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The slow dynamics of postural sway are in the feedback loop

Tim Kiemel^{1,2}, Kelvin S. Oie^{1,3}, and John J. Jeka^{1,3}

¹Department of Kinesiology, University of Maryland, College Park, MD 20742, USA

²Department of Biology, University of Maryland, College Park, MD 20742, USA

³Program in Neuroscience and Cognitive Science, University of Maryland, College Park, MD 20742, USA

Abstract

Postural sway is considered to have two fundamental stochastic components, a slow non-oscillatory component and a faster damped-oscillatory component. The slow component has been shown to account for the majority of sway variance during quiet stance. Postural control is generally viewed as a feedback loop in which sway is detected by sensory systems and appropriate motor commands are generated to stabilize the body's orientation. Whereas the mechanistic source for the damped-oscillatory sway component is most likely feedback control of an inverted pendulum, the underlying basis for the slow component is less clear. We investigated whether the slow process was inside or outside the feedback loop by providing standing subjects with sum-of-sines visual motion. Linear stochastic models were fit to the experimental sway trajectories to determine the stochastic structure of sway as well as the transfer function from visual motion to sway. The results supported a fifth-order stochastic model, consisting of a slow process and two damped-oscillatory components. Importantly, the slow process was determined to be inside the feedback loop. This supports the hypothesis that the slow component is due to errors in state estimation, since state estimation is inside the feedback loop, rather than a moving reference point or an exploratory process outside the feedback loop.

1 Introduction

It is widely recognized that postural sway measured in a single direction, either anterior-posterior or medial-lateral, during standing consists of two components: a slow non-oscillatory component and a faster damped-oscillatory component. Zatsiorsky and Duarte (1999) termed these slow and fast components rambling and trembling, respectively, and proposed a decomposition method of center-of-pressure (COP) trajectories. Dijkstra (2000) modeled the two components of center-of-mass (COM) trajectories as a slow process that acts as the set point for a faster damped-oscillatory system. The set-point dynamics were first-order, the damped-oscillatory dynamics were second-order, and noise was added to both components, leading to a linear third-order stochastic model of sway. Autoregressive moving-average (ARMA) modeling has also pointed to a linear third-order stochastic model as a good approximate description of sway (Johansson et al., 1988; Kiemel et al., 2002).

Characterizing postural sway in terms of its dynamical components is descriptive. The question remains whether different dynamical components correspond to different mechanisms in the postural control system. We use eigenvalues to define and characterize the different dynamical components of sway (see methods). In general, the eigenvalues of a system depend on the

interaction between all system variables and cannot be necessarily associated with different subsystems or mechanisms. However, in particular posture models such an association is often possible. For example, in optimal-control models of posture (Kuo, 1995; van der Kooij et al., 1999; Kiemel et al., 2002), sway eigenvalues can be separated into those associated with state estimation and those associated with feedback control. Also, in models in which a stochastic process outside the feedback loop affects sway dynamics (Peterka, 2000; Masani et al., 2003), sway eigenvalues can be separated into those associated with the outside process and those due to dynamics inside the feedback loop (see methods).

Of the two components of sway described above, the damped-oscillatory component has the clearest mechanistic explanation. In the simplest biomechanical description of postural control, the body is viewed as an inverted pendulum. An inverted pendulum is unstable, and proportional-derivative (PD) feedback is required to stabilize upright stance (Johansson et al., 1988). If the derivative feedback is not too strong relative to the proportional feedback, then the system has damped-oscillatory dynamics.

The mechanistic source for the slow sway component is less clear. Zatsiorsky and Duarte (1999) hypothesized that the slow dynamics are due to a slowly-migrating reference point defined by a central command. In contrast, we have hypothesized that the slow dynamics are due to state estimation (Kiemel et al., 2002). We view the reference point as being fixed and slow changes in posture as the unavoidable consequence of errors in estimating one's position and velocity.

In models of postural control (e.g., Peterka 2000; van der Kooij et al., 2001; Masani et al., 2003), the reference point is an external input into the feedback loop that specifies the preferred orientation of the body (Fig. 1). In this theoretical framework, Zatsiorsky and Duarte's reference-point hypothesis locates the source of the slow dynamics outside the postural control feedback loop. In contrast, state estimation is in the feedback loop (Fig. 1), so our estimation-errors hypothesis locates the dynamics inside the loop.

Understanding the mechanistic source of the slow dynamics is critical to understanding the postural control system. Kiemel et al. (2002) found that most of COM sway variance during quiet stance can be attributed to slow dynamics. As the amount of sensory information increased, sway variance decreased primarily due to a decrease in the slow component of sway. Thus, to understand how the postural control system uses sensory information to decrease sway, it is necessary to understand the mechanistic source of the slow component.

In this paper we use visual motion to test if the source of the slow sway dynamics is inside the feedback loop. Our approach is based on approximating sway dynamics by a descriptive linear stochastic model. The model describes the stochastic components of sway as well as the transfer function from visual motion to sway. The stochastic components of sway are those due to noise in the system. They account for the non-deterministic aspects of sway such as trial-to-trial variability. The transfer function shows how postural response sensitivity (gain) and timing (phase) change as a function of visual stimulus frequency.

2 Methods

2.1 Experimental methods

Subjects—Ten subjects from the University of Maryland participated in the study. Subjects ranged in age from 19 to 33 years and had no known musculoskeletal injuries or neurological disorders that might have affected their ability to maintain balance. All subjects were given both oral and written task instructions and gave written consent according to guidelines

implemented by the IRB at the University of Maryland before undergoing the experimental protocol.

Experimental setup—Each subject stood approximately 40 cm in front of a rear-projected screen (2.0 m × 1.0 m, Da-Lite Screen Company, Inc.) in a parallel stance with the balls and heels of the feet 1 cm apart. Foot position was marked to maintain the same foot position for each trial. Subjects wore goggles that allowed them to wear their prescription eyeglasses, if necessary. The goggles limited their visual range to approximately 100 deg high × 120 deg wide such that potential visual cues for stance control other than the visual display itself, such as the edges of the screen, were not available. Subjects were instructed to keep the knees unlocked and the head level.

Kinematics—Body kinematics were measured using an OptoTrak (Northern Digital, Inc.) system with a 50 Hz sampling rate. Markers were placed at the ankle (lateral malleolus), knee (lateral femoral condyle), hip (greater trochanter) and shoulder (acromium) on the right side of the subject's body.

Visual scene motion—The visual display consisted of a computer-generated pattern of 100 randomly placed triangles (side lengths of approximately 0.2 × 0.2 × 0.3 deg at a distance of 40 cm) that excluded the foveal region. The size and position of the triangles were varied to simulate anterior-posterior (AP) motion of the visual scene, specified by custom D/A Labview software which output a position voltage signal at 50 Hz via an external A/D device (PC-MIO-16E, National Instruments, Inc.). The focus of expansion in virtual space was positioned at the approximate center of the subject's foveal region prior to the start of data collection. The visual display was generated by a graphics workstation (Intergraph, Inc.) at a frame rate of 25 Hz at a spatial resolution of 1024 × 768 pixels with a 75 Hz vertical refresh rate and rear-projected via a CRT projection system (ECP 4500, Electrohome, Inc.).

The simulated AP position of the scene was given by a sum-of-sines function of the form

$$u(t) = \sum_{j=1}^{10} \frac{A}{f_j} \sin(2\pi f_j t) \quad (1)$$

where the vector of frequencies was

$$f = (3, 7, 13, 23, 43, 73, 113, 179, 263, 367)/125$$

in units of Hz. Note that the amplitude of each sinusoid was scaled inversely with frequency so that each sinusoid had the same peak velocity. The frequencies varied from 0.024 to 2.936 Hz and were chosen as prime multiples of a base frequency (0.008 Hz) so that the visual motion repeated every 125 s while avoiding common low-order harmonics.

Experimental conditions—There were two conditions: a low-amplitude condition with $A = 0.05$ cm Hz in Eq. 1 and a high-amplitude condition with $A = 0.10$ cm Hz. Subjects reported that they were aware of the visual motion in both conditions, but that the motion was not predictable. There were eight low-amplitude trials and three high-amplitude trials. We ran more low-amplitude trials, because we expected a smaller sway response in this condition, an expectation that was not borne out by our data (see Results). The length of each trial was 250 s, allowing two repetitions of the visual motion stimulus. The order of the low- and high-amplitude trials was randomized. Of the 110 total trials for the ten subjects, three were unusable and three needed to be truncated due to technical problems during data collection.

2.2 Data analysis methods

2.2.1 Computation of center of mass—We used the method of Winter (1991) to calculate the AP displacement of the estimated center-of-mass based on the ankle, knee, hip and shoulder markers.

2.2.2 Gain and phase functions—For each subject and condition, we computed the frequency-response function (FRF) from simulated AP visual motion to AP center-of-mass displacement at each of the 10 stimulus frequencies. For each trial, we divided the Fourier transform of center-of-mass by the Fourier transform of visual motion and then averaged across trials to obtain the FRF. The FRF is a complex-valued function; its absolute value is gain and its argument is phase. A positive phase indicates that sway led the visual motion.

To characterize the gains and phases of a population of subjects in a given condition, we used the absolute value and argument of the average FRF. We refer to these quantities as *group gain* and *group phase*, respectively. For each condition and stimulus frequency, we used the F-statistic to construct a 95% confidence region in the complex plane with elliptic boundary based on the assumption that the real and imaginary parts of the FRF come from a bivariate normal distribution. We computed the range of absolute values and arguments for points on the boundary to obtain conservative 95% confidence intervals for group gain and group phase.

To compare gain and phase between the low- and high-amplitude conditions at each frequency, we considered the ratio $r = \bar{z}_{\text{high}}/\bar{z}_{\text{low}}$ where $\bar{z}_{\text{low}}$ and $\bar{z}_{\text{high}}$ are the mean FRF values for the low- and high-amplitude conditions, respectively. The absolute value of r is the ratio of group gains, and the argument of r is the difference in group phases. We determined a confidence region R in the complex plane for the ratio r , and then computed the range of absolute values and arguments in R to obtain conservative 95% confidence intervals for the gain ratio and phase difference. The region R was defined as follows. For any possible r , let $p(r)$ be the p -value from testing whether $\bar{z}_{\text{high}} - r\bar{z}_{\text{low}}$ is significantly different from zero using an F-test. Then $R = \{r : p(r) \geq 0.05\}$. R is the complex analog of the Fieller confidence interval for the ratio of two means (Miller, 1986).

2.2.3 Descriptive model—For each subject and condition, we used the anterior-posterior center-of-mass trajectories sampled with a time step h to fit parameters in a descriptive linear continuous-time model of order m ranging from 1 to 7. The time step h was chosen to be either 0.1 or 0.2 s, the values used in the previous studies of Kiemel et al. (2002) and Johansson et al. (1988), respectively. In terms of Laplace transforms, the model is

$$Y_{\text{tot}}(s) = \frac{b(s)}{a(s)} e^{-\tau s} U(s) + \frac{c(s)}{a(s)} \Xi(s). \quad (2)$$

The functions $Y_{\text{tot}}(s)$, $U(s)$ and $\Xi(s)$ are the Laplace transforms of $y_{\text{tot}}(t)$, $u(t)$ and $\zeta(t)$, respectively, where $y_{\text{tot}}(t)$ is the sway trajectory with mean subtracted, $u(t)$ is the visual scene position given by Eq. 1, and $\zeta(t)$ is a white-noise process. The functions $a(s)$, $b(s)$ and $c(s)$ are polynomials of orders m , $m-1$ and $m-1$, respectively:

$$\begin{aligned} a(s) &= 1 + a_1 s + \cdots + a_{m-1} s^{m-1} + a_m s^m, \\ b(s) &= b_0 + b_1 s + \cdots + b_{m-1} s^{m-1}, \\ c(s) &= c_0 + c_1 s + \cdots + c_{m-1} s^{m-1}. \end{aligned} \quad (3)$$

The zeros of $a(s)$ are the eigenvalues of the system. Real eigenvalues correspond to first-order processes and pairs of complex conjugate eigenvalues correspond to damped oscillatory

processes. The polynomial $b(s)$ describes the strength and form of coupling to visual motion. The polynomial $c(s)$ describes the strength and form of influence from noise. The term $e^{-\tau s}$ denotes that the effect of visual motion on sway occurs after a time delay τ . Note that $a(s)$ appears in both $b(s)e^{-\tau s}/a(s)$, the transfer function from the visual scene position to sway position, and $c(s)/a(s)$, the transfer function describing the stochastic aspects of sway.

Without a time delay ($\tau = 0$), model (2) is a general model of an m -dimensional linear stochastic system with one observed variable and with visual scene position as an additive input. Any linear stochastic system will be well approximated by model (2) with m sufficiently large. Adding the time delay to the visual input allows for a more parsimonious model; that is, a model with a smaller m than would otherwise be required. In Kiemel et al. (2002), we used a discrete-time descriptive model to characterize sway dynamics and compared the results to several mechanistic continuous-time models. The descriptive model was similar to model (2), except that it was discrete-time rather than continuous-time and the visual scene was static.

Model parameters were the time delay τ , the $3m$ polynomial coefficients of Eq. 3, and the mean value for each trial. (We did not assume that the mean was equal to the sample mean.) Parameters were determined using the method of maximum likelihood. To compute the conditional log-likelihood function for a given set of parameters, we first subtracted the mean value from each trial to obtain values $y_{\text{tot}}(t)$ at discrete times $t = kh$, where k is an integer. Then, we used Eq. 1 and Eq. 2 to compute the response to the visual drive:

$$y_{\text{vis}}(t) = \sum_{j=1}^{10} \frac{A}{f_j} \{ \text{Re}[F(f_j)] \sin(2\pi f_j t) + \text{Im}[F(f_j)] \cos(2\pi f_j t) \}, \quad (4)$$

where

$$F(f) = \frac{b(2\pi i f)}{a(2\pi i f)} e^{-2\pi i f \tau} \quad (5)$$

is the frequency-response function from visual motion to sway (f is frequency and $i = \sqrt{-1}$).

Next, we computed the residual sway $y(t) = y_{\text{tot}}(t) - y_{\text{vis}}(t)$. When $y(t)$ is considered as a function of continuous time, its Laplace transform obeys the model

$$Y(s) = \frac{c(s)}{a(s)} \Xi(s) \quad (6)$$

Since our fitting was based on data at the discrete times, we converted the continuous-time model (6) to the discrete-time autoregressive moving-average (ARMA) model (Wei, 1990)

$$y_k = \phi_1 y_{k-1} + \dots + \phi_m y_{k-m} + v_k - \theta_1 v_{k-1} - \dots - \theta_{m-1} v_{k-m+1} \quad (7)$$

where $y_k = y(kh)$ and the v_k are independent normally-distributed random variables with standard deviation σ_v . Here, $\phi_1, \dots, \phi_m$ are the autoregressive coefficients, and $\theta_1, \dots, \theta_{m-1}$ are the moving-average coefficients.

For each trial, we used an exact method (cf. Ansley 1979) based on model (7) to compute the log-likelihood of the data starting at time 4 s conditioned on the previous m data points. The

last 2 s of each trial were not used. The conditional log-likelihoods were summed across trials to obtain the conditional log-likelihood for the given parameter set. The parameters were adjusted to maximize the conditional log-likelihood using a quasi-Newton method (Dennis and Schnabel, 1983). Using the conditional log-likelihood allows for transients of model (2) at the beginning of the trial due to the onset of the visual motion or other causes.

Note that all parameters of the models were fit together based on the same criterion, maximizing the conditional log-likelihood. Thus, the coefficients of $a(s)$, which determine the eigenvalues of the systems, were estimated based on both the sway response to visual motion and the stochastic properties of sway. Also, the stochastic properties of sway were explicitly accounted for when estimating and computing the confidence intervals for parameters describing the visual transfer function.

We compared models of different orders m using the Bayesian information criterion (BIC) (Taniguchi and Kakizawa, 2000). The BIC is $-2\log L + k \log n$, where L is the maximum likelihood, k is the number of parameters, and n is the number of data points at which the likelihood is computed. A smaller BIC indicates a better fit after correcting for the number of parameters. The BIC places a greater penalty on additional parameters than other selection criteria such as Akaike's information criterion or the Hannan-Quinn criterion. For ARMA models, the BIC is a consistent estimator of model order (Hannan, 1980), meaning that the probability of selecting the correct order converges to 1 as the amount of data increases.

For a fitted model, we computed the FRF from visual motion to sway using Eq. 5 and the one-sided power spectral density (PSD) of residual sway as

$$P(f) = 2 \left| \frac{c(2\pi i f)}{a(2\pi i f)} \right|^2,$$

which follows from Eq. 6.

Measures based on fitted model: The zeros of $a(s)$ are the eigenvalues of the model. In the case of a fifth-order model with one real eigenvalue, λ_r , and two pairs of complex-conjugate eigenvalues, $\{\lambda_{c1}, \bar{\lambda}_{c1}\}$ and $\{\lambda_{c2}, \bar{\lambda}_{c2}\}$ we used $a(s)$, $c(s)$ and Eq. 6 to compute the autocovariance function of the residual sway:

$$E[y(t)y(t+\delta)] = \kappa_r e^{\lambda_r |\delta|} + \kappa_{c1} e^{\lambda_{c1} |\delta|} + \bar{\kappa}_{c1} e^{\bar{\lambda}_{c1} |\delta|} + \kappa_{c2} e^{\lambda_{c2} |\delta|} + \bar{\kappa}_{c2} e^{\bar{\lambda}_{c2} |\delta|}, \quad (8)$$

where κ_r , κ_{c1} , $\bar{\kappa}_{c1}$, κ_{c2} and $\bar{\kappa}_{c2}$ are the coefficients corresponding to each eigenvalue. The eigenvalue λ_r is typically small. Therefore, $\kappa_r e^{\lambda_r |\delta|}$ is a first-order slow-decay component of the autocovariance function. The remainder of the autocovariance function consists of two damped-oscillatory components, $\kappa_{c1} e^{\lambda_{c1} |\delta|} + \bar{\kappa}_{c1} e^{\bar{\lambda}_{c1} |\delta|}$ and $\kappa_{c2} e^{\lambda_{c2} |\delta|} + \bar{\kappa}_{c2} e^{\bar{\lambda}_{c2} |\delta|}$. These damped-oscillatory components reflect damped-oscillatory modes in the dynamics of the system. We used the following 18 measures to describe the fitted model.

- Slow-decay rate: $\beta = -\lambda_r$.
- Damping of j -th mode: $\alpha_j = -(\lambda_{cj} + \bar{\lambda}_{cj})$ for $j \in \{1, 2\}$.
- Eigenfrequency of j -th mode: $f_j = \sqrt{\lambda_{cj} \bar{\lambda}_{cj}} / 2\pi$ for $j \in \{1, 2\}$.
- Variance of residual sway: $\kappa_{\text{tot}} = \kappa_r + \kappa_{c1} + \bar{\kappa}_{c1} + \kappa_{c2} + \bar{\kappa}_{c2}$

- The normalized real and imaginary parts of the coefficients: $\kappa_r/\kappa_{\text{tot}}$, $\text{Re}(\kappa_{c1})/\kappa_{\text{tot}}$, $\text{Im}(\kappa_{c1})/\kappa_{\text{tot}}$, $\text{Re}(\kappa_{c2})/\kappa_{\text{tot}}$ and $\text{Im}(\kappa_{c2})/\kappa_{\text{tot}}$. We refer to $\kappa_r/\kappa_{\text{tot}}$ as the slow-decay fraction.
- The coupling coefficients $b_0, b_1, \dots, b_4$. The measure b_0 is the gain from visual motion to sway in the limit as the frequency approaches 0 (the DC gain). It is a measure of position coupling. If $b_0 = 0$, then b_1 is the initial slope of the gain function. It is a measure of velocity coupling.
- The in-the-loop measure $b(\lambda_r) = b_0 + b_1\lambda_r + b_2\lambda_r^2 + b_3\lambda_r^3 + b_4\lambda_r^4$. Below we show that if the in-the-loop measure $b(\lambda_r)$ is not zero, then the source of the slow dynamics is inside the feedback loop.
- The time delay τ that appears in the transfer function from visual motion to sway.

Note that two of the measures are redundant; $\kappa_r/\kappa_{\text{tot}} + 2\text{Re}(\kappa_{c1})/\kappa_{\text{tot}} + 2\text{Re}(\kappa_{c2})/\kappa_{\text{tot}} = 1$, and the in-the-loop measure can be computed from β and $b_0, b_1, \dots, b_4$.

Statistics: For model (2), let μ^* be the vector of true model parameters, and let $\hat{\mu}$ be the vector of estimated model parameters. From the asymptotic theory of maximum-likelihood estimation (Harvey, 1990), the estimation errors $\hat{\mu} - \mu^*$ are approximately normally distributed with covariance matrix $-H^{-1}$, where H is the matrix of second derivatives of the log-likelihood with respect to the model parameters, evaluated at $\hat{\mu}$. If G is the derivative matrix of the mapping from model parameters to our measures, evaluated at $\hat{\mu}$, then the estimation errors for our measures are approximately normally distributed with covariance matrix $-GH^{-1}G^T$. For each subject and condition, we used this normal approximation to construct 95% confidence intervals for our measures and to test null hypotheses concerning the value of one or more measures. For example, we tested whether the model with all coupling coefficients fit the data significantly better than the model with only velocity coupling. For averages of measures across subjects, we used t -tests to test whether a given average was significantly different than 0 and paired t -tests to test for condition effects. For all statistical tests, p -values less than 0.05 were considered significant and p -values less than 0.10 were considered marginally significant.

Interpreting the in-the-loop measure: Suppose that $y_{\text{out}}(t)$ is a stochastic variable, such as the reference point in Fig. 1, that affects sway but is outside the feedback loop. Then, a linear model of the postural control system has the form

$$Y_{\text{out}}(s) = \frac{c_1(s)}{a_1(s)} \Xi(s), \quad (9a)$$

$$Y_{\text{tot}}(s) = \frac{b_2(s)}{a_2(s)} e^{-\tau s} U(s) + \frac{c_2(s)}{a_2(s)} \Xi(s) + \frac{d_2(s)}{a_2(s)} Y_{\text{out}}(s), \quad (9b)$$

where $Y_{\text{out}}(s)$ is the Laplace transform of $y_{\text{out}}(t)$; $Y_{\text{tot}}(s)$, $U(s)$ and $\Xi(s)$ are as before; and $a_1(s)$, $a_2(s)$, $b_2(s)$, $c_1(s)$, $c_2(s)$ and $d_2(s)$ are polynomials. Note in (9a) that y_{out} is not affected by the visual scene position u . Visual input depends on the relative position between the visual scene and the eyes, so any variable affected by the visual scene is necessarily also affected by sway. Since we are assuming that y_{out} is outside the feedback loop, and thus not affected by sway, it is not affected by the visual scene.

Writing model (9) in the form of the descriptive model (2) yields

$$Y_{\text{tot}}(s) = \frac{a_1(s)b_2(s)}{a_1(s)a_2(s)} e^{-\tau s} U(s) + \frac{a_1(s)c_2(s) + c_1(s)d_2(s)}{a_1(s)a_2(s)} \Xi(s).$$

In particular, $a(s)$ and $b(s)$ in model (2) are given by $a(s) = a_1(s)a_2(s)$ and $b(s) = a_1(s)b_2(s)$. If λ is an eigenvalue of the stochastic process $y_{\text{out}}(t)$, then from (9a) we have that $a_1(\lambda) = 0$. Therefore, $a(\lambda) = a_1(\lambda)a_2(\lambda) = 0$, so λ is also an eigenvalue of the postural sway dynamics. In addition, $b(\lambda) = a_1(\lambda)b_2(\lambda) = 0$. In particular, if the slow-decay eigenvalue λ_r comes from $y_{\text{out}}(t)$, then the in-the-loop measure $b(\lambda_r)$ is zero. It follows that if the in-the-loop measure $b(\lambda_r)$ is not zero, then the source of the slow dynamics is inside the feedback loop.

3 Results

3.1 Gain and phase functions

Fig. 2A–B shows the gain and phase functions for the low- and high-amplitude conditions. Gain was significantly greater than 0 in both conditions for the eight lowest frequencies of 0.024 to 1.432 Hz ($p < 0.05$), indicating a detectable response to the visual motion. For the two highest frequencies of 2.104 and 2.936 Hz, gain was not significantly greater than 0 in at least one of the conditions ($p > 0.05$). Phase decreased by about a full cycle of 360 deg as frequency increased from 0.024 to 1.432 Hz. At the two highest frequencies phase could not be reliably estimated due to the difficulty in detecting a response to the visual motion.

When the amplitude of the visual motion was doubled, gain decreased significantly at all frequencies from 0.024 to 0.904 Hz (Fig. 2C). At all 10 frequencies the high- to low-amplitude gain ratio was not significantly different than 0.5. A gain ratio of 0.5 corresponds to equal response amplitudes in both conditions. There were no significant differences in phase between the two conditions (Fig. 2D).

3.2 Descriptive model

We fit linear descriptive models of orders $m = 1, \dots, 7$ and with sampling time steps h of 0.1 and 0.2 s. Out of a total of 40 cases (10 subjects times 2 conditions times 2 time steps), the BIC selected $m = 5$ in 20 cases, $m = 6$ in 13 cases, $m = 3$ in 3 cases, $m = 7$ in 3 cases, and $m = 4$ in 1 case. Model fits with $m = 5$ and $h = 0.2$ s produced eigenvalues that were qualitatively similar for all subjects and conditions. With $m = 5$ and $h = 0.1$ s, eigenvalues were qualitatively similar to those with $h = 0.2$ s, except for a couple cases in which the eigenvalues did not match the common pattern. Model fits with $m = 6$ did not produce qualitatively consistent eigenvalues. Based on these considerations, we conclude that a fifth-order model based on a time step of 0.2 s provides a reasonably accurate and interpretable description of the dynamical properties of the sway trajectories in this study. The results from this model are presented in what follows.

Figure 3A shows two versions of the power spectral density (PSD) for a subject in the low-amplitude condition. The version indicated by the solid line was computed directly from the trajectories. The version indicated by the dotted line was computed by first fitting model (2) to the data and then computing the PSD of the fitted model's residual sway. Since the model-based PSD does not include the model's response to visual motion, it does not have the peaks at the stimulus frequencies that are seen in the directly-computed PSD.

Note that there are two broad bumps in the PSDs at about 0.35 and 1.4 Hz. These bumps correspond to two pairs of complex-conjugate eigenvalues in the fitted model that describe damped-oscillatory modes in the sway dynamics. The model's fifth eigenvalue is real-valued and small and thus describes a slow first-order decay component in the sway dynamics. This slow-decay eigenvalue describes the shape of the PSD at low frequencies.

Fig. 3B and C compares the frequency-response function (FRF), in terms of gain and phase functions, of the fitted model to the directly-computed FRF. There is approximate agreement between the directly-computed and model-based FRFs. Note that the model-based gain function in Fig. 3B has its peak near the first eigenfrequency and has a bump near the second eigenfrequency.

Measures describing residual sway—The pattern of one slow-decay eigenvalue and two pairs of damped-oscillatory eigenvalues was seen in both conditions for all ten subjects. Fig. 4 shows measures that characterize these five eigenvalues and the corresponding coefficients of the autocovariance function of residual sway (Eq. 8). For all of these measures, the average across subjects did not show a significant dependence on the visual motion amplitude ($p > 0.1$). Measures were generally more consistent across subjects in the low-amplitude condition, perhaps because more trials were run in this condition. Unless otherwise stated, all results below are for this condition. The mean slow-decay rate was $0.156 \pm 0.025 \text{ s}^{-1}$ (mean $\pm$ SE across subjects; Fig. 4A). For the first damped-oscillatory mode, mean damping was $2.74 \pm 0.18 \text{ s}^{-1}$ and the mean eigenfrequency was $0.420 \pm 0.026 \text{ Hz}$ (Fig. 4B–C). For the second damped-oscillatory mode, mean damping was $4.54 \pm 0.33 \text{ s}^{-1}$ and the mean eigenfrequency was $1.490 \pm 0.066 \text{ Hz}$ (Fig. 4D–E).

The mean variance was $0.402 \pm 0.075 \text{ cm}^2$. The total sway variance κ_{tot} is the sum of the coefficients of the autocovariance function (Eq. 8). Most of this sum is due to the slow-decay coefficient κ_r ; the slow-decay fraction $\kappa_r/\kappa_{\text{tot}}$ was close to one for all subjects (0.986 ± 0.011 ; Fig. 4F) and the other normalized coefficients were small (Fig. 4G–K).

Coupling measures—The fitted model's transfer function describing the effect of visual motion on sway is characterized by the eigenvalue-related measures in Fig. 4A–E and the measures of Fig. 5A–F. Of the coupling coefficients $b_0, b_1, \dots, b_4$, only the velocity coupling coefficient b_1 showed a consistent sign (Fig. 5A–E). The velocity coupling coefficient was significantly positive for all subjects and conditions ($p < 0.05$). Its mean across subjects was significantly positive in both conditions ($p < 0.0002$) and was significantly higher in the low-amplitude condition than in the high-amplitude condition ($p = 0.001$).

Although none of the non-velocity coupling coefficients exhibited a consistent sign across subjects, these coefficients were significantly different than zero ($p < 0.05$) for a substantial number of subjects. For example, in the low-amplitude condition, this was true for 2 subjects for b_0 , 8 subjects for b_2 , 6 subjects for b_3 , and 5 subjects for b_4 . The mean of the position coupling coefficient b_0 across subjects was significantly different in the two conditions ($p = 0.045$), being significantly negative in the low-amplitude condition ($p = 0.021$) and not significantly different than zero in the high-amplitude condition ($p = 0.67$). The means of the coupling coefficients b_2, b_3 and b_4 were not significantly different from zero in both conditions and did not depend significantly on condition ($p > 0.1$).

The time delay τ was significantly positive ($p < 0.05$) for 6 subjects and 3 subjects in the low- and high-amplitude conditions, respectively, and was not significantly different than zero in the remaining cases. The mean of τ across subjects was $0.108 \pm 0.044 \text{ s}$ in the low-amplitude condition and $0.073 \pm 0.037 \text{ s}$ in the high-amplitude condition (Fig. 5F). These values were significantly positive ($p = 0.037$) and marginally significantly positive ($p = 0.082$), respectively. There was no significant difference between the two conditions ($p = 0.57$).

Testing whether a coupling measure is significantly different than zero is one way of evaluating whether the data support including the corresponding term in the model. In addition to testing measures one at a time, we also considered two null hypotheses concerning multiple measures (see methods). The first null hypothesis was that there is only velocity coupling with a time

delay ($b_0 = b_2 = b_3 = b_4 = 0$). This hypothesis was rejected for 6 subjects in the low-amplitude condition and 5 subjects in the high-amplitude condition ($p < 0.05$), indicating support for including non-velocity coupling in about half of the cases. The second null hypothesis was that there is only velocity coupling and no time delay ($b_0 = b_2 = b_3 = b_4 = \tau = 0$). This hypothesis was rejected for all subjects and conditions, indicating support for including either non-velocity coupling or a time delay in all cases.

In-the-loop measure—Recall that if the in-the-loop measure $b(\lambda_r)$ measure is not zero, then the source of the slow dynamics is inside the feedback loop. In the low-amplitude condition, $b(\lambda_r)$ was significantly negative for all subjects ($p < 0.05$; Fig. 5G); in the high-amplitude condition, it was significantly negative for 8 subjects and not significantly different than zero for the remaining 2 subjects. The mean of $b(\lambda_r)$ across subjects was significantly negative in both conditions ($p < 0.001$) and was significantly more negative in the low-amplitude condition ($p = 0.0001$). Based on this evidence that $b(\lambda_r)$ is not zero, we conclude that the source of the slow dynamics is inside the feedback loop.

The in-the-loop measure $b(\lambda_r)$ is equal to the sum $b_0 + b_1\lambda_r + b_2\lambda_r^2 + b_3\lambda_r^3 + b_4\lambda_r^4$. Figure 5H shows $b_1\lambda_r$, the velocity-coupling term in this sum. The in-the-loop measure $b(\lambda_r)$ and $b_1\lambda_r$ had similar values, indicating that the qualitative behavior of $b(\lambda_r)$ was due primarily to the velocity-coupling term. In particular, because $b_1 > 0$ (Fig. 5B) and $\lambda_r = -\beta < 0$ (Fig. 4A), $b_1\lambda_r$ was always negative, as was $b(\lambda_r)$ in all but one case. Therefore, our conclusion that the source of the slow dynamics is inside the feedback loop follows from the fact that $b(\lambda_r)$ is dominated by the velocity-coupling term.

Model without time delay—In previous postural studies that used experimental visual-motion FRFs to fit model parameters, sometimes the model has included a time delay (e.g., Peterka, 2002) and sometimes it has not (e.g., Jeka et al., 2000). To determine whether the primary conclusions of this study depend on our decision to include the time delay τ in model (2), we also fit the model without a time delay ($\tau = 0$). To allow direct comparisons with the results presented above, we consider a fifth-order model based on data sampled with a time step of 0.2 s.

Removing the time delay from the model produced only minor changes in the measures describing residual sway, the position coupling b_0 , the velocity coupling b_1 , and the in-the-loop measure $b(\lambda_r)$. There were only two qualitative changes in the statistical tests reported above: the difference in mean b_0 between conditions went from being significant ($p = 0.045$) to marginally significant ($p = 0.089$), and $b(\lambda_r)$ for subject 7 in the high-amplitude condition became significantly negative.

Removing the time delay produced greater changes in the higher-order coupling coefficients b_2 , b_3 and b_4 . Large values and large confidence intervals for these measures (Fig. 5C–E) both tended to be reduced in size (new values not shown). The higher-order coefficients still did not show a consistent sign across subjects and conditions. However, the mean of b_2 in the low-amplitude condition became marginally significantly negative ($p = 0.077$) and significantly less than its value in the high-amplitude condition ($p = 0.015$). It is not surprising that removing the time delay should have a greater effect on higher-order coupling coefficients than on the position or velocity coefficients, since both a time-delay and higher-order coupling exert their greatest influence on the FRF at higher frequencies.

4 Discussion

4.1 Dynamical components of sway

In this study we used sway trajectories to fit parameters in a descriptive linear stochastic model of sway dynamics. Our results confirm those of previous studies that postural sway dynamics include a slow process that can be descriptively modeled as a first-order decay with noise (Dijkstra, 2000; Kiemel et al., 2002). In addition, since our in-the-loop measure was nonzero, we conclude that the mechanistic source of the slow dynamics is in the feedback loop and not an outside input into the feedback loop (Fig. 1).

By locating the slow dynamics inside the feedback loop, our results are consistent with our previous hypothesis that the slow component of sway is due to state estimation errors (Kiemel et al., 2002; Fig. 1). This hypothesis was motivated by two observations: i) sway has a slow first-order decay component; and ii) the slow-decay fraction remains near 1 as sway variance is decreased by adding or vision and/or light fingertip touch. In Kiemel et al. we proposed a simple mechanistic posture model that accounts for both observations and whose slow dynamics are due to the dynamics of state estimation.

Although our results are consistent with the estimation-errors hypothesis, they do not exclude the possibility of other explanations for the slow dynamics of sway. They might be due to some other mechanism inside the feedback loop besides state estimation or the interaction between multiple mechanisms inside the feedback loop. A postural model with proportional-derivative-integral (PID) control can exhibit a slow-decay eigenvalue (Kiemel et al., 2002). However, the model has a negative slow-decay fraction, rather than a slow-decay fraction near 1 (Fig. 4G). Another possibility is that there are actually multiple slow-decay eigenvalues in the postural control system, but they cannot be distinguished based on sway trajectories because they have similar values. For example, the model of Peterka (2000) has two slow-decay eigenvalues. One is due to an external disturbance torque, and the other is due to PID control. However, the model, as formulated, does not address the question of how the stochastic properties of sway vary across sensory conditions.

Our results are not consistent with the hypothesis that slow dynamics are due to a slowly-changing reference point (Zatursky and Duarte, 1999; Fig. 1). The reference-point hypothesis is similar to the idea that movement variability, rather than serving immediate control objectives, is meant to provide information about the dynamical interaction between the person and the environment (Riccio, 1993). In other words, rather than trying to minimize movement, one purposefully generates movements to explore system dynamics. Associating the slow dynamics of sway to “exploration” places its source outside the feedback loop, contrary to our results. Moreover, the exploration hypothesis fails to explain why postural sway decreases as additional sensory information is provided.

Peterka (2002) has previously measured the frequency-response function (FRF) from visual motion to sway and obtained gain and phase functions that are qualitatively similar to ours in Fig. 2. He fit a non-stochastic third-order model based only on the FRF, whereas we fit a stochastic fifth-order model based both on the FRF and the stochastic components of sway. In our approach, the eigenvalues of the system are reflected in both the FRF and the stochastic components (see Eq. 2), allowing for a unified description of both aspects of sway.

One strength of this unified approach is that we were able to obtain consistent estimates of 16 non-redundant parameters describing sway in response to visual motion. In addition to the commonly described slow first-order (mean rate constant of 0.156 s^{-1}) and damped-oscillatory (mean eigenfrequency of 0.420 Hz) components of sway, we were able to consistently identify and quantify a second damped-oscillatory component with mean eigenfrequency of 1.490 Hz.

These two oscillatory components are often attributed to the dynamics of a multilink pendulum. For example, McCollum and Leen (1989) presumed the existence of two postural modes (ankle and hip strategy) with a biomechanical two-joint model whose characteristic frequencies were estimated to be 0.52 and 1.45 Hz. However, nervous system dynamics also influence these oscillatory components. Begbie (1967) may have been the first to recognize this. Based purely on visual inspection of sway trajectories, he observed that sway consists of two oscillatory components with frequency ranges of 0.5–1 Hz and 1.5–2.5 Hz. Begbie speculated that the fast oscillations were due to stretch reflex pathway characteristics that enhanced somatosensory function when visual or vestibular inputs were disrupted and that slow oscillations emerged from sway corrections based upon vestibular information. More recent studies have shown that other factors such as the length of the support surface (Horak and Nashner, 1986), central set (Horak et al., 1989) and neurological pathologies (Horak et al., 1990) influence the predominance of these two oscillatory modes (i.e., ankle or hip strategy), indicating influence from factors other than just biomechanics.

The dynamical components identified here can be considered to be a superset of those identified in our previous study (Kiemel et al., 2002). In the previous study, we found three eigenvalues that were qualitatively similar across most subjects. Here, we found five eigenvalues that were qualitatively similar across all subjects. The three eigenvalues of the previous study are similar to the first three eigenvalues of this study, leading to a similar mean slow-decay rate (0.19 s^{-1} previously vs. 0.156 s^{-1} here), mean damping for the first mode (2.85 s^{-1} vs. 2.74 s^{-1}), and mean eigenfrequency of the first mode (0.40 Hz vs. 0.420 Hz). These similarities exist even though different stances were used (modified tandem vs. parallel) and sway was measured in different directions (medial-lateral vs. anterior-posterior). Our inability to consistently identify a second damped-oscillatory mode in our previous study may be due to these differences.

4.2 Coupling to the visual scene

In terms of the transfer function from visual motion to sway, the only coupling coefficient to exhibit a consistent sign was the velocity coefficient, not the position coefficient or the higher-order coefficients (Fig. 5A–E). The velocity coefficient was significantly positive velocity for all subjects and conditions. Previous studies have argued for velocity coupling between visual motion and sway based both on theoretical considerations (Schöner, 1991) and empirical evidence (Dijkstra et al., 1994; Jeka et al., 2000). Jeka et al. also argued for position coupling based on a second-order model. Our results here, based on a more accurate fifth-order model, show only weak evidence for position coupling. The mean position coefficient was significantly less than zero in the low-amplitude condition. However, this is most likely due to imperfections in the model, since a negative position coefficient implies that visual motion and sway would be nearly anti-phase at frequencies near zero. While Fig. 3C, for example, shows phase approaching 90 degrees at very low frequencies, in reality, phase is very difficult to measure experimentally at frequencies in which the period is so long. It is worth noting that the robust nature of velocity coupling is not just between postural sway and vision, as previous studies have found similar evidence for the predominance of velocity coupling with proprioceptive and tactile sensory inputs (Jeka et al., 2004; Kiemel et al., 2002).

The finding that postural sway is influenced by visual scene velocity is based on a descriptive model; its interpretation depends on the mechanistic posture model being considered. In the PID-control model of Peterka (2002), which does not include the dynamics of state estimation, the relative amounts of visual position, velocity and acceleration coupling depend on the feedback gains. However, in an optimal-control model (Kuo, 1995; van der Kooij et al., 1999; Kiemel et al., 2002) the link between visual coupling and feedback gains is not as tight. An optimal-control model includes a Kalman filter that generates estimates of body position and velocity based on noisy sensory measurements, and these state estimates are multiplied by

feedback gains to specify the motor command. For such a mechanistic model, a zero position coupling coefficient in our descriptive model implies that state estimates are not based on the position of the visual scene, only its velocity and higher derivatives. It does not imply that the position feedback gain is zero.

4.3 Amplitude-dependent changes in gain

Consistent with previous studies (e.g., Peterka and Benolken, 1995; Oie et al., 2002; Peterka, 2002), we found significant decreases in gain when the amplitude of visual motion was increased (Fig. 2C). Doubling the motion amplitude cut the gain roughly in half, meaning that the sway response amplitude remained roughly constant. Peterka and Benolken varied the amplitude of sinusoidal visual motion and found that response amplitude initially increased with increasing motion amplitude and then reached saturation, resulting in a plateau. Our two motion amplitudes appear to be within the saturation region.

Any amplitude-dependent change in gain indicates some type of nonlinearity in the postural control system. Two sources of the nonlinearity have been proposed: sensory thresholds (Peterka and Benolken, 1995; Mergner et al., 2003) and sensory re-weighting (van der Kooij et al., 2001; Oie et al., 2002; Carver et al., 2005). Since both mechanisms predict a decrease in gain with increasing visual motion amplitude, our data do not clearly distinguish between the two proposals.

5 Conclusion

Many investigations focus on the damped-oscillatory components of postural sway. The present study highlights the crucial nature of the slow sway component embedded within the postural sway trajectory. The slow component is non-oscillatory and corresponds to exponential decay back to equilibrium while being continually perturbed by noise during quiet upright stance. Our conclusion that the source of the slow component is inside the feedback loop supports the hypothesis that the slow component is the manifestation of imperfect estimation. Because the slow component accounts for the majority of sway variance, the results support the notion that most of sway is due to the inability to estimate body dynamics accurately. Human upright stance always has a certain amount of sway because we never know exactly where we are or how fast we are moving.

The results argue against other hypotheses about the slow process; that is, as a moving reference point or an exploratory process, both of which imply that the source of the slow component is outside the feedback loop. The goal seems not to be one of exploring the space around vertical, but to constantly issue commands that return the body to vertical after intrinsic perturbations push the body away from equilibrium. Because errors in the control process of sending out commands appear to play a relatively small role in overall body sway (Kiemel et al., 2002), the precision of controlling upright stance relies primarily on the process of estimation. Characterizing the slow process may hold the key to determining the underlying basis of balance problems in populations with poor balance control.

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Figure 1.

Schematic representation of postural control with a moving visual scene. The source of the slow component of sway may be outside the feedback loop, for example, a slowly changing reference point (Zatsiorsky and Duarte, 1999); or it may be inside the loop, for example, the dynamics of state estimation (Kiemel et al., 2002).

Figure 2.

Gain and phase functions describing the response of the center of mass to motion of the visual scene. Error bars indicate 95% confidence intervals.

Figure 3.

Directly-computed and model-based power spectral densities (PSDs) (A), gain functions (B), and phase functions (C) for subject 1 in the low-amplitude condition (eight trials). The directly-computed PSD was computed using Welch's method with a window size equal to the stimulus period $T = 125$ s and 50% overlap. The model-based PSD does not include the response to the drive. In A, dots indicate stimulus frequencies. In B and C, error bars indicate 95% confidence intervals.

Figure 4.
Model measures describing residual sway. Each symbol type represents a different subject.
Error bars indicate approximate 95% confidence intervals

Figure 5.

Model measures describing the transfer function from visual motion to sway (A–F), the in-the-loop measure (G), and the velocity-coupling contribution to the in-the-loop measure (H). Symbols are as in Fig. 4.