Dynamic Regulation of Sensorimotor Integration in Human Postural Control

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Submitted 28 May 2003; accepted in final form 10 September 2003

Peterka, Robert J. and Patrick J. Loughlin. Dynamic regulation of sensorimotor integration in human postural control. J Neurophysiol 91: 410–423, 2004. First published September 17, 2003; 10.1152/jn.00516.2003. Upright stance in humans is inherently unstable, requiring corrective action based on spatial-orientation information from sensory systems. One might logically predict that environments providing access to accurate orientation information from multiple sensory systems would facilitate postural stability. However, we show that, after a period in which access to accurate sensory information was reduced, the restoration of accurate information disrupted postural stability. In eyes-closed trials, proprioceptive information was altered by rotating the support surface in proportion to body sway (support surface “sway-referencing”). When the support surface returned to a level orientation, most subjects developed a transient 1-Hz body sway oscillation that differed significantly from the low-amplitude body sway typically observed during quiet stance. Additional experiments showed further enhancement of the 1-Hz oscillation when the surface transitioned from a sway-referenced orientation to a reverse sway-referenced motion. Oscillatory behavior declined with repetition of trials, suggesting a learning effect. A simple negative feedback-control model of the postural control system predicted the occurrence of this 1-Hz oscillation in conditions where too much corrective torque is generated in proportion to body sway. Model simulations were used to distinguish between two alternative explanations for the excessive corrective torque generation. Simulation results favor an explanation based on the dynamic reweighting of sensory contributions to postural control rather than a load-compensation mechanism that scales torque in proportion to a fixed combination of sensory-orientation information.

INTRODUCTION

Human bipedal stance is inherently unstable. Small deviations from a perfect upright body position result in a gravity-induced torque acting on the body, causing it to accelerate further away from the upright position. Corrective torque must be generated to counter the destabilizing torque due to gravity. This process of corrective torque generation is not fully understood and controversy remains regarding the organization of sensory and motor systems contributing to postural stability. Numerous studies have demonstrated that quiet stance posture can be perturbed by stimulation of various sensory systems (Day et al. 1997; Horak and Macpherson 1996; Johansson and Magnusson 1991; Kavounoudias et al. 1999; Lee and Lishman 1975; Peterka and Benolken 1995). These results suggest that active feedback-control mechanisms contribute to corrective torque generation based on body motion detected by sensory systems.

However, the organization of these feedback-control mechanisms is unknown, and there is a question about whether feedback mechanisms play a dominant or a minor role in postural control. Some studies have concluded that feedback control alone is insufficient to explain human postural control (Fitzpatrick et al. 1996). Others have suggested an important role for predictive mechanisms (Morasso et al. 1999; van der Kooij et al. 1999) or have concluded that nonlinear mechanisms combining open- and closed-loop control are used for stance control (Collins and De Luca 1993). Additionally, feedback-control limitations demonstrated in other motor systems (Bennett et al. 1994) suggest that similar limitations may apply to postural control. In the following text, we consider these studies and the different hypothesized control strategies, and then present evidence that a dynamically regulated form of feedback control likely does make a major contribution to postural control.

Collins and DeLuca (1993) postulated a combination of open- and closed-loop control to explain their experimental findings. They introduced a new analysis technique called stabilogram diffusion analysis, which measures the average similarity of the center-of-pressure signal at points in time separated by different time intervals. This analysis showed that quiet stance behavior is characterized by “persistence” over short time intervals and “anti-persistence” over longer time intervals. A possible explanation offered for this two-part behavior was that, over short time intervals, the postural system is not controlled (i.e., it operates open-loop), whereas at longer time intervals, there is active feedback control (i.e., closed-loop control). This hypothesized dynamic switching between open- and closed-loop control implies that the overall system cannot be completely characterized as a feedback-control system.

However, a subsequent study (Peterka 2000) showed that a feedback-control model could indeed account for the persistence and anti-persistence behavior revealed by stabilogram diffusion analysis. That is, it is not necessary that the system switch between open- and closed-loop control to explain the experimental findings from stabilogram diffusion analysis of quiet stance center-of-pressure measurements; a simple feedback-control system is sufficient.

Fitzpatrick et al. (1996) concluded from their experimental results that feedback control did not fully account for the torque required to maintain stance. In performing their study, Fitzpatrick et al. made the implicit assumption that various sensory systems make a fixed contribution to torque generation independent of environmental conditions or the reliability/accuracy of the various sensory measures of relative body motion. Based on this assumption, the corrective torque con-
distribution from individual sensory systems was identified in separate experiments and summed to determine the total torque derived from sensory feedback mechanisms. The total torque was found to be insufficient to maintain stance, leading to the conclusion that feedback mechanisms alone are insufficient to explain our ability to maintain stance.

Investigation of the stretch-reflex contribution to limb stabilization has also demonstrated possible limitations in feedback control (Bennett et al. 1994). The results in Bennett et al. (1994) showed that stretch-reflex feedback control can only make a limited contribution to limb stabilization because this reflex (with essentially fixed dynamic properties of the limb, muscles, and stretch receptors) becomes unstable even with fairly low feedback gain. That is, a much higher reflex gain would be needed for adequate compensation of a load disturbance, but this cannot be achieved by a stretch reflex because high gains produce instability. This occurs even though the time delay is relatively short (25 ms transmission delay plus an additional delay with similar magnitude due to muscle activation and force development) (Bennett et al. 1994). Longer time delays exacerbate the stability problem in feedback-control systems (Jacks et al. 1988).

However, a recent study (Peterka 2002) showed that the dynamic behavior of human stance control, in a variety of environmental conditions and in response to various perturbations, could be accounted for by a sensorimotor feedback-control mechanism that did not include predictive or feed forward control and did include a relatively long time delay of 150–200 ms. Two key interpretations of the experimental results from this study illustrate why feedback control can be a dominant contributor to stance control despite the conclusions of previous studies indicating limitations in feedback control (Bennett et al. 1994; Fitzpatrick et al. 1996).

First, the experimental results of Peterka (2002) were consistent with the interpretation that the source of sensory information used for torque generation is dynamically regulated and changes as the environmental conditions change. So for example, during eyes-closed stance on a level fixed surface, subjects use primarily proprioceptive sensory cues, which signal body motion relative to the feet, but if the surface is moving, subjects discount the proprioceptive information and shift toward increased reliance on graviceptive information. The ability of the postural control system to dynamically regulate its source of sensory information was not considered by Fitzpatrick et al. (1996) and likely led to an underestimate of corrective torque generated by feedback mechanisms.

Second, the experimental results of Peterka (2002) were consistent with a negative feedback-control mechanism where the dominant components of the corrective torque are proportional to a summation of angular position and angular velocity of body sway, and where there is a time delay of 150–200 ms in the system. This long time delay suggests that quiet stance is regulated by a higher-order control that requires time for the nervous system to extract and combine information from various sensory sources and to generate a motor command. Even though a 150- to 200-ms delay is long in comparison to delays associated with a direct stretch reflex (Bennett et al. 1994), this long delay is compatible with postural stability if the corrective torque is an appropriate function of body-sway motion.

The conclusion that sensory contributions to postural control are dynamically regulated was obtained from a model-based interpretation of experimental data (Peterka 2002). The model did not include predictive or feed-forward mechanisms but was based entirely on a feedback mechanism where corrective torque is generated in relation to a weighted summation of orientation cues from various sensory systems. A key feature of this feedback model is that the relative weights can and do change, depending on the environmental conditions and available sensory information.

It was shown that sensory-channel weighting factors and the time delay of this model could be estimated from body sway evoked by continuous perturbations applied to the support surface and visual surround (Peterka 2002). For low stimulus amplitudes (0.5 and 1° peak-to-peak stimulus amplitudes) that only weakly perturbed the system away from quiet-stance conditions, there were only small variations in time delay estimates in different test conditions. Therefore the 150- to 200-ms delay appears to be a rather fixed feature that is independent of the particular sensory cues available for postural control. In contrast, the sensory-channel weight estimates, obtained in steady-state conditions, showed large systematic changes as a function of environmental and stimulus conditions.

According to the feedback model-based interpretation of the experimental data in Peterka (2002), the relative contributions of different sensory sources to postural control vary widely in different environmental conditions. This leads to the prediction that there should be functional consequences for postural stability in situations where environmental conditions change suddenly. That is, unless the sensory contributions, represented by sensory-channel weights, adjust instantaneously to environmental changes, a transient period might exist where either too little or too much corrective torque is generated due to sensory weighting that is improper for the new environmental conditions. Although the time delay shows minimal variation with environmental conditions, the time delay has a strong influence over the resonant properties of the postural-control system when too little or too much corrective torque is generated.

There is some experimental evidence demonstrating transient instability after environmental changes. This evidence contradicts the logical prediction that stability should increase with access to additional accurate sensory-orientation cues, as occurs in steady-state conditions. [For example, in steady-state conditions, body-sway levels are less during eyes-open compared with eyes-closed stance on a fixed support surface (Nashner et al. 1982; Prieto et al. 1996).] Specifically, transient increases in body sway, particularly in older adults, were reported after restoration or alteration of visual-orientation cues (Simoneau et al. 1999; Teasdale et al. 1991) and combined visual and proprioceptive cues (Hay et al. 1996). This increase in body sway was attributed to a reduced ability of elderly subjects “to rapidly reconfigure the postural set” (Teasdale et al. 1991), but no specific explanation for this phenomenon was offered.

In experiments designed for other purposes, we occasionally observed transient body-sway motions with characteristic and unanticipated dynamic properties. For example, the center-of-

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1 Graviceptive sensory cues are presumed to provide information about body orientation with respect to earth vertical. Previous results suggest that the vestibular system is the primary source of graviceptive sensory information used for postural control (Peterka 2002).

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J Neurophysiol • VOL 91 • JANUARY 2004 • www.jn.org
pressure recording shown in Fig. 1 illustrates a transient 1-Hz oscillation that occurred while a subject was standing on a level fixed support surface immediately after a time period during which the support surface had been “sway-referenced” by continuously rotating the surface in proportion to the subject’s recorded anterior-posterior (AP) body-sway angle. We were curious to know if this transient 1-Hz oscillatory sway behavior was compatible with the hypothesis put forth in Peterka (2002) that human postural control is achieved primarily by a feedback-control mechanism that includes dynamic regulation of sensorimotor integration by the reweighting of individual sensory channels. Accordingly, we performed new experiments, reported herein, to test this hypothesis.

We also considered the possibility that the transient oscillation might be indicative of changes in a “load-compensation” mechanism that attempts to modulate the magnitude of corrective torque needed to achieve good control of stance. That is, if the main problem with transitions to different environments is that the postural-control system generates too little or too much corrective torque due to a loss or gain of specific sensory-orientation cues, then perhaps a simple solution would be to scale up or down the overall corrective torque rather than alter the weighting of individual sources of sensory-orientation information. In this way, the amount of torque generated would change, but the relative contributions of the different sensory sources would remain fixed, independent of environmental conditions. The scaling up or down of overall corrective torque is a form of load compensation that we have previously observed in postural-control experiments (Peterka 2002) and is recognized as an important aspect of motor control (Duysens et al. 2000).

In this study, we offer new experimental evidence that demonstrates a transient decrease in postural stability after both loss and restoration of accurate sensory information in healthy adults. The postural instability is characterized by transient body-sway oscillations at specific frequencies that are predicted by the hypothesis that the human postural-control system can be characterized as a dynamic feedback-control mechanism with time delay. Feedback is provided by a weighted combination of sensory-orientation cues from various sensory sources, and these sensory weights are dynamically adjusted to maintain stability after changes in environmental conditions that alter the availability of sensory-orientation cues.Transient decreases in postural stability are due to slow adjustments of these weights causing an under- or over-generation of corrective torque. We also explored an alternative control strategy based on a load-compensation mechanism. Load compensation does not dynamically adjust the sensory feedback, but rather corrective torque is scaled in proportion to a fixed combination of sensory-orientation cues. Our results were not compatible with this load-compensation strategy.

**METHODS**

**Subjects**

Fourteen healthy volunteers gave written consent to participate in experimental protocols approved by the Institutional Review Board of Oregon Health & Science University and in compliance with the 1964 Helsinki Declaration. None of the subjects had previously participated in experiments using a sway-referenced support surface. Two of the subjects were excluded because they were unable to maintain stance on a sway-referenced support surface for a sufficient duration to complete experimental trials. The results from the other 12 subjects (age: 23–50 yr; mean: 36 yr; 5 female, 7 male) were analyzed.

**Stimuli and procedures**

Subjects were restrained to sway as a single-link inverted pendulum by use of a backboard assembly that permitted only AP sway about the ankle joint axes (Peterka 2002). Subjects “wore” the backboard like a backpack with straps around the shoulders, with additional straps holding the hips and low thighs against padded supports attached to the backboard, and with the head held against a padded headrest. The weight of the backboard was supported on bearings that were aligned with the ankle joint axes. Therefore when the center-of-mass of the backboard was directly above the bearing axis, subjects did not need to support any additional vertical force. For typical body-sway angles, the vertical force due to the backboard was < 1 N. However, to maintain a given body-sway angle relative to earth-vertical, subjects would need to exert 15–20% additional torque compared with a freestanding condition. We have previously compared postural control behavior in freestanding and backboard restrained subjects and found no differences (Fig. 7 in Peterka 2002), indicating that subjects apparently do compensate for the added mass and moment of inertia of the backboard by appropriately increasing the amount of corrective torque generated in response to body sway (Fig. 12 in Peterka 2002). Use of the backboard simplified the subjects’ biomechanics and control strategies, and permitted a more accurate comparison with modeling results. We are confident that the oscillatory body-sway behaviors we recorded are not an artifact related to use of the backboard because we have previously seen identical oscillatory behavior in freestanding subjects in similar conditions to those used in this study (Fig. 1).

The backboard angular position was recorded using a potentiometer aligned with the rotation axis, and backboard angular velocity was recorded with a rate sensor (Watson Industries, Eau Claire, WI). Eyes were closed throughout trials so that experiments focused on the subjects’ use of proprioceptive and graviceptive cues for postural control. Auditory cues were masked by playing audio tapes of short stories into headphones.

Each subject performed six test trials consisting of three repetitions of two types of trials. The two trial types will be referred to as “sway-referenced” and “reverse sway-referenced” (explained in the following text). These trials were presented alternately, with 5 min seated rest between each trial. With each new subject tested, we changed the first trial type so that some subjects were first exposed to the sway-referenced trial, whereas others were first exposed to the reverse sway-referenced trial. Although this alternating presentation of the two trial types may not be an ideal design for studying learning effects with trial repetition, our primary focus was to characterize changes in dynamic behavior on first exposure to the experimental conditions in subjects naive to our experimental methods.

The sway-referenced trials lasted 180 s and consisted of 60 s of quiet stance on a level fixed support surface, followed by 60 s on a sway-referenced support surface, and finally 60 s on a level fixed support surface immediately after termination of sway-referencing (---).
surface. Sway-referencing (Nashner 1982) was accomplished by using the backboard angular position signal to control the support surface angular position using a servo-controlled motor so that the support surface moved in 1:1 proportion to the subject’s AP body-sway angle. Because the rotation axis of the support surface was aligned with the axes of the ankle joints, sway-referencing maintained a nearly constant ankle joint angle even though the body-in-space sway angle changed over time. Accordingly, during this sway-referencing condition, ankle proprioception, which encodes motion of the body with respect to the feet, is no longer providing information about body sway with respect to earth vertical. A 5-Hz bandwidth of the servo-control system ensured accurate tracking of body sway by the support surface. At the end of the 60-s sway-referenced period, the support surface was smoothly ramped back in 1 s to a level orientation and maintained in this orientation for the final 60 s of the trial.

The reverse sway-referenced trials lasted 240 s and consisted of 60 s of quiet stance on a level fixed support surface, followed by 60 s on a sway-referenced support surface, followed by 60 s on a reverse sway-referenced surface, and finally 60 s on a level fixed surface. Transitions between the sway-referenced and reverse sway-referenced portions of the trial, and between reverse sway-referencing and the final level support surface condition were accomplished smoothly over 1 s. Reverse sway-referencing was accomplished by tilting the support surface in opposite proportion to the subject’s AP sway angle. So, for example, when the subject sways forward 2°, the platform rotates 2° toes up during reverse sway-referencing (in contrast to sway-referencing where the platform would rotate 2° toes down). For a given body-sway relative to earth vertical, reverse sway-referencing of the support surface effectively doubled the change in ankle joint angle compared with stance on a level surface. Therefore proprioceptive cues proportional to ankle joint movement would also be doubled compared with stance on a level surface. A method similar to reverse sway-referencing has been used previously during transient postural disturbances (Bloem et al. 2002). A related method has also been applied to alter visual cues (Nashner and Berthoz 1978).

Data analysis

As in previous analyses of postural sway data (Loughlin and Redfern 2001; Loughlin et al. 1996), the time-varying spectrum of body-sway velocity was estimated by computing a positive time-frequency distribution (TFD) (Cohen 1995) of the data, using a method previously described (Loughlin et al. 1994). This technique combines the time-frequency information from multiple spectrograms, computed with various window lengths, to obtain an improved estimate of the time-varying spectrum compared with that provided by a single spectrogram. In particular, the positive TFD does not suffer from the well-known time-frequency resolution tradeoff inherent to the spectrogram (Cohen 1995; Loughlin et al. 1994). In our analyses, body-sway velocity was initially sampled at 100 Hz. After low-pass filtering at 5 Hz, the velocity time series was down-sampled to 10 Hz. Then the time-frequency information from three different spectrograms, computed using Hanning windows of length 31, 75, and 255 samples, was combined to obtain the positive TFD of the discrete sway velocity time series. For plotting purposes (Figs. 3, 4, 8, and 9), each TFD was normalized by its peak value and the highest 25-dB amplitude values were plotted on a log-amplitude color scale.

From these TFDs, energy levels were computed in specific time-frequency regions to quantify the distribution of spectral energy. The energy within a particular region was computed by summing the values of the discrete TFD over the region (note that summation over the entire time-frequency plane gives the total energy of the signal). The regions over which the energy of body sway velocity was measured consisted of two distinct frequency bands at five different 10-s time windows for the sway-referenced trials (shown in Fig. 3) and six different 10-s time windows for the reverse sway-referenced trials (shown in Fig. 4). The higher frequency band encompassed 0.7–1.3 Hz, which covers the range in which we had previously observed ~1-Hz oscillations (Fig. 1), and the lower frequency band encompassed 0.1–0.7 Hz, which includes the frequency range where the majority of spectral energy is typically located during quiet stance on a fixed support surface (Prieto et al. 1996). For each time window, an energy ratio (ER) was computed as the ratio of energy in the high- to low-frequency bands. Comparisons of these ERs in different time windows were used to demonstrate changes in postural stability associated with transitions between support surface conditions and learning or habituation phenomena associated with the repetition of trials.

Sensory-system descriptions

In discussing the contributions of sensory systems to postural control and in modeling this system, it is necessary to be precise about the definitions of the system’s components. We use the term proprioception to mean ‘‘the sense of position and movement of one’s own limbs and body without using vision’’ (Gardiner et al. 2000) and, more specifically for postural control, the sense of position and movement of the body with respect to the feet. This functional definition of proprioception does not attempt to distinguish among the various sensory receptors (muscle stretch, joint, Golgi tendon, foot pressure, and the skin’s tactile receptors) that contribute to proprioception. This definition also does not consider how the nervous system combines this wide array of afferent information to obtain an internal signal representing body motion relative to the feet. We use the term graviception to refer to the sense of body motion with respect to earth vertical. Experimental results indicate that the vestibular system makes a major contribution to graviception used for postural control (Peterka 2002). However, note that our functional definition of graviception does not exclude other sensory contributions to graviception, such as when a subject lightly touches an earth-fixed object (Jeka and Lackner 1994) or receives tactile cues regarding body motion relative to an earth reference (Rogers et al. 2001) or other nonvestibular graviceptive cues (Mittelstaedt 1998).

Model simulations

A simple closed-loop, negative feedback postural control model (Fig. 2) was used to investigate hypothetical explanations of the experimental results. Previously it was shown that this model could explain the steady-state dynamic behavior of quiet stance control in a variety of environmental conditions (Peterka 2002). Simulations here were performed using the mean values of model parameters (for Eqs. 1 and 2) measured or estimated from the eight subjects who participated in those earlier experiments. The body parameters of the model included body-plus-backboard mass (m = 85 kg), moment of inertia about the ankle joints (I = 81 kg m²), and height of center of mass above the ankle joint axis (h = 0.9 m). The body-plus-backboard was represented by a single-link inverted pendulum, for which the relationship between the corrective torque, Tc, applied about the ankle joint and body sway, BS, relative to earth-vertical is given by the following differential equation

\[
\frac{d^2\text{BS}}{dt^2} = mg\sin(\text{BS}) + T_c, \tag{1}
\]

For small angles of body sway, \(\sin(\text{BS}) \approx \text{BS}\), and the biomechanics become linear.

Sensory integration to form an internal body-orientation estimate is represented by a weighted summation of information provided by proprioceptive (weighting factor \(W_p\)) and graviceptive (weighting factor \(W_g\)) sensory systems (see Fig. 2). The graviceptive system is assumed to signal body orientation in space (BS). The proprioceptive system is assumed to signal body orientation relative to the feet and therefore to the support surface (BS – SS) where SS is support surface

\[J Neurophysiol \cdot VOL 91 \cdot JANUARY 2004 \cdot www.jn.org\]
orientation in space. Therefore the internal orientation estimate is
given by \( e = -W_p BS - W_g (BS - SS) \). The positive directions of BS,
SS, and \( \xi \) are shown in Fig. 2. \( W_p \) and \( W_g \) were initially set to 0.8 and
0.2, respectively, for eyes-closed stance on a level fixed surface
(Peterka 2002). Simulations were performed that allowed \( W_p \) and \( W_g \)
to vary over time to determine if a dynamic regulation of sensory
integration could account for the postural sway observed experimen-
tially.

The model represents the postural-control system as a position
feedback-control system with the proprioceptive and graviceptive
systems encoding body position. This may seem artificial because
many receptors encode velocity-related as well as position-related
information. However, in generating the corrective torque (Eq. 2),
the model utilizes both position and velocity information, the latter being
obtained via differentiation of the position measurement. We could
have reformulated the model so that it explicitly represented both
position and velocity-related sensory information, but the two models
would be mathematically equivalent.

A "neural controller" produces corrective torque, \( T_c \), about the
ankle joint in relation to the internal orientation estimate, \( e \), as follows

\[
T_c(t) = K_e(t - \tau_d) + K_p \frac{de(t - \tau_d)}{dt} + K_{nc} e(t - \tau_d)dt
\]

(2)

where \( K_e = 970 \text{ N m rad}^{-1} \), \( K_p = 344 \text{ N m s rad}^{-1} \), \( K_f = 86 \text{ N m s}^{-1} \)
rad\(^{-1} \), and \( \tau_d = 0.175 \text{ s} \). These parameter values were derived from
experimental data analyzed previously (Peterka 2002) using curve fits
to mean transfer function data obtained in an eyes closed condition
using a low-amplitude support surface stimulus (1° peak-to-peak rotation).
The parameter \( \tau_d \) represents the combined time delays due to
sensory transduction, neural transmission, nervous system processing,
muscle activation, and force development.

The neural controller was followed by a neural controller gain, \( K_{nc} \),
that represents a hypothetical load-compensation factor that scales the
amount of torque generated by the neural controller for a given
amount of body sway. \( K_{nc} \) was nominally set to unity value. In
addition to the dynamic sensory-reweighting simulations discussed in
the preceding text, wherein \( W_p \) and \( W_g \) were varied while \( K_{nc} \)
remained constant (the sensory-reweighting hypothesis), simulations
were also performed to determine if time varying changes in \( K_{nc} \)
(while \( W_p \) and \( W_g \) remained fixed) could account for the dynamic
behavior of postural sway observed experimentally (the load-compen-
sation hypothesis).

Realistic levels of spontaneous body sway are produced by adding
noise to both sensory systems, with the noise in the graviceptive
system about 6 times larger than in the proprioceptive system (van der
Kooij et al. 2001). Sensory-system noise was generated by filtering a
Gaussian white-noise source (0.05- to 2-Hz 1st-order band-pass filter
for the graviceptive and 0.2 to 2 Hz for the proprioceptive system),
and then by further low-pass filtering these time series (0.16-Hz cutoff
of a 1st-order filter). The bandwidths and amplitudes of the filters
were adjusted to approximately match the spectral properties (spectral
amplitude and distribution over frequency) of experimental body-
sway data in the initial fixed surface condition and near the end of the
sway-referenced condition. In the fixed surface condition, it was
assumed that only the graviceptive channel contributed to pos-
tural control.

The mechanism for sway-referencing and reverse sway-referencing
is shown in the model as a feedback loop that connects BS to SS (Fig.
2). When this feedback loop is disconnected and a zero reference
signal is input to SS, the support surface is in a level fixed orientation.
When this feedback loop is connected through a multiplier of +1, the
support surface is in the sway-referenced mode with support surface
angular position tracking the body sway angle within the dynamic
capability of the support surface servo-controlled actuator (modeled by
Eq. 3). When this feedback loop is connected through a multiplier of −1,
the support surface is in the reverse sway-referenced mode with
the support surface rotating opposite the body-sway angle.

Sway-referencing and reverse sway-referencing are tools to manipu-
late the ankle joint angular changes over time to alter the proprio-
ceptive sensory information available for postural control. On a level
fixed surface (SS = 0), the signal sensed by the proprioceptive system
is SS − BS = −BS. For ideal sway-referencing, SS = BS and the

FIG. 2. Feedback model of the postural-control system and system controlling support surface motion. The body is modeled as
a linearized inverted pendulum. Body position in space (BS) is sensed by the graviceptive system, and body position relative to foot
orientation (BF) is sensed by the proprioceptive system. Velocity information is also utilized via differentiation of the body-position
measurements by a neural controller. Each sensory channel includes noise, with the graviceptive channel noise 6 times larger than
the proprioceptive channel noise. An internal orientation estimate is provided by a weighted combination of the graviceptive and
proprioceptive contributions, where \( W_p \) and \( W_g \) are the graviceptive and proprioceptive channel weights, respectively. A neural
controller models the corrective torque generated in response to the internal orientation estimate, \( e \), and is implemented as a simple
proportional-integral-derivative (PID) controller. The neural controller output is scaled by a gain factor, \( K_{nc} \), representing a load
compensation mechanism that scales the amount of corrective torque, \( T_c \), applied to the body to maintain stability. The lower
portion of the model represents the servomechanism that controls support surface rotation angle (SS) to hold the surface level
(SS = 0) or to perform sway-referencing (SS ≈ BS) or reverse sway-referencing (SS ≈ −BS.)

J Neurophysiol • VOL 91 • JANUARY 2004 • www.jn.org
proprioceptive signal is \( SS - BS = BS - BS = 0 \). Thus under this ideal condition, the proprioceptive system signals that there is no motion of the body relative to the feet even though there may be body-sway motion in space. Note that ideal sway-referencing produces an isometric condition where the feet remain in a fixed orientation relative to the body. Therefore one would expect that torque produced about the ankle joint by leg muscle contractions would be effective in producing a change in body orientation in space even though the support surface may be moving. This differs from stance on a compliant surface, such as foam, where ankle torque produces a deformation of the surface and the ankle joint angle is not held constant relative to the body. For ideal reverse sway-referencing, \( SS = -BS \), and the proprioceptive signal is \( SS - BS = -2BS \) or double the signal occurring during stance on a fixed surface for a given amount of body sway.

Because the support surface actuator controlling surface motion is not ideal, sway-referencing cannot be performed perfectly, and the dynamic properties of the actuator must be considered in the simulations. The dynamics of the support surface actuator are represented by the block labeled “support surface actuator dynamics” in Fig. 2. These dynamics were based on a transfer function calculated from experimental data obtained with a subject standing on the support surface. A pseudorandom perturbation with a 15-Hz bandwidth was applied to the support surface, and the actual rotational motion of the support surface was measured. An experimental transfer function was obtained by dividing the cross-power spectrum between the ideal perturbation command signal and the actual surface rotation by the power spectrum of the ideal command signal (Bendat and Piersol 2000). A curve fit to the experimental transfer function was used to obtain parameters for the model simulations. The experimentally determined support surface actuator dynamics were accurately modeled by the following transfer function equation

\[
SA(s) = \frac{SS(s)}{SS_n(s)} = \frac{e^{-\tau_m s}}{s^2\omega_n^2 + 2\zeta s\omega_n + 1} \tag{3}
\]

where \( SS_n \) is the input command signal to the support surface actuator servo control, \( s \) is the Laplace transform variable, \( \omega_n = 33.4 \text{ rad/s} \), \( \zeta = 0.61 \), and motor time delay \( \tau_m = 0.015 \text{ s} \).

All simulations were performed using Simulink with Matlab version 5.2 (The MathWorks, Natick, MA).

RESULTS

AP body sway of test subjects was monitored during eyes-closed stance on a level fixed support surface and in conditions that altered (by sway-referencing or reverse sway-referencing) the available proprioceptive sensory-orientation cues. Particular attention was paid to characterizing body-sway properties after transitions between the different support surface conditions within each test trial to understand how the postural control system adjusts to sudden changes in the available sensory cues.

The general features of body sway recorded during each portion of the two trial types are reported in the next section with emphasis on the most prominent feature, which was a 1-Hz body-sway oscillation after the transitions from sway-referenced to fixed and sway-referenced to reverse sway-referenced conditions. Transient behavior after other transitions were more subtle and are described in the section on time-frequency behavior. Finally, possible explanations for the observed behavior after all transitions are explored in the section on postural control model predictions.

Experimental body-sway responses

SWAY-REFERENCED TRIALS. During the initial 60-s period of stance on a fixed support surface, subjects showed a typical low-amplitude, spontaneous body sway expected in this condition when both proprioceptive and graviceptive sensory cues reliably and accurately contributed to postural control (Prieto et al. 1996). Sway-referencing the support surface resulted in larger-amplitude spontaneous body sway, also consistent with previous findings (Nashner et al. 1982; Peterka and Black 1990).

When the support surface returned, after the 60-s period of sway-referencing, to a level fixed orientation, one might anticipate that body sway would quickly return to the typical low levels of spontaneous body sway seen prior to sway-referencing. However, in 9 of the 12 subjects, a clear, sustained AP body oscillation of ~1 Hz (mean ± SD: 0.87 ± 0.14, range: 0.55–1.08 Hz on the 1st sway-referenced trial) was recorded after the transition from the sway-referenced support surface back to the level fixed support surface. This oscillation, most easily seen in recordings of rotational sway velocity, typically developed immediately after the transition to the fixed surface condition. In some cases, the oscillation was still evident 40 s after sway-referencing ended (Fig. 3A), showing little decay in amplitude but a small decrease in oscillation frequency. In 3 of the 12 subjects, body sway returned rapidly to pre-sway-referencing levels (Fig. 3B). The example subjects in Fig. 3 represent the extremes of the observed behavior. A typical intermediate behavior showed an immediate development of the 1-Hz oscillation, followed by a decay in the amplitude of oscillation over 5–30 s.

REVERSE SWAY-REFERENCED TRIALS. On the reverse sway-referenced trials, the initial 60-s fixed support surface condition and the subsequent 60-s sway-referenced condition were identical to the sway-referenced trials described in the preceding text. As expected, the qualitative features of body sway during the first 120 s were the same as those seen on the sway-referenced trials.

After the transition at 120 s from sway-referencing to 60 s of reverse sway-referencing, a sustained AP body oscillation of ~1–Hz (1.01 ± 0.15, range: 0.61–1.20 Hz on the 1st reverse sway-referenced trial) was recorded in 11 of 12 subjects. The oscillation amplitude was typically largest immediately after the transition to reverse sway-referencing and then declined over time. The amplitude and duration of the 1-Hz oscillations varied widely among subjects. Figure 4 shows recordings from the reverse sway-referenced trials for the same two subjects shown in Fig. 3. Subject 1, who had a prominent sustained 1-Hz oscillation after the transition from sway-referenced to fixed support surface (Fig. 3A), had an even more prominent sustained oscillation after the transition from sway-referencing to reverse sway-referencing (Fig. 4A). Subject 2, who did not have any oscillatory behavior after the transition from sway-referenced to fixed support surface (Fig. 3B), now exhibited a 1-Hz oscillation after the transition from sway-referencing to reverse sway-referencing (Fig. 4B). However, unlike subject 1, the amplitude of subject 2’s oscillation declined in ~5 s to a low level. It was a consistent finding across all subjects that subjects who showed the most (least) oscillatory behavior on the sway-referenced type trials also showed the most
Additionally, among the nine subjects who showed oscillations on the first repetition of both sway-referenced and reverse sway-referenced trials, the oscillation frequency on the reversed sway-referenced trial was significantly greater than on the sway-referenced trial ($P < 0.05$, paired $t$-test; mean paired difference $= 0.12$ Hz).

After the reverse sway-referenced condition, when the support surface returned to a level fixed condition, both subjects in Fig. 4 showed a return to a low level of spontaneous body sway with characteristics similar to spontaneous sway observed in the initial 60-s fixed support surface condition.

**Time-frequency behavior**

Time-frequency analysis of the body sway velocity was conducted to investigate changes in spectral characteristics of sway over time. ERs were computed from the time-frequency distributions over particular time-frequency regions to quantify these changes (see METHODS).

The mean ERs showed about twice as much energy in the lower frequency band (0.1–0.7 Hz) of body sway than in the higher frequency band (0.7–1.3 Hz) during the initial fixed surface condition (Fig. 5, A and B, 1st bar on left). In the period after the start of sway-referencing, there was a small, although not statistically significant, reduction in the mean ER compared with both the prior fixed surface condition and the end of sway-referencing (Fig. 5, A and B, 2nd bar from left). A hint as to the cause of this ER reduction is revealed in the response of the subject shown in Fig. 3A. At the start of sway-referencing, there were body-sway oscillations with period lengths of 8–10 s. The TFD showed that body sway energy is predominant at low frequencies (0.1 Hz) during the initial period of sway-referencing, after which a broader frequency distribution of
sway energy develops that gives rise to a slight increase in ER compared with that at the start of sway-referencing (Fig. 5, A and B, 3rd bar from left). There was no significant difference in ERs between the initial fixed surface condition and the time interval just before the end of sway-referencing.

For the sway-referenced trial types, a post hoc analysis showed that the mean ER after the end of sway-referencing and the return to the final fixed surface condition (the region just after 120 s in Fig. 3) was significantly larger than any of the other ERs (P < 0.05, ANOVA with Tukey-Kramer multiple comparisons test; all statistics performed on ERs used log transformed ER values). In particular, the mean ER (Fig. 5A, 4th bar from left) was about four times larger than in the initial fixed surface condition. This increase in ER was consistent with the presence of the ~1-Hz oscillatory behavior in the majority of subjects after the transition from sway-referencing back to the fixed support surface. The amplitude of this oscillation typically declined over time. Hence, the final ER measured toward the end of the final fixed surface condition was significantly smaller than the ER at the start of the final fixed surface period (P < 0.05, Fig. 5A, 5th bar from left).

For the reverse sway-referenced trial types, the mean ER in the time interval immediately after the transition from sway-referencing to reverse sway-referencing was significantly larger than the ER in any of the prior time intervals (P < 0.05, Fig. 5B, 4th bar from left). This large ER value (~20 times larger than the ER for the initial fixed support surface condition) indicates that body sway in the reverse sway-referenced condition was dominated by the 1-Hz oscillatory behavior in comparison to sway at other frequencies. Because the amplitude of this oscillation typically declined over time, the ER measured at the end of the reverse sway-referenced condition was significantly smaller than the ER at the start of the reverse sway-referenced period (Fig. 5B, 5th bar from left), but was still significantly larger than the ERs in the initial fixed surface condition or in the prior sway-referenced conditions (P < 0.05). Finally, the mean ER at the start of the final fixed surface condition was nearly equal to the mean ER in the initial fixed surface condition.

**Habituation and learning effects**

There was generally less 1-Hz oscillatory sway behavior observed with each repetition of the test trials. This result was quantified by measuring the mean ER for each repetition following the transitions that typically evoked the 1-Hz oscillations (i.e., the sway-referenced to fixed surface transition for the sway-referenced trial type, and the sway-referenced to reverse sway-referenced transition for the reverse sway-referenced trial type). The mean ER versus repetition plots shown in Fig. 6 demonstrate a general decline in the strength of the 1-Hz oscillatory behavior with repetition. This decline was statistically significant for the reverse sway-referenced trials (P < 0.05, repeated-measures ANOVA with log transformed ERs) but not for the sway-referenced trials. The decline occurred despite the fact that the test subjects were given no feedback regarding their performance on each individual trial and no coaching regarding desired behavior other than to maintain their stance. This rapid learning may explain why we seldom see oscillatory sway behavior in subjects experienced with various laboratory tests of balance function. This result is also consistent with demonstrations that subjects with expert motor skills are better able to adjust to rapid changes in the availability of accurate proprioceptive cues (Vuillerme et al. 2001).

**Postural control model predictions**

We used a simple dynamic model of postural control to investigate two possible explanations of the observed behavior...

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**FIG. 5.** Bar graphs of the high- to low-frequency energy ratios (ER) for the 10-s time windows indicated in the TFD plots in Figs. 3 and 4. A: ERs for the 5 time windows shown in Fig. 3 for the sway-referenced trial types. B: ERs for the 6 time windows shown in Fig. 4 for the reverse sway-referenced trial types. Bars indicate the mean ± SE for 12 subjects over all trial repetitions.

**FIG. 6.** Habituation to repetition of test trials. Bar graphs (mean ± SE) showing the reduction with trial repetition of the high- to low-frequency ERs for the 10-s time windows immediately after the end of the sway-referenced portion of test trials. A: for the sway-referenced trial types, this time window occurred at the start of the final fixed support surface condition. B: for the reverse sway-referenced trial types, this time window occurred at the start of the reverse sway-referenced support surface condition.
(see Methods and Fig. 2). The first explanation, which we call the sensory-reweighting hypothesis, is that the relative contributions of proprioceptive and graviceptive information to postural control change during sway-referencing to generate sufficient corrective torque to maintain stable stance. This change leads to an overproduction of corrective torque when the support surface returns to a fixed level orientation, producing 1-Hz body oscillations. The second explanation, which we call the load-compensation hypothesis, is that overall gain of the neural controller is increased during sway-referencing to produce sufficient corrective torque, but the relative contributions of proprioceptive and graviceptive information to postural control remain unchanged. After the end of sway-referencing, the increased neural controller gain produces too much corrective torque, leading to 1-Hz body oscillations.

Both the sensory-reweighting and load-compensation hypotheses are able to predict the occurrence of 1-Hz oscillations after sway-referencing. During sway-referencing, it is also impossible to distinguish between these hypotheses by observing dynamic postural-control behavior in the case where sway-referencing is ideal (i.e., SS = BS). However, when sway-referencing is non-ideal, the load-compensation hypothesis predicts very unusual body-sway dynamics that were not observed experimentally, while the predictions of the sensory reweighting hypothesis are consistent with the experimental results. Simulation examples of the sensory reweighting and load compensation hypotheses are shown in Figs. 8 and 9. Before addressing these in more detail, we first illustrate the model prediction of 1-Hz oscillatory behavior in conditions where there is an overproduction of corrective torque and also show that 0.1-Hz oscillations are predicted when there is an underproduction of corrective torque. We then return to Figs. 8 and 9 to address simulation differences that arise between the load-compensation strategy and the sensory-reweighting strategy.

To illustrate the model’s prediction of postural dynamics, imagine that an external torque, $T_{ext}$, is applied to the body (see Fig. 2). The dynamic properties of body sway evoked by $T_{ext}$ are represented by the following transfer function equation

$$\frac{BS(s)}{T_{ext}(s)} = \frac{B}{1 + K_nc(W_g + W_p - W_f - SA)NC \cdot B}$$

(4)

where $B = BS(s)/T_s(s)$ and $NC = T_s(s)/e(s)$ are transfer functions derived from the Laplace transforms of the differential equations representing body dynamics (Eq. 1) and the neural controller (Eq. 2), respectively, and $SA = SS(s)/BS(s)$ is the support surface actuator transfer function given by Eq. 3.

Under the load-compensation hypothesis, the neural controller multiplicative factor $K_{nc}$ varies to generate increased or decreased corrective torque as warranted by changing external environmental factors, while under the sensory-reweighting hypothesis, it is the sensory channel weights $W_g$ and/or $W_p$ that vary. In the fixed surface condition (modeled by setting $SA = 0$), Eq. 4 shows that a change in $K_{nc}$ has the same influence on the transfer function as does a change in $W_g + W_p$. Accordingly, it is not possible, based on observations of the simulated sway in the fixed surface condition, to distinguish between these two different control strategies. Figure 7 shows a set of transfer function gain curves, calculated from Eq. 4, that describe how the relative amount of body sway evoked by a sinusoidal external torque stimulus changes as a function of the stimulus frequency for different values of $K_{nc}$ and $W$, where $W$ represents the effective sensory gain, given by the sum of the sensory channel weights that are effectively contributing to torque generation (in this fixed surface condition $2W = W_g + W_p$). These curves characterize the change in overall dynamics of the system as a function of the sum of the sensory channel weights, $W$, or the neural controller gain factor $K_{nc}$. Changes in $W$ or $K_{nc}$ change the amount of corrective torque generated for a given amount of body sway. The neural controller parameters ($K_p$, $K_{nc}$, $K_{nc}$ in Eq. 2) are set to generate corrective torque that produces stable and non-resonant dynamic behavior when $W = 1$ and $K_{nc} = 1$, and we assume that these parameters do not change from this initial condition.

If the overall corrective torque is too low ($W$ or $K_{nc}$ approaching 0.8), then our model predicts resonant postural dynamics with a low-frequency resonant peak slightly >0.1 Hz (Fig. 7, top). This means that any noise in the system with component frequencies near 0.1 Hz will excite this resonant mode of the system, producing enhanced low-frequency body sway and, thereby, reducing the measured ER value. If the overall corrective torque is too high ($W$ or $K_{nc}$ approaching 1.7), then our model predicts resonant postural dynamics with a high-frequency resonant peak at ~1 Hz (Fig. 7, bottom) and hence an increased ER value. Additionally, the model system is unstable when $W$ is <0.81 or >1.76.

Both the load-compensation hypothesis and the sensory-reweighting hypothesis are able to predict the occurrence of 1-Hz body oscillation after the end of sway-referencing if we assume that either $K_{nc}$ or $W$ increased during the prior sway-referenced condition and were not able to decrease quickly enough to a value near unity after the end of sway-referencing. The need for an increase in either $K_{nc}$ or $W$ during sway-referencing is easily understood if one considers that in the ideal sway-referenced condition, there is no contribution of proprioceptive channel information to the generation of cor-
For the load-compensation hypothesis, the value of load-compensation hypothesis is just outside of the stability limit. If, after initiation of sway-referencing, \( W_g \) initially increases to a value just above the minimum value needed to maintain stability, the model predicts that there could be enhanced low-frequency sway due to the \( \sim 0.1 \)-Hz resonance of the control system. This prediction is compatible with results of individual experimental (Fig. 3A) and simulation trials (Fig. 8, A and B), and the reduced ER values seen at the start of sway-referencing (Fig. 5, A and B). By the end of the sway-referencing period, we assume \( W_g \) has increased to 1 because experimental results show that the ER returns to a value equal to the ER measured in the initial fixed surface condition (Fig. 5, A and B).

During sway-referencing, very little information flows through the proprioceptive channel, and, therefore, the value of \( W_g \) contributes only a small amount to the generation of corrective torque. This is indicated in Fig. 8 (A and B, top graphs).

SENSORY REWEIGHTING SIMULATIONS. Possible sensory-reweighting strategies that account for our experimental results with the sway-referenced trial types are shown in Fig. 8 (A and B, top two panels). These strategies involve a rapid increase in \( W_g \) at the start of sway-referencing to compensate for a reduction in the contribution of the proprioceptive channel to the effective sensory gain \( \Sigma W \). The dynamics of the system can be characterized by a set of curves calculated from Eq. 4 with \( W_g = 0.8 \), SA defined by Eq. 3, and \( W_f \) varying over its stable range. The system is stable for \( W_g \) values between 0.805 and 1.95, and the curves (not shown) look nearly identical to those in Fig. 7 with the exception that the low-frequency resonant peak is at a slightly lower frequency (0.1 Hz) and the high-frequency resonant peak is at a slightly higher frequency (1.25 Hz).

If, after initiation of sway-referencing, \( W_g \) initially increases to a value above the minimum value needed to maintain stability, the model predicts that there could be enhanced low-frequency sway due to the \( \sim 0.1 \)-Hz resonance of the control system. This prediction is compatible with results of individual experimental (Fig. 3A) and simulation trials (Fig. 8, A and B), and the reduced ER values seen at the start of sway-referencing (Fig. 5, A and B). By the end of the sway-referencing period, we assume \( W_g \) has increased to 1 because experimental results show that the ER returns to a value equal to the ER measured in the initial fixed surface condition (Fig. 5, A and B).

During sway-referencing, very little information flows through the proprioceptive channel, and, therefore, the value of \( W_g \) contributes only a small amount to the generation of corrective torque. This is indicated in Fig. 8 (A and B, top graphs).

**FIG. 8.** Model simulations for the sensory reweighting hypothesis. The model in Fig. 2 was used to simulate body sway during trials equivalent to our experimental sway-referenced trial types. A, top 2 panels: the time course of the effective sensory contribution, \( \Sigma W \), and the individual sensory channel weight changes that account for the observed experimental results in a subject demonstrating prominent 1-Hz resonant behavior after sway-referencing, similar to subject 1 in Fig. 3A. \( W_g \) rises at the start of sway-referencing to maintain sufficient corrective torque for stability. During sway-referencing, no torque is generated by the proprioceptive channel because \( BF = 0 \), even though \( W_p \) remains unchanged (---). A 1-Hz body sway develops immediately after sway referencing because \( \Sigma W = W_p + W_g \) is much \( > 1 \) and \( W_g \) decays slowly. Middle panels: time course of SS, BS, and BS velocity that this model produced for the changing support surface conditions that mimic the experimental trials. Bottom: the TFD of BS velocity. B, top: the time course for \( \Sigma W \), \( W_g \), and \( W_f \) weight changes that account for the observed experimental results in a subject demonstrating no 1-Hz resonant behavior after sway-referencing, similar to subject 2 in Fig. 1B. The time course of individual sensory channel weight changes are the same as in (A), except that \( W_g \) decays rapidly after the end of sway-referencing.
by the fact that the effective sensory contribution, $\Sigma W$, to the generation of corrective torque is dominated by the graviceptive contribution during sway-referencing ($\Sigma W \approx W_p$). If we assume that $W_p$ remains at the value present during the initial fixed surface condition (indicated by the dashed line for $W_p$ during sway-referencing in Fig. 8), then cessation of sway-referencing restores the flow of information through the proprioceptive channel, thereby causing an overproduction of corrective torque ($\Sigma W = W_p + W_g = 1.8$). When the sensory channel weights are slow to readjust to this new fixed support surface environmental condition, the overproduction of corrective torque persists, resulting in $\sim 1$-Hz resonant behavior, which indicates that the postural control system is close to a stability limit (Fig. 8A). When the sensory channel weights rapidly readjust to levels appropriate for stance on a fixed surface ($\Sigma W = 1$), 1-Hz resonant behavior is avoided (Fig. 8B). Thus this model suggests that the large variations among subjects in the presence of 1-Hz oscillatory behavior is associated with large variations in individual sensory integration control strategies. Subjects who were able to make rapid adjustments of sensory channel weights when environmental conditions changed were able to avoid resonant behaviors. In contrast, subjects who made slow adjustments remained close to postural stability limits as indicated by resonant body-sway behavior.

The principles illustrated by the example for the sway-referenced trial types also apply to the reverse sway-referenced trials. The model predicts that non-ideal reverse sway-referencing would nearly double the proprioceptive channel contribution to corrective torque generation. If, at the end of sway-referencing, $W_g = 1$ and $W_p = 0.8$ (as in Fig. 8), then the effective sensory contribution to torque generation at the start of reverse sway-referencing would be $\Sigma W = 2W_p + W_g = 2.6$. According to our model, this value is incompatible with stability. Subjects would need to rapidly decrease $W_p$, $W_g$, or both to reduce $\Sigma W$ to a value less than $\sim 1.6$ to insure stability. However, if $\Sigma W$ remained close to its upper stability limit, then the model predicts that a sustained 1-Hz oscillatory body sway would be present throughout the reverse sway-referenced condition as observed in some subjects (e.g., Fig. 4A). If $\Sigma W$ were reduced to a value closer to 1, then 1-Hz oscillatory behavior would diminish, as seen in other subjects (e.g., Fig. 4B).

The sensory-reweighting model predicts that there would be a possibility of falling after the transition from the sway-referenced to reverse sway-referenced condition because $\Sigma W = 2.6$ is well above the stability limit. In fact, one subject fell on two trials within a few seconds after the transition from sway-referencing to reverse sway-referencing. These falls are consistent with a very large $\Sigma W$ after the transition to reverse sway-referencing, and our model’s prediction that these high effective sensory channel gains cause an overproduction of corrective torque that lead to instability. With repetition of the reverse sway-referenced trials, this subject was eventually able to maintain balance throughout the trial, suggesting a learning effect, although reverse sway-referencing still evoked a sustained 1-Hz oscillation. This sustained oscillation is again consistent with the subject’s inability to quickly reduce his $\Sigma W$ to a value close to unity.

Additionally, the model’s transfer function curves (Fig. 7) show that as $\Sigma W$ approaches the upper stability limit, the frequency of the resonant peak increases from slightly $< 1$ Hz to slightly $> 1$ Hz. Recall that the experimental results showed a slightly higher mean oscillation frequency (1.01 Hz) on the reverse-sway-referenced trials compared with the sway-referenced trials (0.87 Hz). This frequency shift is consistent with subjects being closer to the stability limit after the sway-reference to reverse sway-reference transition compared with the sway-reference to fixed surface transition.

Finally, for the reverse sway-referenced to fixed surface transition, subjects returned rapidly to body-sway behavior consistent with steady-state stance on a fixed surface. This experimental result is consistent with the following scenario. During reverse sway-referencing, subjects would have turned down their graviceptive and/or proprioceptive weights to maintain stability without 1-Hz sway oscillation. One possibility is that graviceptive weights returned to a low value (e.g., 0.2) and proprioceptive weight was reduced to a value approaching half the value seen during stance on a fixed surface (i.e., half of 0.8). At the transition to the fixed platform condition, $\Sigma W$ would then be 0.6, so that too little corrective torque would be generated, and one would expect to see a 0.1-Hz oscillation (see Fig. 7) and an enhancement of low-frequency sway energy relative to high (i.e., a lower ER). Consistent with this prediction, the ER for the time window at the start of the final fixed surface after reverse sway-referencing (Fig. 5B, right-most bar) was slightly reduced compared with the ER in the initial fixed surface condition (Fig. 5B, left-most bar). However, this ER reduction was not statistically significant. This lack of a significant effect may be explained by the fact that we typically observed that the 1-Hz oscillation was not completely absent in most subjects even at the end of the reverse sway-referencing portion of the test trial. Failure to completely suppress the 1-Hz oscillation suggests that subjects were not able to reduce their proprioceptive channel weight by the factor of two necessary to restore non-resonant sway during reverse sway-referencing. Therefore the sum of the sensory channel weights may have been close to unity after the end of the reverse sway-referenced period, resulting in a rather uneventful transition to the final fixed surface condition.

**Load-compensation simulations.** The load-compensation hypothesis assumes that the sensory weights $W_p$ and $W_g$ do not change, but rather the neural controller gain increases during sway-referencing to compensate for the reduced proprioceptive information. However, increasing neural controller gain increases both the graviceptive channel and the proprioceptive channel signal that remains due to non-ideal sway-referencing. This increase in the residual proprioceptive signal has a significant effect on the dynamics of sway predicted by the model. Figure 9A shows the family of transfer function gain curves calculated from Eq. 4 for several values of $K_m$ with $W_p = 0.8$ and $W_g = 0.2$. The system is stable for $K_m$ values from 3.95 to 4.88. All curves show two resonant peaks with the lower frequency peak at $\sim 0.08$ Hz and the higher frequency peak at $\sim 2$ Hz. Accordingly, the load-compensation model simulations (Fig. 9B) display dual resonant body-sway behavior during sway-referencing, with spectral energy concentrated at frequencies near 0.1 and 2 Hz. Because this dual resonant behavior was not observed during sway-referencing in our experimental trials, our experimental results favor the sensory-reweighting hypothesis over the load-compensation hypothesis.
The goal of sensorimotor integration for postural control is to ensure that an adequate amount of corrective torque is generated to resist the destabilizing influence of gravity and other external perturbations. This goal is complicated by the fact that sensory orientation cues can change as environmental conditions change such that some sensory systems no longer reliably signal body orientation in space. We presented subjects with a demanding task that included rapid transitions that altered body-sway information provided by proprioceptive cues to challenge the sensorimotor integration mechanisms that regulate postural control. Our experimental and model-based results suggest that inadequate sensorimotor regulation is signaled by the development of resonant body sways. Enhanced low-frequency (∼0.1 Hz) body sway indicates an under-generation of corrective torque, and enhanced high-frequency (∼1 Hz) sway indicates an over-generation of torque. Modeling results indicate that the postural-control system is operating close to a stability limit when either 0.1- or 1-Hz body sway is present. These findings support the intuitive notion that postural instability can occur when accurate sensory-orientation information is withdrawn but also demonstrate the nonintuitive result that postural instability can also occur when sensory-orientation cues are suddenly restored after exposure to conditions where orientation cues were compromised.

While the laboratory conditions of sway-referencing and reverse sway-referencing used in our experiments are artificial, they provided a well-defined and repeatable means of manipulating proprioceptive sensory cues. This allowed us to systematically alter the relationship between different sensory-orientation cues to characterize transient behavior evoked by sudden transitions that withdrew or restored the normal relationship between proprioceptive and graviceptive orientation cues. Furthermore, sway-referencing and reverse sway-referencing manipulations are easily modeled, in comparison to other methods such as stance on foam, and thus facilitate the use of quantitative models to explore hypotheses regarding the mechanisms contributing to the regulation of human postural control.

By comparing our experimental results to postural-control model simulations, we were able to distinguish between two possible explanations for the overproduction of corrective torque leading to 1-Hz body oscillations. The predictions of the load-compensation hypothesis were not supported because this hypothesis predicted a dual resonant (0.1 and 2 Hz) body-sway behavior during non-ideal (i.e., realistic) sway-referencing, and this behavior was not observed experimentally. In contrast, the predictions of the sensory-reweighting hypothesis were consistent with the experimental data. Although the load-compensation hypothesis could not account for our experimental results, this should not be taken to mean that load-compensation mechanisms do not contribute to the postural-control system. Indeed, we previously obtained results consistent with the existence of load compensation by comparing estimates of subjects’ neural controller stiffness and damping parameters (Kp and KD in Eq. 2) obtained on tests where subjects were freestanding versus backboard supported. Both Kp and KD increased in the backboard supported tests by an amount necessary to compensate for the backboard’s added mass and moment of inertia (Fig. 12 in Peterka 2002). There is also evidence for load-compensation mechanisms contributing to head-movement control (Keshner et al. 1999).

**DISCUSSION**

Our results demonstrate that the apparently simple act of standing upright involves complex, dynamically regulated sensorimotor integration mechanisms that exist in the nervous system. The use of quantitative models to explore hypotheses regarding the mechanisms contributing to the regulation of human postural control.
Our model-based interpretation of experimental results postulates that the corrective torque required to maintain balance is generated in proportion to a weighted combination of sensory-orientation cues. This assumption is consistent with previous studies of sensorimotor integration in limb movement control that have shown that a weighted combination of sensory information can achieve optimal motion and orientation estimates if weighting is adjusted according to the precision of the sensory sources (van Beers et al. 2002). When applied to postural control, these previous results imply that graviceptive or, more specifically, vestibular sensory information is less precise than visual and proprioceptive information (van der Kooij et al. 2001), based on evidence that the postural system makes limited use of graviceptive cues in conditions where multiple sensory systems provide redundant orientation information (Peterka 2002). The low precision (high noise level) of graviceptive cues is also consistent with the larger-amplitude sway observed during support surface sway-referencing when graviceptive cues are presumably the primary source of sensory information for balance control (Nashner et al. 1982). However, postural stability ultimately requires that body sway relative to earth-vertical remain within certain limits defined by foot length and the velocity of body sway (Pai and Patton 1997). Because the vestibular system is the primary sensory system that provides graviceptive body-orientation information, there is presumably an increased dependence on vestibular information for postural control in conditions where orientation information from other sensory systems becomes less reliable. This increased vestibular contribution is represented as an increase in the graviceptive system weighting in our model.

In developing models of sensorimotor systems, it is necessary to use simplified representations of complex systems. The representation of proprioceptive and graviceptive systems by weights in our model is a simplification that does not consider the detailed dynamic and nonlinear properties of the various sensory receptors contributing to these sensory systems. For the proprioceptive system, a number of different sensory receptors (muscle stretch, joint, Golgi tendon, foot pressure, and the skin’s tactile receptors) contribute to an overall sense of body motion relative to the feet. For modeling purposes, we assume that the nervous system has experience with the complex array of sensory cues that occurs with body sway and is able to extract a signal that accurately encodes ankle joint motion over a wide dynamic range (Cordo et al. 2002). Detailed psychophysical studies of motion perception support the representation of proprioceptive sensory information by a non-dynamical linear element such as a weighting factor (Mergner et al. 1991). For the graviceptive system, neither the vestibular system’s semicircular canals nor otolith organs directly sense head orientation with respect to gravity in dynamic conditions, but there is evidence that the nervous system combines information from canals and otoliths to obtain a wide-dynamic-range estimate of the direction of gravity with respect to the head (Angelaki et al. 1999; Merfeld and Zupan 2002; Zupan et al. 2002).

The inclusion of these various simplifying assumptions in our model allowed us to focus on the dynamic behavior of the entire system as predicted by a sensorimotor integration mechanism based on feedback of a weighted combination of sensory-orientation cues. The close correspondence between experimental and predicted results inspires some confidence that our model, based entirely on a negative feedback-control mechanism, captures important attributes of the human postural-control system related to sensorimotor integration. That is, the model did not require the inclusion of more complex features, such as feed forward or predictive control as previously suggested (Fitzpatrick et al. 1996; Morasso et al. 1999; van der Kooij et al. 1999), to explain the experimental results. The validity of the model is further supported by the fact that we did not have to alter the model’s structure or its parameters (other than sensory weights) that were previously shown to account for postural dynamic behavior in a variety of conditions (Peterka 2002). However, we recognize that this model does not account for all postural behavior such as voluntary control or preparatory postural adjustments (Cordo and Nashner 1982) or perturbations that might trigger specific compensatory motor programs (Horak et al. 1989). The model also does not predict how sensory weights are selected or how they change over time, although this is an important issue for future consideration. Finally, the feedback mechanism represented as a weighted summation in our model is quite possibly a simplification of a system using internal models to interpret sensory and motor commands (van der Kooij et al. 1999; Wolpert et al. 1995).

Our results offer a possible explanation of oscillatory sway behavior reported in previous studies. Spontaneous body-sway motions with a predominant oscillatory component in the 0.5- to 1-Hz range have been reported in some patients with Friedreich’s ataxia (Diener et al. 1984a) and with tabes dorsalis (Mauritz and Dietz 1980). Normal subjects have also shown 1-Hz oscillations after ischemic blocks of leg afferents (Diener et al. 1984b; Mauritz and Dietz 1980). These previous findings are consistent with inadequate postural system regulation resulting in the generation of too much corrective torque in proportion to body sway, but these results alone cannot be used to distinguish between inadequate load-compensation or sensory-rewighting mechanisms. Recent data from two Parkinson’s disease patients showed 0.1-Hz resonant body sway during quiet stance on a sway-referenced surface but not during stance on a fixed support surface (Creath et al. 2002). These data are potentially consistent with a failure of these patients to adequately increase their utilization of graviceptive information in the sway-referenced condition, resulting in too little corrective torque generation.

Finally, our results have potentially important implications regarding the cause of falls. While diminished sensory function has long been recognized to contribute to postural instability and increased risk of falls, particularly in the elderly (Lord et al. 1991), our results highlight the role played by the dynamic regulation of sensorimotor integration. In particular, our results suggest that inadequate regulation resulting in an over production of corrective torque may be an underappreciated cause of instability. Furthermore, our results predict that the risk of falling increases after any environmental change that alters the available sensory-orientation cues even if this change restores accurate orientation information.

**Acknowledgments**

We thank S. Clark-Donovan and J. Roth for their assistance.
GRANTS
This work was supported by National Institutes of Health Grants AG-17960 to R. J. Peterka and DC-04455 to P. J. Loughlin.

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