Sensory reweighting dynamics in human postural control

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Abstract

Healthy humans control balance during stance using an active feedback mechanism that generates corrective torque based on a combination of movement and orientation cues from visual, vestibular and proprioceptive systems. Previous studies found that the contribution of each of these sensory systems changes depending on perturbations applied during stance and on environmental conditions. The process of adjusting the sensory contributions to balance control is referred to as sensory reweighting. To investigate the dynamics of reweighting for the sensory modalities of vision and proprioception 14 healthy young subjects were exposed to six different combinations of continuous visual scene and platform tilt stimuli while sway responses were recorded. Stimuli consisted of two components: 1) a pseudorandom component whose amplitude periodically switched between low and high amplitudes and 2) a low amplitude sinusoidal component whose amplitude remained constant throughout a trial. These two stimuli were mathematically independent of one another and, thus, permitted separate analyses of sway responses to the two components. For all six stimulus combinations, the sway responses to the constant amplitude sine were influenced by the changing amplitude of the pseudorandom component in a manner consistent with sensory reweighting. Results show clear evidence of intra- and inter-modality reweighting. Reweighting dynamics were asymmetric with slower reweighting dynamics following a high to low transition in the pseudorandom stimulus amplitude as compared to low to high amplitude shifts and were also slower for inter- as compared to intra-modality reweighting.

Keywords

Humans, balance, sensory integration, posture control, reweighting
Introduction

The main sensory cues involved in human balancing stem from visual, vestibular and proprioceptive systems (Horak and Macpherson 1996). The relative contribution of each sensory system changes depending on environmental conditions, a phenomenon referred to as ‘sensory reweighting’ (Nashner and Berthoz 1978). Peterka (2002) showed that human sway response behavior could be explained using a relatively simple feedback mechanism with a linear combination of appropriately weighted sensory cues. Furthermore, the study confirmed the existence of sensory reweighting by demonstrating that quantitative estimates of sensory weights changed depending on the availability of sensory information from visual or proprioceptive systems and depending on the amplitude of perturbations provided by visual surround (VS) or platform (PF) tilts.

The results of Peterka (2002) and consistent results of other studies (Maurer et al. 2006, Oie et al. 2002) demonstrated that sensory reweighting is a major contributor to limiting body sway amplitudes when balance is perturbed by platform tilts and visual scene motions. However, these findings are based on long duration experimental trials that allow subjects to reach steady-state conditions. Relatively little is known about the time course of sensory reweighting following a sudden change in environmental or stimulus conditions. The speed of reweighting is functionally important because failure to adjust rapidly enough can result in instability and falls when subjects either fail to generate sufficient corrective torque to resist gravity or generate too much torque resulting in resonant behavior (Peterka and Loughlin 2004).

Only a limited number of studies have addressed transition effects that likely involve sensory reweighting. Most studies concentrated on the transition effects when adding or removing cues from one or more sensory systems such as vision, touch, or proprioception (Teasdale et al. 1991; Hay et al. 1996; Sozzi et al. 2012). Only two studies addressed the transition effects that occur following amplitude changes of a stimulus (Jeka et al. 2008; Polastri et al. 2012).
In the first study, Jeka et al. (2008) measured the time course of the response to a continuous, oscillating translational visual stimulus following sudden changes in the stimulus amplitude. Subjects stood in semi-tandem stance facing a translucent screen onto which the stimulus was projected. The time course of the change in body sway amplitude at the visual stimulus frequency was considered indicative of changes in the relative contribution of visual cues to stance control. Results showed more rapid changes in sway responses following low-to-high changes in visual stimulus amplitude, whereas the response following the high-to-low transition showed a slower change. This behavioral asymmetry was interpreted as being functionally relevant for preventing instability, because a failure to adjust quickly in a low-to-high transition would result in large sway responses to the large stimulus, whereas high-to-low transitions are not threatening and the system can change more slowly.

The second study (Polastri et al. 2012) used a continuous sinusoidal visual stimulus to estimate the sensitivity of the visual response in combination with a sinusoidal PF tilt stimulus whose amplitude changed. Again, the amplitude of the body sway responses at the stimulus frequencies were taken as a measure of the relative sensory contributions to balance control with results showing both slow and fast changes. Because this study simultaneously presented a PF stimulus (with changing amplitude) and a VS stimulus (with constant amplitude), the study was able to distinguish between two effects. The 'intra-modality' effect was defined as being present if the change in PF stimulus amplitude resulted in a change in the body sway response at the frequency of the PF stimulus. The 'inter-modality' effect was defined as being present if the change in PF stimulus amplitude resulted in a change in body sway response at the frequency of the VS stimulus.

Previous model-based interpretations of body sway responses evoked by pseudorandom PF or VS stimuli of various amplitudes indicated that a change in test conditions that evoke a weight change in one sensory system was always compensated by changes in the weights of other sensory systems (Peterka 2002; Cenciarini and Peterka 2006). This coordinated change in weights (i.e. a reweighting rather than a change in only one sensory weight) was assumed to be necessary in order to maintain a consistent level of
sensory feedback to stabilize the body against gravity without changing the overall dynamic characteristics of the balance control system. Using the terminology of the Polastri et al. (2012) study, a stimulus that evokes an intra-modality effect should also show inter-modality changes. While intra-modality changes were consistently seen in response to PF amplitude changes in the Polastri study, the inter-modality changes were not always seen. Specifically, following the transition of the PF stimulus from high to low amplitude, the sway response to the VS stimulus did not show an inter-modality change. In the current study a variety of PF and VS amplitude transitions were investigated with sway responses analyzed to determine if intra- and inter-modality changes always occurred together in a manner consistent with sensory reweighting.

The results from Jeka’s laboratory (Jeka et al. 2008, Polastri et al. 2012) are limited in some aspects. The dynamic changes of the sway responses can result not only from a change in the sensory weights (reweighting dynamics), but also from the change of the stimulus amplitude itself. More specifically, a dynamic system without any reweighting would also show a transient response following a change in stimulus amplitude, in which the body sway response follows a transient time course until it reaches a new steady-state condition. Thus, while the results from the Jeka laboratory clearly demonstrated changes in responsiveness, consistent with reweighting, to the changing amplitude of visual (Jeka et al. 2008) and proprioceptive (Polastri et al. 2012) stimuli, the detailed interpretation of the time course of sway changes following a stimulus amplitude change is confounded by the response being a combination of reweighting and transient effects.

To overcome the ambiguity of attributing transient responses following amplitude changes to reweighting dynamics versus system dynamics, the current study combined two independent stimuli. The first stimulus component was a broadband pseudorandom waveform that provoked reweighting through changes in its amplitude. Following an amplitude change, the response to this stimulus included a transient response that consists of sway responses caused by the dynamic characteristics of the balance control system (independent of whether or not sensory reweighting occurred) as well as transient sway
responses caused by sensory reweighting. The second stimulus component was a constant amplitude sinusoidal waveform applied at a frequency where the pseudorandom stimulus had no energy. As the amplitude of the sinusoidal component did not change throughout an experimental trial, changes of the sway response at the frequency of the sine wave will not include an amplitude-related transient response and therefore sway response changes at the sinusoidal frequency can be mainly attributed to sensory reweighting dynamics.

Another potential limitation of results from Jeka’s laboratory is that the visual stimulus was based on a projected visual field simulating an anterior-posterior directed optic flow pattern on a screen that was fixed in space. This stimulus is ambiguous in itself, as subjects perceive not only the projected optic flow stimulus, but further visual cues from estimates of the relative motion to the fixed screen, e.g. from accommodation of the lenses, convergence of the eyes, binocular disparity and occlusion (for a current review see Blake and Wilson 2011). This ambiguity might affect the visual input and alter sway responses in comparison to those evoked by a visual structure that is actually moving. For example, a study by Mergner et al. (2005) found that sway evoked by a projected moving visual scene was about half that of sway evoked by a similar physically moving visual surround. The current study generated visual stimuli using a movable visual screen with an illuminated pattern. This physical moving visual surround provided an unambiguous, congruent visual input.

Twelve experimental trials with 6 experimental conditions were performed to obtain a description of the time course of intra- and inter-modality response sensitivity following changes in the PF and VS stimulus amplitude during eyes open conditions and during conditions without visual input or with minimized proprioceptive contributions. The current set of experimental results complements previous results of Jeka and colleagues in that it identifies an extensive set of intra- and inter-modality weighting dynamics and provides an accurate characterization of reweighting dynamics.

**Methods**
Subjects

Fourteen healthy subjects (age 26.0 +/- 4.1 years, 7 female, 7 male) participated in this study after giving their informed consent. The study was approved by the Internal Review Board of the Oregon Health & Science University and is in accordance with the 1964 declaration of Helsinki.

Experimental setup

Experiments were performed using a custom made device that provided servo-controlled independent motions of the platform and visual surround (half cylinder with 70-cm radius). Both tilted in AP direction about the ankle joints (see Peterka 2002). The visual surround was covered by a pattern of horizontal and vertical grey, white and black stripes of various spatial frequencies and was illuminated by two attached lights to exclude visual distractions from outside the half cylinder. The platform had a custom-made force plate to record center of pressure shifts (CoP). Stimulus delivery and data collection were performed at a sampling frequency of 200 Hz using a custom program written in LabView® (National Instruments, Austin, USA).

Subjects were free standing on the platform, with hands crossed in front at waist level. Subjects wore a harness with two straps attached to the ceiling to prevent falls. The straps were attached with sufficient slack such that they did not support the subject or provide any additional sensory cues. Fixed to the head was an IMU to measure head motion (data were not included in the analysis). Two hooks were attached to the harness at shoulder level and to a Velcro belt worn around the hips at the height of the greater trochanter. The hooks guided horizontal rods attached to earth-fixed potentiometers to measure the AP sway at hip and shoulder levels. From the potentiometer angles, AP displacements of hip and shoulder were derived using appropriate trigonometric calculations. Instrumentation noise in the recording system was very low (rms noise measures of 0.002° for the measurement of body sway angles at hip and shoulder levels) such that body sway could be measured accurately even though sway amplitudes were small.
The main output for the analysis was considered to be the whole body center of mass (COM) sway angle with respect to the space vertical. COM sway was calculated from the hip and shoulder displacements using information derived from a calibration trial (see Peterka 2002). In the 120-s long calibration trial subjects performed very slow movements at the hip and ankle joints. The measured CoP was taken as a vertical projection of the COM (Breniére 1996) and a linear regression analysis was used to determine the relationship between hip and shoulder displacements and COM displacement. COM displacements during the experimental trials were then calculated from the hip and shoulder displacements using the parameters from the linear regression. Finally, the COM sway angle at each sample point was calculated from the COM displacement and the COM height, with COM height estimated from anthropometric measures and relative body mass distributions (Winter 2005).

Stimuli

The study consisted of six experimental conditions (Exps. 1-6; Fig. 1B). In each condition the stimuli consisted of two parts; a sinusoidal waveform and a pseudorandom waveform based on a pseudorandom ternary sequence (prts). The prts was an 80 state sequence with 0.18s state duration (Davies 1970). Each prts cycle had 14.4-s duration and was presented either with a low amplitude (LO condition; 1° peak-to-peak; pp) or with a high amplitude (HI condition; 4° pp for the visual surround; 8° pp for the platform, shown in Fig. 1A). Each trial started with two LO condition cycles and was followed by five repetitions of two HI and two LO prts cycles each, i.e. a total of 22 prts cycles with 316.8-s trial duration (Fig. 1C).

The frequency of the sinusoidal waveform (sine for PF and cosine for VS motion) was ~0.56 Hz (8 cycles / 14.4 s = 0.56 Hz). This frequency made the sinusoidal component mathematically independent of the prts waveform, which has no energy at even harmonics of the fundamental prts frequency. The amplitude of the sine wave was 0.3° pp and remained constant throughout each trial. Note that the sine-wave amplitude was small compared to the prts peak-to-peak amplitude, even in the LO condition.
All six experimental conditions were performed twice, with the sine-wave stimulus of one trial inverted as compared to the sine-wave stimulus on the other trial. This sine-wave inversion on separate trials was used in the analysis to separate the COM sway response to the prts stimulus from that to the sine wave (see below).

Three of the 6 experimental conditions investigated reweighting dynamics following amplitude changes in the PF prts stimulus (Exps. 1, 2, 3) and three the reweighting dynamics following amplitude changes in the VS prts stimulus (Exps. 4, 5, 6). In the first set, the alternating PF prts amplitude was combined with a PF sine (Exp. 1) and a VS sine (Exp. 2) during eyes open in order to estimate inter- and intra-modality reweighting effects, respectively, by tracking changes in COM sway responses at the sinusoidal frequency. The third experimental condition, with alternating PF prts amplitude combined with a constant amplitude PF sine (Exp. 3), focused on the intra-modality reweighting during eyes closed, where mainly proprioceptive and vestibular cues contribute to balance control. In the second set of experimental conditions, all tests were performed with eyes open, while an alternating-amplitude VS prts stimulus was combined with a PF sine (Exp. 4) and a VS sine (Exp. 5) to provide the time course of inter- and intra-modality reweighting, respectively. The sixth experimental condition used PF sway-referencing to minimize the proprioceptive contribution to balance control by minimizing ankle joint motions (Nashner and Berthoz 1978). Sway-referencing was implemented by continuously measuring the lower body sway angle (based on the hip displacement measure) and commanding the servo-controlled PF to track the lower body sway angle. In Exp. 6 sway-referencing of the PF was applied throughout the test while alternating VS prts amplitudes were combined with a constant-amplitude VS sine stimulus. Exp. 6 investigated intra-modality changes in the visual contribution to balance under conditions where mainly visual and vestibular systems contribute to balance control.

Protocol

Subjects’ anthropometric measures were taken and they were asked to perform the calibration trial. The calibration trial was followed by a ‘warmup’ trial consisting of a series of
different stimuli from Exps. 1-6 in order to familiarize subjects with the experiment. Then the
twelve experimental trials (two 316.8-s duration trials per experimental condition) were
presented in randomized order with a break of 3-5 min given at least every three trials, or
upon request of the subject. During experiments, subjects were asked to look straight ahead
(or close their eyes) and stand upright. To distract subjects from the balancing task and to
minimize auditory orientation cues, subjects listened to an audio book via headphones.

Analysis – separation of prts and sine responses
The recorded data was exported to Matlab® (The Mathworks, Natick, MA, USA) for
further analysis. The first and last cycle of each trial were discarded to avoid uncontrolled
transient effects. For each of the six experimental conditions, the COM sway responses of
the two paired trials, i.e. the responses to the stimuli that included positive and negative sine-
wave components, were taken as one set (Fig. 2, left column). Adding the two COM signals
of each set (and dividing by two) yielded the response to the prts stimulus, while the
response to the sine wave canceled out (Fig. 2, COM response to prts). Subtracting the two
signals of each set (and dividing by two) canceled the response to the prts stimulus, yielding
the response to the sine wave (Fig. 2, COM response to sine). The stimulus and response
sequences were further separated into prts HI condition and prts LO condition segments and
these HI and LO segments were further divided into steady-state and transition periods (Fig
1C). In the two paired trials (positive and negative sine) of each experimental condition the
prts HI/LO segments were repeated five times in each trial and therefore a total of 10 HI/LO
segments for each experimental condition were used for each subject’s analysis.

Time domain analysis
To reduce low frequency drifts, the derivative of the raw COM sway data (i.e., sway
velocity) were used for all time domain and frequency analyses. The sway velocity data were
also filtered with a 10 Hz butterworth low-pass filter using the Matlab® zero-phase digital
filter function ‘filtfilt’. The mean COM velocity response to the sine component was calculated
for each subject and across all subjects using data from all 10 HI/LO segments. These data were used for display and for the fitting of mathematical functions to characterize transient changes (see below).

Frequency domain analysis

Frequency domain analyses of the prts and sine-wave stimuli and COM responses of each subject were performed using discrete Fourier transform methods that were appropriate for data collected using periodic stimuli (Pintelon and Schoukens, 2001). Frequency response functions were calculated from the ratio of the complex discrete Fourier transform components (real and imaginary parts) of the COM response to those of the stimulus at the sine component frequency and at each frequency where the prts had stimulus energy. Gain and phase values at each frequency point were obtained by calculating the magnitude (absolute value) and the angle (four-quadrant inverse tangent) of the mean complex vector at each frequency point in the frequency response function.

To obtain an estimate of frequency response functions representing dynamic behavior in the 14.4 s steady-state portions of the data sets for both the prts LO and HI amplitude conditions the procedures described above were applied at all prts and sine component frequencies. The across-subject mean frequency response functions for data from each of the six experimental conditions were calculated by averaging the real and imaginary parts from the individual frequency response functions at each frequency point prior to calculating the mean gain and phase values. 95% confidence limits on the mean frequency response function gain and phase data were obtained using approximations based on F-statistics described by Otnes and Enochson (1972).

Across-subject mean frequency response function values (also expressed as gain and phase values) at the sine component frequency were also calculated for each of the 32 sine cycles associated with a set of LO, HI, HI, LO changes in the prts stimulus amplitude.

Individual and across-subject mean frequency response function values of the responses at the sine component frequency during the HI and LO prts steady-state periods
were calculated from frequency response function data of the 8 sine cycles in each prts steady-state period. A two-step statistical analysis was performed to account for the multivariate nature of the frequency response function values. First, Hotellings $T^2$ was used to test for differences between the complex values of the frequency response function of HI and LO steady-state conditions (Calkins 1998). Second, bootstrapping methods were performed to separately test for differences in gain and phase (Zoubir and Boashash 1998).

**Descriptions of transient response behavior**

Quantitative descriptions of the temporal dynamics of the COM velocity response to the sine component following the LO/HI and HI/LO transitions of the prts stimulus were obtained using model fits to the experimental COM velocity data. The across-subject mean COM sway velocity following the prts stimulus amplitude transitions were the input to the fitting procedure. Several different mathematical models of varying complexity were fit to the sway data. Because additional model parameters reduced the error between model fit and experimental data, the tradeoff between reducing the fit error and adding parameters was considered. We used F-test statistics as described in Johannson (1993) to account for this tradeoff with a more complex model accepted only when the test showed a significant improvement in fit error ($p<0.05$). After an appropriate model was identified, the 95% confidence intervals of the model’s parameters were calculated using bootstrap methods that resampled the mean COM responses of each of the 14 subjects 1000 times (with replacement) and performed the fits to the mean of each resampled dataset (Zoubir and Boashash 1998).

COM velocity data for the 28.8-s period (i.e., for the duration of 2 prts cycles) following the LO/HI and HI/LO transitions were fit with functions of the following form:

$$y(t) = A(t) \cdot \sin(\omega t + \Phi(t)) \quad \text{for } t > \Delta t$$  \hspace{1cm} (1)

$$y(t) = a \cdot \sin(\omega t + \varphi) \quad \text{for } t < \Delta t$$  \hspace{1cm} (2)
where $\omega$ is the sine frequency (in radians/s), $A(t)$ represents the time-varying modulation of the amplitude of the sine function, and $\Phi(t)$ represents the time-varying modulation of the phase of the sine function. For fits that included a time delay parameter, $\Delta t$, the fit assumed that the amplitude, $a$, and phase, $\varphi$, of the COM sine response remained the same (for the first $\Delta t$ seconds after the transition) as the amplitude and phase of the COM sine velocity at the end of the steady-state cycle just before the prts amplitude transition. The $a$ and $\varphi$ values were determined from fits of a sine function to the COM velocity data in the last 3 sine cycles before the transition.

For fits that included a single exponential term, the $A(t)$ and $\Phi(t)$ functions are given by:

$$A(t) = a + b \left( 1 - e^{-\frac{(t-\Delta t)}{\tau_1}} \right)$$

(3)

$$\Phi(t) = \varphi + \Delta \varphi \left( 1 - e^{-\frac{(t-\Delta t)}{\tau_1}} \right)$$

(4)

where $b$ and $\Delta \varphi$ represent the amount that the amplitude and phase, respectively, of the COM sine response changed over the 28.8-s time course following the transition, and $\tau_1$ is the time constant of the exponential change. The value of $b$ was found by first fitting a sine function to the COM velocity data from the 3 sine cycles at the end of the 28.8-s period and then taking the difference between the amplitude value from this fit and the parameter value $a$ (see equation 2 description). The parameter $\Delta \varphi$ was similarly calculated as the difference between the phase value from the fit to the last 3 sine cycles and the value of $\varphi$ (see equation 2 description).

For fits that included two exponential terms, the $\Phi(t)$ function was the same as in equation 4 but the $A(t)$ function had the form:

$$A(t) = a + b \cdot \left( 1 - e^{-\frac{(t-\Delta t)}{\tau_1}} \right) + c \cdot \left( e^{-\frac{(t-\Delta t)}{\tau_2}} - e^{-\frac{(t-\Delta t)}{\tau_1}} \right)$$

(5)
where $\tau_2$ is the time constant of the second exponential term and $c$ represents the amount of change in the amplitude of the COM velocity sine response over a slow exponential time course represented by $\tau_2$ where $\tau_2 > \tau_1$.

Two sets of fits were made to the COM velocity data of the sine-component. One set assumed that there was no time delay ($\Delta t$ set to zero) in the onset of changes in the COM response following the prts amplitude transition. The second set assumed there could be a time delay and allowed the value of $\Delta t$ to be determined by the fit procedure. For single exponential fits, the fit procedure provided an estimate of $\tau_1$ (when $\Delta t$ was set to zero) or $\tau_1$ and $\Delta t$ (when $\Delta t$ was allowed to vary). For double exponential fits, the fit procedure provided estimates of $\tau_1$, $\tau_2$, and $c$ (when $\Delta t$ was set to zero) or $\tau_1$, $\tau_2$, $c$, and $\Delta t$. For all fits, the values of parameters $a$, $b$, $\varphi$, and $\Delta \varphi$ were pre-calculated based on steady-state values prior to the transition and at the end of the fit period.

The fits were performed on 28.8-s segments of mean COM sway velocity data following the HI/LO and LO/HI changes in prts amplitude. The 28.8-s segments included both the “transition” and “steady-state” periods as defined in Fig. 1C. The fits were made using the Matlab® function ‘fit’ from the “Curve Fitting Toolbox”. This function performs a least squares minimization using a ‘trust-region-reflective’ algorithm. The fit function called a custom user-defined function that used case selection commands to specify the discontinuity caused by inclusion of a time delay parameter in the fit equation.

**Results**

We first present frequency response functions demonstrating the intra-modality modulation of the steady-state COM responses to the prts stimulus at LO and HI prts amplitudes as well as the associated intra- and inter-modality modulation of responses to the constant-amplitude sine component in the LO and HI prts steady-state conditions. Then a qualitative description is given of the time courses of COM responses to the sine component.
following the sudden changes in the VS or PF prts stimulus amplitudes. The final section
presents quantitative estimates of the reweighting dynamics derived from fits to the COM
responses to the sine component.

Steady-state intra- and inter-modality reweighting

Steady-state COM sway responses to the prts PF and VS stimuli were analyzed by
calculating frequency response functions using COM sway data from the second prts cycles
following the transitions from LO to HI and from HI to LO amplitudes. The frequency
response function gain data are shown in Fig. 3 for PF prts stimuli (top row) and VS prts
stimuli (bottom row). The general pattern of gain change as a function of stimulus frequency
are consistent with previously reported responses to prts stimuli (Peterka 2002) with the
largest gains occurring at ~0.2 Hz and declining gains with increasing frequency. Also
consistent with previous results (Peterka 2002), the frequency response function gains were,
on average, much larger for the LO- compared to HI-amplitude prts stimuli in each of the 6
experimental conditions. Thus, the COM sway responses showed strong intra-modality
modulation of sensitivity for both PF and VS prts stimuli of different amplitudes.

Fig. 3 also overlays the gain values derived from the COM responses to the constant-
amplitude sinusoidal PF or VS stimuli (data points plotted within the gray bars). The COM
data for these gain calculations came from the steady-state time periods used for the LO-
and HI-amplitude prts frequency response function calculations. In all six experimental
conditions there were differences in sine gain values associated with the LO and HI prts
conditions. In experimental conditions where the sine and the prts stimuli were of the same
type (both PF in Exps. 1 and 3; both VS in Exps. 5 and 6), the sine gain differences

corresponding to the LO and HI prts conditions showed evidence for intra-modality
modulation of the sine response sensitivity consistent with the intra-modality modulation
identified from responses to the prts stimuli. Specifically, when the PF prts amplitude was
LO, the gain of the response to the sine PF component was larger than the PF sine gain
value when the PF prts amplitude was HI. Thus, the change in prts amplitude was associated
with a change in the sensitivity of the COM response at the PF sine frequency even though
the amplitude of the PF sine stimulus was constant throughout the experimental conditions.
Similarly when prts and sine stimuli were both applied to the VS, the sine gain value
associated with the LO amplitude VS prts stimulus was larger than the VS sine gain value
when the VS prts amplitude was HI.

In experimental conditions where the sine and the prts stimuli were of different types
(PF prts and VS sine in Exp. 2; VS prts and PF sine in Exp. 4), the sine gain values
corresponding to the LO and HI prts conditions showed evidence for inter-modality
modulation of response sensitivity. For Exp. 2 with PF prts amplitude changes, the gain value
for the VS sine stimulus was largest when the PF prts amplitude was HI. Similarly for Exp. 4
with VS prts amplitude changes, the gain value for the PF sine stimulus was largest when the
VS prts amplitude was HI.

The results presented in Fig. 3 also suggest that some form of interaction occurred
that influenced the COM response to PF stimuli in the experimental conditions where both
the sine and prts components were PF stimuli (Exps. 1 and 3) and the prts amplitude was
LO. In both of these experimental conditions the prts gain values at frequencies immediately
adjacent to the sine component frequency were noticeably lower than the sine gain value.
This notch in the prts gain values in the vicinity of the sine component frequency was not
expected based on previous results using only PF prts stimuli (Peterka 2002) where results
showed a quite uniform decline in gain with increasing frequency in this 0.3 to 0.8 Hz
frequency region. No gain notch was evident in these same experimental conditions when
the PF prts was HI. Also, no similar interaction was evident in experimental conditions where
both the sine and prts components were VS stimuli.

Time course of sensory reweighting

The COM response to the constant-amplitude sine stimulus was separated from the
response to the prts stimulus in order to track the time course of sensitivity changes of sway
responses to the PF or VS sine stimuli (Fig. 2).
Fig. 4 shows the COM sway velocity responses to the sine stimuli as well as the corresponding gain and phase values calculated from each individual sine cycle and plotted over time for all 6 experimental conditions. Changes in responses to the PF and VS sine stimulus were considered to reflect changes in the relative sensory contributions (of proprioception and vision, respectively) to balance control. The sway responses to the sine component during both PF prts and VS prts amplitude changes showed statistically significant gain differences between prts HI and LO conditions. The phases showed large variability in conditions where the gain was low, due to the low amplitude of stimulus-evoked sway in comparison to the amplitude of ongoing, naturally occurring body sway motions that were not correlated with the stimulus. However, the phase was found to change significantly between HI and LO conditions in all experimental conditions except Exp. 4 (Table 1). For PF prts changes and for PF sine responses, this phase change is in agreement with previous findings (Peterka 2002). In contrast, the phase during different VS amplitudes was found to be unchanged by Peterka (2002), while the phase showed significant changes following transitions in the VS intra-modality conditions (Exps. 5 and 6). While these phase changes in Expts. 5 and 6 are not explained by current theories, the high phase variability during the VS prts HI amplitude conditions calls into question the meaningfulness of the identified phase changes despite the statistical significance.

For experimental conditions with PF prts amplitude changes (Exps. 1-3), the sine gain changes between PF prts HI and LO conditions were all large ranging from a factor of 2.2 increase (in VS sine gain where PF prts changed from LO to HI) to 3.6 decrease (in PF sine gain when PF prts changed from LO to HI when eyes were closed). Comparing eyes open and closed (Exp. 1 and 3), PF sine gain was 1.6 times higher when eyes were closed during PF prts LO, but the PF sine gains had similar low values during PF prts HI.

The low PF sine gains in PF prts HI conditions in Exps. 1 and 3 were likely caused by different sensory reweighting combinations. In Exp. 3 with eyes closed, where proprioception and vestibular systems were the main contributors to balance control, it is likely that the decreased response to the PF sine was associated with an increased contribution of the
vestibular system (Cenciarini and Peterka 2006). In contrast, in Exp. 1 where vision was available, the suppression of the PF sine response in the PF prts HI condition is likely to be mainly associated with an increased contribution of the visual system, although some vestibular contribution is also possible. This increased utilization of vision is supported by results from Exp. 2 where the sensitivity to the VS sine stimulus increased greatly when the PF prts amplitude was HI.

During VS prts amplitude changes (Exps. 4-6, bottom row in Fig. 4), gain differences were less pronounced compared to Exps. 1-3 with the exception of Exp. 6 where the proprioceptive contribution was minimized by PF sway referencing. During conditions without sway referencing (Exps. 4 and 5), there were only small changes in the responsiveness to the sine component between prts HI and LO conditions. One possible reason is that the VS prts gain values (Exp. 4) and the VS sine gain during VS prts LO (Exp. 5) were already quite low indicating the vision was providing a relatively small contribution to balance control even in the VS prts LO condition. Thus the visual contribution was limited in how much it could further decrease in the VS prts HI condition. A low contribution from vision is consistent with proprioception providing much larger contribution to balance control, as indicated by the large PF sine gain during VS prts LO of Exp. 4. Because the visual contribution to balance decreased only by a small amount in the VS prts HI compared to LO condition (Exp. 3), only a comparably small increase in the proprioceptive contribution was necessary to compensate for the small decrease in the visual contribution (Exp. 4). Thus, there was only a small increase in the PF sine gain in Exp. 4 in the VS prts HI condition. When proprioceptive cues were minimized by PF sway referencing (Exp. 6), the visual contribution greatly increased, with VS sine gains being ~5.5 times higher in both the VS prts HI and LO conditions as compared to the fixed PF condition (Exp. 5). Although the VS sine gain was strongly reduced during VS prts HI sway-referenced conditions, a considerable visual contribution remained, which was still higher than the visual contribution in the VS prts LO condition without sway referencing.
Quantitative descriptions of transient response behavior

Sway response velocities of PF sine and VS sine following the PF and VS prts HI/LO transitions were described by mathematical functions. Fig. 5 displays the first 3 sine cycles of the best fit to the experimental COM velocity data following HI/LO and LO/Hi prts amplitude transitions of each experimental condition. For comparison, the mean experimental COM sway velocity responses, as well as the mean experimental steady-state COM sway velocity time series previous to the HI/LO or LO/HI prts transition are shown. In all experimental conditions, the fits (black lines in Fig. 5) closely resemble the experimental data (grey lines in Fig. 5) following all HI/LO and LO/HI transitions. Furthermore, the differences between the previous periods’ steady-state responses (dashed lines in Fig. 5) and the transitional responses (experimental data and fits) are clearly visible with the exception of Exp. 4. In Exp. 4, the difference in steady-state amplitudes between LO and HI prts conditions was relatively small (~1.25 gain-change factor) and there was a slow time course of amplitude change (exponential time constants $\tau_1 = 4.9$ s for LO to HI and $\tau_1 = 9.3$ s for HI to LO; Table 2) such that very little change was evident in the first 3 cycles displayed in Fig. 5.

COM sway velocity following LO to HI transitions was best described by an exponential change of amplitude and phase following a time delay for all experimental conditions except Exp. 4 (Table 2, upper part). The fit statistics did not justify a time delay for Exp. 4 and the data was best described by an exponential change of amplitude and phase. We note that Exp. 4 had the longest time constant ($\tau_1 = 4.9$ s) of all the LO to HI transitions. This slow change in amplitude represented by the long time constant may have precluded the detection of a time delay less than ~1 s as identified on LO to HI transitions in all other experimental conditions. For all experimental conditions other then Exp. 4, the exponential time constants were quite short and in most cases shorter than the time delay. Thus, the time delay of 0.5-0.8 s is the dominant consideration in describing the dynamics of COM sway velocity changes following the LO to HI transition.

For HI to LO transitions (Table 2, lower part), the identified functions that best represented the experimental data were less consistent across experimental conditions
compared to results for LO to HI transitions. Time delays were only found for Exps. 1, 2 and 
6, although the time delay values in these cases were similar to those for LO to HI 
transitions. In two experimental conditions (Exp. 1 and 5), a second exponential term was 
required to account for a small and slow decay in COM sway amplitude (decay amplitude $c$
$\approx$0.1 deg/s; time constants $\tau_2 \approx$10 s), following an initial, fairly rapid exponential rise in COM 
amplitude (time constant $\tau_1 \approx$0.6 s).

In all experimental conditions, initial gain and phase changes following HI to LO 
transitions were found to be consistently slower as compared to LO to HI transitions. The 
slower changes in HI to LO transition are represented by the generally larger values of $\tau_1$
time constants for HI to LO compared to LO to HI. Additionally, a second dynamic amplitude 
change represented by a second exponential term was required in two experimental 
conditions to account for slow changes that occurred following HI to LO transitions.

For both LO to HI and HI to LO transitions, results from experimental conditions 
investigating inter-modality reweighting had ~5 times slower transitions as compared to 
experimental conditions investigating intra-modality reweighting for PF prts transitions (Exp. 
2 compared to Exp. 1) and >17 times slower transitions for VS prts transitions (Exp. 4 
compared to Exp. 5). That is, a change in prts stimulus amplitude that primarily affected one 
sensory system resulted in a rapid reweighting of that sensory system's contribution to 
balance control. In contrast, reweighting was slower in another sensory system that was not 
primarily affected by the change in prts stimulus amplitude.

Discussion

Our study was designed to investigate inter- and intra-modality sensory reweighting of 
the human balance control system and the dynamic changes that follow sudden transitions in 
stimulus amplitude of platform and visual surround tilt motions. The presented approach 
aimed at separating the dynamics of sensory reweighting from the transient response to the 
amplitude change itself in order to provide a detailed analysis of the temporal dynamics 
immediately following an amplitude transition. First, we will discuss the influence of passive
mechanical ankle torque contributions on the reweighting results. Then, the general
reweighting effects of the prts and the sine components will be addressed, followed by a
discussion of the temporal dynamics, with emphasis placed on differences of our findings as
compared to previous studies. Finally we will focus on some unexpected findings in the prts
responses at frequencies close to the sine frequency.

Influence of passive mechanics on sway responses

In order to understand the extent to which changes in the amplitude of sway
responses to the sine-component stimuli are attributable to sensory reweighting, it is
necessary to consider the extent to which the passive mechanical properties of muscles,
tendons, and joints influence the evoked body sway. The influence of passive mechanics of
sway evoked by PF and VS stimuli can be estimated based on a previously developed
feedback model of balance control (Peterka 2002). This model showed that the gain of sway
responses in a mid-frequency region, where response gain is largest, is determined mainly
by the “stiffness” parameters in the system. These stiffness parameters include both passive
and active stiffness. The passive stiffness of the system generates a restoring ankle torque
proportional to the ankle joint angle. The active stiffness generates an ankle torque
proportional to the deviation of a sensory-derived estimate of body orientation from an
internal reference orientation. The presence of a non-zero passive stiffness influences the
mid-frequency gain of responses to both PF and VS stimuli, but its influence is different for
the two stimuli. Specifically, the mid-frequency gain for PF stimuli, $G_{PF}$, is given by the
equation:

$$G_{PF} = \frac{K_{pas}+K_{act}W_{prop}}{K_{pas}+K_{act}W_{prop}+mgh}$$  \hspace{1cm} (6)

and for VS stimuli the gain, $G_{VS}$, is given by:

$$G_{VS} = \frac{K_{act}W_{vis}}{K_{pas}+K_{act}W_{vis}+mgh}$$  \hspace{1cm} (7)
where $K_{pas}$ is the passive stiffness factor, $K_{act}$ is the active stiffness factor, $W_{prop}$ is the proprioceptive weight, $W_{vis}$ is the visual weight, $m$ is body mass, $h$ is COM height, and $g$ is the gravity constant. The sensory weights represent the relative contributions of sensory systems to balance control and thus are restricted to the range 0 to 1. Model parameters estimated in Peterka (2002) showed the $K_{act}$ was about 1/3 larger than $mgh$. If we define $R$ as the ratio of $K_{pas}$ to $K_{act}$ and substitute $K_{act} = (4/3)*mgh$ into equations 6 and 7 we get:

$$G_{PF} = \frac{R+W_{prop}}{R+0.25} = \frac{R}{R+0.25} + \frac{W_{prop}}{R+0.25}$$ \hspace{1cm} (8)

$$G_{VS} = \frac{W_{vis}}{R+0.25} \hspace{1cm} (9)$$

For visual stimuli, equation 9 shows that the visual response gain is proportional to the visual sensory weight independent of the value of $R$ (assuming $R$ is constant) although the gain will be smaller when $R$ is larger (i.e., when passive stiffness is larger relative to active stiffness).

For platform stimuli the relationship between response gain to PF stimuli and the proprioceptive sensory weight is more complex. If $R$ is small then $G_{PF}$ is approximately proportional to $W_{prop}$ and, therefore, changes in $G_{PF}$ are essentially proportional to proprioceptive weight changes. If $R$ is larger (e.g., $R$ could be greater than unity) then $G_{PF}$ will still vary with changes in $W_{prop}$, but the change in $G_{PF}$ would be small even if the change in $W_{prop}$ were large. Additionally, even if the proprioceptive weight were zero the platform response gain would be equal to $R/(R+0.25)$ and thus there could be a large response that approaches unity gain if the passive stiffness were large relative to active stiffness.

Finally, for both PF and VS stimuli, gain changes could also occur if the ratio of passive to active stiffness changed with stimulus amplitude even if the sensory weights did not change.

Although the above considerations cast some doubt on whether it is appropriate to primarily attribute gain changes to sensory weight changes, the results from the study by Peterka (2002) suggest that this interpretation is appropriate. Specifically, the model-based
analysis of experimental responses to PF and VS stimuli under conditions similar to the current study estimated that the passive stiffness contribution to balance control was about 10% of the active contribution and thus $R=0.1$. With this small $R$ value, equation 8 predicts that the gain of the sway response to the platform stimulus could not be smaller than 0.29. This gain value corresponds closely to the PF sine gains measured in the prts HI condition in Exps. 1 and 3 (Table 1: mean gains were 0.25 and 0.28, respectively), and suggests that the proprioceptive contribution to balance in the prts HI condition was very low. Furthermore, the low PF sine gain values in the prts HI conditions of Exps. 1 and 3 tend to rule out the possibility that the passive stiffness contribution to balance control could be large relative to the active contribution under our test conditions. For example, if passive stiffness was half the value of the active stiffness, equation 8 predicts that the lowest possible mid-frequency PF sine gain would be 0.66; a value that is more than twice as large as the gains recorded in the prts HI conditions of Exps. 1 and 3. Finally, the results from Peterka (2002) showed no large changes in the passive stiffness parameter with changing stimulus amplitude indicating that it is unlikely that gain changes could be attributed to amplitude dependent changes in passive stiffness.

Inter- and intra-modality reweighting effects

The prts response gain values during steady-state cycles were greatly reduced during HI amplitude prts conditions as compared to LO conditions across all prts frequencies in all experimental conditions (Fig. 3). This effect is a well-known property of the human balance control mechanism that has been attributed to sensory reweighting (Peterka 2002). The use of a constant-amplitude PF or VS sine wave, as a concurrently applied second stimulus, allowed us to monitor intra- and inter-modality weights as they were influenced by changing PF and VS prts amplitudes. The results showed that in prts conditions where intra-modality gain was reduced, the inter-modality gain was increased and vice-versa. This result gives direct experimental evidence that the balance control mechanism uses complementary weight changes in response to amplitude transitions in PF and VS stimuli. A limitation of our
study is that we did not obtain a quantitative measure of the dynamic changes in the vestibular contribution to balance. However results from previous studies indicate that the vestibular contribution would be expected to change. Experiments with vestibular loss subjects (Peterka 2002; Maurer et al. 2006; Mergner et al. 2009a) and model simulations (e.g. Peterka 2002; Mergner et al. 2009b) have shown that the vestibular system contributes considerably during experimental conditions with moving support surface (as in Exps. 3 and 6). Additional, for frontal plane balance control, results consistent with sensory reweighting have been reported for proprioceptive-vestibular interactions by Cenciarini and Peterka (2006) and for somatosensory (moving touch plate)-visual interactions (Oie et al. 2002; Allison et al. 2006).

Our findings differed from those of Polastri et al. (2012), who did not find evidence for inter-modality reweighting of the responsiveness to a VS sine stimulus when a PF sine of a different frequency was changed from HI to LO amplitude. However, they did find that an inter-modality reweighting effect was present following the LO to HI transition in the PF sine stimulus. Thus, their results were asymmetric for HI to LO versus LO to HI changes in PF amplitude and are, therefore, not consistent with complimentary reweighting of sensory contributions to balance. In contrast, our results (Exp. 2) showed inter-modality related increases and decreases in responsiveness to the VS sine when the PF prts amplitude was changed, and these sway changes were quite large (factor of 2.2; Fig. 4 and Table 1).

It is difficult to reconcile the differences between our results in Exp. 2 and the asymmetric changes in visual weighting reported in Polastri et al. (2012). The combination of two sine waves, used in the study of Polastri et al. (2012), has potential drawbacks. The use of predictable sine waves may have evoked learning effects. In contrast, prediction and learning effects were less likely with our stimuli where the amplitude of the sine component was quite small compared to the prts and the pseudorandom prts stimulus was continuously present. Another aspect that should be considered in the Polastri study is the occurrence of a beat frequency when two sine waves of similar frequencies are combined. Even though each sine was applied to a different sensory system, both were combined in the nervous system, with
the beat-frequency modulation possibly having effects on the sway responses due to an
internal waxing and waning of the combined sensory signal as the separate sensory signals
move in and out of phase with one another.

Transitions following PF amplitude changes

PF prts HI to LO transitions (Exps. 1-3) show about five times longer time constants
compared to the PF prts LO to HI transitions in both inter- and intra-modality reweighting.
This asymmetry between HI to LO and LO to HI dynamics has not been previously reported
for the proprioceptive contribution to balance control. However, Jeka et al. (2008) previously
reported an asymmetry for visual reweighting where LO to HI transitions produced faster
visual response changes compared to HI to LO transitions. Jeka et al. argued in favor of a
functional reason for the different reweighting speeds following LO to HI as compared to HI
to LO transitions for the visual weight. Similar arguments can be made for proprioceptive
reweighting. Specifically, PF prts LO to HI transitions are a potential threat to stability if the
subject makes no adjustments and continues to rely heavily on proprioceptive information.
For example, subjects with bilateral vestibular loss, who rely heavily on proprioceptive cues
for balance and show minimal ability to reweight, are unable to maintain balance on 8° PF
prts tests (Peterka 2002). Therefore, LO to HI transitions require quick reweighting. In
contrast, HI to LO transitions present no immediate danger to stability and allow for slower
reweighting.

During eyes open tests of proprioceptive intra-modality reweighting (Exp. 1), the
responsiveness to the PF sine following the PF prts HI to LO transition showed an initial
rapid increase in gain, but this was followed by a slow decay in gain (τ_2=9.7 s time constant)
by a small, but significant amount(c=0.1 deg/s). The functional relevance of the slow decay is
unclear. One interpretation could be that the balance control system switched to a default
weight distribution immediately after the HI to LO transition, with this default weight
distribution being one that is appropriate for stance on a fixed platform. Following this
immediate fast reweighting, the balance control system engaged some slow reweighting
mechanism that adjusted weights to those appropriate for the PF prts LO condition and thereby slowly reduced its reliance on proprioceptive information as indicated by the slow reduction in sway amplitude.

The increase of the visual contribution following the PF prts LO to HI transition (Exp. 2: LO to HI $\tau_1 = 0.64$ s) was five times slower compared to the decrease of the proprioceptive contribution (Exp. 1: $\tau_1 = 0.12$ s). Therefore, a short time period existed after the transition in which the sum of the visual and proprioceptive contributions to balance was reduced in comparison to steady-state conditions. This reduced sum of the two weights could indicate that too little torque was produced during this short period of time leading to a brief period of reduced stability. Alternatively, the reduction in the visual and proprioception contributions could have been compensated by an increase of the vestibular contribution, although this is speculative since the vestibular contribution was not measured.

Transitions following VS amplitude changes

In VS prts experimental conditions, the consistently large sway responses to the PF sine component (Exp. 4) and the small responses to the VS sine component (Exp. 5) indicate that the visual contribution to balance control was small and the proprioceptive contribution large throughout both HI and LO prts conditions in these experimental conditions. The small differences in sway responses to the sine component between HI and LO prts conditions had the drawback that they limited our ability to characterize the properties of the transition dynamics. This limitation is reflected by large confidence intervals for some of the parameters of Exp. 4 (Table 2). In contrast in Exp. 6, the large differences in sway responses to the VS sine between LO and HI prts conditions provided better circumstances for investigating transition dynamics.

Our results investigating intra-modality changes in the visual contribution to balance (Exps. 5 and 6) showed asymmetries in response dynamics following LO to HI versus HI to LO transitions. These asymmetries are qualitatively similar to those described previously in experimental conditions where the amplitude of a sinusoidal visual stimulus was first
increased and then decreased (Jeka et al. 2008). Data from the Jeka et al. (2008) paper were discussed in a preliminary presentation (Oie et al. 2005) where the response asymmetry was represented quantitatively by the different values of exponential time constants with a LO to HI time constant of 2.1 s and a HI to LO time constant of 8.2 s. This preliminary analysis motivated the development and investigation of models that could predict this type of asymmetry (Carver et al. 2006). However, the later analysis presented in Jeka et al. (2008) gave evidence for asymmetry based mainly on their being a delay in the increase in sway-response amplitude following the HI to LO transition while there was no delay following the LO to HI transition.

Our quantitative analysis of transition dynamics, based on a mathematical description of the time course of sway velocity following prts amplitude changes, had a higher time resolution compared the Jeka et al. (2008) analysis based on cycle by cycle changes in response gain. With our higher time resolution, we identified transition dynamics that differed in some ways from those described previously. The visual intra-modality changes we identified in Exps. 5 and 6 were characterized by asymmetric time constants (shorter time constant for LO to HI than for HI to LO). This asymmetry in time constants is qualitatively in agreement with Oie et al. (2005) but our identified time constants were much shorter (< 1 s). We did not find evidence for a full cycle time delay (as in the Jeka et al. 2008 analysis) following the HI to LO transition in Exp. 4, but did identify an ~0.5-s delay in Exp. 6. In fact in many of our experimental conditions, we identified a delay of ~0.5 to 0.8 s followed by fairly rapid (most time constants < 1 s) transitions to a new steady-state value. It is not surprising that our results differ from the limited results from previous studies since the experimental paradigms were quite different, but a common theme is that the changes following HI to LO transitions have slower dynamics than those following LO to HI transitions.

Frequency selective interactions between PF prts and sine components

An unexpected finding was that COM sway responses in experimental conditions that combined PF prts and PF sine stimuli (Exps. 1 and 3) showed a local frequency-specific
interaction. Specifically, the frequency response function gain values for the PF prts frequency components immediately below (0.49 Hz) and above (0.63 Hz) the 0.56-Hz frequency of the PF sine component had noticeably lower gain values than the gain of the sine component. Additionally, the gains at these two prts frequencies were also lower than at other prts frequencies immediately below and above 0.49 and 0.63 Hz, respectively. A gain notch in this frequency region was not expected based on previous results using prts stimuli alone (Peterka 2002). Furthermore, this frequency specific depression in PF prts gain was only present in results from the PF prts LO condition. In the HI condition, the gain values at the sine frequency and at prts frequencies in the vicinity of the sine frequency all had similar values. Finally, no similar interaction was evident in experimental conditions that combined VS prts and VS sine stimuli (Exps. 5 and 6) for either VS prts LO or HI conditions.

This PF prts and PF sine interactioneffect on COM sway was not expected based on a common understanding that reweighting scales a sensory system's contribution to corrective torque generation across all frequencies (Oie et al. 2002; Peterka 2002). That is, sensory reweighting is typically represented as a change in internal scale factors that relate motion information encoded by sensory systems to corrective torque. These weighting factors affect overall response gain across a wide bandwidth of frequencies. Therefore, the gain during intra-modality experimental conditions would be expected to be similar across neighboring frequencies, as it was for the VS intra-modality experimental conditions. Thus, the reduced PF prts gain at frequencies close to the PF sine frequency suggests a more local reweighting phenomenon during PF tilts than can be explained by simpler ideas about sensory reweighting.

To the best of our knowledge, the observed local reweighting phenomenon has not been reported in previous studies. The presence of local reweighting could indicate the existence of more complex reweighting mechanisms for balance control than are represented in current quasi-linear models (Oie et al. 2002; Peterka 2002; van der Kooij 2001; Kuo 2005; Carver et al. 2006). These mechanisms might be based on parallel, frequency-selective channels as has been suggested as a mechanism for vestibulo-ocular
reflex adaptation (Lisberger et al. 1983). A possible neural substrate for postural reweighting based on frequency-selective channels can be seen in recordings of pyramidal tract and rubrospinal tract neurons in cats during sinusoidal platform tilts (Beloozerova et al. 2005; Zelenin et al. 2010) where they found a nearly uniform distribution of the phases of neural responses in relation to the platform sine motion. Such a broad encoding of sensorimotor information offers considerable flexibility in shaping the final motor output to achieve particular behavioral goals.

Thresholds

Some authors have suggested the involvement of threshold mechanisms in human balancing (Fitzpatrick and McCloskey 1994; Peterka and Benolken 1995; Mergner et al. 2003; Mahboobin et al. 2009; Mergner 2010). Traditionally thresholds were observed in perceptual studies, where subjects verbally reported or had to indicate their perception of a physical stimulus. The study of Fitzpatrick and McCloskey (1994) estimated perceptual thresholds in a setup that allowed the isolated stimulation of the vestibular, ankle proprioceptive, and visual sensory systems. The perceptual thresholds observed by Fitzpatrick and McCloskey (1994) may or may not be related to those suggested for the sensory feedback mechanisms (Peterka and Benolken 1995; Mergner et al. 2003; Mahboobin et al. 2009; Mergner 2010). Balance control models that use internal thresholds in the feedback loop account for a wide variety of experimental data involving somatosensory-proprioceptive-vestibular interactions as well as interactions with externally applied forces (Maurer et al. 2006; Mergner 2010). Thresholds like those implemented in the model of Mergner (2010) do not involve active or adaptive processes to change sensory weights, but rather the thresholds effectively adjust the sensory contributions to balance control depending on when and for how long a signal or a combination of signals exceeds a certain threshold value.

Our analysis of sway changes following LO to HI transitions showed that the time constants of intra-modality transitions were very short, suggesting that the time delay is the
main factor determining reweighting dynamics. It seems plausible that these fast reweighting
dynamics following LO to HI transitions could be explained by a balance control mechanism
that uses internal thresholds to rapidly adjust sensory weights. However, it is necessary to
also explain why the time delays found in our experiments (0.5-0-8 s) were relatively long as
compared to time delays of 0.1-0.2 s found in previous studies (Peterka 2002; Maurer et al.
2006). It is also questionable whether threshold mechanisms can explain the longer time
constants that were found for HI to LO transitions. However, intuitive predictions about the
dynamic properties of complex, non-linear, closed-loop systems are of limited utility.
Therefore, the current threshold-based models need to be extended to include visual
interactions and possible changes in strategies associated with the control of multi-
segmental body motion. Then simulations need to be performed to determine whether they
can explain the experimentally observed time courses of body sway associated with intra-
and inter-modality sensory reweighting.
Acknowledgements

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Disclosures

There are no conflicts of interest.

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Figure Legends:

Fig. 1. A: Sinusoidal and prts stimulus components (left) and combinations of sine and prts (right) which were applied to either the platform (PF) or the visual surround (VS) in the six experimental conditions. Note that the ordinate has different scales for the sine and the prts components. B: Description of the six experimental test conditions. Each test condition consisted of two separate trials with the sine wave having opposite signs in the two trials. The two stimulus components (prts and sine) were either applied on PF and VS separately (Exps. 2 and 4) or combined, i.e. the sum of prts and sine on the PF (Exps. 1 and 3) or on the VS (Exps. 5 and 6). C: Full length PF tilt stimulus for one trial of Exp. 2 (the VS sine stimulus is not shown) and the evoked COM sway response of one subject. Two high amplitude prts cycles (prts HI) were alternated with 2 low amplitude cycles (prts LO). The first cycle following a change in prts amplitude was defined as a transition (trans) period and the second cycle was defined as a steady-state period.

Fig. 2. Analysis scheme for the separation of responses to the prts and the sine stimulus components. Adding the COM responses of a pair of trials (and dividing by two) yields the COM response to the prts while the response to the sign-opposed sine stimulus components are canceled out. Subtracting the COM responses of a pair of trials (and dividing by two) yields the sine response and cancels out the prts response.

Fig. 3. Gain versus stimulus frequency plots characterizing COM sway dynamics at the sine frequency (indicated by grey bar) and the prts frequencies. Gains were calculated from data during the steady-state cycles of prts LO conditions (open symbols) and prts HI conditions (filled symbols). Shown are mean gain values (±95% confidence limits) for PF prts (top row; EC=eyes closed) and VS prts experimental conditions (bottom row, s.r.=sway referenced). Circles indicate response gains to PF stimuli, triangles indicate response gains to VS stimuli. Note the ordinate scale difference in Exp. 6.
Fig. 4. Analysis of COM responses to the 0.56-Hz sinusoidal stimulus component in the six experimental conditions. The vertical dashed lines demarcate the steady-state and transition periods of the prts HI amplitude and LO amplitude conditions. Top plot in each experimental condition shows the mean COM velocity responses to the sine component. Middle and lower plots for each experimental condition show mean gain and phase values, respectively, calculated for each individual sine cycle. Gain is the ratio of COM response amplitude to stimulus amplitude, while phase represents the temporal dynamics. Mean values of gain and phase during steady-state periods are given in Table 1. Grey shaded areas in gain and phase plots indicate 95% confidence limits.

Fig. 5. Results for all six experimental conditions of mathematical fits to the COM sway velocity responses evoked by the 0.56-Hz sine stimulus following LO to HI (top plot in each experimental condition) and HI to LO (bottom plot in each experimental condition) transitions in the prts stimulus amplitude. Shown for each experimental condition are the first 5.4 s (3 sine cycles) of the COM sway and fit results following a prts amplitude transition. Grey lines: experimentally measured across-subject mean COM velocity responses following prts amplitude transitions; black lines: mathematical fits to the mean COM velocity data (fit parameters in Table 2); dotted lines: virtual continuations of COM velocity responses to the sine component assuming there were no changes in sway characteristics from the end of the previous steady-state prts period.
Figure 1
Figure 2
Figure 3
Figure 4

Exp 1: PF prts; PF sine

Exp 2: PF prts; VS sine

Exp 3: PF prts; PF sine; EC

Exp 4: VS prts; PF sine

Exp 5: VS prts; VS sine

Exp 6: VS prts; VS sine; PF s.r.
Figure 5
Table 1: Statistical comparison of sine-component responses during LO and HI steady-state conditions

<table>
<thead>
<tr>
<th>#</th>
<th>Experiment</th>
<th>Hotelling T^2 test</th>
<th>LO</th>
<th>HI</th>
<th>Hypothesis test</th>
<th>95% c.i.</th>
<th>Δgain bootstrap</th>
<th>LO</th>
<th>HI</th>
<th>Hypothesis test</th>
<th>95% c.i.</th>
<th>Δphase bootstrap</th>
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<td>PF prts PF sine</td>
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</tbody>
</table>
### Table 2: Parameters of fits to mean COM sway velocity responses to sine following transitions

<table>
<thead>
<tr>
<th></th>
<th>Experiment</th>
<th>a (deg/s)</th>
<th>b (deg/s)</th>
<th>c (deg/s)</th>
<th>ϕ (deg)</th>
<th>Δϕ (deg)</th>
<th>τ₁ (s)</th>
<th>τ₂ (s)</th>
<th>Δτ (s)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>LO to HI transition</strong></td>
<td>#</td>
<td>mean 95% c.i.</td>
<td>mean 95% c.i.</td>
<td>mean 95% c.i.</td>
<td>mean 95% c.i.</td>
<td>mean 95% c.i.</td>
<td>mean 95% c.i.</td>
<td>mean 95% c.i.</td>
<td>mean 95% c.i.</td>
</tr>
<tr>
<td>1</td>
<td>PF prts PF sine</td>
<td>0.31</td>
<td>-0.16</td>
<td>16</td>
<td>31</td>
<td>0.12</td>
<td>0.55</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>0.28/0.36</td>
<td>-0.2/-0.12</td>
<td>10/22</td>
<td>23/40</td>
<td>0.01/0.18</td>
<td>0.46/0.86</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>PF prts VS sine</td>
<td>0.40</td>
<td>0.48</td>
<td>47</td>
<td>32</td>
<td>0.64</td>
<td>0.49</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.33/0.48</td>
<td>0.41/0.56</td>
<td>35/57</td>
<td>26/38</td>
<td>0.33/1.6</td>
<td>0.07/0.67</td>
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</tr>
<tr>
<td></td>
<td>PF prts VS sine, eyes closed</td>
<td>0.52</td>
<td>-0.33</td>
<td>16</td>
<td>17</td>
<td>0.13</td>
<td>0.49</td>
<td></td>
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<td></td>
<td></td>
<td>0.46/0.57</td>
<td>-0.41/-0.22</td>
<td>12/20</td>
<td>5/34</td>
<td>0.03/0.7</td>
<td>0.37/0.59</td>
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<tr>
<td>4</td>
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<td>0.51</td>
<td>0.14</td>
<td>-17</td>
<td>-2</td>
<td>4.9</td>
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<tr>
<td></td>
<td></td>
<td>0.46/0.57</td>
<td>0.10/0.19</td>
<td>-22/-10</td>
<td>-6/3</td>
<td>1.8/8.2</td>
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<tr>
<td>5</td>
<td>VS prts VS sine</td>
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<td>-0.06</td>
<td>50</td>
<td>52</td>
<td>0.13</td>
<td>0.80</td>
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<tr>
<td></td>
<td></td>
<td>0.071/0.12</td>
<td>-0.07/-0.03</td>
<td>40/63</td>
<td>32/52</td>
<td>0.012/0.3</td>
<td>0.41/1.5</td>
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<tr>
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<td>VS prts VS sine, PF sway ref.</td>
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<td>-0.40</td>
<td>40</td>
<td>37</td>
<td>0.005</td>
<td>0.72</td>
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<tr>
<td></td>
<td></td>
<td>0.49/0.68</td>
<td>-0.47/-0.29</td>
<td>34/47</td>
<td>21/54</td>
<td>0.005/0.25</td>
<td>0.61/0.86</td>
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</tr>
<tr>
<td><strong>HI to LO transition</strong></td>
<td>#</td>
<td>mean 95% c.i.</td>
<td>mean 95% c.i.</td>
<td>mean 95% c.i.</td>
<td>mean 95% c.i.</td>
<td>mean 95% c.i.</td>
<td>mean 95% c.i.</td>
<td>mean 95% c.i.</td>
<td>mean 95% c.i.</td>
</tr>
<tr>
<td>1</td>
<td>PF prts PF sine</td>
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<td>0.16</td>
<td>0.10</td>
<td>47</td>
<td>-31</td>
<td>0.64</td>
<td>9.7</td>
<td>0.82</td>
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<tr>
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<td></td>
<td>0.12/0.2</td>
<td>0.12/0.2</td>
<td>0.057/0.19</td>
<td>40/57</td>
<td>-41/-23</td>
<td>0.44/0.85</td>
<td>2.0/15</td>
<td>0.66/1.2</td>
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<tr>
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<td>-0.48</td>
<td>78</td>
<td>-32</td>
<td>2.5</td>
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<td></td>
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<td>0.82/0.97</td>
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<td>69/86</td>
<td>-38/-25</td>
<td>1.5/3.9</td>
<td>0.16/0.99</td>
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<td>PF prts PF sine, eyes closed</td>
<td>0.19</td>
<td>0.33</td>
<td>34</td>
<td>-17</td>
<td>0.96</td>
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<td>0.12/0.3</td>
<td>0.21/0.41</td>
<td>19/52</td>
<td>-34/-6</td>
<td>0.39/1.5</td>
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<td>4</td>
<td>VS prts PF sine</td>
<td>0.66</td>
<td>-0.14</td>
<td>-19</td>
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<td>9.3</td>
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<td>0.63/0.69</td>
<td>-0.19/-0.10</td>
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<td>5</td>
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<td>0.059</td>
<td>0.07</td>
<td>103</td>
<td>-52</td>
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<td></td>
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<td>0.028/0.064</td>
<td>0.028/0.073</td>
<td>0.04/0.096</td>
<td>80/143</td>
<td>-92/32</td>
<td>0.27/0.89</td>
<td>7.4/17</td>
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<tr>
<td>6</td>
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<td>0.18</td>
<td>0.40</td>
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<td>0.63</td>
<td>0.49</td>
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<td>0.13/0.3</td>
<td>0.29/0.47</td>
<td>63/92</td>
<td>-54/-21</td>
<td>0.07/1.5</td>
<td>0.12/0.95</td>
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</table>