Position and Velocity Coupling of Postural Sway to Somatosensory Drive

JOHN JEKA, KELVIN OIE, GREGOR SCHÖNER, TJEERD DIJKSTRA, AND ELAINE HENSON

1Department of Kinesiology, University of Maryland, College Park, Maryland 20742; 2Centre de Recherche en Neurosciences Cognitives, Centre National de la Recherche Scientifique, 13402 Marseille 20, France; and 3Department of Psychology, Ohio State University, Columbus, Ohio 43210


Light touch contact of a fingertip to a stationary surface provides orientation information that enhances control of upright stance. Slight changes in contact force at the fingertip lead to sensory cues about the direction of body sway, allowing attenuation of sway. In the present study, the coupling of postural sway to a moving contact surface was investigated in detail. Head, center of mass, and center of pressure displacement were measured as the contact surface moved rhythmically at 0.1, 0.2, 0.4, 0.6, and 0.8 Hz. Stimulus amplitude decreased with frequency to maintain peak velocity constant across frequency. Head and body sway were highly coherent with contact surface motion at all frequencies except 0.8 Hz, where a drop-off in coherence was observed. Mean frequency of head and body sway matched the driving frequency ≤0.4 Hz. At higher frequencies, non-1:1 coupling was evident. The phase of body sway relative to the touch plate averaged 20–30° at 0.1-Hz drive and decreased approximately linearly to −130° at 0.8-Hz drive. System gain was ~1 across frequency. The large phase lags observed cannot be accounted for with velocity coupling alone but indicate that body sway also was coupled to the position of the touch plate. Fitting of a linear second-order model to the data suggests that postural control parameters are not fixed but adapt to the moving frame of reference. Moreover, coupling to both position and velocity suggest that a spatial reference frame is defined by the somatosensory system.

INTRODUCTION

For humans to remain upright, it is crucial to know the position of different body segments relative to the surrounding environment. How we construct such an internal model is unknown, but it is thought to be heavily dependent on information from visual, vestibular, and somatosensory sources. Consequently, an intensive research effort during the last two decades has contributed considerable knowledge about properties of sensory information that are important for human postural control and spatial orientation (for reviews see Horak and MacPherson 1996; Nashner 1981).

One of the primary methods to investigate “sensorimotor integration” or “perception-action coupling” stems from linear systems theory. Subjects typically are “driven” by an oscillating pattern of sensory information. The resulting postural or orientation responses of the body are measured to determine “system” control properties. For example, the sinusoidal vertical axis rotation (SVAR) technique rotates seated subjects at a range of frequencies to measure the gain and phase of eye movements in the dark as a measure of vestibular function (Howard 1982; Krebs et al. 1993). Likewise, an oscillating visual “moving room” has been used to demonstrate the coupling of visual information with whole-body posture (Berthoz et al. 1979; Dijkstra et al. 1994a,b; Lee and Lishman 1975; Peterka and Benolken 1995; Soechting et al. 1979; Talbott and Brookhart 1980; van Asten 1988). These techniques have determined that rate information is derived from sensory stimuli, that is, the vestibular system provides information about angular acceleration of the head and linear acceleration of the body (Benson 1982), whereas the visual system is sensitive to the velocity of a stimulus (Dijkstra et al. 1994b; Schöner 1991).

Such control theory techniques have not been implemented for somatosensory function with regard to upright stance control. Extensive empiric studies have determined that the primary role of somatosensation is to provide information concerning contact surface forces and properties such as texture and friction and the relative configuration of body segments (Dietz 1992; Horak and MacPherson 1996). Moreover, there is evidence that somatosensory inputs provide the most sensitive means of perceiving small increments of postural sway (Fitzpatrick and McCloskey 1994). However, it remains unclear how somatosensory information acts on posture, that is, what properties of the somatosensory stimulus couple to posture.

We have begun to address this question through a series of studies that illustrate that somatosensory cues derived from light-touch fingertip contact to a stationary surface provide orientation information for improved control of upright stance. Contact at the fingertip with a stationary rigid surface led to sensory cues about body motion, allowing attenuation of sway (Holden et al. 1994; Jeka and Lackner 1994, 1995). Further, the influence of fingertip contact with a moving surface on whole-body posture was as dramatic as with full-field vision (Jeka et al. 1994, 1997). When the contact surface moved sinusoidally, head/body sway adopted the frequency of contact surface motion. Predictions of a second-order, linear model supported the hypothesis that body sway was coupled to the contact surface through the velocity of the somatosensory stimulus at the fingertip.

In the present study, we examine further the issue of veloc-
ity-dependent coupling of head and body sway to the motion of a somatosensory stimulus. In the study by Jeka et al. (1997), all subjects showed a constant head gain as stimulus frequency increased, even though phase lags as large as −90° were observed (body sway temporally behind the contact surface movement). The constant gain suggested that the postural system may be adapting its own control system parameters (e.g., eigenfrequency) to remain sensitive to a stimulus that was not compatible with its “natural frequency” of sway. However, no conclusive statements could be made because the peak velocity of the contact surface increased with increasing stimulus frequency (i.e., movement amplitude was held constant across frequency). As a result, stimulus intensity also increased with frequency, which means that constant gain across frequency could result from either increased somatosensory drive or adaptation of postural control parameters. The increase in stimulus intensity makes it difficult to sort out potential adaptive properties of the postural control system. Therefore, in the current study, peak velocity of the stimulus motion was held constant by decreasing amplitude across frequency. We asked the questions: does the postural sway response across stimulus frequencies indicate velocity coupling or are other properties of the stimulus also relevant? Does the gain response with a constant sensory drive indicate adaptive effects? The temporal relationship between dynamic somatosensory cues and whole-body postural sway was examined in terms of model predictions.

METHODS

Subjects

Three male and three female undergraduate students at the University of Maryland (ages 20–22 yr) participated in the study. The participants had no known musculoskeletal injuries or neurological disorders that may have affected their balance control. All subjects gave written consent according to procedures approved by the Institutional Review Board at the University of Maryland.

Apparatus

Figure 1 illustrates the experimental setup. Each subject stood on a force plate in a tandem Romberg position (heel-to-toe) with eyes closed and with the tip of the right index finger in contact with a moving touch plate. Subjects placed their fingertip on a thin circular self-sticking paper dot (1.5 cm diam) in the middle of the touch plate to minimize fingertip sliding and ensure contact with the touch plate throughout the trial.

FINGERTIP CONTACT FORCES. A circular metal plate 5 cm in diameter mounted on a tripod was positioned to the right of each subject at approximately hip level to provide the stimulus (i.e., touch plate motion) through fingertip contact. A motor controlled by a torque servo drive (Compumotor OEM670T) was used to rhythmically move the touch plate from side to side parallel to the subject’s frontal plane. The touch plate measured lateral (Tx and Ty directions) and vertical (Tz direction) fingertip contact forces through three strain gauges mounted to the metal plate. A computer monitored the applied forces and emitted an auditory alarm when the threshold force of 1 N was exceeded in any direction.

HEAD AND CENTER OF MASS MOTION. Medial-lateral head (Hx) and center of mass (CMx) displacements were measured using a multiple receiver 6D tracking system (Logitech). The system consisted of a control unit, two small triangular ultrasonic receivers (7 × 7 × 7 cm) and a triangular transmitter (25 × 25 × 25 cm). The transmitter was mounted to a tripod positioned ~1 m behind the subject. One receiver was mounted to the subject’s waist with a velcro waistband. The other receiver was mounted on an adjustable lightweight headband. Each receiver measured three directions of rotation (yaw, pitch, roll) with a resolution of 0.1°.

CENTER OF PRESSURE. Medial-lateral position of center of pressure (CPx) was calculated from ground reaction forces measured by a force plate (Kistler Model 9261A). All signals were sampled at 50 Hz in real time.

Stimuli

The touch plate was driven rhythmically by a torque servo drive at frequencies of 0.1, 0.2, 0.4, 0.6, and 0.8 Hz with peak-to-peak displacements of 18, 9, 4.5, 3, and 2.25 mm, respectively. Covarying the amplitude of the displacement with frequency kept the peak velocity constant at 0.65 cm/s at all driving frequencies. Control of the servomotor allowed only for peak velocity and acceleration to be defined within a cycle not instantaneous velocity and acceleration. Consequently, touch plate movement approximated sinusoidal motion. Touch plate position was measured using a precision encoder attached to the end of the servomotor. The encoder produced 1,000 pulses per revolution. A custom circuit monitored the motor’s

1 The ultrasonic tracker provides an approximation of the center of mass only if the body is swaying like an inverted pendulum. In the present study, relative phase values at the head, waist and feet were equivalent at all frequencies (see Fig. 6), which indicates inverted pendulum motion of the body.
direction and counted the number of encoder pulses to enable D/A conversion at a resolution of 0.0004 cm.

**Procedure**

Each subject stood barefoot on the force plate with the right foot in front of the left and with knees slightly bent. Foot position was marked with chalk on a hard rubber mat placed securely over the force plate so that the same foot position was maintained for each trial. The height and lateral position of the touch plate then were adjusted to a comfortable position, which was approximately at hip level with the elbow slightly bent ($=165^\circ$).

The subject was instructed to maintain the heel-to-toe stance with eyes closed while keeping the fingertip force on the touch plate $<1$ N. The subject was not told that the touch plate would move. Subjects reported that the movement of the touch plate was ambiguous. They knew that it was not stationary, but they could not decipher the frequency or amplitude of its movement. Trial duration was 90 s. Five trials at each frequency were performed in random order, with the first two trials at 0.2 Hz to allow subject adaptation. The experiment lasted ~2 h.

**Analysis**

**LINEAR SYSTEMS ANALYSIS.** Spectral analysis was performed to determine the magnitude squared coherence (MSC), gain and phase between all three measures of body sway (CPx, CMx, and Hx) and touch plate displacement (TPx). Spectra were evaluated only at the stimulus frequency, which was the only frequency at which systematic peaks were observed. A Welch procedure (Marple 1987) was employed to calculate the spectra using seven segments and factor 3 zero padding. MSC is a measure of how strong body motion is coupled with the stimulus (i.e., touch plate movement). An increase in MSC to a maximum of 1 indicates stronger coupling. Gain was defined as the ratio of the amplitude spectrum of CPx, CMx, or Hx to the touch plate amplitude spectrum at the driving frequency.

**TIME SERIES OF RELATIVE PHASE.** Discrete time series of relative phase between center of pressure (CPx) and touch plate displacement, center of mass (CMx) and touch plate displacement, and head (Hx) and touch plate displacement were calculated. The data were first smoothed using a Gaussian window with a standard deviation of 0.18 s. The significant extrema were picked in the position and velocity curves of each measure. To calculate relative phase, the time difference between an extremum of the target signal (CPx, CMx, or Hx) and an extremum of the reference signal (TPx) was taken and divided by the time difference of two extrema in the reference signal. The phase angle then was converted to degrees. Mean and angular deviation of relative phase were calculated for each trial.

**RESULTS**

Subjects exhibited strong coupling between body sway and touch plate movement, but the strength of this coupling was frequency dependent. Figures 2 and 3 show the time series, amplitude spectra, and relative phase of center of mass (CMx) and touch plate (TPx) displacement of typical trials from one subject at 0.2 and 0.6 Hz, respectively. Center of pressure (CPx) and head (Hx) displacement showed behavior similar to CMx. The time series in Fig. 2A illustrates that CMx displacement is frequency-locked with TPx movement at 0.2 Hz, supported by the amplitude spectrum shown in Fig. 2B, showing a definite peak at the driving frequency. In Fig. 2C, the relative phase time series at 0.2 Hz illustrates strong phase entrainment with a consistent mean relative phase of $\sim0^\circ$ (i.e., in-phase).

By contrast, in Fig. 3A, a 1:1 frequency relationship between center of mass and touch plate displacement was not evident at 0.6 Hz. A clear amplitude peak at $\sim0.6$ Hz was observed for CMx displacement in Fig. 3B, but substantial broadband amplitude also was observed at lower frequen-
The relative phase time series in Fig. 3C shows a mean phase lag of approximately $-90^\circ$ (CMx displacement temporally behind touch plate displacement) with discontinuities indicating skipped cycles. A consistent mean phase along with discontinuities suggests relative coordination (von Holst 1973).

**CONTACT FORCES.** Touch contact forces were maintained at comparable levels across all conditions. Collapsed across subjects and frequency, anterior-posterior (Ty) and mediolateral (Tx) forces averaged 0.018 and 0.015 N, respectively, and showed no statistical differences across frequency for individual subjects ($P > 0.1$). Vertical contact forces ($Tz$) averaged $-0.4$ N, showing no differences across frequency for all subjects ($P > 0.05$), except subject 4, who showed a significant frequency effect for Tz. The maximum mean Tz force for subject 4 was 0.46 N at 0.6 Hz, which was well below the required threshold of 1 N.

An analysis of the contribution of touch plate forces to peak angular acceleration of the body was done by computing the peak angular body accelerations that may be generated by the touch forces and by comparing these to the observed peak angular acceleration of sway. The analysis showed a potential mechanical contribution from touch plate forces to the peak angular acceleration of the body at the 0.1-Hz driving frequency (contribution of $T_x + T_z = 72\%$), which drops off sharply as driving frequency increases (e.g., 0.8 Hz: $T_x + T_z = 5\%$). One may hypothesize that at low frequencies, the body is linked rigidly to the force plate and thus swaying purely because that force plate moves. This rigid body link implies that touch forces and touch plate position are in-phase and touch forces exactly match the sway forces. However, such a rigid link hypothesis is not feasible for the following reasons.

1) **Strict mechanical coupling implies perfect coherence (MSC = 1)** between touch forces and body sway. An analysis of the coherence between touch forces and the center of mass showed an average MSC of 0.68 at all frequencies (collapsed across subjects). This is much lower than the coherence between touch plate position and body sway (see **MEAN SQUARED COHERENCE**). If force causes sway, then force should be equally or more coherent with body sway than touch plate position.

2) The results presented below for the relative phase between body sway and touch plate position show that the body leads touch plate movement by $\sim 30^\circ$ at 0.1 Hz. Pure mechanical coupling requires an in-phase relationship and points to the importance of other factors than mechanical coupling.

3) **Body sway frequency increased with touch plate frequency (see frequency).** Because the velocity of the touch plate movement was kept constant across frequency, peak acceleration of the touch plate increased with frequency. Increasing peak acceleration suggests increasing peak touch forces if mechanical coupling plays an important role. However, we observe constancy of peak touch forces across frequency, arguing against an important role of force to drive body sway.

**FREQUENCY.** Mean frequency of Hx and CMx displacement matched the stimulus frequency $\leq 0.4$ Hz but dropped below the driving frequency $>0.4$ Hz. In Fig. 4, A–C, the 1:1 frequency relationships between the drive and a body component are illustrated (— — —). Head and center of mass displacement frequency were clearly lower than the touch plate frequency at driving frequencies $>0.4$ Hz. CPx displacement followed the drive more closely than CMx or Hx at higher stimulus frequencies. Center of pressure is known to contain higher frequency components than center of mass (Winter et al. 1990). Statistical analysis revealed significant frequency effects for CPx, CMx, and Hx mean sway frequency for all subjects ($P < 0.0001$).

**MEAN SQUARED COHERENCE.** The coupling between touch plate movement and body sway was strong $<0.4$ Hz and decreased at higher stimulus frequencies. In Fig. 5, A–C, mean squared coherence between touch plate displacement and CPx, CMx, and Hx displacement was $>0.95$ at frequencies $<0.4$ Hz with a slight drop off at higher frequencies. Significant effects for MSC as a function of frequency emerged for: CPx MSC ($P < 0.01$) for subjects 1, 2, and 4, CMx MSC ($P < 0.05$) for all subjects, and for subjects 1, 3, and 5 with Hx MSC. The significant effects were due primarily to the reduction in MSC at frequencies $>0.4$ Hz.

**PHASE.** Mean relative phase steadily decreased with increasing stimulus frequency. Figure 6, A–C, illustrates that with a touch plate frequency of 0.1 Hz, mean phase is positive for CPx, CMx, and Hx, indicating that body sway is leading touch plate movement. As the driving frequency increased, CPx, CMx, and Hx displacement fell temporally behind touch plate movement, shown by a steadily increasing phase lag, with a maximum lag of $\sim 130^\circ$ at 0.8 Hz.

Relative phase for CPx, CMx, and Hx maintained consistent...
mean values across all stimulus frequencies but showed relative coordination behavior >0.4 Hz, where non-1:1 frequency relationships were adopted. The angular deviation of relative phase, plotted in Fig. 7, also showed a clear modulation with frequency, with a minimum at 0.2 Hz and an increase toward higher frequencies in all subjects. Significant effects ($P < 0.0001$) for frequency emerged for CPx, CMx, and Hx mean relative phase and the angular deviation of relative phase with all subjects.

**Mean gain.** Maximum gain was observed ~0.4 Hz for head (Hx) and center of mass (CMx) motion for all subjects, as seen in Fig. 8, A and B. In Fig. 8C, center of pressure (CPx) gain increased and leveled off with increasing drive, showing a differential gain response when compared with both CMx and Hx. A significant effect for frequency was observed for Hx, CMx, and CPx gain for all subjects ($P < 0.0001$).

**Theoretical model**

We studied the coupling between a rhythmic somatosensory stimulus at the fingertip and body sway, extending previous results that had suggested that body sway was coupled to the velocity of the somatosensory stimulus (Jeka et al.
In this previous study, coherence increased with frequency and gain remained constant, which was surprising in view of the large phase lags observed at the larger frequencies. Although such strong coupling might have been indicative of adaptive changes of the postural sway system that enable it to follow somatosensory inputs to relatively high frequencies, the previous data could not be unequivocally interpreted in this way because the peak velocity of the somatosensory drive increased with frequency (i.e., amplitude was kept constant as frequency increased). The stimulus may have provided stronger input to the postural system at higher frequencies than at lower frequencies. In this study, we kept peak velocity of the somatosensory drive constant across frequency by decreasing the amplitude of touch plate movement with increasing frequency. The following results were obtained for all subjects.

1) Strong coupling was observed at frequencies <0.6 Hz with coherence values consistently >0.95 for all subjects. Coherence dropped off at 0.6 and 0.8 Hz. These higher frequencies are well above the eigenfrequency of body sway (≈0.2 Hz) and non-1:1 coupling was clearly evident.

2) Relative phase was slightly above zero at 0.1 Hz (body
sway phase leads the touch plate) and decreased approximately linearly as touch plate frequency increased. The maximum phase lag was $\approx 130^\circ$ at 0.8 Hz.

3) Gain showed weak resonance for head and center of mass motion. Gain showed a steady increase for center of pressure.

To the extent that we exclude the rigid link hypothesis, we must recognize that the forces at the touch plate arise because the body-finger tip ensemble resists the touch bar motion with finite eigenfrequency and damping. This resistance is generated actively by the nervous system. Thus the relevant question is how the nervous system couples to this position input. In other words, the moving touch plate causes both body sway and touch force in a manner structured by nervous system properties. The fact that a certain amount of the acceleration of the center of mass is caused potentially by touch bar forces does not contradict the notion that sensory coupling to somatosensory information underlies the temporal relationships observed between body sway and touch plate motion.

Qualitatively, these results are consistent with the previously proposed account of the influence of somatosensory cues on posture, in which the postural system is conceived of as a stable control system that receives as one source of input the somatosensory signal (Jeka et al. 1997). This
argument can be made more explicit and exact by formulating a concrete mathematical model and comparing it with the experimental data. This is worthwhile because the way in which such a model falls short of a good fit is revealing of mechanisms that have not been taken into account. We proceed in two steps: first, we recall the simplest model used previously, in which somatosensory velocity provides the input signal to the postural system. The model is fitted to the data, and the remaining discrepancy analyzed as a function of frequency. This motivates an extension of the model that includes position coupling. A best fit leads to an improved account, but still falls short of a correct description. Again, the remaining discrepancy reveals a clear dependence of frequency, which enables us to interpret this error in terms of adaptive processes.

A theoretical model can be based on the following assumptions (cf. Schöner 1991): 1) The state of the postural control system can be characterized by the lateral position, $x$, of the center of mass and its velocity, $\dot{x}$; 2) The overall stability properties of the postural system (including both plant and controller) can be characterized as a second-order dynamical system with the two parameters eigen-
frequency, $\omega$, and damping (or viscosity), $\alpha$; and 3) Somatosensory information contributes to postural control as an on-line contribution that stabilizes the resting state in the relevant frame of reference. The relevant frame of reference is the inertial frame for contact with a stationary surface and a moving frame of reference for contact with a moving surface.

The simplest model, proposed previously (Jeka et al. 1997), postulates that the somatosensory velocity at the fingertip, $(\dot{d} - \dot{x})$, is the relevant signal coupling into postural control

$$\ddot{x} + \alpha \dot{x} + \omega^2 x + \sqrt{Q}\xi = c_i(\dot{d} - \dot{x})$$

Here, $d(t) = d_0 \sin(2\pi f_d t)$, is the time varying position of the touch plate in the inertial frame, so that $d - \dot{x}$ is the relative velocity between touch plate and center of mass. The parameter, $c_i$, represents the strength of the somatosensory input. Noise is added ($\sqrt{Q}\xi$) to capture the random influences on the equilibrium state. Somatosensory input contributes both as a driving force ($c_i \dot{d}$) and as an additional source of damping ($-c_i \dot{x}$). The damping contribution accounts for the reduction of sway observed with a stationary touch bar (Jeka and Lackner 1994). The effective damping with touch is therefore $\dot{\alpha} = \alpha + c_i$.

The model predicts how gain and relative phase depend on the frequency, $f_d$, of the touch plate (cf. Schöner 1991,
maximum of gain is located at too low a frequency, as reflected by the fitted value of eigenfrequency.

These results clearly indicate that velocity coupling cannot account for the large phase delays observed at higher frequencies. The underestimation of gain is consistent with this observation, because the model is far from resonance at the higher frequencies. Overestimation of gain at the resonance frequency is a trade-off of the minimization.

These results point to the need to consider coupling to position related somatosensory signals. Because position lags 90° behind velocity, such coupling might account for the large phase delays observed at higher frequencies. Introducing one additional coupling constant $c_p$, the extended model reads

$$\ddot{x} + \alpha \dot{x} + \omega^2 x + \sqrt{Q} \dot{Q} \xi = c_v (\dot{x} - \dot{y}) + c_p d(t)$$ (2)

The choice of multiplying the position coupling term by $d$ rather than $d_0 x$ (as with the velocity coupling term) is motivated by experimental findings with a stationary touch plate (Jeka and Lackner 1994). With a stationary touch plate, $d$ and $d_0$ are both zero, allowing the corresponding $x$ and $i$ terms to be added on the left side of Eq. 2. This operation increases the damping and eigenfrequency of postural sway. The corresponding experimental findings with a stationary contact surface are consistent with an increase in damping (i.e., a decrease in sway amplitude) but not with an increase in eigenfrequency, because no change in the frequency spectrum of body sway was observed with light touch contact (Jeka and Lackner 1994). Consequently, position coupling must not contain a contribution to stiffness, that is, no term proportional to $x$.

Fig. 9. Fitted gain (A) and phase (B) functions of CMx displacement for the model with velocity coupling.

for the formulas, which carry over from the case of visual input). Therefore the model can be compared with the experiment by fitting the parameters $\omega$, $\alpha$, and $c_v$ to minimize the sum of squared differences between measured and predicted relative phase and gain.$^4$

The fits lead to parameter values for each subject and trial (mean over subjects and trials: $\alpha = 1.5$ s$^{-1}$, $\omega = 1.3$ s$^{-1}$, which corresponds to a frequency of $\omega/2\pi = 0.21$ s$^{-1}$ and $c_v = 2.4$ s$^{-1}$). The fitted phase and gain functions are shown in Fig. 9, and the difference between fitted and observed gain and phase is plotted as a function of frequency in Fig. 10. The residual error is not small and a pattern of systematic error is clearly visible: 1) Relative phase always is overestimated, and this error is more pronounced at high and very low frequencies; 2) Gain is underestimated at all except the lowest frequencies, near the fitted eigenfrequency of 0.21 Hz, gain is slightly overestimated; and 3) The resonance

$^4$ A Levenberg-Marquardt nonlinear least squares procedure was used to fit individual transfer functions by minimizing the error in the complex (Gaussian) plane. For each subject, gain and phase values were available from five trials at each frequency. These were combined into five different estimates of the transfer function considered as a function of somatosensory frequency $f_d$. The real part of the transfer function was calculated as gain·cos(phase) and the imaginary part as gain·sin(phase). The mean and SD across the five estimates were determined both for the fitted parameter values as well as for the predicted gain and phase as functions of frequency. We report results for fits based on center of mass displacement data. A similar pattern emerges for fits of center of pressure and head displacement data.
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The dynamical model also predicts the stability of the phase. The phase variability, for instance, is, in the model, inversely proportional to the square root of \( \alpha \), the proportionality factor being the noise strength, another model parameter (cf. Schöner 1991). The constant parameter model thus predicts that phase variability is independent of the frequency of the somatosensory input. The observed increase of phase variability with frequency (Fig. 7) therefore provides evidence for an adaptive decrease of the parameter \( \alpha \) with frequency, leading to reduced stability of phase as frequency is increased. This form of adaptation has been observed in the visual moving room (Giese et al. 1996). Reduced damping at higher frequencies is consistent with the observed larger than predicted gains as well as with the observed drop in coherence at these high frequencies. Moreover, this adaptive effect also can account for the characteristic frequency dependence of the deviation of the predicted from the observed phase. Reduced damping “sharpens” the phase-frequency function, so that at frequencies larger than the eigenfrequency phase \( \text{lags} \) more than predicted (overestimation) and at frequencies smaller than the eigenfrequency phase \( \text{leads} \) more than predicted (underestimation—see Fig. 12). Note that the mechanical contribution of the touch forces to sway at low frequencies attracts phase toward zero. Therefore, the enhanced phase advance at 0.1 Hz is in the opposite direction than that produced by mechanical coupling, implying that adaptation of the sensory contribution to postural sway is accounting for the observed behavior.

An adaptive change of the second parameter, eigen-frequency \( \omega_c \), cannot be excluded. The underestimation of gain at the highest somatosensory driving frequency is con-

For reference we list the mean fitted parameters of this model: \( \bar{\alpha} = 1.6 \; \text{s}^{-1} \), \( \omega = 2.4 \; \text{s}^{-1} \), corresponding to a frequency of 0.38 Hz, \( c_v = 1.6 \; \text{s}^{-1} \) and \( c_p = 4.6 \; \text{s}^{-2} \). The fitted gain and phase functions are shown in Fig. 11. The residual error, plotted as a function of driving frequency in Fig. 12, is clearly much smaller than without position coupling (there is also, of course, 1 additional parameter). More interestingly, the pattern of systematic error is also quite different. 1) Relative phase is approximated very well around the fitted eigenfrequency of 0.38 Hz. At the highest frequency, relative phase is again overestimated, that is, the actual sway is lagging further behind the touch plate than predicted. At the lowest frequency, by contrast, relative phase is underestimated, that is, actual sway leads the touch plate more than predicted. 2) Gain is well described up until 0.6 Hz, where it starts to be underestimated. 3) The resonance maximum of gain is now correctly located near 0.4 Hz.

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An adaptive change of the second parameter, eigen-frequency \( \omega_c \), cannot be excluded. The underestimation of gain at the highest somatosensory driving frequency is con-
sistent with such a notion: adaptive shift of eigenfrequency with driving frequency leads to the system never being as far removed from resonance as in the constant parameter model and, consequently, remaining at higher levels of gain than predicted. Direct evidence for such an adaptation effect has been provided in studies that drove the postural system by visual input (Giese et al. 1996).

In summary, these fits support the notion that a combination of position and velocity coupling can account for the observed pattern of results. The deviations from the extended model, are also quite interesting, however, in that they provide evidence for adaptive change of the postural control system in response to periodically structured somatosensory input. We emphasize, however, that the evidence for adaptation is not conclusive, but merely the most feasible interpretation of the deviations from the model predictions.7

DISCUSSION

We extended our earlier findings on the continuous coupling of somatosensory signals into the postural control system (Jeka et al. 1997) by investigating the system with a constant peak velocity signal into higher frequencies. This led to the discovery of a position-related input signal. In hindsight, it is easy to understand why this position coupling contribution was not detected in the earlier study: at high frequencies, the position signal was swamped by the massive input from the velocity related signal, the amplitude of which increased with increasing peak velocity (due to constant amplitude across frequency). At the lower frequencies, the system operates close to its eigenfrequency, so that only modest effects of the somatosensory input are observable through gain and phase. Quantitative comparison of a model with and without position coupling supported our conclusion that somatosensory position contributes to postural control. Even when both position and velocity dependent coupling was taken into account, however, characteristic deviations of the model from the data remained. These were interpreted in terms of adaptive changes of the parameters of the postural control system.

Spatial reference frames

The sensitivity to position sets somatosensation apart from the other major sensory inputs to postural control. Body sway is known to be sensitive to the velocity of visual drive (Dijkstra et al. 1994b; Schöner 1991). Vestibular information provides accelerative (Benson 1982) and some argue, velocity-dependent input (Howard 1982) for spatial orientation. Position- and velocity-dependent input, however, seems to be conveyed simultaneously through the somatosensory system. The neurophysiological basis for velocity-dependent somatosensory afferent activity is well documented at the peripheral (Johansson et al. 1982; Matthews 1988) and central levels (Esteky and Schwark 1994). Moreover, there is much evidence to suggest that muscle spindle signals interpreted in relation to motor commands are the primary source of information for the position sense representation of the body and about body orientation relative to a support surface (Lackner 1988; Matthews 1988). The fine acuity of cutaneous stimulation at the fingertip in combination with muscle spindle stimulation allows for precise detection of both position and rate of body sway with fingertip contact of a surface.

Consequently, a spatial reference frame is defined by the somatosensory system because the sensory signal depends on position in space. Thus the sensory signal in principle could be calibrated to measure position. By contrast, the visual input at the level of the optic flow field does not depend on the position in space only on relative motion. All positions in space give equally zero optic flow if the system is at rest. Of course, there exists monocular and binocular visual information for spatial cues through stereo, depth perception, etc. (Sekuler and Blake 1994), but it remains controversial whether spatial cues such as absolute depth are derivable from optic flow (Simpson 1993). More specifically, one can say that optic flow does not define a spatial reference frame, only a velocity reference frame.

Adaptation

This experiment considerably strengthened the evidence for adaptation of the postural control system to the moving haptic world over the previous study (Jeka et al. 1997). Specifically, the convergent observations of the increase of phase deviation with increasing frequency, the concomitant decrease in coherence, and the characteristic deviation of predicted from observed phase all supported the notion that the postural control system decreases its damping with increasing frequency of the somatosensory drive. Such an adaptive reduction of damping is also consistent with the larger-than-expected gain at large frequencies, although an adaptation of eigenfrequency likewise could have caused this effect. Moreover, alternatives to our “adaptive” hypothesis are feasible (see footnote 7) and further experiments are necessary to identify adaptation conclusively.

This form of adaptation is most interesting and, probably, counterintuitive, as it leads to larger amounts of sway rather than to a reduction of sway. At reduced damping, the system is capable of generating the large sway motions in the inertial reference frame in response to the small somatosensory input signal so as to achieve approximate posture in the haptic reference frame. Thus a putative adaptive process would lead toward stabilization of posture in the moving haptic frame of reference rather than the inertial frame of reference.

More definitive evidence has been provided for adaptive...
reduction of damping and increase of eigenfrequency with increasing frequency of a visual stimulus with perturbation techniques (Giese et al. 1996). These perturbations involve reversals of the driving stimulus midway through the cycle, forcing the system to change its rhythm temporarily to maintain the same preperturbation phase relationship. Perturbations enable separation of the transient from the stationary components of the system and allow estimation of model parameters at each frequency. If parameters such as damping and eigenfrequency change across frequency to necessitate a good fit of the data, then adaptation is suggested much more clearly than with the present techniques. Such experiments are presently underway.

Relatedly, Dijkstra et al. (1994a) observed that postural sway closely matched the amplitude of visual motion even as distance to the visual display was strongly increased. By contrast, early experiments with a visual moving room (e.g., Berthoz et al. 1979; Soechting and Berthoz 1979) showed sharp decreases in gain with similar phase lags. These differences in gain response between earlier and more recent studies may be due to the amplitude of the visual stimulus, which was much smaller in Dijkstra’s study than used previously and more closely matched to the typical sway amplitudes observed with human stationary stance. Precise matching of sensory and sway amplitude may result in stronger coupling than previously observed and allow adaptive mechanisms to unfold. By analogy, in the present experiment, the small amplitude of touch plate motion may be crucial to bring about the adaptation effect. The contact surface must be interpretable to the postural system as “background” information about a relevant reference frame to trigger the adaptive processes that aim to stabilize posture in that reference frame.

Conclusions

The potential outcome of studies using the present techniques is to identify two sources of sensorimotor integration. On the one hand, there is the notion of coupling to sensory information that underlies the stabilization of posture in stationary environments. On the other hand, components of the postural control system that are not directly time-varying with sensory information contribute to postural stabilization by adapting to the sensed environment. Therefore sensory deficits may have two distinct origins: lack of coupling or inflexible adaptation to environmental conditions.

Systematically moving the sensory environment and studying how humans couple to it has proven to be a sensitive technique to determine postural capabilities. With the “moving room” technique, the sources of sensory information to which the system is coupled can be established. This is nontrivial because the total amount of sway in a stationary environment might remain constant as a sensory source is decoupled due to adaptive influences. Conversely, the system may destabilize its state in the inertial frame to achieve posture in the moving sensory environment. Experimental studies have shown that young children (Forsberg and Nashner 1982) as well as elderly individuals (Horak et al. 1989) use inflexible postural control “strategies” that suggest a relatively fixed (nonadaptive) control system. Our methods provide for assessment of postural control in human development and aging by separating the coupling to sensory information from adaptive properties of the postural control system.

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Address reprint requests to J. J. Jeka.

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