Controlling Human Upright Posture: Velocity Information Is More Accurate Than Position or Acceleration

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1Program in Neuroscience & Cognitive Science, 2Departments of Kinesiology and 3Biology, University of Maryland, College Park, Maryland 20742-2611; and 4Neurological Sciences Institute, Oregon Health & Science University, Portland, Oregon 97239-3098

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Jeka, John, Tim Kiemel, Robert Creath, Fay Horak, and Robert Peterka. Controlling human upright posture: velocity information is more accurate than position or acceleration. J Neurophysiol 92: 2368–2379, 2004. First published May 12, 2004; 10.1152/jn.00983.2003. The problem of how the nervous system fuses sensory information from multiple modalities for upright stance control remains largely unsolved. It is well established that the visual, vestibular, and somatosensory modalities provide position and rate (e.g., velocity, acceleration) information for estimation of body dynamics. However, it is unknown whether any particular property dominates when multisensory information is fused. Our recent stochastic analysis of postural sway during quiet stance suggested that sensory input provides more accurate information about the body’s velocity than its position or acceleration. Here we tested this prediction by degrading major sources of velocity information through removal/attenuation of sensory information from vision and proprioception. Experimental measures of postural sway were compared with model predictions to determine whether sway behavior was indicative of a deficit in velocity information rather than position or acceleration information. Subjects stood with eyes closed on a support surface that was fixed, 2 foam, or 3 sway-referenced. Six measures characterizing the stochastic structure of postural sway behaved in a manner consistent with model predictions of degraded velocity information. Results were inconsistent with the effect of degrading only position or acceleration information. These findings support the hypothesis that velocity information is the most accurate form of sensory information used to stabilize posture during quiet stance. Our results are consistent with the assumption that changes in sway behavior resulting from commonly used experimental manipulations (e.g., foam, sway-referencing, eyes closed) are primarily attributed to loss of accurate velocity information.

INTRODUCTION

A common experimental technique in the postural control literature is to remove, or at least attenuate, a particular sensory modality and measure how this changes sway behavior. Such changes can then be used to determine how that sensory information is instantiated in the underlying control system. Removing sensory information with a healthy adult population typically leads to an increase in mean sway amplitude (e.g., Woollacott et al. 1986), although certain populations (e.g., children) do not consistently display this result (Ashmead and Horak 2000; Lacour et al. 1997; Newell et al. 1997). Reduced sensory information means that the nervous system has less information to accurately estimate center of mass dynamics (i.e., position and velocity) and, consequently, sway control is less precise. However, an increase in mean sway amplitude resulting from reduced sensory information is not particularly helpful to understand the underlying control system for posture because most models predict this relationship (e.g., Peterka 2002; Schöner 1991; van der Kooij 1999). Additional properties/constraints are necessary if modeling is to be used to understand the mechanisms underlying the estimation and control of posture. In this paper, we illustrate a much richer view of how the removal/attenuation of sensory information can lead to changes in postural sway behavior.

Properties of sensory information

It is relevant to ask what information is lost when a sensory modality is removed or degraded as the result of injury or an experimental manipulation. Studies on the psychophysical properties of a particular sensory modality, such as tactile afferents, categorize neurons in terms of rapidly adapting and slowly adapting properties, referring to the time taken to return to a baseline activity after stimulation (Kandel et al. 1991). More detailed classification schemes identify the physical aspects of the stimulus to which a neuron responds (Burgess and Perl 1973; Esteky and Schwark 1994). For example, slowly adapting neurons are generally considered sensitive to position, responding tonically throughout an entire ramp displacement and displaying sensitivity to the size of the displacement. Many rapidly adapting neurons respond primarily during a ramp stimulus and increase their firing rate with increasing stimulus velocity regardless of displacement, indicating sensitivity to stimulus velocity. Other rapidly adapting neurons respond vigorously to rapid/high-frequency stimuli and are considered transient detectors, more tuned to the acceleration of a stimulus. These classification schemes do not necessarily separate afferents into distinct groups because neurons often respond to more than one physical property.

When investigating the properties of sensory receptors associated with human postural control, it is important to bear in mind that the information conveyed by individual receptors is less relevant than the collective activity transmitted through large populations of receptors distributed throughout the body and then integrated by the central nervous system. Consequently, stimulus properties are often described in terms of the role they play in functional behavior. For instance, the classical view of somatosensation is that it provides information concerning: 1) contact surface forces and properties such as texture and friction; and 2) the relative configuration of body segments (Dietz 1992; Horak and Macpherson 1996). Despite their
accurate velocity information

In Kiemel et al. (2002), we analyzed the stochastic structure of postural sway and demonstrated that this structure imposes important constraints on models of postural control. To briefly summarize our approach, we first analyzed experimental postural sway trajectories using an autoregressive moving-average (ARMA) technique, to derive descriptive model parameters (i.e., stochastic parameters) that can be used to create postural sway trajectories that are statistically equivalent to the experimental sway trajectories. We then tested whether these descriptive results could be reproduced by a mechanistic model, such as optimal control models commonly used in the postural control literature (e.g., Kuo 1995). We found that such models reproduce the stochastic structure of postural sway only when noise is added to the process of fusing sensory information from multiple modalities, which we refer to as the “noisy-computation” model (Kiemel et al. 2002), whose main features are described in the APPENDIX.

An important prediction from the noisy-computation model was that the postural control system (during quiet stance) operates in a parameter regime in which sensory input provides more accurate information about the body’s velocity than its position or acceleration. The models considered in Kiemel et al. (2002) did not associate different forms of sensory information (position, velocity, and acceleration) with specific sensory modalities. Instead, the emphasis was that the behavior of a postural control model depends on which form of sensory information is assumed to be most accurate, regardless of the sensory modalities involved.

Of the 5 stochastic postural sway measures (see METHODS below) considered in Kiemel et al. (2002), the noisy-computation model predicts that 3 measures should depend on the degradation of velocity information. However, when vision and/or light touch information at the fingertip were manipulated in Kiemel et al. (2002), only the sway variance showed a statistically significant dependency on sensory condition. We hypothesize that predictions from the noisy-computation model were not observed because the support surface was stable in all conditions. With a fixed surface, proprioception through the feet/ankles provides accurate velocity information and may limit the overall degradation in velocity information when vision or light touch information is removed. Thus, a further test of the noisy-computation model would be to create experimental conditions that produce a greater degradation in velocity information. If the degradation is sufficiently large, then additional measures beyond sway variance would be predicted to show changes large enough to be detected.

Here we show results from an experiment designed to test the idea that velocity information is most accurate for the control of quiet stance by removing/attenuating 2 primary sensory modalities that provide velocity information about center of mass dynamics: vision and proprioception from the feet/ankles. Stochastic measures derived from both experimental sway trajectories and the noisy-computation model will be compared. Use of the term “degraded” is motivated by the fact that we cannot assume that all sources of velocity information can be removed entirely through experimental manipulation. Vestibular input also provides velocity information in our experimental setting, although arguably less salient than that provided by proprioception during stance on a fixed surface (see DISCUSSION).
for small rapid oscillations about the local COM position indicative of AP body acceleration) (Brenière 1996; Winter et al. 1998). In subsequent trials, Eq. 1 was used to calculate AP COM displacement from measures of $x(t)$ and $x(t)$. An estimate of the subject’s COM height (based on anthropometric measures) above the ankle joint was then used to calculate the COM rotation angle. Thus, COM sway angle was defined as the angle between the subject’s center of mass, the ankle (also the rotational axis of the platform), and vertical.

Subjects wore a safety harness that was secured to fixed brackets by 2 connecting straps. The straps were adjusted to allow for the subjects’ body sway before becoming taut. The platform displacement signal and potentiometer voltages were sampled at 100 Hz.

**Procedures**

Subjects stood upright with feet shoulder-width apart and eyes closed in 3 conditions: 1) fixed surface; 2) sway-referenced surface; and 3) foam surface. Three trials of 364 s each were run in each condition. The platform position was stationary on the fixed surface and foam surface trials. For the sway-referenced trials, the platform rotated in the A–P direction an amount equal to the angular hip displacement as determined by the hip rod potentiometer signal. For the foam surface trials, subjects stood on a 4-in.-thick piece of Summate Temper medium-density foam placed on the platform. Because of the long trials, the sway-referencing condition was run after the fixed surface condition to minimize any possible effects of fatigue. The foam surface was run last because it required repositioning the rigid rods to accommodate the increased height of the foam surface. Before performing the sway-referenced trials, subjects completed 2 shorter practice trials to familiarize themselves with the condition to minimize any learning effects that might occur as a result of the long trial duration and the unfamiliar nature of the task. Background sound was masked with a tape-recorded text played through ear-covering headphones. One trial was discarded because of technical difficulties and one trial was shortened to 300 s because of a loss of balance near the end.

**Analysis**

**ARMA MODELS.** For every subject and condition, an autoregressive moving-average (ARMA) model (Wei 1990) was used to characterize the statistical properties of the anterior–posterior center of mass (COM) angular displacement trajectories. Every tenth point of the trajectories was used for analysis, corresponding to a time step $h$ of 0.1 s. Increasing the time step in this way reduces the effect of any low-amplitude, high-frequency components of the measured sway trajectories, which presumably are attributable mainly to measurement noise (see **STATISTICS** below). The 3 trials were used together to fit parameters in the $(p, q)$ ARMA model

$$X_{1}^{(k)} = \tilde{x}_{1}^{(k)} + \phi_{1}[X_{1}^{(k-1)} - \tilde{x}_{1}^{(k-1)}] + \ldots + \phi_{p}[X_{1}^{(k-p)} - \tilde{x}_{1}^{(k-p)}] + \alpha_{1}^{(k)}$$

$$+ \theta_{1}\alpha_{1}^{(k-1)} - \ldots - \theta_{q}\alpha_{1}^{(k-q)}$$

where $X_{1}^{(k)}$ is the $k$th value of the sway time series on the $j$th trial. The subscript 1 indicates position (see **APPENDIX**). The $\alpha_{1}^{(k)}$ are independent normally distributed random variables with SD $\sigma_{a}$. The integers $p$ and $q$ are the autoregressive order and moving-average order, respectively, $\phi_{1}, \ldots, \phi_{p}$ are the autoregressive coefficients and $\theta_{1}, \ldots, \theta_{q}$ are the moving-average coefficients. The parameters $X_{1}^{(k)}$ are the asymptotic means for each trial. Sampling one variable from a $p$th-dimensional linear (in the narrow sense) stochastic differential equation (Arnold 1974) at fixed time intervals produces a $(p, q – 1)$ ARMA process. Therefore, we let $q = p – 1$.

Parameters were fitted for models of order $p = 1, \ldots, 5$ using the method of maximum likelihood. No assumption was made that the process was initially in its equilibrium state. Thus, our fitting procedure allowed for the possible existence of transients. In particular, a slow trend in the data could be interpreted by the fitting procedure as a slowly decaying transient rather than stochastic variation. See Kiemel et al. (2002) for additional details.

The 5th-order model was compared to the models of orders $p = 1, \ldots, 4$ using a likelihood-ratio test at significance level 0.05. In all but one case (the 3 trials combined from subject 4 in the foam condition), the 5th-order model was significantly better than all lower-order models. In these cases, the 5th-order model was selected. In the remaining case, the 5th-order model was better than the 3rd-order model, but not the 4th-order model. In this case, the 4th-order model was selected.

For the selected model, we computed the coefficients $\kappa_{1}, \ldots, \kappa_{p}$ and eigenvalues $\lambda_{1}, \ldots, \lambda_{p}$ of its autocovariance function

$$E[(X_{1}^{(t)} - \tilde{x}_{1}^{(t)})(X_{1}^{(t+h)} - \tilde{x}_{1}^{(t+h)})] = \kappa_{1}\kappa_{h}^{1} + \ldots + \kappa_{p}\kappa_{h}^{p}$$

where $X_{1}^{(t)} = X_{1}^{(t)}$ and $\tau$ is a multiple of $h$. The terms on the right-hand side of Eq. 2 were arranged so that $|\kappa_{1}\kappa_{h}^{1}| \geq \ldots \geq |\kappa_{p}\kappa_{h}^{p}|$. We then denoted the first real-valued eigenvalue by $\lambda_{1}$ and the first pair of complex-conjugate eigenvalues by $\lambda_{1, \lambda_{2}}$. The corresponding coefficients were denoted by $\kappa_{1, \kappa_{2}}$ and $\kappa_{1, \kappa_{2}}$ respectively. Typically, $\kappa_{1}\kappa_{h}^{1}, \kappa_{1}\kappa_{h}^{2}$, and $\kappa_{1}\kappa_{h}^{*}$ were the first 3 terms on the right-hand side of Eq. 2, although not necessarily in that order, and the remaining terms were small. The term $\kappa_{1}\kappa_{h}^{1}$ represents a first-order decay component of the autocovariance function and $\kappa_{1}\kappa_{h}^{*} + \kappa_{1}\kappa_{h}^{1}$ represents a damped-oscillatory component. Thus, the autocovariance function can be decomposed into a first-order decay component, a damped-oscillatory component, and a remaining component that is typically small. With this decomposition in mind, we define the following 6 measures that (at least partially) characterize the stochastic structure of postural sway.

1) The slow-decay rate $\beta = -\lambda_{1}$, which describes how quickly the first-order decay component of the autocovariance function decays with time delay $\tau$. Note that based on its definition, the slow-decay
rate $\beta$ is not necessarily slow. The term “slow-decay rate” is based on
the experimental results from Kiemel et al. (2002). The slow-decay
process can be thought of as a deviation from the baseline level of
time delay. A damped-oscillatory component of the autocovariance function decays
with time delay $\tau$. The rate constant of the decay is $a/2$.

2) The damping $\alpha = -(\lambda_1 + \lambda_2)$, which describes how quickly
the damped-oscillatory component of the autocovariance function decays
in 2 respects; the previous study used sway variance instead of
relative size of the damped-oscillatory component of the autocovari-
ance of position, the SD of velocity, and the mean speed. A forward
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directly from

3) The eigenfrequency $\omega_0 = \sqrt{\lambda_1 \lambda_2}$, which is the approximate
angular frequency of the damped-oscillatory component if $\alpha$ is small.

4) The SD $\sigma_{COM} = \sqrt{\kappa_{tot}}$ of the model’s sway trajectories,
where $\kappa_{tot} = \kappa_1 + \ldots + \kappa_n$ is the variance. Typically,
$\sigma_{COM} = \sqrt{\kappa_1 + \kappa_2 + \kappa_3}$. In most cases, $\sigma_{COM}$ is also approximately
equal to the average variance of the 3 sway trajectories used to fit
the ARMA model. However, slow trends in the data that are not modeled
as stochastic variation do not contribute to $\sigma_{COM}$ (see discussion of
slow trends above).

5) The slow-decay fraction $\kappa_1/\kappa_{tot}$, which describes the relative size
of the slow-decay component of the autocovariance function.

The ARMA fitting procedure described above is the same as that
used in Kiemel et al. (2002) except in 2 respects. In the previous study
we used $(p, p)$ ARMA models. Here we use $(p, p - 1)$ ARMA models
because their autocovariance function (Eq. 2) has a simpler form.
Also, in the previous study we tested models up to order 8, rather than
up to order 5. Although higher-order models often provide statistically
significant improvements in the quality of the fit, the measures
computed from such models are, in some cases, less consistent across
subjects.

COM VARIABILITY. In addition to the sway SD $\sigma_{COM}$ based on
ARMA model parameters, 3 measures of variability were computed
directly from filtered COM angular displacement trajectories: the SD
of position, the SD of velocity, and the mean speed. A forward–
reverse cascade of a 2nd-order Butterworth filter was applied to each
trajectory using the Matlab function filtfilt, resulting in a 4th-order
zero-phase filter with a cutoff frequency of 3 Hz (Winter 1990). (We
chose the cutoff frequency based on the shape of the power spectral
densities; see STATISTICS below). Finite differences where used to
calculate velocity and speed (the absolute value of velocity).

COM POWER SPECTRAL DENSITY. The average power spectral den-
sity (PSD) of the COM angular displacement was calculated from 3
trials in each condition for each subject (one subject had only 2 foam
trials) using the Matlab spectrum function, which implements Welch’s
averaged periodogram method (Marple 1987). PSD calculations used
a 100-s Hanning window with a one-half window overlap. Means
were subtracted from each trial before computing the PSD. Spectral
density was plotted on a log–log scale to make it easier to observe the
distribution of power at higher frequencies, which is typically small
and difficult to resolve visually on a linear scale.

STATISTICS. Each of our 6 measures based on ARMA parameters
was analyzed separately at significance level 0.05. We first used the
Hotelling $T^2$ statistic to test for significant differences among the 3
surface conditions. If a significant difference was found, paired t-tests
were used to make pairwise comparisons among the conditions.
Because there are only 3 conditions, this procedure controls the
familywise type I error rate (Hochberg and Tamhane 1987).

For each condition, the log of the PSD was averaged across subjects
and paired t-tests were used to detect differences between conditions.
Tests were performed at 300 equally spaced frequencies from 0.01 to
3 Hz. (Above 3 Hz the PSDs begin to level off, presumably because of
measurement noise.) For each of the 3 types of condition effects
(fixed vs. foam, fixed vs. sway-referenced, and foam vs. sway-
reference) we used the procedure of Benjamini and Hochberg (1995)
to control the false discovery rate (FDR) at a significance level 0.05.
The FDR is the expected value of the ratio $n_{null}/n_{tot}$, where $n_{null}$ is
the number of null hypotheses falsely rejected and $n_{tot}$ is the total number
of null hypotheses rejected. When $n_{tot} = 0$, the ratio is defined to be
0. Controlling the FDR is more liberal than the traditional approach of
controlling the familywise type I error rate but is more conservative
than controlling the per-comparison error rate. The Benjamini
and Hochberg procedure controls the FDR in the case of independent test
statistics. In our case of dependent test statistics, the control of the
FDR is only approximate.

For each of the 3 sway variability measures (position SD, velocity
SD, and mean speed), each individual subject was tested for condition
effects with a one-way ANOVA. Analyses were based on the log of
each measure to reduce differences in intertrial variance across con-
ditions. (Because coefficients of variation were small, the log trans-
formation had only a small effect on the skewness of the distribu-
tions.) A Bonferroni test was applied to the 8 resulting $P$-values to
select those subjects that showed a significant condition effect. For
those subjects, unpaired t-tests were used to test for pairwise differ-
ces between conditions. Because there were only 3 conditions, this
procedure controls the familywise type I error rate for each subject.

RESULTS

Figure 2 shows an example of the COM sway angle time
series for each surface condition from one representative sub-
ject. As many other studies have found, the center of mass
amplitude increases when standing on a foam (e.g., Hytonen
et al. 1993; Rogers et al. 2001) or sway-referenced surface (e.g.,
Horak et al. 2002; Kuo et al. 1998; Nashner et al. 1982; Peterka
and Benolken 1995) when compared to the fixed surface
condition. Measures from the noisy-computation model below
illustrate more detailed differences in the structure of postural
sway trajectories between conditions.

Model predictions

Figure 3 illustrates the predictions of the noisy-computation
model as position, velocity, or acceleration sensory information
is degraded. The assumptions underlying these predictions
are described in the APPENDIX. Moving right along the horizon-
tal axis in Fig. 3 represents increasing degradation of position,
velocity, or acceleration information. The model predicts that
as velocity information is degraded (i.e., $\sigma_v$ is increased),

- The slow decay rate ($\beta$) will increase (Fig. 3A).
- The damping ($\alpha$) and eigenfrequency ($\omega_0$) are not depen-
dent on velocity information and will remain constant
(Fig. 3, B and C).
- The SD of the COM position ($\sigma_{COM}$) will increase (Fig.
3D).
- The damped-oscillatory fraction ($2 \kappa_1/\kappa_{tot}$) will increase
(see Fig. 3F and APPENDIX).

There is no prediction concerning the slow-decay fraction
(\(\kappa_1/\kappa_{\text{total}}\)) such that it can either increase or decrease as velocity information is degraded, depending on the values of the other model parameters. With our choice of model parameters, the slow-decay fraction remains roughly constant (Fig. 3E). Note that the predictions for degrading position and acceleration information are substantially different from those for degrading velocity information. For example, the slow-decay rate and the damped-oscillatory fraction are predicted to decrease as position and acceleration information degrade, contrary to the increase predicted with degraded velocity information.

Model measures

Figure 4, A–F shows the average results across subjects for each of our 6 measures. On the left side of Fig. 4 are 3 measures based on the eigenvalues of the descriptive model: the slow-decay rate (B), the damping (\(\alpha\)), and the eigenfrequency (\(\omega_0\)). On the right side of Fig. 4 are 3 measures based on the coefficients of the model’s autocovariance function (Eq. 2): the sway SD (\(\sigma_{\text{COM}}\)), the slow-decay fraction (\(\kappa_1/\kappa_{\text{total}}\)), and the damped-oscillatory fraction (2\(\kappa_1/\kappa_{\text{total}}\)).

Of the 6 measures, the slow-decay rate, the sway SD, and the damped-oscillatory fraction showed significant differences across the 3 surface conditions (\(P < 0.05\)). Pairwise tests revealed that the slow-decay rate and the damped-oscillatory fraction were larger on the foam surface (\(P < 0.01\)) and sway-referenced surface (\(P < 0.05\)) than on the fixed surface. Sway SD was significantly greater in the sway-referenced condition than in the fixed and foam conditions (\(P < 0.05\)). Damping and eigenfrequency showed no significant change across surface condition. All of these results are consistent with model predictions in the case of degraded velocity information. The mean slow-decay fraction also showed no significant change across surface condition. The mean slow-decay fraction also showed no significant change across surface condition. This measure was much more variable across subjects in the foam and sway-referenced conditions than in the fixed condition (compare error bars in Fig. 4E).

COM variability and power spectral density

Figure 5A shows the SD of COM displacement for each of the 8 subjects. Only 5 of the 8 subjects (1–4 and 7) showed a significant dependency of COM displacement on surface condition (Bonferroni-adjusted \(P < 0.05\); see METHODS). In addition, subject 2 did not exhibit a significant difference between the foam and sway-referenced conditions, and subject 7 exhibited a significantly lower SD of position in the foam condition than in the fixed and sway-referenced conditions. Thus, only 3 of the 8 subjects showed a significant condition ordering of the form fixed < foam < sway-referenced (\(P < 0.05\)).
The lack of consistency across subjects in COM SD is reflected in the distribution of COM spectral power at low frequencies. Figure 5, B and C shows log–log plots from 2 different subjects representing the averaged spectral density of the COM angular displacement from 3 trials in each condition. At low frequencies, there is no consistent ordering of spectral density across condition in the 2 subjects. However, in a middle range of frequencies, spectral density is consistently highest in the sway-referenced condition and lowest in the fixed condition for both subjects. This condition hierarchy for spectral density was observed for all subjects in a middle-frequency band from 0.37 to 1.79 Hz. Recall that the variance of COM position is the integral of the COM power spectral density (PSD). Because most of the power of COM position is at the low frequencies, it is the PSD at low frequencies that largely determines the variance, and hence the SD, of COM position.

Figure 6A shows the geometric mean PSDs across subject for each condition. There were no significant differences among conditions at the lowest frequency of 0.01 Hz. At higher frequencies, the mean PSDs were significantly different with a condition ordering of Fixed < Foam < Sway-Referenced (false discovery rate < 0.05; Fixed < Foam for 0.03–2.95 and 2.98–3.00 Hz; Fixed < Sway-Referenced for 0.02–3.00 Hz; Foam < Sway-Referenced for 0.10–3.00 Hz).

Figure 6, B–D illustrate PSDs predicted from the noisy-computation model based on changing levels of position, velocity, and acceleration noise. The 3 values of the sensory-noise level correspond to the 3 experimental conditions. The pattern of spectral power differences across condition, based on changing velocity noise, are the most similar experimental PSDs in Fig. 6A in that the differences of the 3 PSDs are smallest at low frequencies and largest in the mid-frequency range. PSDs based on position or acceleration noise levels are largest at low frequencies and smallest in the mid-frequency range, contrary to the pattern observed in the experimental mean PSDs.

**COM velocity**

Because the PSD of COM velocity is \((2\pi f)^2\) times the PSD of COM position, where \(f\) is frequency, the variance of velocity (the integral of the velocity PSD) depends very little on the position PSD at low frequencies and is largely determined by the position PSD at higher frequencies. Because the subjects showed consistent condition effects in the position PSD at higher frequencies, this suggests that the SD of velocity will also show consistent condition effects. Figure 7A shows that this was the case. All subjects showed a significant dependency of velocity SD on condition (Bonferroni-adjusted \(P < 0.01\)) and a significant condition ordering of the form Fixed < Foam < Sway-Referenced (\(P < 0.01\)).

Another measure that has been used to quantify sway variability is mean path length per unit time (Hufschmidt et al.)
This measure is often used to describe sway in 2 dimensions (anterior–posterior and medial–lateral) but can also be used in one dimension (in our case, anterior–posterior). Mean path length per unit time is equal to mean speed. Given that speed is the absolute value of velocity, one would expect that mean speed and the SD of velocity would show similar condition effects. This was true (Fig. 7B); the statistical results for the SD of velocity also held for mean speed.

**DISCUSSION**

Here we tested the prediction of the noisy computation model (Kiemel et al. 2002) that the stochastic properties of sway will change if the major sources of sensory information related to velocity are degraded, that is, by removing/attenuating vision and proprioception. Our results showed that 3 of the 6 model measures, the slow-decay rate, the damped-oscillatory fraction, and the sway SD showed a significant increase from the fixed surface to the foam and/or sway-referenced conditions, as predicted. Two other parameters, the damping and eigenfrequency, showed no significant change as a function of surface condition, also as predicted. The results were not consistent with predictions based on degrading position or acceleration information, suggesting that our experimental manipulation was successful in primarily degrading velocity information.

**Regimes of accurate sensory information**

The motivation of this study was based on the suggestion of Kiemel et al. (2002) that the postural control system (during quiet stance) operates in a parameter regime in which sensory input provides more accurate information about the body’s velocity than its position or acceleration. This suggestion was based on comparing the behavior of the noisy-computation model to experimental data. Figures 3 and 4 illustrate this comparison. ARMA modeling of sway trajectories yielded measures for the fixed condition that were compatible with those under conditions of accurate velocity information. For example, the slow-decay rate was found to be small, indicating a long time constant. Likewise, the damped-oscillatory fraction was found to be small, suggesting that the damped-oscillatory component of sway accounts for only a small proportion of the total sway variance. These 2 results are more compatible with the assumption of accurate velocity information than accurate position or acceleration information.

In Kiemel et al. (2002), only the total amount of sway showed a statistically significant dependency on the experimental conditions tested. The current experiment was designed...
to produce a greater degradation of velocity information so that predicted changes in additional postural sway measures would be observed. In particular, the noisy-computation model predicts that the slow-decay rate will become faster and the damped-oscillatory fraction will increase if velocity information is sufficiently degraded (Fig. 3, A and F), which is what we observed experimentally (Fig. 4, A and F). In contrast, degrading position or acceleration information is predicted to produce the opposite behavior in both measures.

Damping and eigenfrequency for the noisy-computation model show no change as a function of degrading any form of sensory information. The reason is that the damping (\( \alpha \)) and eigenfrequency (\( \omega_0 \)) depend only on the control-function coefficients \( c_1 \) and \( c_2 \) and the inverted-pendulum parameter \( \gamma \) and not on any of the sensory-noise levels (see APPENDIX). Because our experimental manipulations were aimed at varying sensory information, the prediction would then be that damping (\( \alpha \)) and eigenfrequency (\( \omega_0 \)) should be constant across our experimental conditions. Our experimental results, which did not show a significant dependency of \( \alpha \) and \( \omega_0 \) on experimental condition, are consistent with this prediction.

Many studies have found an increase in mean sway amplitude when sensory information was removed (for reviews, see Dietz 1992; Horak and Macpherson 1996; Nashner 1981). However, mean sway amplitude is not a very useful measure to distinguish different mechanisms underlying postural control because most models predict such an increase. Figure 3D illustrates this idea; any form of sensory loss is predicted to

![Figure 5](image5.png)

**FIG. 5.** A: average center of mass (COM) angular displacement SD for individual subjects show that there was not a consistent increase across conditions for all subjects. COM power spectral density (PSD) plots for (B) S1 and (C) S5 show that there was no consistent pattern of spectral power distribution at low frequencies. At high frequencies, a consistent ordering of fixed < foam < sway-referenced spectral power is observed. Error bars denote SE of the mean.

![Figure 6](image6.png)

**FIG. 6.** A: geometric mean across subjects of the PSD for COM angular displacement in the 3 surface conditions. B–D: PSDs of the noisy-computation model for 3 values of the position sensory-noise level \( \sigma_p \), velocity sensory-noise level \( \sigma_v \), and acceleration sensory-noise level \( \sigma_a \). These 3 parameter values are meant to represent the 3 experimental conditions in A. Note the similarity between experimental PSDs in A and model PSDs based on velocity noise levels in C. See APPENDIX for other parameter values.
increase sway SD. Our results supported the prediction that sway SD would increase as velocity information was degraded, although this result was inconsistent across subjects. In contrast, the SD of COM velocity displayed systematic condition effects for all subjects; lowest on a fixed surface and highest on a sway-referenced surface (see Fig. 7, A and B). Consistent with the COM velocity SD results, power spectral densities showed a systematic ordering across condition in the middle-frequency range. Such results indicate that foam and sway-referenced support surfaces do not necessarily increase the amount of sway, but influence the dynamics of sway by increasing sway velocity.

**Accurate velocity information**

The basis for the accuracy of velocity information may be attributable to the underlying physiology of sensory receptors related to postural control, which generally favor rate information rather than absolute position information. The proprioceptive, tactile, and visual systems are all thought to be velocity sensitive (Dijkstra et al. 1994a; Esteky and Schwark 1994; Jeka et al. 1997, 1998; Matthews 1972). Position information is clearly available from proprioceptive and otolith information, but may not play as prominent a role as velocity in the small corrections required during quiet stance (Masani et al. 2003).

Considering that subjects relied primarily on vestibular information during the sway-referencing condition and to a lesser extent, the foam condition, in the present study, it is useful to consider what information is provided about body sway by the vestibular system. Semicircular canals are effectively integrating angular accelerometers because of their biophysics, and therefore convey angular velocity information to the CNS over a broad range of frequencies (Fernandez and Goldberg 1971; Goldberg and Fernandez 1971a,b; Miles and Braithman 1980). At very low frequencies, the canal response conveys angular acceleration, although this signal is thought to be noisy. One source of the noise is the wide range of head movements over which the canals are designed to operate essentially linearly (up to several hundred deg/s) to accurately encode head motion for the generation of compensatory eye movements [vestibulo-ocular reflex (VOR)]. Body sway velocities in our results were approximately 1 deg/s or lower on all surfaces (see Fig. 7). This is on the order of 1% of the dynamic range of the canals. Therefore, it would be reasonable to expect that the signal-to-noise ratio of the canal signal would be fairly low during operation in the restricted range of motions associated with spontaneous body sway, although compensation for this deficit may be achieved by combining otolith and canal information (Schmid-Priscoveanu et al. 2000).

A second source of noise is ascribed to their anatomical location in the head; the canals sense head velocity and not COM velocity. Therefore, some transformation of this canal information would be necessary to obtain COM velocity. The simplest transformation would be to combine the vestibular head-in-space information with proprioceptive head-on-body information to estimate trunk-in-space information. A more complicated transformation would be the down-channeling and up-channeling mechanism proposed by Mergner and Rosemeier (1998) that would include additional proprioceptive-based transformations. Assuming the simplest model, these transformations would be additive, and therefore the noise properties of the various sensory processes would also be additive. Therefore, the noisy vestibular information would become more noisy in the process of estimating COM velocity in space.

In summary, stance on foam or sway-referencing requires an increased reliance on vestibular-derived motion information (increased weighting of the vestibular channel; see Peterka and Loughlin 2004). This increased weighting of vestibular information reveals the relatively high noise level of the vestibular signal at the low frequencies of stimulation during quiet stance and sway-referencing. In contrast, subjects rely primarily on proprioceptive cues during stance on a fixed surface (Peterka 2002), whose noise level is low relative to vestibular cues (Mergner et al. 1993; van der Kooij et al. 2001). The observed differences between stance on foam versus a sway-referenced surface (e.g., see Fig. 6) can be attributed to a higher vestibular weighting during sway-referencing than during stance on foam. There is ankle joint motion during stance on foam and thus some useful proprioceptive information can contribute to postural reactions. Sway-referencing is never quite ideal but comes very close to stabilizing ankle joint motion, providing less useful proprioceptive information than a foam surface.

**Limitations of the noisy-computation model**

Our modeling approach has been to obtain multiple measures of postural sway across different experimental conditions.
and then identify a simple mechanistic model whose behavior is qualitatively consistent with these measures. This approach led us to the noisy-computation model (Kiemel et al. 2002). Even though the present results are consistent with the predictions of this model, there are potential deficiencies in our modeling approach worth addressing. For example, our simple model lacks features found in more complicated models of the postural control system such as sensory time delays, sensory dynamics, and multiple body segments (see, for example, Kuo 1995; Peterka 2000, 2002; van der Kooy et al. 1999, 2001). We have chosen to forgo these features because they are not required to obtain qualitative agreement with the data we have considered. However, it will be important to compare our model to more detailed models to investigate whether they can be thought of as refinements of our simple model, or whether they offer fundamentally different interpretations of experimental data.

Another possible deficiency of our modeling approach concerns how we have interpreted our model’s parameters. One important parameter is the inverted-pendulum parameter γ, which determines the amount of torque that needs to be counteracted from acceleration resulting from gravity. The question is the extent to which this torque is produced by passive (e.g., tendon) or active (e.g., neurally mediated muscle activity) components of the ankle–foot muscle/joint complex. Presently, our model assumes that the counteracting force is mediated only by active changes in muscle force resulting from changes in sensory noise levels. However, this assumption would be erroneous if passive ankle forces play a significant role. Winter et al. (1998) proposed that passive ankle muscle stiffness alone was capable of maintaining upright stance. However, a number of studies have argued against purely passive control (Loram and Lakie 2002; Morasso and Sanguineti 2002; Morasso & Schieppati 1999; Peterka 2002). For example, Loram and Lakie (2002) used small mechanical perturbations to the foot to measure intrinsic ankle stiffness (stiffness not attributed to neurally mediated feedback) during quiet stance. They found that intrinsic ankle stiffness was, on average, 91% of that necessary to minimally counteract the torque produced by gravity. Peterka (2002) developed a PID control model for human postural control that argued for much lower levels of the passive ankle component (10% passive vs. 90% active). Although the actual contribution of passive ankle stiffness remains controversial, the important point is that attributing the inverted pendulum parameter (γ) to purely active control is most likely an overestimate and may affect the qualitative behavior of the model. Moreover, intrinsic ankle stiffness may play less of a role during sway-referencing than during quiet stance. If so, the effective γ might be different for the different experimental conditions in the current study. This would be counter to our assumption that differences between experimental conditions are primarily sensory in nature and can be modeled by changing only sensory-noise levels.

In conclusion, these results support previous findings (Kiemel et al. 2002), suggesting that velocity information is the most accurate form of sensory information used to stabilize posture during quiet stance. We are not suggesting that position and acceleration information are unimportant for postural control, but rather that healthy postural behavior reflects the availability of accurate velocity information. Reflecting the inherent redundance of sensory information for postural control, velocity information is derived from more than one sensory modality. As long as velocity information is available, the noisy computation model predicts that the qualitative stochastic structure of sway should not change. If one source of velocity information is lost while another remains available, sway variability may increase because the nervous system cannot estimate the center of mass velocity as precisely, although the fundamental characteristics of sway remain unchanged. Only severe degradation of velocity information is predicted to change the basic structure of sway.

A P P E N D I X

Here we briefly summarize the noisy-computation model of Kiemel et al. (2002). The model has 4 variables: the position \(x_1\), the velocity \(x_2\), the estimated position \(\hat{x}_1\), and the estimated velocity \(\hat{x}_2\). In this paper, position \(x_1\) is the anterior-posterior angle of the center of mass. The time derivatives of the variables are given by

\[
\begin{align*}
\dot{x}_1 &= x_2 \\
\dot{x}_2 &= \gamma x_1 - c_1 \dot{x}_1 - c_2 \dot{x}_2 + a \sigma(t) \\
\dot{\hat{x}}_1 &= \hat{x}_2 + K_1(x_1 - \hat{x}_1) + K_2(z_1 - \hat{x}_1) + K_3(z_1 - \gamma \dot{x}_1) + \sigma_1 \epsilon \dot{\xi}(t) \\
\dot{\hat{x}}_2 &= \gamma \hat{x}_1 - c_1 \hat{x}_1 - c_2 \hat{x}_2 + K_4(z_1 - \hat{x}_1) + K_5(z_1 - \gamma \dot{x}_1) + \sigma_2 \epsilon \dot{\xi}(t)
\end{align*}
\]

where

\[
\begin{align*}
z_1 &= x_1 + \sigma_1 \epsilon \dot{\xi}(t) \\
z_2 &= x_2 + \sigma_2 \epsilon \dot{\xi}(t) \\
\epsilon &= z_1 + \sigma_1 \epsilon \dot{\xi}(t) + c_1 \epsilon \dot{\xi} + c_2 \epsilon \dot{\xi} \\
\dot{\xi}(t), \dot{\xi}_1(t), \dot{\xi}_2(t), \epsilon(t), \epsilon_1(t), \epsilon_2(t), \text{and } \epsilon_3(t) \text{ are independent white-noise processes, and the } K_\text{th} \text{ are chosen to minimize the estimation performance index}
\end{align*}
\]

\[
J = E[d_1(x_1 - \hat{x}_1)^2 + d_2(x_2 - \hat{x}_2)^2]
\]

where \(d_1\) and \(d_2\) are positive.

Equations A1 and A2 describe the dynamics of an inverted pendulum: The right-hand side of Eq. A2 consists of γx1, the acceleration produced by gravity, and \(-c_1 \dot{x}_1 - c_2 \dot{x}_2 + \sigma(t)\), the acceleration produced by muscle activity, where \(u(\hat{x}_1, \hat{x}_2) = -c_1 \dot{x}_1 - c_2 \dot{x}_2\) is the control function and \(\sigma(t)\) is process noise. Equations A3 and A4 describe the dynamics of estimating position and velocity based on noisy sensory measurements defined in Eqs. A5–A7. \(z_1\) is a noisy measurement of position, \(z_2\) is a noisy measurement of velocity, and \(\epsilon_3\) is a noisy measurement of acceleration, transformed by subtracting the control function \(u(\hat{x}_1, \hat{x}_2)\). The coefficients \(K_\text{th}\) are sensory weights. They are chosen to minimize the weighted sum of squared estimation errors given by the performance index (Eq. A8). The weighting of position and velocity errors does not effect the choice of sensory weights. Therefore, we set the performance-index coefficients \(d_1\) and \(d_2\) both equal to 1 in their respective units.

When the sensory weights \(K_\text{th}\) are zero, Eqs. A3 and A4 are an internal model of the inverted pendulum. The terms \(\sigma_1 \epsilon \dot{\xi}_1(t)\) and \(\sigma_2 \epsilon \dot{\xi}_2(t)\) describe computation noise. Computation noise is meant to model errors made by the neural systems that fuse sensory information to produce the state estimates \(\hat{x}_1\) and \(\hat{x}_2\). It differs from measurement noise in that it affects the dynamics of estimation even in absence of the sensory information. When the computation-noise levels \(\sigma_1\) and \(\sigma_2\) are zero, Eqs. A3 and A4 are a Kalman filter (Bryson and Ho 1975).
The model has a total of 9 parameters: the inverted-pendulum parameter $c_2$; the control-function coefficients $c_1$ and $c_2$; the process-noise level $\sigma_2$; the sensory-noise levels $\sigma_1$, $\sigma_2$, and $\sigma_3$; and the computation-noise levels $\sigma_{1,2}$ and $\sigma_{2,3}$.

The autocovariance function of the model has the form

$$E[x(t)x(t+\tau)] = k_{0}\epsilon^{2\tau} + k_{1}\epsilon^{2\tau} + k_{2}\epsilon^{2\tau} + k_{3}\epsilon^{4\tau} \quad (A9)$$

The eigenvalues $\lambda_{1,2}$ are called the "estimation eigenvalues"; they describe the dynamics of estimation errors and depend only on $\gamma$ and the noise-level parameters. The eigenvalues $\lambda_{1}$ and $\lambda_{2}$ are called the "function-eigenvalues"; they depend only on $\gamma$ and the control-function coefficients $c_1$ and $c_2$.

$$\lambda_{1,2} = -c_2\epsilon \pm i \sqrt{c_1 - \gamma - c_2^2/4} \quad (A10)$$

Based on comparisons of the model to experimental data (Kiemel et al., 2002), we hypothesize that $c_1 > \gamma + c_2^2/4$ so that the control-function eigenvalues are complex-valued, corresponding to a damped oscillation. We further hypothesize that the postural control system under normal sensory conditions resides in a parameter regime in which the process-noise level $\sigma_2$, the velocity sensory-noise level $\sigma_2$, and the position computation-noise level $\sigma_{1,2}$ are all small. This hypothesis is stated mathematically by assuming that these parameters are of order $\epsilon$, where $\epsilon$ is a small parameter. Then one estimation eigenvalue, $\lambda_{1,2}$, is of order $\epsilon$, indicating a slow rate constant; and the other estimation eigenvalue, $\lambda_{1,2}$, is of order $1/\epsilon$, indicating a fast rate constant. The control-function eigenvalues $\lambda_{1}$ and $\lambda_{2}$ are of order 1, indicating dynamics on an intermediate timescale.

The largest coefficient of the autocovariance function is the estimation coefficient $k_0$, which is of order $\epsilon$. The control-function coefficients $k_1$ and $k_2$ are of order $\epsilon^2$, and the second estimation coefficient $k_3$ is of order $\epsilon^3$. Therefore, the eigenvalues of a descriptive ARMA model (see METHODS) can be related to the eigenvalues of the mechanistic noisy-computation model: the real-valued eigenvalue $\lambda_0$ corresponds to the estimation eigenvalue $\lambda_{1,2}$, and the complex-valued eigenvalues $\lambda_1$ and $\lambda_2$ correspond to the control-function eigenvalues $\lambda_{1,2}$.

The default values of the parameters are $\gamma = 8 \, s^{-2}$, $c_1 = 14.25 \, s^{-2}$, $c_2 = 3 \, s^{-3}$, $\epsilon = 0.25 \, deg \, s^{-3/2}$, $\sigma_1 = 1 \, deg \, s^{-1/2}$, $\sigma_2 = 0.05 \, deg \, s^{-1/2}$, $\sigma_3 = 2 \, deg \, s^{-3/2}$, $\sigma_{1,2} = 0.03 \, deg \, s^{-1/2}$, and $\sigma_{2,3} = 5 \, deg \, s^{-3/2}$.

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## References


