Vertical torque responses to vestibular stimulation in standing humans

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Non-technical summary Galvanic vestibular stimulation (GVS) is a method for activating the human vestibular nerve with electricity. It induces sensations of head movement which cause sway and eye movements, and affect navigation. GVS is used here to demonstrate a novel vestibular reflex. Stimulation of standing subjects caused them to generate torque around a vertical axis, resulting in trunk rotation. Response magnitude and direction were systematically altered by head orientation in a manner consistent with GVS causing a sensation of head roll. This is relevant for balance control because vestibular information is only useful for fall prevention when interpreted in the context of head orientation. These findings therefore provide a method for investigating this neural transformation process. This can be used to diagnose deficiencies in the vestibular control of balance caused by ageing and/or neurological disease.

Abstract The effects of electrical vestibular stimulation upon movement and perception suggest two evoked sensations: head roll and inter-aural linear acceleration. The head roll vector causes walking subjects to turn in a direction dependent on head pitch, requiring generation of torque around a vertical axis. Here the effect of vestibular stimulation upon vertical torque (T_z) was investigated during quiet stance. With the head tilted forward, square-wave stimuli applied to the mastoid processes evoked a polarity-specific T_z response accompanied by trunk yaw. Stochastic vestibular stimulation (SVS) was used to investigate the effect of head pitch with greater precision; the SVS–T_z cross-correlation displayed a modulation pattern consistent with the head roll vector and this was also reflected by changes in coherence at 2–3 Hz. However, a separate response at 7–8 Hz was unaffected by head pitch. Head translation (rather than rotation) had no effect upon this high frequency response either, suggesting it is not caused by a sense of body rotation induced by an inter-aural acceleration vector offset from the body. Instead, high coherence between medio-lateral shear force and T_z at the same frequency range suggests it is caused by mechanical coupling to evoked medio-lateral sway. Consistent with this explanation, the 7–8 Hz response was attenuated by 90 deg head roll or yaw, both of which uncouple the inter-aural axis from the medio-lateral sway axis. These results demonstrate two vertical torque responses to electrical vestibular stimulation in standing subjects. The high frequency response can be attributed to mechanical coupling to evoked medio-lateral sway. The low frequency response is consistent with a reaction to a sensation of head roll, and provides a novel method for investigating proprioceptive-vestibular interactions during stance.

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Abbreviations COP, centre of pressure; GVS, galvanic vestibular stimulation; SVS, stochastic vestibular stimulation.

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Introduction

When walking or stepping on the spot, galvanic vestibular stimulation (GVS) causes subjects to turn in a direction which depends upon head orientation and stimulus polarity (Fitzpatrick *et al.* 2006). For example, tilting the head backwards with the anode electrode behind the right ear causes a leftward turn. Reversing the polarity or tilting the head forwards causes a rightward turn. These effects can be explained as counteractive movements in response to a sense of head rotation about a naso-occipital axis (Day & Fitzpatrick, 2005).

Locomotor turning requires generation of torque about a vertical axis, so it follows that GVS must be capable of inducing such a response. Whether this occurs during quiet standing is open to question, since double-stance imposes mechanical limits upon the duration and magnitude of body yaw. Furthermore, having both feet in contact with the floor would provide additional proprioceptive information, conflicting with the sense of rotation induced by GVS. It is well established that GVS-induced sway responses are attenuated in the presence of veridical sensory input (Day & Cole, 2002; Horak & Hlavacka, 2001; Day & Guerraz, 2007).

The nature of any torque response would depend on the mechanism of action of GVS. Previous research suggests two CNS effects. Firstly, it causes a sense of head roll around a naso-occipital axis, thought to be due to stimulation of semicircular canal afferents (Fitzpatrick & Day, 2004). This induces perceptions of rotation (Day & Fitzpatrick, 2005) and locomotor steering responses, as described above (Fitzpatrick *et al.* 2006). When standing, it causes sway towards the anode electrode (Lund & Broberg, 1983). Secondly, GVS results in a sense of inter-aural linear acceleration, possibly due to effects upon otolith afferents (Cathers *et al.* 2005; although see Mian *et al.* 2010). This causes an earlier but smaller sway response in the opposite direction (Cathers *et al.* 2005). How would these effects of GVS manifest as vertical torque? Presumably, vertical torque would be generated only to compensate for a sense of rotation around a vertical axis. This would obviously be caused by a sense of head roll, assuming the head is first tilted up or down. However, the acceleration vector might also result in a sense of body rotation, if the head is displaced from the axis of body rotation, by leaning forwards for example. Hence, although the largest contributor to vertical torque is likely to be the canal stimulus, both actions of GVS could conceivably contribute.

Here, vertical torque responses to vestibular stimulation are measured during quiet stance. GVS is used initially to establish the existence and nature of the response. Stochastic vestibular stimulation (SVS) is subsequently employed to determine precisely how the response is modulated by head orientation, due to its increased signal-to-noise properties (Fitzpatrick *et al.* 1996; Pavlik *et al.* 1999; Dakin *et al.* 2007, 2010; Reynolds, 2010). SVS has been used to determine changes in the direction of shear force with head yaw (Mian & Day, 2009). The present study extends this capability, reporting changes in the direction of the vestibular-evoked vertical torque response with head pitch.

Methods

Subjects

Twenty-four healthy subjects (6 female, 21–34 years old) gave written informed consent to participate in this study. Permission was obtained from the ethics committee of the School of Sports and Exercise Sciences at The University of Birmingham, and experiments conformed to the *Declaration of Helsinki*. Six main experiments are reported here, plus two presented as supplementary data. Seven individuals participated in two or more experiments.

Vestibular stimulation

Vestibular stimulation was applied via the mastoid processes using 56×39 mm carbon rubber electrodes coated with conductive electrode gel, attached with adhesive tape. Some subjects reported minor discomfort during stimulation but this was alleviated by recoating the electrode with conductive gel. Computer-generated waveforms were delivered to a stimulus isolator (Model 2200; AM Systems, Carlsborg, WA, USA). GVS stimuli were 2 mA in magnitude and 1.5 s in duration. SVS stimuli were generated by passing white noise through a digital filter. First, a low pass second order 5 Hz butterworth filter was used, resulting in a very shallow cut-off which gave a gradual reduction in power with frequency. This is termed the broadband stimulus. To isolate responses to low and high frequency stimulation, a 10th order low pass and band pass filter was used to generate 0–5 Hz and 5–10 Hz stimuli, respectively. The power spectra of all three stimuli can be compared in Figure 1. In all cases SVS current magnitude was 1.5 mA RMS. Freshly generated stimuli were used for each trial. Positive values of current represent anode-right stimulation for both GVS and SVS stimuli.

Protocol

Subjects stood barefoot on a force plate with eyes closed and feet together, and were asked to stand still but relaxed. GVS was delivered in sequences of 20 stimuli with random polarity and a variable gap of 2–2.5 s (each sequence lasting ~80 s). Participants were asked to hold their head level, or to tilt it forward in a position which could be held comfortably for the duration of the trial, without the chin touching the chest. Eighty stimuli (40 for each polarity) were delivered for both head positions. Effects of head orientation were investigated further with SVS stimuli lasting 80 s. Head orientation was manipulated by aligning a head-mounted laser crosshair to lines placed at 1 m distance, corresponding to specified angles of head yaw, pitch and roll. Once aligned, subjects closed their eyes and attempted to maintain head orientation while vestibular stimulation was delivered. Two trials were recorded for each head orientation. Trial order was randomised.

Effects of head position (not orientation) and body lean on the response to the high frequency stimulus (5–10 Hz) were investigated by asking subjects to adopt specific postures. Real-time centre of pressure (COP) position was displayed on a computer screen, allowing subjects to adopt reproducible body leans at the beginning of each trial. To dissociate effects of body lean and head position, subjects also attempted leaning while maintaining head position. The various postures are depicted in Fig. 6*B*.

The main experiments are listed below with a brief description of their aims:

1) Response to GVS ($n = 9$; Fig. 2). Square-wave stimuli were used to establish the existence of a vertical torque response to vestibular stimulation.
2a) Effect of head pitch on SVS response ($n = 8$; Figs 3 and 4*A* and *B*). Stochastic stimuli were used to examine the effect of head pitch on the response. This also allowed the response to be characterised in the frequency domain.
2b) High and low frequency SVS stimuli ($n = 6$; Fig. 5). Different stimulus bandwidths were applied separately to determine how the response differs at high and low frequency.
3) High frequency coupling between shear force and vertical torque ($n = 6$; Fig. 4*C*). The relationship between lateral force (F_x and F_y) and vertical torque (T_z) was examined in the absence of vestibular stimulation.
4) Effect of head position and body lean on the high frequency SVS response ($n = 3$; Fig. 6). The physiological origin of the high frequency response was investigated by independently manipulating head position and body lean.
5) Effect of head orientation on the high frequency response SVS response ($n = 5$; Fig. 7). To gain further insight into the high frequency response, head orientation was manipulated up to 90 deg in yaw, pitch and roll.

Two additional experiments are reported as supplementary data:

S1) Comparison of GVS and SVS–evoked torque response ($n = 4$).
S2) Effect of stance position on force–torque coupling ($n = 1$).

Data acquisition and analysis

Ground reaction forces were transduced by a Kistler 9281B force platform and sampled at 1 kHz (Kistler Instrumente AG, Winterthur, Switzerland). These were used to calculate vertical torque in terms of the free moment (T_z), which refers to torque around a vertical axis positioned at the centre of pressure (COP). This is derived from torque around the centre of the force platform (M_z) as follows: $T_z = M_z - (F_y \times \mathrm{XCOP}) + (F_x \times \mathrm{YCOP})$, where F_x and F_y are shear forces. Calculation of T_z ensures that a shear force applied from a position offset from the platform centre will not be misinterpreted as vertical torque. Crucially, this means that a particular behaviour will generate the same T_z value regardless of where the subject stands on the force platform. See Fig. 1 for force and torque conventions.

Head and trunk Euler angles were sampled at 50 Hz using two Fastrak sensors (Polhemus Inc., Colchester, VT, USA). These were attached to a welding helmet frame worn on the head and a wooden plate traversing the shoulder blades secured by webbing. Head yaw, pitch and roll, and trunk yaw were obtained from Fastrak Euler angles in Matlab (The Mathworks Inc., Natick, MA, USA), using a rotation matrix according to the Tait–Bryan rotation sequence (i.e. yaw → pitch → roll using a rotating sensor reference frame). Head pitch was expressed relative to the orientation in which Reid's plane (the line between the inferior orbital margin and external auditory meatus) is horizontal. Any offset between the orientation of the helmet sensor and Reid's plane was measured with a separate sensor secured to a flat plate, and subsequently subtracted. Negative values of pitch refer to downward head tilt.

T_z was derived from filtered force signals (10 Hz low-pass 2nd order butterworth). Responses to GVS were averaged after subtracting the mean baseline for each trial (between −1 and 0 s). The root-mean-square (RMS) value between 0 and 1 s was used to assess response magnitude. Within-subject variability was characterised by the mean standard deviation of the averaged response during the same time period. Trunk yaw was filtered in the same way and then differentiated to derive angular velocity before baseline subtraction and averaging. Ninety-five per cent confidence intervals were calculated to determine if responses differed from zero. Student's *t* test was were used to compare GVS responses in two head positions. Bonferroni adjustment was applied for multiple comparisons.

SVS responses were analysed in the time domain by cross-correlation and in the frequency domain by coherence. Cross-correlations were performed using the

Matlab XCOV function with the 'coeff' option activated. This removes the mean and normalises the signals to unit variance resulting in a correlation coefficient which varies between −1 and 1. Coherence was calculated using the method of Halliday *et al.* (1995), implemented using Neurospec 2 for Matlab (www. neurospec.org). Coherence is the squared magnitude of the cross-spectrum divided by the product of the input and output spectra. It measures linear dependence between two signals as a function of frequency, providing a dimensionless value between 0 and 1. It can be interpreted in a similar way to the squared correlation coefficient. SVS and T_z signal pairs were split into segments of 2048 samples (i.e. 2.048 s), giving a frequency resolution of 0.488 Hz. Cross-spectra were calculated for each segment, allowing mean coherence and 95% confidence intervals to be calculated. Trial data for each subject were concatenated. For graphical purposes, subject data were concatenated to provide pooled group data (Amjad *et al.* 1997). Mean coherence and RMS cross-correlation values were analysed by ANOVA to determine effects of head orientation. One-way ANOVA was used to investigate significant interactions following a two-way ANOVA. $P < 0.05$ was considered significant for all tests.

Results

Experiment 1: response to galvanic vestibular stimulation

With the head tilted down (HD), anode-right stimulation caused a positive T_z deflection starting around 90 ms, resulting in clockwise trunk rotation at ∼140 ms (Fig. 2*A* and *B*). The T_z response peaked and then underwent a negative deflection, returning to baseline at 700–1000 ms. Anode-left stimulation caused an equal and opposite response, as did stimulus cessation. The magnitude of the initial T_z response was 3.24 ± 0.65 N cm at 215 ± 37 ms (anode left and right combined). The subsequent negative peak was -3.12 ± 1.31 N cm at 532 ± 96 ms. Trunk yaw velocity reached a maximum of 0.38 ± 0.17 deg s^{-1} at 409 ± 58 ms.

Holding the head upright (HU) had no affect on response magnitude, as measured by the RMS value of torque between 0 and 1 s (Fig. 2*C*; HD: 1.84 ± 0.52 N cm; HU: 1.68 ± 0.45 N cm; $t = 0.67$, $P = 0.53$). However, it did increase response variability, in terms of within-subject SD (HD: 8.7 N cm; HU: 10.8 N cm; $t = 2.7$, $P = 0.03$). Trunk yaw showed the same pattern, i.e. no effect of head orientation upon magnitude (HD: 0.18 ± 0.08 deg s^{-1}; HU: 0.18 ± 0.07 N cm; $t = 0.67$, $P = 0.53$), but increased variability (HD: 0.83 deg s^{-1}; HU: 0.99 deg s^{-1}; $t = 2.7$, $P = 0.03$). The variable nature of the head up response made it impossible to identify consistent torque or yaw peaks for each subject.

Experiment 2: effect of head pitch on SVS response

Compared with the average T_z response to GVS, the SVS–T_z cross-correlation (CC) displayed approximately twice the signal-to-noise ratio (see supplemental Fig. 1). Significant T_z responses were seen at all head pitch angles (i.e. 95% CI deviates from zero in Fig. 3*A*). However, there was a progressive change in CC amplitude and shape with head pitch. The peaks and troughs apparent at –40 deg are progressively attenuated and eventually reversed as the head is tilted backward. At 7 deg the response is an amalgamation of the two extreme pitch angles, initially resembling head down and later switching to head back. This modulation pattern can be seen more clearly in Fig. 3*B* where the same data are plotted in three dimensions. Response magnitude displayed a U-shaped function of head pitch (Fig. 3*C*; $F_{6,42} = 9.18$, $P <$ 0.001).

Figure 4*A* shows SVS–T_z coherence for the same data in Fig. 3. At all head angles coherence was significantly greater than zero. However, its magnitude varied as a function of head pitch. This can be seen at 2–3 Hz, where the gradual increase in coherence as the head deviates from horizontal reflects the cross-correlation findings in Fig. 3. However, at 7–8 Hz there is a second peak unaffected by head pitch. A comparison of mean coherence at low (0–5 Hz) and high (5–10 Hz) frequencies reveals an interaction between head pitch and frequency ($F_{6,42} = 5.94$, $P < 0.001$). One-way ANOVA confirms that this interaction is due to a significant effect of head pitch upon the low frequency response ($F_{6,42} = 7.84$; $P < 0.001$) but not the high frequency response ($F_{6,42} = 1.85$; $P = 0.11$).

Narrow bandwidth stimuli (0–5 and 5–10 Hz; Fig. 1) were used to further investigate the two frequency responses identified by the coherence analysis. Figure 5*A* shows the low frequency response is reversed by head tilt, whereas high frequency response is unaffected, both in terms of amplitude and polarity.

When the high and low frequency responses are summed (Fig. 5*B*), the resulting waveform resembles the broadband response (Fig. 3*A*). In particular, the apparent latency difference between the two head positions is recreated, with the head down response peaking earlier (Fig. 5*B*; HD: 132 ms; HU: 183 ms versus red and black traces in Fig. 4*A*; HD: 124 ms; HU: 173 ms).

Experiment 3: high frequency coupling between shear force and vertical torque

F_x–T_z coherence from experiment 2 is shown in Fig. 4*B*. For all head orientations, there is a peak at 7–8 Hz which is aligned to the high frequency T_z response in Fig. 4*A*. This is also seen in the absence of vestibular stimulation, and so is an inherent characteristic of normal stance (Fig. 4*C*). Furthermore, it is restricted to medio-lateral force and does not occur for sagital force (compare F_x and F_y in Fig. 4*C*). A comparison of different stance positions confirmed that the coupling is fixed in body coordinates (see supplemental Fig. 2). Hence, the apparent high frequency T_z response may be secondary to an evoked medio-lateral sway response. This could be caused by a response to an inter-aural acceleration vector (Cathers *et al.* 2005).

Experiment 4: effect of head position and body lean on the high frequency response

An alternative possibility is that the linear acceleration vector could induce a sense of body rotation, *if* head position is offset from the axis of body rotation (Fig. 6*A*). Hence, the high frequency T_z response could be a reaction to this sensed rotation. To address this possibility, subjects were asked to adopt various body postures in order to dissociate the effect of body lean and head position (Fig. 6*B*). Head pitch was maintained between 7 and 9 deg for all conditions.

COP position was the same for both forward lean conditions (Fig. 6*C*; 1 and 3; $P = 0.06$; Bonferroni-adjusted $\alpha = 0.0125$), whereas head position differed by 6.7 cm ($P = 0.004$). Despite this difference, there was no change in response shape or magnitude (see red traces in Fig. 6*D*; $t = 0.5$, $P = 0.66$). Similarly, for backward lean conditions (2 and 4), COP was constant ($P = 0.40$) while head position differed by 11.8 cm ($P = 0.01$). Again, despite the large difference in head position, there was no difference in response magnitude (blue traces; $t = 0.68$, $P = 0.68$). The results therefore provide no evidence of modulation by head position.

However, there was an effect of body lean upon response magnitude, with the combined forward lean conditions being larger than backward lean ($t = 13$, $P = 0.006$). In addition, there was a tendency for the response to reverse direction during backward lean, with the forward lean conditions showing an average phase difference of 155 deg compared with backward lean (mean phase shift between 5–10 Hz). This suggests the coupling between medio-lateral shear force and T_z is affected by the point of application of the force at the feet (Fig. 6*E*).

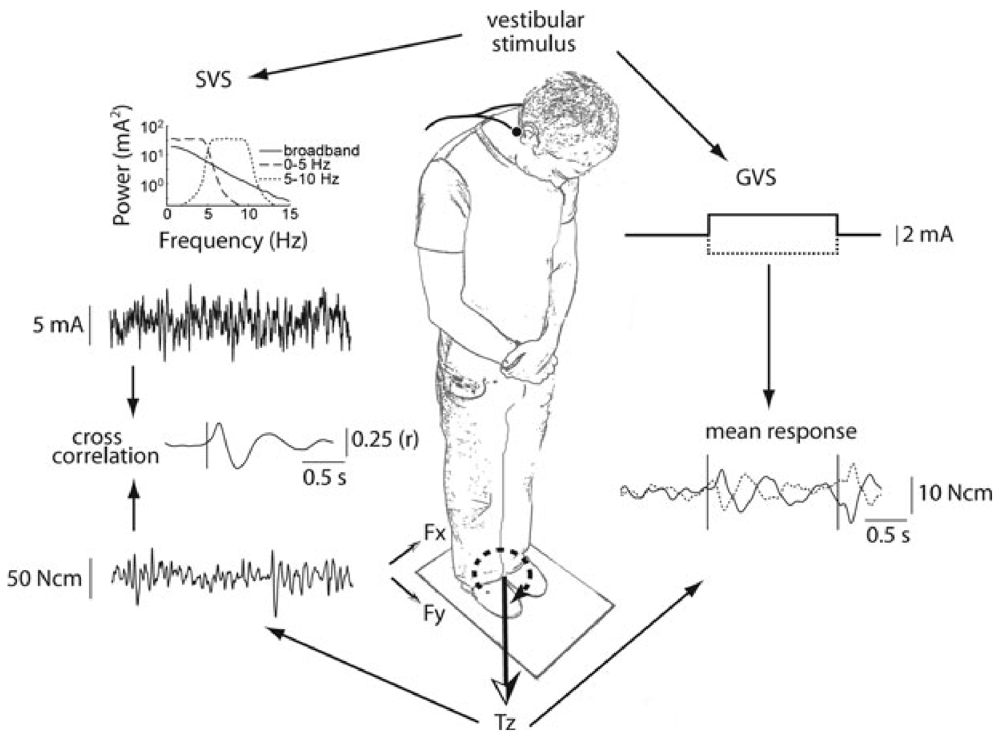

Figure 1. Methods of vestibular stimulation and analysis
Electrical stimuli were applied to the mastoid processes to determine the effect upon vertical torque (free moment; T_Z). Two types of stimuli were employed. Shown on the right are single subject responses to galvanic vestibular stimulation (GVS). Continuous and dashed traces show anode right and left conditions, respectively. The top left graph shows log power spectra for the three stochastic vestibular stimuli (SVS) used in the study. Below this, 20 s of broadband SVS is shown, with a concurrently recorded T_Z signal on the bottom left. The SVS response was analysed by cross correlation, and also by coherence (not shown). Positive values of T_Z represent a downward-directed torque vector acting upon the body, according to the right-hand convention. The directions of shear force vectors F_x and F_y are also depicted.

Experiment 5: effect of large head rotations on the high frequency response

The data suggest that the high frequency T_z response is caused by coupling to evoked medio-lateral sway induced by the inter-aural acceleration vector. If this is the case, then it should attenuate if the evoked sway direction is *not* medio-lateral. This would occur if the inter-aural axis is uncoupled from the medio-lateral direction by head yaw or roll. To test this, subjects adopted ±30, 60 and 90 deg head roll, yaw and pitch (Fig. 7). Response magnitude was reduced by yaw and roll ($F_{6,24} \geq 3.9$, $P \leq 0.007$), but not by pitch ($F_{6,24} = 1.5$, $P = 0.21$), thus confirming the prediction.

Discussion

With the head tilted forwards, GVS caused significant T_z oscillations accompanied by trunk rotation. These were polarity-specific and reversed direction when the current was switched off. Indirect evidence of vestibular-evoked vertical torque responses comes from a study by Fitzpatrick *et al.* (2006) in which walking subjects were steered in a controlled fashion by GVS. Such turning behaviour requires generation of torque around a vertical axis, but other studies of locomotor turning suggest this occurs primarily during single stance, when the body is free to rotate around the stance leg (Xu *et al.* 2006; Orendurff *et al.* 2006). The results here provide direct evidence of vertical torque responses evoked by vestibular stimulation when standing quietly with both feet in contact with the floor.

Modulation of vertical torque by head pitch

With the head upright response variability increased, suggesting modulation by head pitch. This was confirmed by the SVS response. When head pitch changed from +45 to −45 deg the response initially attenuated, reached a

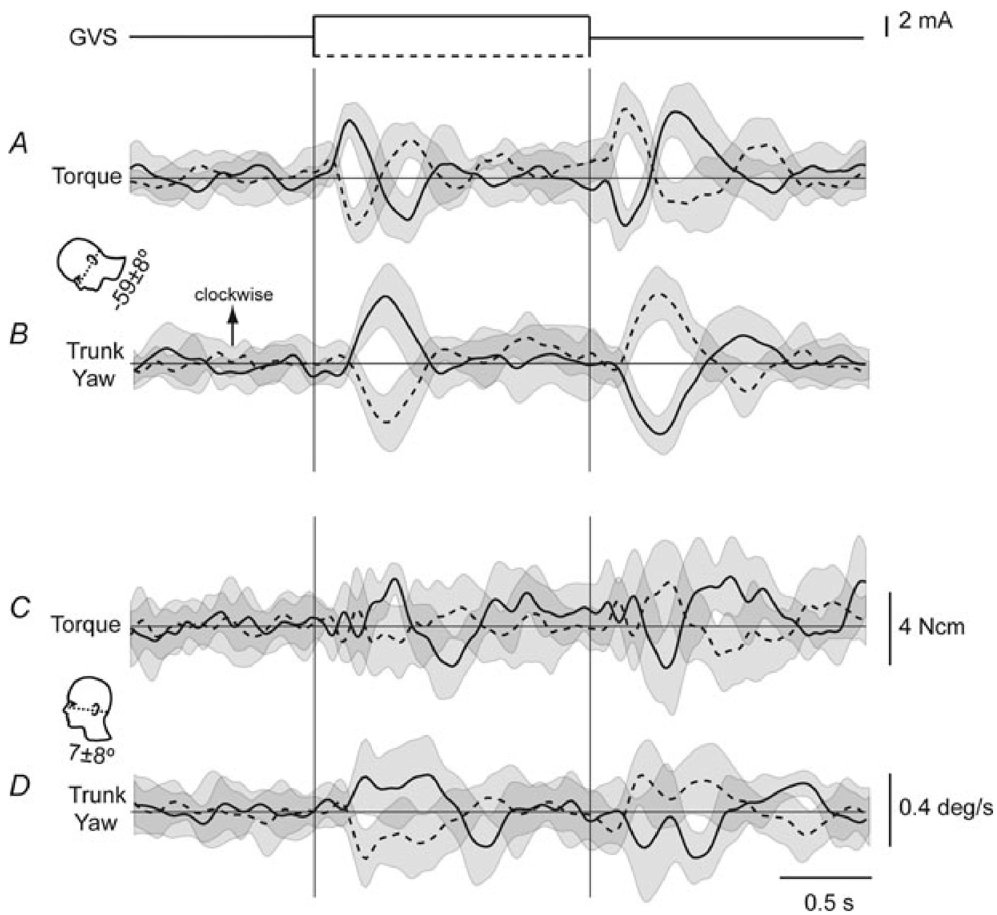

Figure 2. Vertical torque and trunk yaw responses to GVS (mean ± 95% CI; *n* = 9)
Group mean torque and trunk yaw velocity responses to 2 mA stimuli are shown. Anode right and left conditions are shown by continuous and dashed traces, respectively. Each subject was stimulated with the head tilted forwards (*A* and *B*), and upright (*C* and *D*). The angle of Reid's plane with respect to horizontal is shown for both conditions (mean ± SD).

nadir at +7, and finally reversed polarity and regained magnitude with further tilt (Fig. 3*A*–*C*). This is consistent with the effect of head orientation upon vestibular-evoked turning behaviour (Fitzpatrick *et al.* 2006) and can be explained by stimulation of semicircular canal afferents causing virtual head roll around a naso-occipital axis (Fitzpatrick *et al.* 2002; Fitzpatrick & Day, 2004; Day & Fitzpatrick, 2005). When this axis is aligned to vertical the CNS interprets the stimulus as whole body rotation about the vertical. The observed torque response is therefore produced to compensate for this sensed rotation.

Mian & Day (2009) applied SVS to study the effect of head orientation upon vestibular-evoked shear force. They showed that changes in the direction of evoked force caused by head yaw are accurately quantified by the SVS–force cross-correlation. The present results show that head pitch causes a systematic change in the SVS–T_z response. These techniques can be used to assess deficits in vestibulo-motor transformation processes underlying balance disorders. To transform a vestibular signal into

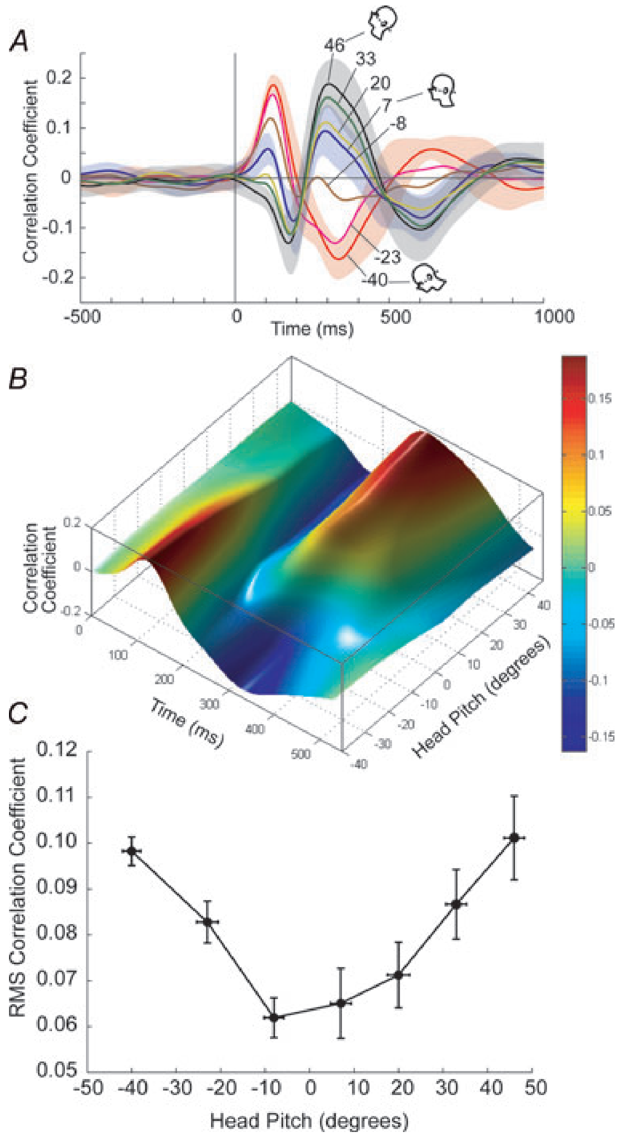

Figure 3. Effect of head pitch on SVS response (*n* = 8)
A, mean SVS–T_z cross correlations are shown for seven different head postures. Inset values show the angle of Reid's plane with respect to horizontal. Shaded bands depict 95% confidence intervals for the 46, 7 and –40 deg conditions, but are omitted from the other conditions for clarity. *B*, the same data plotted in 3D with an interpolated connecting surface. *C*, the RMS cross correlation between 0 and 1 s shown with standard errors.

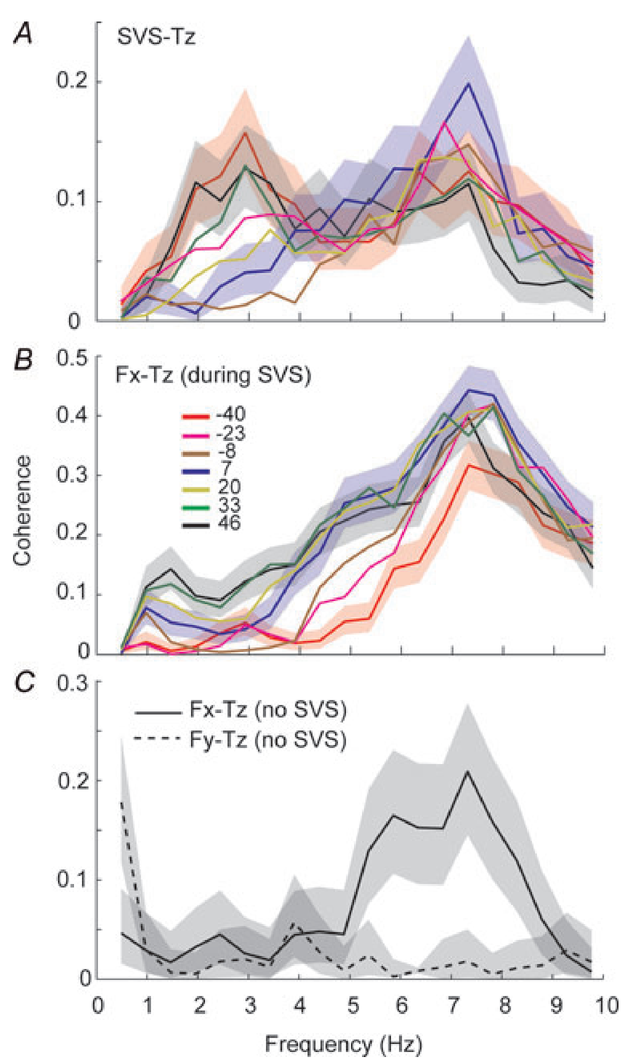

Figure 4. Coherence between vertical torque and SVS/shear force
A, pooled coherence between SVS and T_z is shown for all head pitch angles for the same subjects presented in Figure 3. *B*, coherence between T_z and medio-lateral shear force (F_x). *C*, coherence between anterior–posterior shear force (F_y) and T_z, as well as between F_x–T_z for a group of six subjects standing quietly without vestibular stimulation. Shaded bands show 95% confidence intervals.

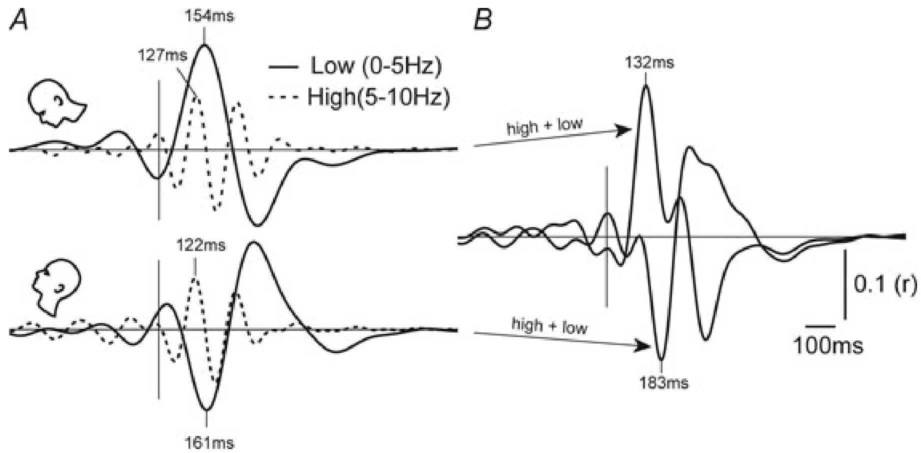

Figure 5. Effect of head pitch on high and low frequency SVS response ($n = 6$)
Mean SVS–T_z cross correlations are shown for two different stimulus bandwidths and two head pitch positions (45 deg up and down). *A*, separate responses to high and low frequency stimulation. The low frequency response is clearly modulated by head position, whereas the high frequency response remains constant. *B*, summed (high + low) responses for both head positions. Summation causes an apparent difference in peak timing, also seen in the broadband response (Fig. 3*A*; compare red and black traces).

an appropriate whole-body movement, the CNS must estimate the orientation of the head with respect to the ground. With the eyes closed, this information is presumably derived from memory, proprioception, motor efference copy and otolith input. Any error in this estimation process, resulting in either illusory bias or uncertainty of head orientation, would be expected to cause a concomitant change in the vestibular response.

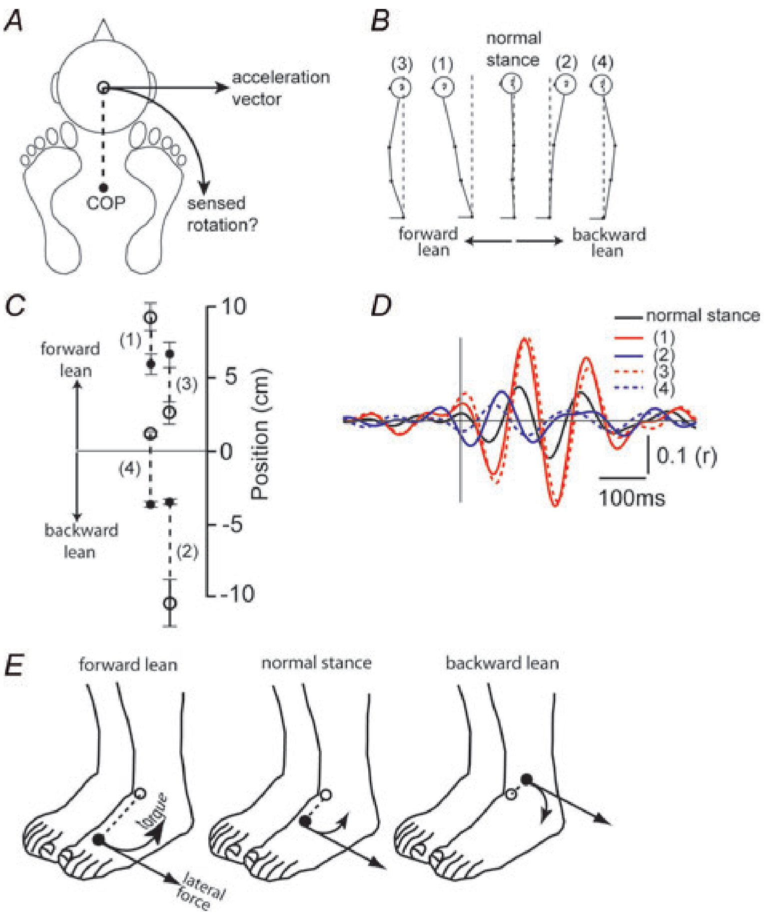

Figure 6. Effect of head position and body lean on the high frequency SVS response ($n = 3$)
A, schematic diagram showing how an inter-aural acceleration vector could theoretically produce a sense of body rotation around a vertical axis, when leaning displaces the head from the body's centre of rotation. *B*, subjects were stimulated in various body postures in order to dissociate effects of COP from head position. *C*, sagittal COP (filled circles) and head position (open circles) are shown for each posture, relative to normal stance (±SEM; points shifted laterally for clarity). *D*, SVS–T_z cross-correlations for each posture. *E*, proposed mechanism of force–torque coupling. Assuming the axis of body rotation lies between the ankle joints (open circles), application of lateral force from a forward COP position (filled circles) will evoke torque around this axis, causing bodily rotation. As body motion reverses due to elastic forces, it will produce a rebound torque around the COP. The magnitude of the torque response will increase with forward lean and reverse with backward lean.

Specifically, the U-shaped curve in Fig. 3*C* would shift laterally or flatten out with changes in bias and uncertainty, respectively. Hence, the vertical torque response can be used to assess the efficacy of vestibular-evoked reflexes.

Two responses identified in the frequency domain

Frequency analysis revealed two coherence peaks which were affected differently by head orientation. The 2–3 Hz peak reflected the overall pattern of the cross-correlation, changing with head pitch. In contrast, the 7–8 Hz peak was unchanged. Separate application of low and high frequency stimuli supported this observation: The 0–5 Hz stimulus produced a response which reversed polarity between head-up and head-down in a symmetrical fashion, whereas the response to 5–10 Hz stimulation was completely unaffected by ±45 deg head pitch. When these separate responses were summed in the time domain, the resulting waveform resembled the broadband response in Fig. 4*A*. Although this comparison is limited by the unequal spectral content of the stimuli, it is clear that the gross characteristics of the broadband response were recreated by summation. In particular, the asymmetry between the head-up and head-down down response was seen, with the latter peaking earlier. These comparisons suggest that the broadband response may be an amalgamation of two mechanisms operating in parallel. The physiological origins of these two responses are discussed below.

Physiological origins of the two torque responses

Lateral sway responses to vestibular stimulation consist of two parts; a small initial sway directed towards the cathode electrode followed by a much larger sway in the opposite direction (Marsden *et al.* 2002; Cathers *et al.* 2005). Systematic manipulation of head orientation has led to the conclusion that the early response is due to a sense of inter-aural linear acceleration, whereas the latter response is caused by a head roll vector (Fitzpatrick & Day, 2004). These virtual head movements have been attributed to stimulation of otolith and semicircular canal afferents, respectively (Cathers *et al.* 2005), although the otolith theory has recently been disputed (Mian *et al.* 2010).

How can these two mechanisms explain the vertical torque responses seen here? As discussed above, the low-frequency T_z response is readily explained by a virtual head roll vector, and so is likely to be caused by stimulation of canal afferents. But the origin of the high frequency T_z response is less obvious. Since it was not modulated by head pitch, it cannot be attributed to the same roll vector, and so is presumably related to the inter-aural linear vector. However, one would only expect to see vertical torque in response to a sense of body rotation, which raises the question: Why would a *linear* vector elicit *rotation*? One possibility is that when this vector is displaced from the axis of body rotation, it is interpreted as rotation. This is analogous to an accelerometer placed at the periphery of a rotating carousel, registering a signal as the carousel begins to rotate. Similarly, if the head is displaced from the axis of body rotation, a sense of inter-aural acceleration could be interpreted as body rotation around a vertical axis (Fig. 6*A*). However, the results of the leaning experiment do not support this hypothesis. Although the SVS–T_z cross-correlation was altered by forward or backward lean, it was unaffected by large changes in head position. Hence, the high frequency torque response cannot be attributed to a sense of rotation caused by a linear vector offset from the centre of rotation. Instead, the results point towards mechanical coupling between medio-lateral force and vertical torque.

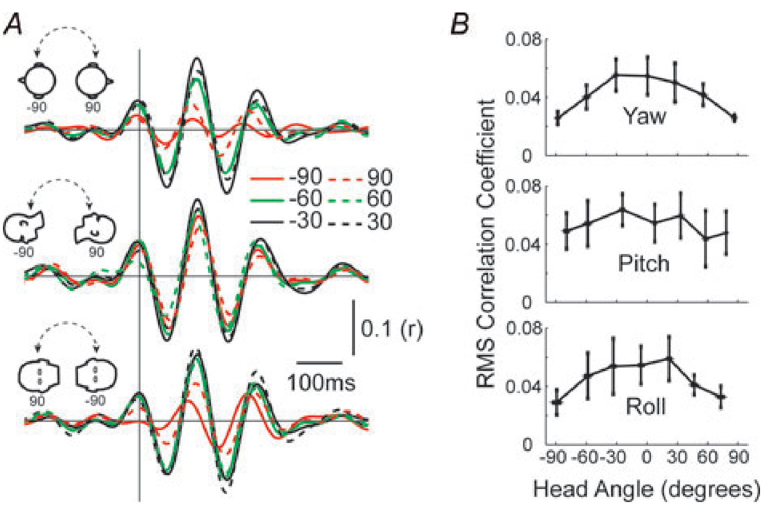

Figure 7. Effect of head orientation on the high frequency SVS response ($n = 5$)
A, mean SVS–T_Z cross correlations for the 5–10 Hz stimulus. Head-neutral position is omitted for clarity. Vertical lines show time zero. *B*, RMS values of cross-correlations between 0 and 1 s.

Coupling between vertical torque and shear force

Coherence analysis revealed that T_z was strongly coupled to shear force (F_x) at precisely the same range as the high frequency response (i.e. 7–8 Hz). This is inherent to normal stance since it occurred without vestibular stimulation. This suggests that the high frequency response is secondary to an evoked shear force manifesting as vertical torque through a pre-existing mechanical coupling. This coupling was restricted to the medio-lateral direction (i.e. the frontal body plane). When the inter-aural axis was uncoupled from the medio-lateral direction by head yaw or roll, the response was attenuated. In this case, the direction of stimulus-evoked sway is no longer aligned with the frontal plane, and therefore it does not transfer to vertical torque. In contrast, head pitch had no effect since it does not change the orientation of the inter-aural vector.

While head *position* had no effect, forward lean did increase the magnitude of the high frequency response. Backward lean had limited effect on magnitude, but caused a reversal in polarity. This observation leads to the following hypothesis to explain the mechanical coupling: assuming the axis of body yaw rotation lies between the ankle joints, application of lateral force from a position displaced from this axis will evoke torque around it (see Fig. 6*E*). This would cause the body to rotate, albeit by a tiny amount. As the body subsequently returns due to mechano-elastic forces, it would evoke a rebound torque, registering as T_z. Any tendency for the body to resonate in yaw at 7–8 Hz would exacerbate this torque. In support of this, the resonant frequencies of the human spine and abdomen exposed to vertical vibration are close to this frequency range (10–12 and 4–8 Hz, respectively; Rasmussen, 1983; Kitazaki & Griffin, 1998). Changes in the pattern of coupling caused by leaning can be attributed to an altered moment arm between the ankle joint and the point of application (COP). During normal stance the COP lies forward of the ankle joint. Leaning further forward will increase the magnitude of the moment arm while backward lean will reverse it, causing an increase or reversal in the F_x–T_z cross-correlation, respectively (Fig. 6*E*). Further work is required to confirm the nature of the force–torque coupling. But whatever its cause, these results suggest it underlies the high frequency vertical torque response to vestibular stimulation.

In summary, two separate vertical torque responses to vestibular stimulation have been identified. The low frequency response was modulated by head orientation in a way consistent with a naso-occipital roll vector caused by stimulation of canal afferents. The high frequency response could not be explained in the same way. Convergent data from several experiments suggest that it is secondary to an evoked lateral sway response which is mechanically coupled to vertical torque.

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