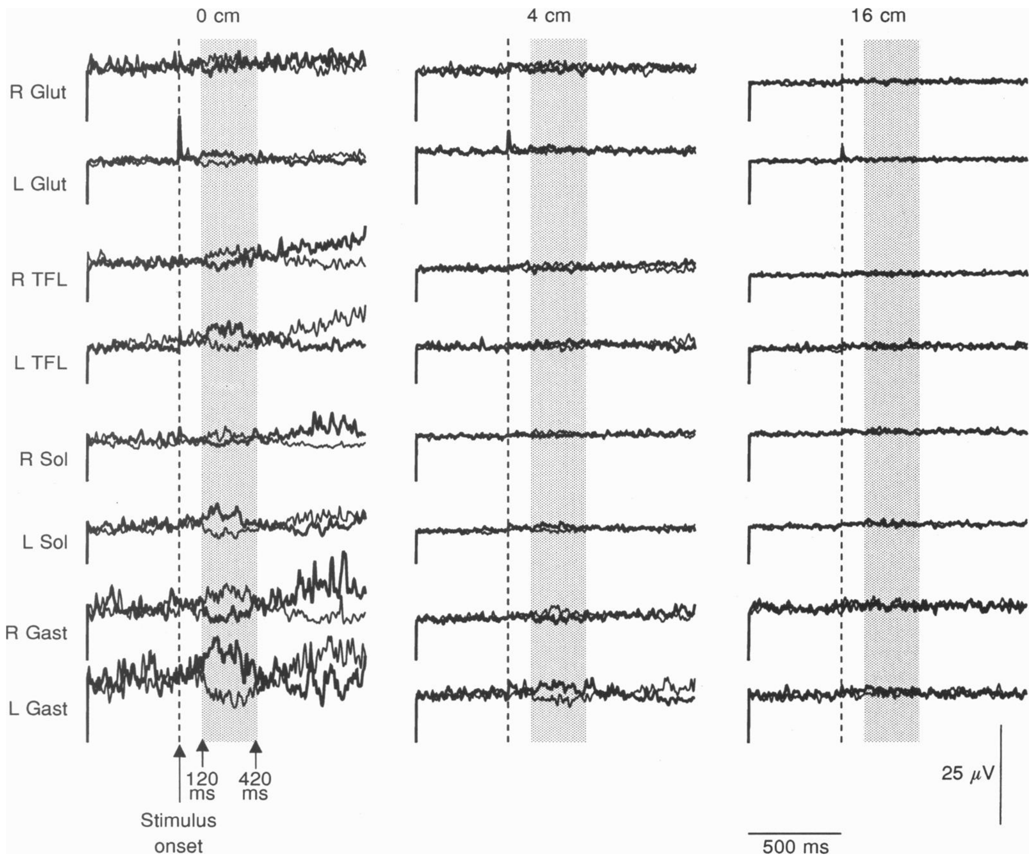

Figure 4. Effect of stance width on leg EMG responses

Group mean rectified EMG from four muscles of the right and left leg obtained with three stance widths (0, 4 and 16 cm). Responses to the two polarities of stimulation have been superimposed (thick line, anode right; thin line, anode left). The time of stimulus onset is denoted by the vertical dashed lines. A stimulus artefact is apparent at this time in some traces. The vertical grey bars indicate the period over which the initial EMG response occurred when the feet were together (0 cm).

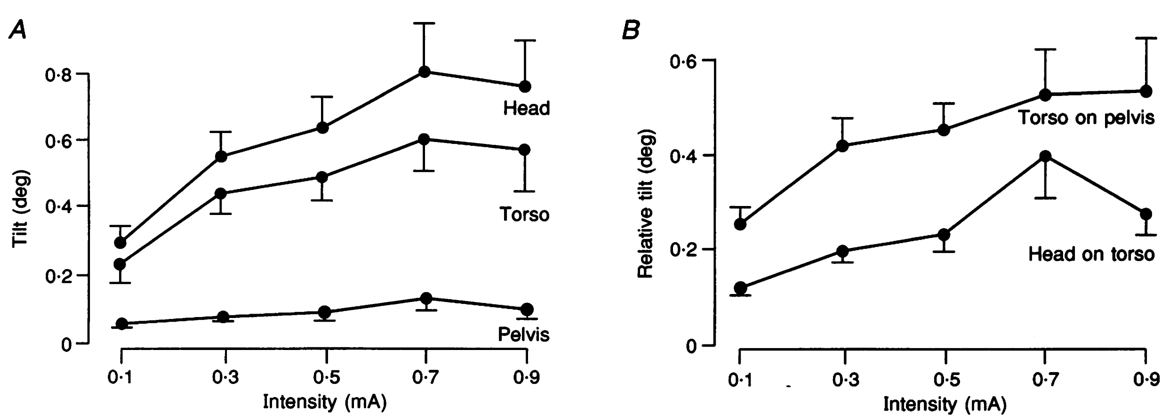

Figure 5. Effect of stimulus intensity on body-segment tilts

A, maximum (mean ± S.E.M.) tilt in space for each of the three body segments plotted against stimulus intensity. *B*, maximum (mean ± S.E.M.) relative tilt between adjacent segments. Data were obtained with subjects standing, feet 16 cm apart and eyes closed.

was turned off. The body did not appear to tilt as a rigid structure since the magnitude of tilt was not the same for all segments.

Effect of stimulus intensity on tilt amplitude

The relationship between stimulus current and body segment tilt was investigated in subjects standing with their feet 16 cm apart. Figure 5 shows the effect of stimulus intensity on the maximum values of tilt obtained for each body segment in space (Fig. 5*A*) and on the maximum relative tilt between adjacent body segments (Fig. 5*B*). Greater tilts in space were recorded from higher body segments and greater relative tilt occurred between the torso and the pelvis than between the head and the torso. The amplitude of tilt in space of each of the three body segments, as well as the relative tilt between segments, was influenced by the intensity of stimulation (head, $P < 0.05$; torso, $P < 0.05$; pelvis, $P < 0.01$; head on torso, $P < 0.01$; torso on pelvis, $P < 0.05$). The amplitude of lateral tilt increased with stimulus intensity over the range 0·1–0·7 mA.

Effect of stance width and sitting on tilt of body segments

For this experiment an intensity of stimulation of 0·7 mA was used based on the above finding that this intensity produces a maximal response. As shown on the left of Fig. 6, the latency and direction of tilt was similar for all postural conditions. When standing, tilts in space were greater the higher the body segment (Fig. 7; $P < 0.001$) indicating that the body did not tilt as a rigid structure about the ankles. When seated, a similar pattern was seen in that higher body segments tilted more than lower segments (Fig. 7; $P < 0.001$). When standing, an increase in stance width reduced the tilt of all body segments in space (Fig. 7; $P < 0.01$). Further decreases in tilt occurred when subjects were seated (Fig. 7; $P < 0.01$).

The tilt in space of a body segment depended upon the tilt of segments below it. To assess how the reduction of tilt in space with stance width was distributed across joints we calculated the relative tilts of adjacent body segments. The group mean relative head-on-torso and torso-on-pelvis tilts

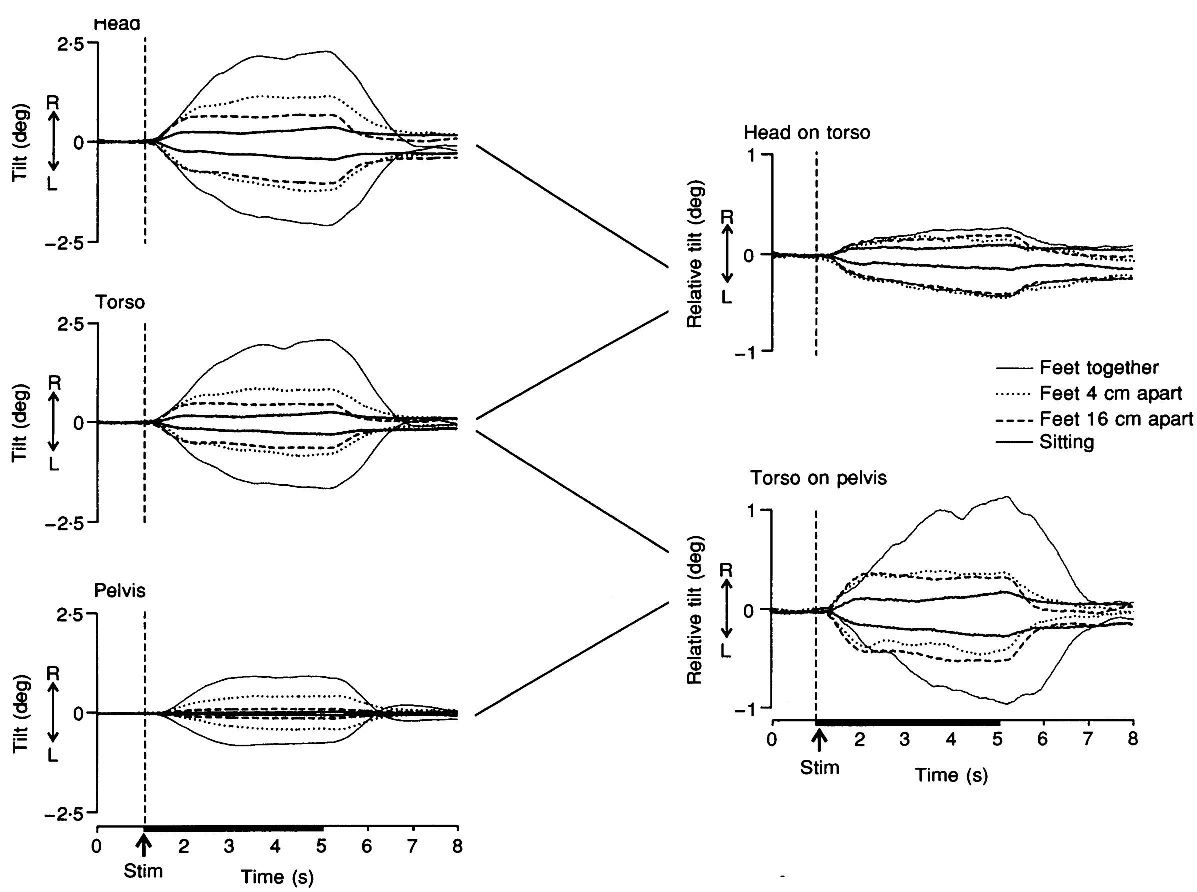

Figure 6. Effect of stance width and sitting on GVS-evoked body-segment tilts

Grand mean tilt in space of body segments (left column) and relative tilt between adjacent segments (right column) evoked by GVS (0·7 mA) in subjects standing with three different stance widths and when sitting (see key). Period of stimulation is shown by thickened portion of time axis. Positive values indicate tilt in the direction of right ear down. Positive-going traces were obtained with the anode on the right, negative-going traces with the anode on the left.

are shown on the right of Fig. 6. For all postural conditions there were small but significant amounts of relative tilt between body segments. The head tilted relative to the torso and the torso tilted relative to the pelvis and these relative tilts were in the same direction such that the body appeared to bend as well as lean towards the anode. The relative tilts were smaller when seated than when standing with feet 16 cm apart (Figs 6 and 7; $P < 0.01$). When standing, changes in stance width had much greater impact on tilt of the lower body structure with respect to the ground than on the relative tilts of higher body segments. The relative head-on-torso tilt was unaffected by changes in stance width (Fig. 7; $P > 0.05$). The relative torso-on-pelvis tilt remained constant for stance widths of 4 and 16 cm (Fig. 7; $P > 0.05$) but was significantly greater when the feet were placed together (Fig. 7; $P < 0.05$). However, this increase may be artefactual because when the feet were together a current strength of 0·7 mA evoked lateral motion of the body which was large enough to threaten balance. This often appeared to induce balance-restoring reactions involving the torso which may well have contributed to the measured value of maximum relative tilt between the torso and pelvis. This explanation was borne out by the results obtained from a separate experiment in which a smaller current strength of 0·5 mA was used. For this condition, changing the stance width from 0 to 16 cm had no significant effect on either the relative head-on-torso tilt or the torso-on-pelvis tilt (Fig. 7; $P > 0.05$), although the tilt in space of all three segments was reduced as before (Fig. 7; $P < 0.05$).

Effect of stance width and sitting on horizontal translation of the head and the centre of mass of the body

Finally, we estimated the effect of stance width and sitting on some translational (as opposed to rotational) parameters of body motion during the experiment in which a stimulus intensity of 0·7 mA was used. Lateral translation of the head was estimated from the mid-position of the two IREDs fixed to the helmet. Lateral translation of the body's centre of mass was estimated from the centre of pressure record. If it is assumed that the body is approximately stationary prior to and at the end of the stimulation period then at these times the position of the centre of mass in the horizontal plane would coincide with the position of the centre of pressure. As shown in Fig. 8 the lateral displacement of both the head and the centre of pressure was dramatically attenuated when standing subjects increased their stance width, and was further reduced when subjects were seated.

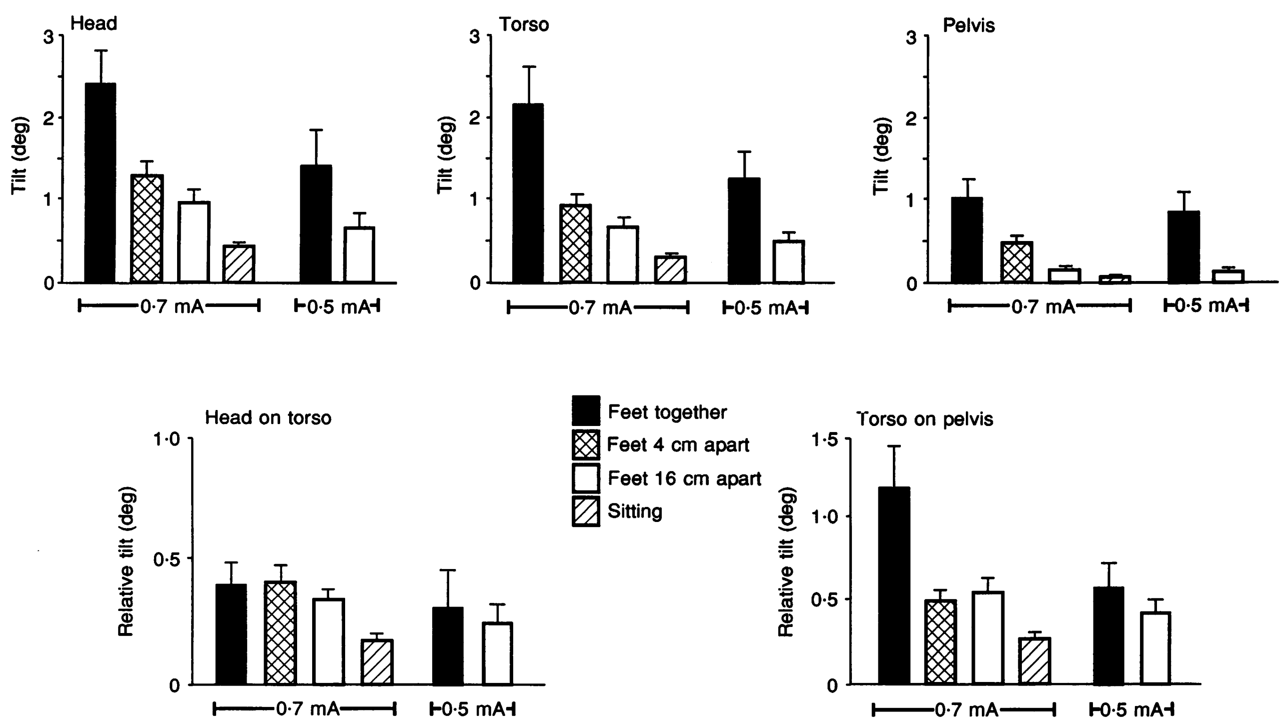

Figure 7. Effect of stance width and sitting on maximum evoked tilts

Upper graphs show mean (+S.E.M.) maximum tilt of the three body segments when standing with three different stance widths and when sitting (see key). Lower graphs show mean (+S.E.M.) maximum relative tilt between adjacent body segments. The data of the four bars on the left of each graph were obtained using a stimulus intensity of 0·7 mA. The two bars on the right (standing with feet together and 16 cm apart) were obtained in a separate experiment using a stimulus intensity of 0·5 mA.

DISCUSSION

As outlined in the Introduction, the motor response to GVS is highly context dependent with characteristics which suggest it is organized to serve some function. The broad question being asked here is what is the CNS attempting to control with this motor response? Two possibilities are considered. Either it is concerned with stabilization of the head or stabilization of the body.

Basic characteristics of the response

Under all stance conditions the response evoked by GVS conformed to the principle of movement towards the anodal ear (Lund & Broberg, 1983). When standing with feet together this movement was produced, in part, by changes in activity of leg muscles at a latency of around 120 ms. The latency of the leg EMG response was similar to that which produces anteroposterior body sway in subjects facing sideways (Nashner & Wolfson, 1974; Britton *et al.* 1993; Fitzpatrick *et al.* 1994). However, the smaller, short-latency component of EMG response that has been observed at around 60 ms in lower leg muscles (Britton *et al.* 1993; Fitzpatrick *et al.* 1994) was not apparent in the present experiments. This may have been due to the lower intensity of stimulation that was used here (0·5 mA *vs.* > 1·0 mA). The response acted first to accelerate the body sideways and then to hold it tilted at a small angle with respect to gravity. A new finding is that the upper body also receives motor drive since the torso adopted a static tilt with respect to the pelvis and the head tilted with respect to the torso. Thus, the response may be described as a leaning and bending of the body towards the anodal ear. A second new observation concerns the response of seated subjects to GVS. Previous reports have shown that leg EMG responses disappear when subjects sit down (Britton *et al.* 1993; Fitzpatrick *et al.*

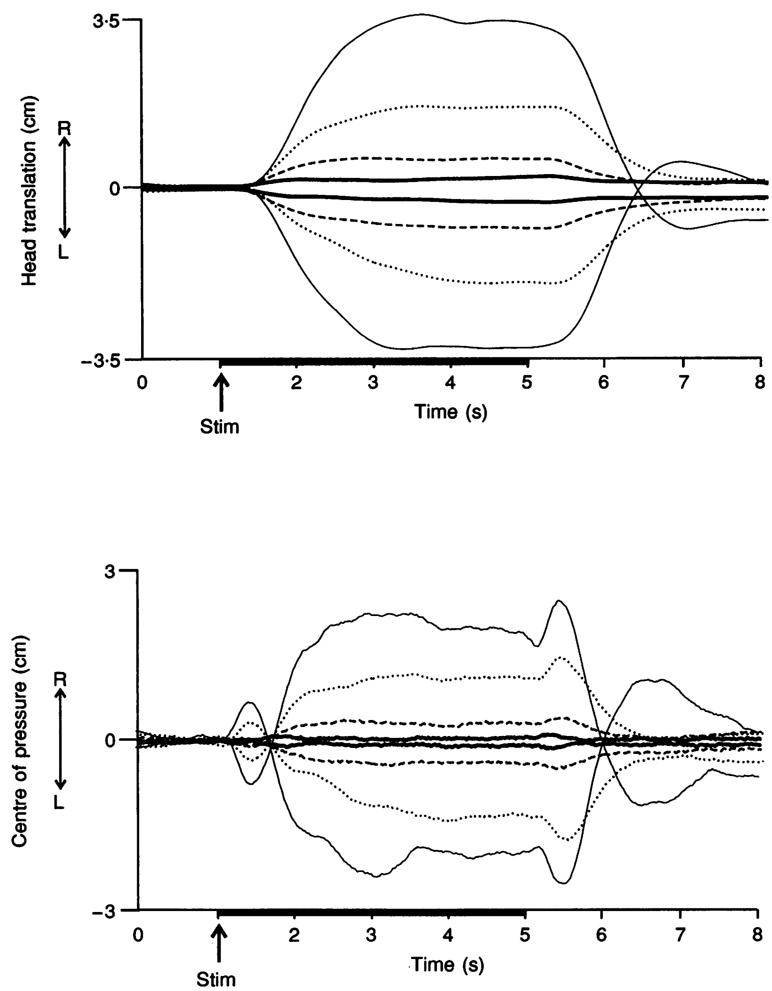

Figure 8. Effect of stance width and sitting on head translation and centre of pressure

Group mean lateral translation of the head (upper panel) and of the centre of pressure (lower panel) evoked by GVS (0·7 mA) in subjects standing with three different stance widths and when sitting (see Fig. 6 for key to traces). Period of stimulation is shown by thickened portion of time axis. Positive-going traces were obtained with the anode on the right, negative-going traces with the anode on the left. Note that the initial portion of the centre of pressure trace moves in the opposite direction to that of the main response.

1994). The present results extend this observation and demonstrate that the vestibular input is not simply disregarded when the subject is seated. Instead, the upper body segments are driven to produce small lateral tilts of the torso and the head.

Changes in the response with changes in support conditions

The response was found to be extremely sensitive to stance width. Responses were largest when subjects stood with their feet together and rapidly became smaller as stance was widened. The leg EMG response became attenuated and tilt of the lower body structure (incorporating the feet, legs and pelvis) was reduced. However, the relative tilts at higher segments of the body were generally unaffected by this manoeuvre (see Results for an explanation of a departure from this rule). Thus, when stance width was increased the response adapted with a specific reduction in the motor outflow to leg muscles. When subjects changed from standing to sitting the motor outflow to upper body segments was also affected resulting in a reduction in the relative torso-on-pelvis and head-on-torso tilts.

Are changes in the response due to changes in motoneurone excitability?

An important question is whether these observed modifications of the response represent a change in the pattern of descending motor drive to the various motoneurone pools. A simpler explanation could be that the vestibularly evoked descending drive remains constant but the final motor output to muscles is modulated at a low level by changes in the background excitability of the individual motoneurone pools. On some occasions the response size did appear to be related to motoneurone excitability if we assume that this is reflected in the mean prestimulus level of rectified EMG (e.g. compare Gast values at stance widths of 0 and 4 cm, Fig. 4). However, there were other examples which showed a reduction in response size without a concomitant reduction in background EMG level (e.g. compare hip abductor muscles at stance widths of 0 and 4 cm, Fig. 4). Further difficulties with this explanation arise when we consider the reduction in response size when subjects were seated. Although we did not measure activity in the muscles responsible for the upper body response it seems reasonable to assume that, to keep the torso and head upright, those muscles would be active to a similar extent irrespective of whether the subject stands with a wide base or sits on a high stool. Change in motoneurone excitability, therefore, may contribute partly to the reduction in response size but does not explain fully the observed behaviour. We suggest that changes in the initial posture of the body modify the vestibularly evoked drive to muscles at a premotoneuronal stage. If this is the case then the observed modifications of the response pattern are achieved actively, presumably to fulfil a function.

Is the response organized to stabilize the head or body in space?

Are these response patterns and adaptations compatible with a control system which functions to stabilize the head? Our measurements showed that the changes in response pattern resulted in a net change in head motion. Either an increase in stance width or changing from a standing to a sitting posture produced a reduction in both lateral translation of the head and tilt of the head in space. Thus, although vestibular input can only signal a change in motion or orientation of the head, it appears that GVS-evoked input is not used to maintain a set head position. This implies that the function of the response is not simply to stabilize the head in space. The displacement of the body's centre of mass also varied across stance conditions and so by the same token could be taken to mean that the response is not organized to stabilize the centre of mass in space.

Is the response organized to keep the body vertical?

How then is the observed response to GVS to be interpreted? Hlavacka, Krizkova & Horak (1995) suggested that the function of the GVS-evoked response is to keep the body vertical so that postural muscle activity is minimized. To achieve this, they suggested that three independent estimates of the orientation of the body are made on the basis of vestibular, proprioceptive and visual information. These are then combined to produce an overall estimate. According to this idea, GVS changes the vestibular component leading to a new estimate of verticality and consequently a realignment of the body. Our results present two problems for this hypothesis. First, if the aim is to minimize postural muscle activity, then one might expect all segments to be aligned to the same perceived vertical such that the body remains straight. However, we find that the body bends as well as leans. Second, a fixed stimulating current might be expected to produce the same realignment of the body under different stance conditions, given that the other components of the estimate (proprioceptive and visual) remain undistorted. However, we find that the evoked tilts of body segments are altered by a change in stance width or by sitting down.

Is the input interpreted as a tilt of the support surface?

Why does the body respond to GVS by leaning and bending? And why does a change in stance width or sitting alter the magnitude of tilt in space of body segments? To address these questions it is helpful to consider natural situations which might produce a vestibular input similar to that produced by GVS. We start by assuming that GVS evokes a signal akin to that produced by a tilt of the head in a gravitational field. Under natural circumstances, such a tilt could occur because the support surface has become inclined. Purdon Martin (1967) investigated the response to changes in support surface inclination by filming blindfolded subjects seated on a table that was tilted unpredictably in the frontal plane. The evoked responses, although considerably larger, are reminiscent of those produced by GVS. The films show that normal subjects respond to a lateral tilt by leaning and bending their upper body against the tilt, back into a more upright (vertical) position. A response of this sort will have the effect of reducing the lateral excursion of the body's centre of mass and will thus help keep the body in balance in the face of the tilting. Labyrinthine-defective subjects did not appear to re-orientate their upper body in this way when the table was tilted. In sharp contrast to the normal subjects they tried to maintain a fixed posture relative to the table until the tilt was so great that they started to topple. Allum & Pfaltz (1985) obtained a related result in patients with bilateral vestibular deficits. These patients tended to fall over backwards when they stood, without vision, on a platform that rotated upwards (toe up). Thus, proprioceptive information on its own does not appear to inform on changes in body tilt produced by rotation of the support surface. By exclusion, the response evoked in blindfolded, healthy subjects on Purdon Martin's tilt apparatus would appear to be elicited by vestibular input in comparative isolation, as is the case during GVS. This, together with the fact that both types of stimulus evoke a similar pattern of adjustment (a leaning and bending of the body), suggests that the CNS may interpret the GVS-evoked vestibular input as a change in tilt of the support surface.

Is the response a balance protection mechanism?

With this interpretation, the GVS-evoked response may be thought of as a protective manoeuvre that is organized to help keep the vertical projection of the centre of mass of the body away from the boundaries of the support base such that the body does not reach a position where it comes close to toppling. We envisage that a protective manoeuvre of this type is not organized to maintain a precise position of the centre of mass. Rather, the adjustment would be sufficient only to keep the centre of mass within safe limits. The height of the centre of mass above the base and its horizontal distance from the edge of the support base determines the critical angle through which the support surface could be rotated before the body starts to topple. This critical angle is changed, therefore, by altering the dimensions of the support base. Standing with the feet further apart increases the critical angle for rotations in the frontal plane. A given support surface rotation would then take the vertical projection of the centre of mass less near to the edge of the support base and so would represent less of a threat to balance requiring less compensation. This may explain why in the present experiments the lateral motion of the centre of mass was found to diminish with greater stance width. However, it does not explain why this is achieved by altering the response of the lower body while leaving that of the upper body relatively unchanged. In this regard, it would be of interest to know whether subjects adopt the same strategy when standing with different stance widths on an inclined surface.

Why should the response change when seated?

The width of the support base is about the same when sitting as when standing with feet wide apart, so why should there be additional reductions in the degree of upper body bending to GVS when the subject is seated? The critical angle, as defined above, depends not only upon the width of support but also upon the height of the body's centre of mass above the support surface. The lower the centre of mass, the greater is the critical angle. Thus, lowering the centre of mass relative to the support surface by sitting means that a given rotation of the surface would not take the centre of mass as close to the boundary of safety as when standing with a wide stance. This may explain the additional reductions in the GVS-evoked body tilt when seated. This idea is similar to the concept of 'stability limits' put forward by Forssberg & Hirschfeld (1994). They used this concept to explain why postural responses evoked by support platform disturbances (in the sagittal plane) in seated subjects have considerably higher thresholds than those reported for similar disturbances in standing subjects. They suggested that internal representations of the body contain information about such 'stability limits'. Presumably, this information could be used to pre-set the sensitivity of a wide range of postural responses.

Conclusions

In conclusion, we suggest that GVS produces a vestibular input akin to that produced by a lateral tilt of the head in a gravitational field. The adjustment may be viewed as one stabilizing either the head in space or the body. We favour the latter and suggest that the postural adjustment might be similar to that evoked by an inclined support surface. The aim of a such an adjustment would be to avoid any threat to balance by keeping the centre of mass of the body within safe limits.

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