Stimulus-Dependent Changes in the Vestibular Contribution to Human Postural Control

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Cenciarini, Massimo and Robert J. Peterka. Stimulus-dependent changes in the vestibular contribution to human postural control. J Neurophysiol 95: 2733–2750, 2006. First published February 8, 2006; doi:10.1152/jn.00856.2004. Humans maintain stable stance in a wide variety of environments. This robust behavior is thought to involve sensory reweighting whereby the nervous system adjusts the relative contribution of sensory sources used to control stance depending on environmental conditions. Based on prior experimental and modeling results, we developed a specific quantitative representation of a sensory reweighting hypothesis that predicts that a given reduction in the contribution from one sensory system will be accompanied by a corresponding increase in the contribution from different sensory systems. The goal of this study was to test this sensory-reweighting hypothesis using measures that quantitatively assess the relative contributions of the proprioceptive and graviceptive (vestibular) systems to postural control during eyes-closed stance in different test conditions. Medial/lateral body sway was evoked by side-to-side rotation of the support surface (SS) while simultaneously delivering a pulsed galvanic vestibular stimulus (GVS) through electrodes behind the ears. A model-based interpretation of sway evoked by SS rotations provided estimates of the proprioceptive weighting factor, $W_p$, and showed that $W_p$ declined with increasing SS amplitude. If the sensory-reweighting hypothesis is true, then the decline in $W_p$ should be accompanied by a corresponding increase in $W_g$, the graviceptive weighting factor, and responses to the GVS should increase in proportion to the value of $W_g$ derived from responses to SS rotations. Results were consistent with the predictions of the proposed sensory-reweighting hypothesis. GVS-evoked sway increased with increasing SS amplitude, and $W_g$ measures derived from responses to GVS and from responses to SS rotations were highly correlated.

INTRODUCTION

During stance, stability is maintained by generating a control torque at the level of the ankle joint that counteracts the destabilizing torque due to gravity (Johansson et al. 1988). Results from a previous study (Peterka 2002) indicate that active sensorimotor feedback control mechanisms are a dominant contributor to the torque required for stance control. This study showed that a relatively simple feedback-control model could account for the dynamic behavior of the postural control system in response to support surface (SS) or visual surround rotational perturbations over a bandwidth of 0.05 to 1.2 Hz. Others have also shown that simple feedback control models are able to characterize the dynamics of the human postural control system (Ishida and Imai 1980; Ishida and Miyazaki 1987; Johansson et al. 1988). Peterka (2002) showed that parameters of the proposed postural control model could be estimated from the anterior-posterior (AP) body sway response to a pseudorandom stimulus that controlled the rotational motion of the SS or visual surround. Specifically, stimulus/response data were used to estimate experimental transfer functions (TFs) that characterized the postural control system’s response sensitivity (gain) and timing (phase) as a function of the stimulus frequency. Then model parameter estimates were obtained from a curve fit of the model’s TF equation to the experimental TF data.

A key experimental result was that the TF gain decreased with increasing stimulus amplitude, but the overall shape of the TF gain and phase curves remained nearly unchanged. The model-based interpretation of this result was that a decrease in the relative contribution (sensory channel weight) of one sensory source (visual, proprioceptive, or graviceptive) was always accompanied by an increase in the contribution of other sensory sources and that other aspects of the system remained essentially unchanged. That is, a sensory reweighting mechanism is a dominant feature of postural regulation. This is in contrast to other potential interpretations where the contribution of only one sensory source might change and all other aspects of the control system remain constant, the overall stiffness (due to a combination of neurally mediated mechanisms and passive mechanics) might change to alter the amount of sway evoked by a given perturbation, or some nonlinear phenomenon might limit the amplitude of evoked sway.

The experimentally observed uniform TF gain changes imply that the amount of corrective torque generated in relation to a combined sensory error signal remains essentially constant across test conditions (Peterka 2002). This relation between corrective torque and sensory error was referred to as the “torque normalization hypothesis,” and this hypothesis leads directly to what we refer to as the “sensory reweighting hypothesis” in the current study.

Specifically, under eyes-closed conditions with a SS perturbation, the model introduced in Peterka (2002) indicated that the corrective torque was determined primarily by a “neural controller” acting on the value of a “sensory error signal”, $e$, given by

$$ e = W_p \cdot (SS - BS) - W_g \cdot BS $$

$$ = W_p \cdot SS - (W_p + W_g) \cdot BS $$  \hspace{1cm} (1)

where $SS$ is the support surface tilt angle, $BS$ is the body sway angle, $W_p$ is the proprioceptive channel weighting factor, and $W_g$ is the graviceptive channel weighting factor.
$W_g$ is the graviceptive channel weighting factor. The first line of Eq. 1 shows that $e$ includes proprioceptive and graviceptive contributions related to the ankle joint angle (SS-BS) and to body sway (BS) relative to the earth vertical, respectively. The second line of Eq. 1 is rearranged to show another interpretation of $e$. The first term, $W_p \cdot SS$ produces torque that is related to the external SS perturbation. It is presumably desirable for the postural control system to reduce the disturbance caused by an external perturbation, such as surface tilt. A reduction in $W_p$ alone would seem to satisfy the requirement for reducing the effect of such a disturbance.

However, the second term, $(W_p + W_g) \cdot BS$ shows that a reduction in $W_p$ would also cause a reduction in torque related to body sway relative to earth vertical. Modeling results demonstrate that such a reduction would produce resonant behavior and ultimately would result in instability if corrective torque was reduced below the level needed to resist gravity (Peterka and Loughlin 2004). The disturbance caused by a tilt perturbation can be reduced and resonant behavior and instability avoided if a decrease in $W_p$ is accompanied by a corresponding increase in $W_g$.

Although sudden changes in the availability of sensory information can induce transient resonant behavior (Peterka and Loughlin 2004), experimental results obtained under steady-state conditions suggest that the postural control system is regulated in a manner that avoids resonant behavior (Peterka 2002). This type of regulation can be represented by the equation $W_p + W_g = \text{constant}$. This equation is consistent with the torque normalization hypothesis when the neural controller properties and other passive mechanical factors contributing to corrective torque (associated with muscle and joint properties) do not change with stimulus conditions. Experimental results indicate that there are only small changes in neural controller and passive properties with changing stimulus amplitude (Peterka 2002). This equation is also an explicit representation of the sensory reweighting hypothesis. Furthermore, there is no loss in generality (see METHODS) in representing the sensory reweighting hypothesis by the equation $W_p + W_g = 1$ where the sensory weighting factors represent the relative contributions of the two sensory systems.

A previous analysis of AP sway evoked by SS stimuli of different amplitudes yielded $W_p$ estimates that decreased from 0.70 at the lowest SS stimulus amplitude tested (0.5° peak to peak) to 0.24 at the highest amplitude (8° peak to peak) in subjects with normal sensory function and with eyes closed (Peterka 2002). Because this analysis assumed that the sensory reweighting hypothesis was true (i.e., $W_g = 1 - W_p$), these results predict that $W_g$ increased from 0.30 at the lowest stimulus amplitude to 0.76 at the highest amplitude. The primary goal of the current study is to quantitatively test that $W_g$ increases with increasing SS amplitude in a manner predicted by the sensory reweighting hypothesis by comparing $W_g$ measures derived from the TF analysis to $W_g$ measures derived from an independent analysis method.

In developing an experimental test of the sensory reweighting hypothesis, we must first consider the possible sensory sources that contribute to $W_g$. An obvious contributor to graviception is the vestibular system, but others might include somatosensory sources related to the pressure distribution on the feet (Maurer et al. 2001) and other nonvestibular sources (Mittelstaedt 1998). Our previous results indicate that nonvestibular sensory sources do not contribute to graviception over the 0.05 to 1.2 Hz frequency bandwidth under our experimental conditions (Peterka 2002).

If vestibular information is the sole source of graviceptive information under our experimental conditions, then a galvanic vestibular stimulus (GVS) can be used to test the prediction that $W_g$ changes with SS stimulus amplitude. GVS is known to alter the activity of vestibular nerve afferents by acting directly on the nerve spike trigger zones (Goldberg et al. 1984). Although GVS is a crude stimulus, in that it is uncertain what combination of vestibular receptor afferents are stimulated (Schneider et al. 2002; Wardman and Fitzpatrick 2002), it has long been known that robust postural perturbations are evoked by GVS applied through electrodes placed on the mastoid processes (Day et al. 1997; Hlavacka and Nijoki 1985; Lund and Broberg 1983; Nashner and Wolfson 1974; Séverac Cauquil and Martinez 2000). The uncertainty about which vestibular afferents are activated is not critical for the test of the sensory-reweighting hypothesis because we are primarily interested in determining whether or not the body-sway response to a given fixed intensity of the GVS current scales in proportion to estimates of $W_g$ derived from responses to SS stimulation. In fact, we will go beyond this demonstration by showing that $W_g$ estimates can be derived from GVS responses so that these GVS-derived $W_g$ estimates can be directly compared with the $W_g$ estimates derived from responses to SS stimulation.

The most robust responses to GVSs are obtained with a bipolar-binaural electrode configuration where current is passed between the two ears through electrodes applied to the mastoid processes (Séverac Cauquil and Martinez 2000). However, this bipolar-binaural stimulation evokes medial-lateral (ML) sway. Because measures of $W_g$ obtained in previous experiments were based on SS stimuli that evoked AP body sway (Peterka 2002), it was necessary to first demonstrate that analogous results were obtained from SS stimuli that evoke ML body sway.

The goal of the current study was to quantitatively test the prediction of the sensory reweighting hypothesis that a change in the proprioceptive contribution to postural control will be accompanied by an equal and opposite change in the graviceptive contribution under eyes closed conditions. To accomplish this, we first showed that ML body-sway responses to SS stimulation were analogous to our earlier AP results. We then analyzed body sway evoked by the simultaneous presentation of a pulsed GVS and a pseudorandom SS stimulus. The TF analysis method was applied to SS responses to derive estimates of $W_g$ and thereby obtain model-based estimates of $W_g = 1 - W_p$. A separate analysis of GVS responses provided a second estimate of $W_g$ for comparison. Results showed a close correspondence between the two $W_g$ measures.

METHODS

Subjects

All subjects completed a medical screening prior to being tested to confirm that they had no history of balance problems or neurological defects and gave their informed consent prior to being tested using a
protocol approved by the Institutional Review Board at Oregon Health & Science University and in accordance with the 1964 Helsinki Declaration.

Thirteen subjects (6 males and 7 females) participated in this study. The results from one subject were excluded due to extremely large amounts of oscillatory body-sway behavior, which differed considerably from the results of the other subjects. The remaining 12 subjects’ ages ranged from 21 to 48 yr [mean: 29 ± 7.5 (SD) yr].

Equipment

Subjects stood on a servo-controlled SS that could be rotated side to side using a servo-controlled motor. The SS rotational axis, orthogonal to the frontal plane, was centered between the subject’s two feet and located 8 cm above the surface of the platform at a height approximately equal to ankle joint height.

To ensure that body movements remained similar to that of a single link inverted pendulum with sway only in a ML direction, most tests were performed with the subject’s body secured to a backboard assembly with a padded headrest and straps that held the subject against padded supports at knee, hip, and shoulder levels. The backboard was free to rotate about an axis aligned with the rotational axis of the support surface. The backboard rested on its own set of bearings, so the subject did not support the backboard weight, although its mass and moment of inertia (11.4 kg and 12.9 kg m², respectively) were accounted for in the data analysis.

Eight subjects performed all tests with the backboard assembly. These subjects stood with their feet close together in a comfortable position, and this position was used throughout testing. The mean distance between the center of the two heels was 15.24 cm (mean ± 1 SD). Four additional subjects performed a set of tests both with the backboard and freestanding. Their center-to-center heel distance was 15 cm on both backboard and freestanding trials.

An isolated galvanic current generator (A-M Systems analog stimulus isolator Model 2200, Carlsborg, WA) was used to pass current through two electrodes (Reusable Self-Adhering TENS/NMES/FES electrodes, 3.17 cm in diameter, # 626SS; UNI-PATCH) placed on the right and left mastoid processes in a bipolar binaural configuration. With the head facing forward on the body, this electrode configuration evoked ML body sway toward the anode (positive electrode) (Severac and Martinez 2000). The impedance measured across the two electrodes, 3.17 cm in diameter, # 626SS; UNI-PATCH) placed on the right and left mastoid processes in a bipolar binaural configuration. The impedance was always <3.5 kΩ. Throughout the experiment, a voltage proportional to the galvanic current was monitored on an oscilloscope and recorded using an isolated current probe amplifier (Tektronix AM503) to ensure correct delivery of the galvanic current.

Stimulus delivery and data sampling were computer controlled (DEC LSI 11/73) using custom programs. The data-sampling frequency was 100/s. Sampled data included the SS angular position measured by a potentiometer, the backboard angular position measured by a potentiometer, backboard angular velocity measured by a rate sensor (Watson rate sensor, ARS-C141-1A, Watson Industries, Eau Claire, WI), and a voltage signal proportional to the galvanic current. Because the body was restrained to sway as a single-link inverted pendulum, the backboard angular position and velocity measures provided direct measures of the body center-of-mass (COM) angular sway and sway velocity. COM sway and sway velocity were considered to be the output variables of interest for data analysis.

In the freestanding tests, the method previously used to measure AP COM angular sway (Jeka et al. 2004; Peterka 2002) was applied to measure ML COM angular sway, which was considered to be the output variable of interest. Briefly, lateral body motion was measured using two horizontal rods that rotated in relation to ML displacement at shoulder and hip levels. Rotational positions of the rods were measured by two earth-fixed potentiometers. Trigonometric conversions were used to calculate lateral body displacements from the rotational positions of the rods. Based on results from a prior calibration trial, the COM lateral displacement was calculated from hip and shoulder displacements. Then the COM rotation angle was determined using estimates of the subject’s COM height (based on anthropometric measures) above the ankle joint.

GVS and SS stimuli

Two different types of stimuli were used to evoke body sway. One was mechanical, the rotational motion of the SS, and the other was electrical, the GVS. SS rotation was used to provide a specific perturbation to identify input/output dynamics of postural control following the methods in Peterka (2002) or to limit the contribution of proprioceptive cues to postural control using “sway-referencing” (Peterka and Loughlin 2004). GVS was used to perturb the vestibular system, to determine the extent to which vestibular information was contributing to postural control in different test conditions.

We used a pseudorandom SS rotational stimulus based on a pseudorandom ternary sequence (Davies 1970) that was similar to the one used previously to characterize the dynamics of AP-evoked sway (Peterka 2002). The ternary sequence was mapped into a set of rotational velocities of +v, 0, or −v/3 that were held throughout each of the n = 242 states of the pseudorandom sequence with a state duration of Δt = 0.20 s. The period of the pseudorandom stimulus was N Δt = 48.4 s. The velocity (v) was selected so that the mathematical integral of the pseudorandom stimulus (Fig. 1A) provided peak-to-peak rotations of 0 (control), 1, 2, 4, and 8° on different trials. The stimulus was symmetric, providing equal tilts to the right and left. Six consecutive cycles were presented during each test trial.

Sway-referencing of the SS was used on some trials to limit the contribution of proprioceptive cues to postural control. Sway-referencing was accomplished by commanding the servo-controlled platform to rotate in equal proportion to the instantaneously measured body-sway angle. Sway-referencing maintained a nearly constant angle between legs and the SS and thereby produced an unchanging proprioceptive signal of body sway relative to the support surface even though there was body sway relative to earth-vertical (Peterka and Loughlin 2004). In the sway-referenced condition, SS rotation is determined by the subject’s sway, and no pseudorandom SS stimulus was presented.

The GVS consisted of a succession of positive pulses alternating with negative pulses (Fig. 1B). The positive polarity was defined as a right-side anodal, left-side cathodal stimulation. The pulse duration was 0.5 s (50-ms rise and fall time). The pulse amplitude was 0 (control), 0.25, or 0.75 mA. The time period between the onset of each pulse was 6.05 s, whereas the time period between successive pulses of the same polarity was 12.1 s, which corresponded to one quarter of the period of the SS stimulus. A total of 24 positive and 24 negative pulses were presented during a test trial.

On some trials, the GVS and the pseudorandom SS stimulus were given simultaneously. However, these two stimuli were designed to be mathematically uncorrelated so that responses to the two stimuli could be isolated from one another and analyzed separately. Spectral analysis demonstrates that the GVS and SS stimuli are uncorrelated (Fig. 1C and D). The pseudorandom SS stimulus has energy only at odd harmonic frequencies (dark vertical lines in Fig. 1C and D). The pulsed GVS has energy only at even harmonic frequencies of the SS fundamental frequency (gray vertical lines in Fig. 1C and D) where the pseudorandom SS stimulus has zero energy.

Separability of responses is guaranteed in the case of linear responses to the stimuli. For each SS stimulus amplitude, essentially linear responses to the SS stimulus were expected based on previous results from the characterization of AP sway dynamics (Peterka 2002). Although less is known about the linearity of responses to GVS, there is some evidence that responses are quite linear for small current amplitudes (Hajos and Kirchner 1984). However, even strong static nonlinearities, such as a rectification, in the GVS response would produce response components only at frequencies that are even integer multiples of the frequency components in the GVS. Therefore...
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These tests included the four different amplitudes of the pseudorandom SS stimulus (1, 2, 4, and 8° peak to peak) performed in both freestanding or backboard-supported conditions. No GVS was used in these experiments. Tests were completed in two sessions on two different days. All tests in each session were either freestanding or backboard supported, and the four SS amplitudes were presented in randomized order. Two of the subjects performed freestanding tests prior to backboard-supported tests, and the other two performed backboard-supported before freestanding tests.

All subjects were instructed to maintain a relaxed upright stance position. Subjects wore headphones and listened to audiotapes of short stories to mask equipment sounds and to maintain alertness.

Data analysis

PSEUDORANDOM SS STIMULUS/RESPONSE ANALYSIS. The body-sway response to the SS stimulus was analyzed using methods described previously (Peterka 2002). Spectral analysis methods were applied to sway data to compute a transfer function, relating the body-sway response to the SS stimulus, and a coherence function, indicating the degree of linearity between stimulus and response and the presence of noise in the system (Bendat and Piersol 2000). Each transfer function was expressed as a gain and phase function over a range of stimulus frequencies. The power and cross-power spectra used to compute transfer and coherence functions were calculated using the discrete Fourier transform to decompose the SS stimulus (SS angular velocity) and COM response (backboard angular velocity) waveforms into their spectral components. For each of the last five stimulus cycles (1st cycle was excluded to avoid initial transient responses), spectral components were calculated at 150 frequencies ranging from 0.021 Hz ($f_1 = 1/48.4$) to 3.1 Hz ($f_{150} = 150/48.4$) where 48.4 s is the period length of the SS stimulus. Because the SS stimulus has zero energy at all even harmonic frequencies of the fundamental, all even frequencies were discarded leaving 75 odd harmonic frequency samples. Power and cross-power spectra were computed by averaging the remaining 75 odd harmonic spectral components across the stimulus cycles. To further reduce the variability of the power spectra at higher frequencies, the higher frequency portion of the power spectra was smoothed by averaging spectral point first at adjacent frequencies to obtain final power spectra at 17 frequencies ranging from 0.021 to 2.79 Hz and spaced at approximatively equal intervals on a logarithmic frequency scale. Specifically, the lowest two odd-harmonic components were not averaged with adjacent frequencies, but adjacent odd-harmonic components at higher frequencies were averaged. The number of adjacent components included in an average increased with increasing frequency such that the highest frequency component was derived from an average of the highest 15 of the 75 odd harmonic components.

GVS ANALYSIS. Responses to the GVS were analyzed by computing a pulse-triggered average response for both the positive and negative GVS pulses. A pulse-triggered average was computed for both COM body-sway angle and angular velocity data. Because the body-sway responses to the initial set of GVS pulses were often larger than responses later in the trial, consistent with habituation to the GVS as characterized in previous studies (Johansson et al. 1995; Magnusson et al. 1990), data from the first 48.4 s of each test trial, corresponding to the first cycle of the SS stimulus, were not included in the pulse-triggered average to avoid transient responses.

The pulse-triggered average was formed by averaging 6.05-s segments of body-sway or sway-velocity data after the beginning of each pulse, with separate averages formed for the responses to positive and exception of one subject who was unable to complete the sway-referenced SS condition with 0.75-mA GVS even after many attempts.

Four subjects performed tests designed to determine if the backboard affected postural responses to the SS stimulus in the ML direction. These tests included the four different amplitudes of the pseudorandom SS stimulus (1, 2, 4, and 8° peak to peak) performed in both freestanding or backboard-supported conditions. No GVS was used in these experiments. Tests were completed in two sessions on two different days. All tests in each session were either freestanding or backboard supported, and the four SS amplitudes were presented in randomized order. Two of the subjects performed freestanding tests prior to backboard-supported tests, and the other two performed backboard-supported before freestanding tests.

Eight of the 12 subjects performed tests consisting of various combinations of SS rotation and galvanic stimulation. All of these tests were performed using the backboard. These tests included six different SS conditions for each of the three different galvanic stimulus conditions. The six SS conditions included a fixed SS, four different amplitudes of the pseudorandom stimulus (1, 2, 4, and 8° peak to peak), and a sway-referenced SS. The GVS conditions included 0- (no-GVS), 0.25-, and 0.75-mA pulse stimulus amplitudes. Data were collected in two 2-h sessions on separate days. The test sequence was randomized to avoid habituation that might occur when similar trials were presented in succession and to reduce possible habituation to galvanic stimulation characterized by a reduction of body sway evoked by GVS. The eight subjects included in this portion of the study were able to complete all trials presented with the

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These higher frequency GVS harmonics, which are due to nonlinear responses, would still be at frequencies that are even harmonics of the fundamental frequency of the SS stimulus. Analysis of the experimental results showed that our separability assumption was justified.

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Pseudorandom support surface (SS) stimulus and galvanic vestibular stimulus (GVS) characteristics. A: angular position waveform of the pseudorandom SS stimulus is the time integral of the angular velocity that was derived from a pseudorandom ternary sequence with a length of 242 states and a state duration of 0.20 s producing a stimulus with 48.4-s period. A 2° peak-to-peak stimulus is shown. B: 4 cycles of a pulsed GVS are shown with alternating positive and negative 0.5-s pulses during each 12.1-s cycle. C: spectrum of the pseudorandom SS velocity stimulus (black lines) for a SS stimulus with 1° peak-to-peak amplitude and spectrum of the pulsed GVS (gray lines). D: enlargement of the spectrum shown in C from 0 to 0.5 Hz to highlight the noninterference between the 2 stimuli in the frequency domain.

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negative pulses. Data from a total of 20 positive and 20 negative pulses were averaged to form the pulse-triggered average responses. The value of the first point in each 6.05-s segment was subtracted from all of the data samples in that segment prior to averaging so that the first sample in the pulse-triggered average was always zero. The peak amplitude and time to peak of each pulse-triggered average response was measured for both body-sway angle and angular velocity averages. The time-to-peak measures from GVS trials were used to define a window that was subsequently used to search for peak values on no-GVS control trials.

Model-based interpretation

A theoretical model of postural control was used to interpret the experimental results. The model represents a quantitative hypothesis whereby we explicitly state our assumptions about the organization of the postural control system. These assumptions can be later confirmed or refuted based on experimental results. The model in Fig. 2 is based on a modified version of the “independent channel model” described previously (Peterka 2002) but includes a torque feedback mechanism and excludes the visual channel because eyes were closed during all trials.

In the model, corrective torque is generated by both active sensory-related responses and passive mechanical properties of muscles and joints. The passive properties are represented by a stiffness factor, $K$, and a damping factor, $B$, that generate passive torque, $T_p$, in proportion to body sway and sway velocity, respectively, relative to the SS. The sensory-related responses generate an active torque, $T_a$, based on a weighted sum of graviceptive (vestibular) and proprioceptive signals with the weights represented by $W_g$ and $W_p$, respectively, and a torque-related feedback mechanism that accounts for low-frequency dynamic behavior (Peterka 2003).

The model assumes that the CNS is able to derive a veridical estimate of body sway from vestibular sensory receptors (otoliths and semicircular canals) and a veridical estimate of body sway relative to the feet from the various proprioceptive sensory receptors (Gardiner et al. 2000). That is, the sensory systems represented in the Fig. 2 model do not include the complex dynamics of individual sensory receptors or the dynamics of different sensory subsystems, such as the semicircular canals, but rather represent the final outcome of the CNS’s processing of motion information encoded by individual receptors. For the vestibular system, this assumption is consistent with experimental results showing that rotational information from the semicircular canals can be combined with linear acceleration and gravity signals from the otolith organs to accurately distinguish head tilt (rotation) with respect to gravity from head translation (linear motion) over a wide range of frequencies (Angelaki et al. 1999, 2001; Merfeld and Young 1995; Merfeld et al. 1999). Similarly, for the proprioceptive system, a huge array of sensory signals with various dynamic properties are available from individual sensors. However, the detailed studies of motion perception by Mergner and colleagues indicate that subjects have a veridical perception of body kinematics derived from proprioception over a wide range of frequencies (Mergner et al. 1983, 1991, 1993). Additional neurophysiological evidence (Bosco and Poppele 2000; Bosco et al. 2000) is available indicating that sensory neurons in the CNS encode more global parameters of limb movement and posture rather than specific muscle and joint parameters.

There is some evidence that force sensors, such as Golgi tendon organs or pressure sensors in the feet, contribute to postural control (Maurer et al. 2001), but this influence seems to be limited to low-frequency corrections (Mergner et al. 2003; Peterka 2003). The Fig. 2 model uses force sensors to detect the corrective torque, $T_c$, applied to the body. The model assumes that the torque signal is low-pass filtered ($1^{st}$-order filter with gain, $K_p$, and time constant, $\tau_c$), fed back, and summed together with the graviceptive and proprioceptive signals to form the sensory error signal, $e$. The sign of the torque feedback is positive. As discussed in Peterka (2003), this form of positive torque feedback provides a mechanism that corrects for low-frequency deviations of body orientation away from vertical and accounts for the low-frequency phase lead and gain decline observed in experimental TFs. When torque feedback is included in the model,
it is no longer necessary to include an integral control factor in the
neural controller, as used in previous models (Peterka 2002; Peterka
and Loughlin 2004), to account for low-frequency data. Others have
suggested roles for positive force feedback in motor control systems
(Duyssen et al. 2000; Geyer et al. 2003; Prochazka et al. 1997a,b).

Inclusion of a torque feedback mechanism does not alter the basic
concept behind the torque normalization hypothesis. Torque feedback
influences low-frequency behavior and provides a relatively small
contribution to \( \varepsilon \) in comparison to the proprioceptive and graviceptive
contributions. In contrast, the proprio- and graviceptive contributions
influence the dynamic behavior of the postural control system over its
entire bandwidth. The experimental results support the limited influ-
ence of torque feedback. Eyes-closed subjects with absent vestibular
function fall without evidence for any corrective action when the SS
is sway-referenced (Nashner et al. 1982) suggest that force feedback is
a minor contributor to stance control. In addition, the analysis of
responses to pseudorandom SS rotations in eyes-closed vestibular-loss
subjects identified \( W_p \) values of 1.0 (Peterka 2002), suggesting that
these subjects were relying entirely on the wide bandwidth informa-
tion available from proprioceptive sensory cues to maintain stability
and that the torque feedback only modulated the low-frequency
behavior.

The weighted sum of vestibular, proprioceptive, and torque feed-
back signals, represented by \( \varepsilon \) in Fig. 2, results in the generation of \( T_a \)
via the action of a “neural controller.” The active torque generated by
the neural controller includes two components, which are respectively
proportional to \( \varepsilon \) (gain constant \( K_p \)) and to the rate of change of \( \varepsilon \) (gain
constant \( K_\varepsilon \)). A time delay, \( \tau_a \), accounts for neural transmission,
processing, and muscle activation and torque generation delays.

For ML body sway with the feet placed at approximately hip width,
the pelvis and legs move as a parallelogram with the pelvis remaining
parallel to the SS, and the upper body, when constrained by a
backboard assembly, tilts with respect to the pelvis when the body is
not aligned with the SS. These mechanics are more complex than a
simple inverted pendulum. Also in contrast to a simple inverted
pendulum, where torque is applied at one joint, torque can be applied
at a combination of ankle and hip joints to control lateral body sway.
However, with regard to the control of COM motion, Winter et al.
(1998) showed that for small sway amplitudes, the equations of
motion that govern a simple inverted pendulum are the same as those
for the more complex lateral sway mechanics. Therefore for our
study, the body was modeled as a linearized single-link inverted
pendulum (Eq. 11, Peterka 2002).

Estimates of the sensory channel weights as well as other postural
control parameters were obtained by fitting the experimental transfer
function data to the model equation given by

\[
\frac{BS(s)}{FS(s)} = \frac{W_p \cdot IPB \cdot NC \cdot TD + IPB \cdot P}{1 - T \cdot N \cdot TD + IPB \cdot P + (W_p + W_g) \cdot IPB \cdot NC \cdot TD}
\]

(2)

where \( s \) is the Laplace transform variable, \( FS \) and \( BS \) are, respectively,
the foot-in-space angular position and body-in-space angular position,
\( IPB = 1/(Js^2 - mg) \) is the inverted pendulum body moment, \( NC = K_p + K_{p,b} \)
is the neural controller model, \( TD = e^{-\tau_a} \) represents the
time delay, \( P = K + B \) models the passive mechanical properties,
and \( T = K_\varepsilon(\tau_a s + 1) \) models the torque feedback low-pass filter. The
feet remain in contact with the support surface, therefore \( FS = SS \).

The biomechanics of the human body are represented by \( I, m, h, \) and
g, which are, respectively, body moment of inertia about an axis at
ankle joint level, body mass (excluding mass of the feet), COM height
of the body above the ankle joints, and gravitational acceleration.
The mass \( m \) was determined by directly weighing each subject, subtracting
2.6% of body mass to account for the mass of the feet (Diffrient et al.
1974). The moment of inertia and COM height was obtained using
anthropometric measures from each subject and formulas from Winter
(2004). In tests using the backboard support, mass and moment of
inertia of the backboard were added to \( m \) and \( J \), respectively, and \( h \)
was adjusted to account for the backboard.

The curve fits of Eq. 2 to the experimental TF data were performed
using a constrained nonlinear optimization implemented in the Matlab
Optimization Toolbox (The MathWorks, Natick, MA) to minimize an
error function based on the normalized difference between model and
experimental TF data (Eq. 9 in Peterka 2002). We found that Eq. 2
provided a good description of TF data in the low- and mid-frequency
range of 0.021 to 1.47 Hz, but data above this frequency range were
not always adequately described. Specifically, the higher frequency
TF data showed greater phase lag than the fit. When TF data at all
frequencies were included in the fit procedure, the fit typically showed
resonant properties in the mid-frequency range that clearly deviated
from TF data in this region. Therefore we chose to focus on the
mid-frequency region that appears to be particularly affected by
interactions associated with sensory integration. Accurate fits of Eq. 2
to the low- and mid-frequency TF data were obtained by excluding
the highest four TF frequencies.

We tried variations of the model to improve the quality of the fit
over the full range of frequencies. The most successful variation was
to add an acceleration component to the neural controller. This
addition accounted for the high-frequency phase but also resulted in
unrealistically large time delay estimates. Because the inclusion of
the acceleration component did not noticeably change the estimates of
parameters other than the time delay, the conclusions of this study
regarding sensory reweighting were not affected by the use of the
simpler model without an acceleration component. It is likely that
higher frequency dynamics are influenced by several mechanisms that
are not fully accounted for in our model. These could include a more
complex neural controller that includes an acceleration component,
separate neural controllers for each sensory channel, different time
delays in each sensory channel, shorter latency contributions from
stretch reflexes (Mirbagheri et al. 2000), muscle activation dynamics,
and dynamics of the muscle/tendon system (Zajac 1989). Future work
is needed to develop a comprehensive model that can explain the full
range of data.

Without loss of generality, we define the sensory channel weighting
factors, \( W_p \) and \( W_g \), so that they represent the relative contributions to
postural control of the graviceptive and proprioceptive systems, re-
spectively. That is

\[
W_p + W_g = 1
\]

(3)

This definition does not place any additional constraint on the model
because a gain factor multiplying the neural controller (i.e., scaling
the values of \( K_p \) and \( K_\varepsilon \)) can always be found such that Eq. 3 is satisfied.
A major goal of this study was to measure \( W_p \) values based on a TF
analysis of responses to the pseudorandom SS stimulus, the “TF-\( W_g \)”
estimates, and to compare these TF-\( W_g \) estimates to \( W_p \) values
obtained from responses to GVS, the “GVS-\( W_g \)” estimates. The
TF-\( W_g \) estimate was obtained by substituting Eq. 3 into Eq. 2,
performing a curve fit of this simplified version of Eq. 2 to obtain an
estimate of \( W_p \) and then calculating \( W_p = 1 - W_g \).

The quality of the model fits was assessed by using model param-
eters derived from each test trial’s TF data to simulate (using Matlab
Simulink) the steady-state time course of the response to the SS
stimulus for that trial. The input to the model was the SS angular tilt
recorded during the test trial. The output was the simulated body sway
angle response. The “residual sway” over one stimulus cycle was
caclulated by subtracting the mean experimental body sway from the
simulated body sway. The proportion of the variance accounted for
by the model was determined by taking the difference between the
mean squared value of the experimental body sway and the mean
squared value of the residual sway and then normalizing by the mean
squared value of the experimental body sway. The expectation was
that on trials with combined GVS and SS stimuli, the residual sway traces
should reveal the isolated responses to the GVS.
If the contribution of passive components (K and B) to the generation of corrective torque is small relative to contribution of active components and if the time delay and neural controller parameters do not change across stimulus conditions, then Eq. 2 shows that $W^g$ is the major determinant of the overall gain of the transfer function and that changes in the value of $W^g$ will only minimally influence the overall shape of the gain or phase functions. Therefore experimental conditions that yield higher transfer function gains without changing the transfer function shape are associated with greater utilization of proprioceptive cues for postural control (i.e., larger values of $W^g$). Because the sensory channel weights represent the relative contribution of each sensory system to postural control, a larger $W^g$ value implies a smaller $W^p$ value because $W^o = 1 - W^o_p$ in our hypothesized formulation of the sensory reweighting hypothesis (Eq. 3).

The Fig. 2 model includes a switch for turning on sway-referencing. When this switch is closed, the body-sway angle, BS, is used to control the angle of the support surface. For ideal sway-referencing, SS = BS, and therefore the body-on-foot angle, BF, which is sensed by the proprioceptive system, is always zero. Therefore information from the proprioceptive system should not contribute to the generation of corrective torque in the sway-referenced condition. However, information from the vestibular system still can contribute to the generation of corrective torque, and, in fact, subjects with normal vestibular function are able to maintain their balance during sway-referencing (Peterka and Black 1990), but subjects with a bilateral vestibular function are not able to maintain their balance during sway-referencing (Peterka and Black 1990), but subjects with a bilateral vestibular loss cannot (Nashner et al. 1982). Based on these considerations, we assume that to generate sufficient corrective torque, $W^g$ must be increased in the sway-referenced condition compared with other conditions where proprioceptive cues contribute to postural control, to compensate for reduced availability of reliable proprioceptive orientation cues. To obtain good dynamic control over balance, it is reasonable to assume that $W^g = 1$ in the sway-referenced condition (Peterka 2002; Peterka and Loughlin 2004).

The model includes a GVS input that is assumed to perturb the afferent activity of vestibular receptors leading to an altered internal vestibular-based estimate of body-in-space position, $bs + bsv_{av}$. The model predicts that the body-sway response to the GVS should be largest in the sway-referenced condition where we assume $W^o = 1$ and should decrease in proportion to $W^o$ in other conditions where proprioceptive cues are also contributing to postural control in which we assume that $W^o > 1$ and $W^o_p = 1 - W^o_p$.

Based on the model predictions, a method was devised to calculate $W^g$ from responses to GVS. Specifically, with the assumption that $W^o = 1$ in the sway-referenced condition and that neural controller parameters are constant across test conditions, an "uncorrected" GVS-$W^g$ estimate in a particular test condition was calculated by dividing the peak GVS response in that condition, obtained from the pulse-triggered average, by the peak GVS response in the sway-referenced condition (Cenciarni 2001). However, because passive mechanical properties do not contribute to the corrective torque in the sway-referenced condition, the uncorrected GVS $W^g$ would be in error if the postural control system does not compensate for the loss of passive torque in the sway-referenced condition. Through simulation studies, we found that the difference between the actual $W^g$ and uncorrected $W^g$, normalized by the actual $W^g$, varied systematically as a linear function of both $K$ and $B$ over the range of $K$ and $B$ values determined from the experimental data. Regression fits were used to calculate the coefficients of this linear function using data from simulation results. Separate regressions were used to fit data for $W^g$, values obtained from peak position and peak velocity responses to GVS. These linear functions were solved to calculate the "corrected GVS-$W^g$" for the given values of $K$, $B$, and the uncorrected $W^g$ obtained from each test trial. Comparisons were then made between both the uncorrected and the corrected GVS-$W^g$ estimates and the TF-$W^g$ estimates obtained from the same trial data. Favorable comparisons would support the Fig. 2 model and the assumptions made in determining values of $W^g$ from both GVS and SS stimulation.

**RESULTS**

COM body-sway traces evoked by four different amplitudes of the pseudorandom SS stimulus are shown in Fig. 3 for a representative subject using a backboard to maintain an approximate inverted pendulum body configuration. In particular, the top trace of each pair of traces in Fig. 3B shows the mean body-sway responses, averaged over the last five pseudorandom stimulus cycles, for each amplitude of the SS stimulus without simultaneous presentation of the GVS. This ML-evoked sway is very similar to AP-evoked sway reported previously (Peterka 2002). Specifically, subjects tended to orient to the support surface, and therefore the body-sway response had a similar time course to the pseudorandom stimulus. The amplitude of the body sway was larger than the SS stimulus amplitude for both the 1 and 2° peak-to-peak stimuli. However, with increasing stimulus amplitude, the body-sway amplitude did not continue to increase in proportion to the stimulus but rather showed a saturation effect where the COM body-sway response was clearly smaller than the stimulus amplitude for the 4° and 8° stimuli.

The top trace of each pair of traces in Fig. 3C shows the mean body-sway responses when the 0.75-mA pulsed GVS was simultaneously presented with the pseudorandom SS stimulus. The overall body-sway response had a similar time course to the response without GVS, but responses to the GVS pulses were superimposed with a positive (rightward) deflection of body sway after each positive GVS pulse and a negative (leftward) body sway after each negative GVS pulse. The arrows in Fig. 3C indicate the characteristic response peak to the third positive GVS pulse in the stimulus cycle.

The bottom trace in each pair of traces in Fig. 3B and C, shows the residual sway after subtracting the sway predicted from model simulations using parameters obtained from fits to TF data for each trial. The residual sway traces for trials shown in Fig. 3B demonstrate that the model accounted for most of the variability in the sway responses apart from some higher-frequency variability that likely remained because the TF fit did not fully account for the higher-frequency TF data. The average of residual error variance across all subjects and all no-GVS trials showed that the model accounted for 92 ± 4% of the sway variance.

The residual sway traces for trials shown in Fig. 3C demonstrate that the model accounted for most of the variability in the sway responses to the SS stimulus. The residual sway traces clearly revealed the individual responses to the GVS. The general trend is evident for an increasing GVS response amplitude with increasing SS stimulus amplitude.

**Transfer functions characterizing responses to SS stimulation**

**EXAMPLE TRANSFER FUNCTIONS.** Figure 4 shows two example transfer functions calculated from body-sway responses of one representative backboard-supported subject to a 2° peak-to-peak pseudorandom SS stimulus. The TF in Fig. 4A was calculated from a trial where no GVS was presented, whereas the TF in Fig. 4B was from a trial with a simultaneous presentation of a 0.75-mA pulsed GVS. There was no obvious distortion of the transfer function gain and phase data caused by the simultaneous presentation of the GVS, and no clear difference between TF gain and phase results obtained from
trials both with and without GVS. The general pattern of the gain and phase changes as a function of stimulus frequency was similar to those shown in Fig. 4 for all subjects and test conditions.

Examples of model curve fits of Eq. 2 to the experimental TF data are also shown in Fig. 4 (—). The model TF equation (Eq. 2) provided good fits to the experimental data for all subjects and all test conditions, both with and without concurrent GVS, over the frequency range of 0.021 to 1.47 Hz (Fig. 4, F). TF data were sometimes not well explained by the model, suggesting that additional dynamic components, which are not included in the Fig. 2 model, are required to account for the higher frequency postural dynamics.

MEAN TRANSFER FUNCTIONS—BACKBOARD VS. FREESTANDING. Figure 5 shows two sets of the mean gain, phase, and coherence functions for the four subjects who performed both backboard-supported and freestanding trials in response to 4 SS amplitudes. These results are similar to results comparing TFs characterizing AP-evoked sway in freestanding and backboard-supported conditions (Fig. 7 in Peterka 2002). The mean ratio of freestanding to backboard TF gains across all frequencies and for all stimulus amplitudes was 0.89, suggesting that subjects did not fully compensate for the added mass and moment of inertia of the backboard. However, the general pattern of TF gain decrease with increasing stimulus amplitude was similar in the backboard-supported and freestanding trials.

Curve fits of Eq. 2 were made to the TFs from individual trials to estimate the parameters of the Fig. 2 model. There was no significant difference in the passive stiffness and damping factors between the freestanding and backboard conditions (K: 2.06 and 1.66 Nm/°; B: 1.02 and 0.72 Nms/° in freestanding and backboard conditions, respectively), indicating that the backboard did not restrict lateral sway even though there was a mechanical mismatch between backboard motion about a single axis at ankle level and the more complex motion associated with lateral body sway. The mean $K_D + K$ and $K_D + B$ values in the backboard condition were 1 and 15% larger, respectively, than in the freestanding condition, indicating that

![Fig. 3. Examples of body-sway responses to perturbations. A: 1 cycle of the pseudorandom SS stimulus waveforms with 1, 2, 4, and 8° peak-to-peak amplitudes. B: each pair of traces shows the mean ML body-sway response (top trace of each pair) to the corresponding pseudorandom SS stimuli shown in A and the residual sway after subtracting the transfer function (TF) model prediction of SS-evoked sway (bottom trace of each pair). Responses are from a representative backboard-supported subject during the no-GVS test condition. —, mean sway, in degrees, obtained from the final 5 cycles of the pseudorandom stimulus. □, 95% confidence interval about the mean. C: each pair of traces shows the mean ML body-sway response (top trace of each pair) to simultaneously presented 0.75-mA GVS (bottom) and pseudorandom SS stimuli shown in A, and the residual sway after subtracting the TF model prediction of SS-evoked sway (bottom trace in each pair). The sway responses to GVS are evident in the residual sway traces. →, peak body-sway response to the 3rd positive GVS pulse identified (···). ← in B, placed at the same point in the SS stimulus cycle as in C to indicate the absence of those peaks when no GVS is delivered.](http://jn.physiology.org/doi/10.1152/jn.00753.2005)
the postural control system partially compensated for the 16% increased mass and 19% increased moment of inertia of the backboard-supported subject derived from responses to a 2° pseudorandom SS stimulus with a concurrently presented 0.75-mA pulsed GVS.

MEAN TRANSFER FUNCTIONS ACROSS GVS CONDITIONS. Figure 6 shows a summary of the mean gain, phase, and coherence functions for the eight backboard-supported subjects in the three GVS conditions at four SS amplitudes. For all GVS conditions, the TF gain functions at frequencies below ~1.6 Hz were largest for the 1° SS stimulus amplitude and progressively decreased with increasing stimulus amplitude. At frequencies above ~1.6 Hz, TF gain values were indistinguishable from one another. For all GVS conditions, the family of phase functions converged at lower frequencies (below ~0.1 Hz) but showed increasing separation with increasing stimulus frequency with phase functions from larger-amplitude SS trials showing less phase lag (less negative) at a given frequency.

Coherence functions show only small changes with SS amplitude and no apparent change with increasing levels of GVS. Coherence functions were indistinguishable from one another at the highest SS amplitudes of 4° and 8°. Coherence values were only slightly lower for the 1° SS amplitude consistent with there being a reduced signal-to-noise ratio of body sway evoked by this very low amplitude SS stimulation.

Coherence function values of unity are indicative of a linear stimulus/response relationship with no noise in the system. The fact that coherence values were large and did not change appreciably with SS stimulus amplitude suggests that the postural response to SS stimulation was well characterized by linear system behavior for each SS stimulus amplitude. However, the overall behavior of the postural control system was nonlinear because gain declined and phase showed some changes with increasing SS amplitude. Furthermore because simultaneous presentation of the pulsed GVS did not alter the qualitative pattern of responses to SS stimulation, GVS can be used to test the sensory-reweighting hypothesis.

MODEL TRANSFER FUNCTION PARAMETERS. For the eight backboard-supported subjects who performed trials that included GVS, Fig. 7 shows the mean values of the TF parameters as function of the SS stimulus amplitude for each of the GVS conditions. The effects on each parameter of the SS stimulus amplitude and GVS condition were tested using repeated-measures ANOVA and the Tukey-Kramer multiple comparisons test.

Statistical analysis revealed that $K_P$, $K_B$, and $\tau_d$ were not significantly affected by changes in the GVS condition ($P > 0.2$). The parameter $K_D$ was significantly lower in the 0.25-mA GVS condition ($P < 0.05$) compared with the 0.75-mA GVS condition, although the difference in mean $K_D$ values between GVS conditions was very small. The parameters $K_P$, $K_D$, and $\tau_d$ showed significant changes with increasing SS stimulus amplitude ($P < 0.003$). $K_P$ and $K_D$ increased, whereas $\tau_d$ decreased with increasing SS stimulus amplitude.

The median values of torque feedback parameters, $K_T$ and $\tau_T$, are also shown in Fig. 7. The distributions of these parameters were highly skewed with half the values of $K_T$ between 0.02 and 0.09°/Nm and of $\tau_T$ between 2 and 12 s. These parameters exerted their largest influence on the TF dynamics at frequencies below ~0.1 Hz where they produced a gain decline and phase advance. The limited amount of low-frequency
TF data likely reduced the accuracy with which these parameters were identified, resulting in the skewed distributions.

The proprioceptive channel weighting factor, $W_p$, showed a large and significant decrease with increasing SS stimulus amplitude. Post hoc analysis revealed that $W_p$ was significantly different at each SS amplitude from the values at the other SS amplitudes. This effect was not found for any of the other model parameters. The mean $W_p$ (across all subjects and GVS conditions) was 0.76 at the 1° SS amplitude and decreased to 0.36 at the 8° amplitude. Also evident in Fig. 7, the mean $W_p$ values obtained during simultaneous presentation of the 0.75-mA GVS were consistently larger than the mean $W_p$ values in the no-GVS or 0.25-mA GVS conditions, although the difference was significant only between the 0.25- and 0.75-mA GVS conditions ($P < 0.05$). There was no significant difference in $W_p$ values between the no-GVS and 0.25-mA GVS conditions. Across all SS amplitudes, the mean value of $W_p = 0.62$ in the 0.75-mA GVS condition was on average 10% greater than in the no-GVS or 0.25-mA GVS condition.

Figure 8 shows mean $W_g$ values based on $W_p$ estimates from TF curve fits and the relation $W_g = W_p - 1$. The sensory-reweighting hypothesis will be supported if GVS responses and corresponding GVS-$W_g$ estimates show a similar dependency on SS amplitude.

Responses to galvanic stimulation

Figure 9 shows examples of responses to positive GVS pulses determined by calculating a pulse-triggered average from sway position data (Fig. 9A) and from sway-velocity data (Fig. 9B) from a representative subject. The 0.75-mA pulsed GVS (Fig. 9C) was delivered concurrently with a 2° pseudorandom SS stimulus. In all cases, the position pulse responses to the GVS had a characteristic peak that was directed toward the anodal electrode. A second peak, smaller and in the opposite direction, sometimes followed the first peak in agreement with previous studies (Hajos and Kirchner 1984). The velocity pulse response had a biphasic waveform with the first peak always toward the side of the anode. Responses to positive and negative pulses were similar to each other with only the direction differing.

For a given SS condition and GVS amplitude, the magnitudes of the peak GVS responses to positive and negative pulses were not significantly different from one another for either the position ($P > 0.31$) or velocity responses ($P > 0.96$) as determined by repeated-measures ANOVA. Therefore the peak response magnitudes from positive and negative GVS pulses were combined to obtain a single peak position and a single peak velocity magnitude in each test condition which we refer to as the GVS peak position and GVS peak velocity responses.

The time to the first peak was, on average, 1.26 ± 0.14 and 0.83 ± 0.08 (SD) s for position and velocity responses, respectively. The peak amplitude of GVS responses increased with increasing SS amplitude. Body-sway responses from a representative subject to a 0.75-mA positive galvanic pulse are shown in Fig. 10 during all of the SS conditions tested. The body-sway response to the galvanic stimulus was smallest for TF data likely reduced the accuracy with which these parameters were identified, resulting in the skewed distributions.
a fixed surface, increased with increasing pseudorandom SS amplitude, and was largest in the sway-referenced SS condition. The peak amplitudes measured from body sway-velocity responses showed an analogous trend with changes of SS condition.

Figure 10 also shows an example of a control trial (no-GVS) response during concurrent pseudorandom SS stimulation with a 4° amplitude. For this control trial response calculation, the pulse-triggered average was computed as if GVS pulses had occurred in a normal sequence. The no-GVS pulse-triggered average in Fig. 10 shows that no false peak was present, consistent with there being no unexpected interaction between the simultaneously presented pseudorandom SS stimulus and GVS pulses. In addition, the low amplitude of this no-GVS...

FIG. 7. Summary of mean model parameters derived from curve fits to TF data from each of the 4 pseudorandom SS stimulus amplitudes (1, 2, 4, and 8° peak-to-peak) and the 3 GVS conditions (0, 0.25, and 0.75 mA). Parameter estimates for $W_p$, $K_p$, $K_T$, $B$, and $\tau$ were obtained by averaging model parameters obtained from 8 backboard-supported subjects using curve fits of Eq. 2 to individual subject transfer function data as shown in Fig. 3 for 1 representative subject. Error bars (±SD) are shown for data from the 0-mA GVS condition. The SDs of parameters on other GVS conditions were similar. The median values are shown for the parameters $K_T$ and $\tau$. The mass, moment of inertia, and COM height for the 8 subjects was 84.3 ± 11.1 (SD) kg, 85.2 ± 17.3 kg m², and 0.92 ± 0.06 m. These values include the contribution of the backboard.

FIG. 8. Mean graviceptive sensory channel weight estimates, $W_g$, as a function of pseudorandom SS stimulus amplitude. $W_g$ values were derived from the model parameter $W_p$ obtained from curve fits of Eq. 2 to TF data transfer function data using the relationship $W_g = 1 - W_p$. $W_g$ values were obtained in each of the 3 GVS conditions (0, 0.25, and 0.75 mA). Error bars (±SE) are shown for data from the 0.75-mA GVS condition. Error bars for the other GVS conditions were of comparable magnitude.

FIG. 9. Example of a ML body-sway response to a 0.75-mA pulsed GVS obtained by pulse-triggered averaging of sway data from a typical subject. A pseudorandom SS stimulus with 2° peak-to-peak amplitude was delivered concurrently with the pulsed GVS. A: characteristic average body-sway position response to the 20 positive GVS pulses delivered during the last 5 cycles of the pseudorandom SS stimulus. The response was quantified by measuring the peak amplitude and time of the peak relative to the onset of the GVS pulse. B: characteristic biphasic average body-sway velocity response to the 20 positive GVS pulses delivered during the last 5 cycles of the pseudorandom SS stimulus. The response was quantified by measuring the amplitude of the 1st peak after the GVS pulse and time of that peak relative to the onset of the GVS pulse. C: time course of the 0.75-mA GVS pulse. The time base of 6.05 s is the time between the onsets of 2 consecutive pulses of alternating polarity.
waveform indicates that body-sway responses evoked by the concurrent SS stimulus were effectively canceled by the pulse-triggered averaging procedure. Similar results were obtained for the pulse-triggered average of body-sway velocity (not shown) in no-GVS control trials. The absent GVS pulse response (position and velocity) obtained in no-GVS control trials was consistent across all subjects.

The summary of GVS peak position and GVS peak velocity responses is shown in Fig. 11 for responses averaged across subjects at each test condition. The peak responses were smallest when subjects stood on a fixed SS (0°), and both position and velocity peak responses increased with increasing SS stimulus amplitude. Peak responses were consistently larger in the sway-referenced SS condition than in any other condition for a given GVS amplitude.

ESTIMATES OF Wg FROM RESPONSES TO GVS. Four sets of uncorrected Wg estimates were obtained for each SS condition by calculating the ratio of the GVS peak response on a given SS condition to the GVS peak response on the sway-referenced SS condition. Two sets were from the peak position responses and two sets were from the peak velocity responses to the 0.25- and 0.75-mA pulsed GVS. These four sets of estimates of Wg are plotted in Fig. 12 as a function of the pseudorandom SS amplitude. Results were similar for the Wg estimates derived from peak position data and peak velocity data. The major qualitative difference between Wg estimates from 0.25- and 0.75-mA GVS is that the Wg values from the 0.25-mA GVS were noticeably smaller than the corresponding estimates from the 0.75-mA GVS. The trend of increasing GVS-Wg estimates with increasing SS stimulus amplitude is similar to the trend seen in TF-Wg estimates for SS amplitudes ranging from 1° to 8° (Fig. 8).

Comparison of Wg estimates from TF and GVS analysis

Comparisons of both corrected and uncorrected GVS-Wg estimates with corresponding TF-Wg estimates are shown in Fig. 13. Paired comparisons of both the corrected and uncorrected GVS- and TF-Wg estimates showed high correlations ranging from 0.58 to 0.90 with the correlations being the same or slightly greater for the uncorrected compared with the corrected GVS-Wg data (Fig. 13). Correlations were lower for the comparisons based on 0.25-mA GVS responses than for 0.75-mA GVS responses, consistent with higher variability in GVS responses to lower-amplitude GVS pulses. Correlations were higher for GVS-Wg estimates based on peak velocity than for estimates based on peak position.

On average, the values of the corrected GVS-Wg estimates were larger than the uncorrected estimates, but the uncorrected GVS-Wg estimates were closer to the TF-Wg estimates. This result suggests that the assumptions made in deriving the correction factor for the GVS-Wg estimates were incorrect and that no correction factor was needed for the calculation of the GVS-Wg values. The Wg correction was based on the assumption that neural controller properties remained constant across test conditions. Therefore the net amount of corrective torque generated in relation to body sway would be less in the sway-referenced condition because there is no passive corrective torque contribution in the sway-referenced condition.
However, if the torque normalization hypothesis applies to the sway-referenced condition, then the postural control system may have altered its properties (i.e., increased neural controller gain) to compensate for the loss of the passive torque contribution. If such a compensation occurred, then uncorrected GVS-Wg estimates would not need to be corrected for the loss of passive torque in the sway-referenced condition.

Paired $t$-test showed no significant differences ($P > 0.19$) between uncorrected 0.25-mA GVS-Wg values and TF-Wg values for the GVS-Wg values derived from both peak position and peak velocity measures. However, there were significant differences ($P < 0.003$) between uncorrected 0.75-mA GVS-Wg and TF-Wg values. The GVS-Wg values, based on peak position and peak velocity measures, were on average 0.07 larger than the TF-Wg values.

Linear regression analyses were applied to uncorrected GVS-Wg and TF-Wg estimates using GVS-Wg estimates derived from both GVS amplitude conditions (0.25 and 0.75 mA) and from sway-position (Fig. 13A) and sway-velocity data (Fig. 13B). The regression analyses were performed using the paired-Wg estimates from each individual subject for each SS stimulus condition even though Fig. 13 shows only the mean ($\pm$ SE) uncorrected GVS-Wg and mean ($\pm$ SE) TF-Wg estimates obtained at the four pseudorandom SS amplitudes. For three of the four sets of data shown in Fig. 13, the regression lines that best fit the data had intercepts that were not significantly different from 0 ($P > 0.12$), and the 95% of confidence limits on the linear regression slopes included the slope of 1. The exception was the Wg comparison based on the 0.25-mA GVS sway-position data. Considering the results from both the paired comparisons and linear regressions, the closest match between TF-Wg and uncorrected GVS-Wg estimates was obtained for the 0.25-mA GVS peak-velocity data.

**DISCUSSION**

The current study was performed to quantitatively test the sensory-rewriting hypothesis (Peterka 2002), which postulated that the decreased responsiveness to larger-amplitude SS stimuli was caused by both a decrease in the contribution of proprioceptive information and a corresponding increase in the contribution of graviceptive sensory information to postural control. If this hypothesis is true and if the vestibular system is the primary source of graviceptive information used for postural control, then a direct vestibular stimulus provided by pulses of galvanic current should evoke body-sway responses in proportion to the predicted contribution of graviceptive or more specifically vestibular cues.

A number of assumptions and practical considerations were required to develop a protocol for testing the sensory-rewriting hypothesis. These include the applicability of the sensory-rewriting hypothesis to the control of ML sway for which GVS evokes a robust sway response, the separability of sway responses to concurrently applied GVS and support surface stimuli, and the validity of the assumptions made in the calculation of graviceptive weights from responses to GVS and SS stimuli. These considerations are discussed in the following text and are followed by additional discussion of interaction.

**FIG. 12.** Mean uncorrected graviceptive sensory channel weight estimates, $W_g$ as function of the SS condition (fixed SS, 1, 2, 4, and 8° pseudorandom SS stimulus amplitudes) are shown for the 2 levels of GVS amplitude (0.25 and 0.75 mA). Uncorrected weights for each subject on each SS condition were obtained by normalizing the peak GVS response magnitude by the peak GVS response magnitude obtained in the sway-referenced SS condition. The $W_g$ values obtained using the 0.75-mA GVS are from 7 backboard-supported subjects because 1 of the subjects was unable to complete the sway-referenced condition with the 0.75-mA pulsed GVS. A: mean uncorrected $W_g$ estimates from GVS peak position data. B: mean uncorrected $W_g$ estimates from GVS peak velocity data.
effects between GVS and SS stimuli, and a comparison of our results with previous evidence of sensory reweighting.

**ML postural dynamics resemble AP dynamics**

Results shown in Figs. 3–8, compared with the AP results from a previous study (Figs. 3, 5, 6, 10, and 14 in Peterka 2002), confirmed that ML sway evoked by SS tilts had properties similar to AP-evoked sway. Specifically, ML body-sway responses to increasing amplitudes of SS stimuli showed a saturation phenomenon (Fig. 3). Like the AP responses, this saturation was not likely due to some static nonlinearity, which would be expected to cause a reduction of coherence function values at increasing SS amplitudes. Results showed that the coherence functions remained essentially unchanged or even increased slightly with increasing SS amplitude (Fig. 6). This implies that the stimulus/response behavior was essentially linear at each SS amplitude tested even though the overall behavior was clearly nonlinear because the overall responsiveness to the SS stimulus declined with increasing SS amplitude. Additionally, the overall shape of ML transfer function gain and phase curves (Figs. 4–6) were similar to those derived from AP-evoked sway and showed only small changes in shape with changing SS amplitude.

Curve fits of Eq. 2 provided a very good description of the data over a frequency range of 0.021 to 1.47 Hz (Fig. 4). The values of the model parameters derived from these curve fits showed systematic changes with SS amplitude (Fig. 7) that were very similar to those previously shown for AP-evoked sway (Fig. 10 in Peterka 2002). A minor difference between ML and AP results was that the mean value of \( W_g \) was \( \sim 37\% \) higher for ML than AP results, indicating that subjects tend to make greater use of proprioceptive cues for controlling ML sway than for AP sway under the conditions tested. A greater reliance on proprioceptive information is potentially consistent with proprioceptive cues being more sensitive and accurate for ML compared with AP sway due to the involvement of a greater number of joints and muscles during ML sway. Day et al. (1993) showed that ML sway involves both ankle and hip joints, and the hip joint motion increases with increasing stance width. They speculated that the reduction in GVS-induced sway observed at greater stance widths could be due to increased reliance on proprioceptive information because this information becomes more accurate when more joints and larger joint motions are involved in the sway.

The similarities between the results of ML and AP sway evoked by pseudorandom SS stimulation suggest that there are similar underlying mechanisms involved in the control of balance in both directions of sway. Hence we concluded that the original sensory-reweighting hypothesis developed from AP body-sway experiments also applies to postural mechanisms controlling ML sway.

**Separability of SS and GVS responses**

Testing of the sensory-reweighting hypothesis relied on our ability to separate responses to simultaneously presented GVS and SS stimuli. The stimuli were specifically designed to be mathematically uncorrelated (Fig. 1) to facilitate later separation of the responses to each stimulus component. For uncorrelated stimuli, the superposition principle (Bendat and Piersol 2000) guarantees that responses to the two stimuli are separable if the response to each stimulus component is linearly related to that component.

Our results and the results of others suggest that there is good reason to expect linear responses from GVS and SS stimuli. A previous study found an approximately linear dependence on galvanic current amplitude and the amount of GVS-evoked body sway (Hajos and Kirchner 1984). The high coherence function values derived from ML-evoked sway responses to SS stimuli (Figs. 5 and 6) suggest that the linearity assumption is justified for ML sway evoked by each amplitude of the SS stimulus. Results of the analyses of sway responses to simultaneously presented GVS and SS stimuli and comparisons to control-trial results (no-GVS condition) suggest that the responses to GVS and SS stimuli were separable. There were no obvious distortions of TF estimates due to simultaneous presentation of the GVS (Figs. 4 and 6). When the pulse-triggered averaging for GVS analysis was applied to SS stimulation trials performed without GVS, there was no false pulse response detected even when the SS amplitude was large (control trials responses in Figs. 10 and 11).

**Estimating \( W_g \) from GVS responses**

Previous experimental results suggest that the graviceptive contribution to postural control increases in the sway-referenced condition to ensure that sufficient corrective torque is generated to maintain balance (Peterka and Loughlin 2004). If we assume that \( W_g = 1 \) during sway-referencing, the model predicts that the amplitude of GVS-evoked sway in the sway-referenced condition should be larger than in any other condition and should be indicative of the full contribution to body sway caused by the GVS-induced perturbation to vestibular afferent firing rate. Then in any other condition, the reduction in the amplitude of GVS-evoked sway is indicative of a reduction in \( W_g \) and “uncorrected” \( W_g \) estimates can be obtained by taking the ratio of the GVS pulse-response amplitude in that condition to the pulse-response amplitude in the sway-referenced condition.

The potential error in this method for estimating \( W_g \) is that muscle/joint mechanics contribute passive torque in all conditions except the sway-referenced condition. In the sway-referenced condition, the surface tracks the rotational body-sway motion, and there is no change in body orientation relative to the surface over time. Because \( BF = 0 \) in the model, the model predicts that the muscle/joint mechanics make no passive torque contribution. If the nervous system does not compensate for the loss of the passive torque component during sway-referencing, the GVS response amplitude in the sway-referenced condition will be too large, and the uncorrected GVS-\( W_g \) estimates will be too small.

Alternatively, if the nervous system does fully compensate for the loss of passive torque in the sway-referenced condition, then the “uncorrected” GVS-\( W_g \) estimates would provide an accurate measure of \( W_g \), whereas the corrected measure will be too large as also shown in Fig. 13. Such a compensation would be consistent with the torque normalization hypothesis (see INTRODUCTION) and could occur by increasing the neural controller gain. We currently have no method for measuring the neural controller parameters in the sway-referenced condition to determine whether there was a compensation for the loss of
passive torque. However, the results in Fig. 7 show small increases in the neural controller gain factors $K_p$ and $K_D$ with increasing SS amplitude, suggesting that the nervous system is able to adjust the neural controller gain. Furthermore, the uncorrected GVS-$W_g$ estimates were more closely matched to the TF-$W_g$ estimates than were the GVS-$W_g$ estimates corrected for the assumed loss of passive torque in the sway-referenced condition (Fig. 13). A parsimonious interpretation of these results is that the torque normalization does occur in the sway-referenced condition, and therefore the uncorrected $W_g$ estimates are more accurate than the corrected $W_g$ estimates.

Even though the uncorrected GVS-$W_g$ estimates were closer to the TF-$W_g$ estimates than the corrected GVS-$W_g$ estimates, there were still some systematic differences between the uncorrected 0.75-mA GVS-$W_g$ estimates and TF-$W_g$ estimates (Fig. 13, right). Specifically, the 0.75-mA GVS-$W_g$ estimates were slightly larger than the corresponding TF-$W_g$ estimates. Such a discrepancy could occur if the peak response to the 0.75-mA GVS obtained on the sway-referenced SS was biased toward a lower value. This may have occurred for responses to 0.75-mA, but not 0.25-mA pulses, because responses to the 0.75-mA pulses in the sway-referenced condition brought subjects close to the limits of stability. Indeed one subject was unable to complete a full sway-referenced trial with the 0.75-mA GVS. Such a large response may have triggered the participation of other nonvestibular sensory systems, such as somatosensory cues signaling excessive sway based on pressure cues from the feet or loading/unloading cues in the legs (Dietz 1998; Maurer et al. 2001) and therefore reduced the sway-evoked responses primarily under three conditions: tasks performed with limited visual and/or proprioceptive cues (Day and Bonato 1995; Day et al. 1993; Fitzpatrick et al. 1994; Nashner and Wolfson 1974; Welgampola and Colebatch 2001), when subjects stand on a moving surface (Inglis et al. 1995), and when pathology limits the somatosensory contribu-

**Interactions between SS and GVS responses**

The primary interaction of interest in our study was the effect of SS stimulus amplitude on the response to the GVS. The qualitative prediction of the sensory-reweighting hypothesis was that the body-sway response to the pulsed GVS should increase with increasing SS amplitude. This prediction was confirmed (Figs. 10 and 11). Additionally, the model-based interpretation of experimental results allowed a quantitative test of the sensory-reweighting hypothesis by comparing estimates of $W_g$ from the TF analysis of responses to SS stimulation with $W_g$ estimates from the GVS analysis. The comparison of TF $W_g$ estimates with GVS $W_g$ estimates (Fig. 13) showed a close correspondence and therefore quantitatively confirms the sensory-reweighting hypothesis.

A secondary interaction between SS condition and GVS responses was also observed. The estimates of $W_g$ derived from TFs during concurrent application of the 0.75-mA GVS were larger than $W_g$ estimates from the no-GVS or 0.25-mA GVS conditions (Fig. 7). No other model parameter showed any systematic influence of concurrent GVS presentation. The larger $W_g$ values mean that subjects relied more on proprioceptive cues and less on graviceptive cues during trials that concurrently presented the larger amplitude GVS. Such a result indicates that the GVS stimulus produced a change in the responses to SS stimulation. A change toward increased reliance of proprioceptive information is consistent with the general predictions of a recently developed optimal control model of postural control (van der Kooij et al. 1999, 2001) and is consistent with other motor-control models (van Beers et al. 1999, 2002). These models predict that in obtaining an optimal internal estimate of important system variables, such as the position and velocity of body or limb movement, the nervous system weights sensory information in inverse proportion to the amount of variability (noise) in the sensory-channel signals. Therefore adding significant “noise” to the vestibular channel by applying the larger amplitude GVS caused a detectable shift toward greater use of proprioceptive information. Similarly, increasing the SS stimulus amplitude effectively increases the variability in the proprioceptive channel, producing a reduction in use of proprioceptive cues for postural control with increasing SS amplitude.

**Comparison with previous studies**

The idea that sensory reweighting and sensory substitution contribute to human postural control is not new. However, consideration of the feedback model structure (Fig. 2) and the torque normalization hypothesis provides a quantitative understanding of the benefits of sensory reweighting. Specifically, sensory reweighting affords the ability to reduce the effect of an external perturbation while preserving stability by maintaining a constant amount of corrective torque in relation to sway about the upright position (see Eq. 1).

Previous studies have identified many qualitative examples that are consistent with the idea that the nervous system alters the sources of sensory orientation information used for balance control as environmental, biomechanical, and pathological conditions change. Studies have shown increases in GVS-evoked responses primarily under three conditions: tasks performed with limited visual and/or proprioceptive cues (Day and Bonato 1995; Day et al. 1993; Fitzpatrick et al. 1994; Nashner and Wolfson 1974; Welgampola and Colebatch 2001), when subjects stand on a moving surface (Inglis et al. 1995), and when pathology limits the somatosensory contribu-
It is clear from several studies that vestibular information is most relevant to the postural control system when it is critical for maintaining balance (Day et al. 2002; Fitzpatrick et al. 1994; Peterka 2002; Welgampola and Colebatch 2001). That is, in conditions where information from other sensory systems is compromised, a sensory reweighting occurs, causing an increased reliance on vestibular information while decreasing reliance on other sensory information. The increased reliance on vestibular information is supported by the increased responsiveness to GVS (Fitzpatrick et al. 1994; Welgampola and Colebatch 2001) and by decreased responsiveness to other sensory cues (Ivanenko et al. 1999). In fact, when all three primary sensory inputs (visual, proprioceptive, and vestibular) are available and are providing veridical cues regarding body orientation in space, it is generally accepted that the vestibular system contributes less than the visual or proprioceptive systems. For example, using very-small-amplitude perturbations from SS or visual surround motions that were typically not perceived by the subjects, Peterka (2002) showed that the proprioceptive, visual, and vestibular systems contributed ~50, 35, and 15%, respectively, to quiet stance control. Peterka (2002) also demonstrated experimental results consistent with sensory reweighting for a wide range of conditions that manipulated visual, proprioceptive, and combinations of these two orientation cues.

Others have considered models and mechanisms to account for sensory interactions for postural control. Various related models have been used to understand the influence of different perturbations (visual, light touch on a moving surface, and combinations of the two) on stance control (Dijkstra et al. 1994; Giese et al. 1996; Jeka et al. 1998, 2000; Kiemel et al. 2002; Oie et al. 2002). These models differ from the Fig. 2 model in that they do not consider the influence of time delay in the feedback system, and they characterize the effect of a perturbation on a system that is a priori stable. In contrast, the stability of the Fig. 2 model depends on the regulation of the sensory integration process represented by the selection of sensory channel weights.

Building on earlier studies of the perception of head/neck movements (Mergner et al. 1983, 1991, 1993), Mergner and colleagues have developed a model that accounts for body sway evoked by sinusoidal external force perturbations in different surface conditions (Mergner et al. 2003). This model includes multiple nonlinear threshold elements that alter the contribution of different sensory systems to corrective torque generation as a function of stimulus conditions and body sway. Effectively, these thresholds provide a mechanism for changing weights, and therefore there is some resemblance to the Fig. 2 model.

Optimal control models have also been developed recently that include high dimensionality and predictive control (van der Kooij et al. 1999, 2001). In contrast, the Fig. 2 model is of low dimensionality and does not include prediction. Prediction could play a role in the responses to our pseudorandom stimulus because the stimulus is, in fact, deterministic. Even if it was not, the postural control system could still use prediction to take advantage of the statistical properties of the stimulus and internal knowledge about body dynamics to improve performance and to compensate for feedback time delay. However, the Fig. 2 model provided a good description of the experimental data without including any predictive mechanism.

**Summary**

We have demonstrated that GVS can be used to quantitatively measure the vestibular contribution to postural control under steady-state conditions. In addition, we have shown that our indirect, model-based estimate of $W_g$, based on the TF analysis of SS-evoked body sway, can also be used to quantify the vestibular contribution to postural control. In deriving our $W_g$ estimates, we made several assumptions that we considered to be reasonable but that could have been potentially untrue. Effectively these assumptions represent hypotheses about the functional structure of the postural control system and about how experimental manipulations, such as sway-referencing, alter the sensory information available for balance control. The fact that there was a very close correspondence between the $W_g$ estimates obtained using very different analysis methods supports the validity of our assumptions. These assumptions include: 1) steady-state body sway evoked by surface rotations is well characterized as a response of a linear system at any given stimulus amplitude; 2) the overall nonlinearity of body-sway responses to concurrently applied GVS and SS stimuli are sufficiently linear to insure separability of these responses when these two stimuli are mathematically uncorrelated; 3) surface sway-referencing effectively eliminates the contribution of proprioceptive cues to the generation of corrective torque for postural control with proprioceptive defined as sensory information signaling the kinematic aspects of body motion relative to the surface; and 5) the model in Fig. 2 provides a quantitative representation of the human postural control system that is consistent with the available experimental data.

**References**


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