

## Sensory reweighting dynamics in human postural control

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Healthy humans control balance during stance by 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 intermodality reweighting. Reweighting dynamics were asymmetric, with slower reweighting dynamics following a high-to-low transition in the pseudorandom stimulus amplitude compared with low-to-high amplitude shifts, and were also slower for inter- compared with intramodality reweighting.

humans; balance; sensory integration; posture control; reweighting

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 by 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 PF 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 have concentrated on the transition effects when adding or removing cues from one or more sensory systems such as vision, touch, or proprioception (Hay et al. 1996; Sozzi et al. 2012; Teasdale et al. 1991). Only two studies have addressed the transition effects that occur after 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 “intramodality” effect was defined as being present if the change in PF stimulus amplitude resulted in a change

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in the body sway response at the frequency of the PF stimulus. The “intermodality” 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 evoked a weight change in one sensory system was always compensated by changes in the weights of other sensory systems (Cenciari and Peterka 2006; Peterka 2002). 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. In the terminology of the Polastri et al. (2012) study, a stimulus that evokes an intramodality effect should also show intermodality changes. While intramodality changes were consistently seen in response to PF amplitude changes in the Polastri study, the intermodality changes were not always seen. Specifically, after the transition of the PF stimulus from high to low amplitude, the sway response to the VS stimulus did not show an intermodality change. In the present study a variety of PF and VS amplitude transitions were investigated with sway responses analyzed to determine whether intra- and intermodality 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 present study combined two independent stimuli. The first stimulus component was a broadband pseudorandom waveform that provoked reweighting through changes in its amplitude. After 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 (AP)-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 also 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 compared with 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 evoked by a similar physically moving visual surround. The present study generated visual stimuli by using a movable visual screen with an illuminated pattern. This physical moving VS provided an unambiguous, congruent visual input.

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

## METHODS

**Subjects.** Fourteen healthy subjects (age  $26.0 \pm 4.1$  yr; 7 women, 7 men) participated in this study after giving their informed consent. The study was approved by the Internal Review Board of the Oregon Health and Science University and is in accordance with the 1964 Declaration of Helsinki.

**Experimental setup.** Experiments were performed with a custom-made device that provided servo-controlled independent motions of the PF and VS (half-cylinder with 70-cm radius). Both tilted in the AP direction about the ankle joints (see Peterka 2002). The VS was covered by a pattern of horizontal and vertical gray, 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 (CoP) shifts. Stimulus delivery and data collection were performed at a sampling frequency of 200 Hz with a custom program written in LabVIEW (National Instruments, Austin, TX).

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 with appropriate trigonometric calculations. Instrumentation noise in the recording system was very low (rms noise measures of  $0.002^\circ$  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 with 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 (Brenière 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 with 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 0.18-s 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 VS, 8°pp for PF; 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 with 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 compared with the sine-wave stimulus of 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 six experimental conditions investigated reweighting dynamics following amplitude changes in the PF prts stimulus (*Exps. 1, 2, 3*) and three 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 intramodality 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 intramodality reweighting during eyes closed, where mainly proprioceptive and vestibular cues

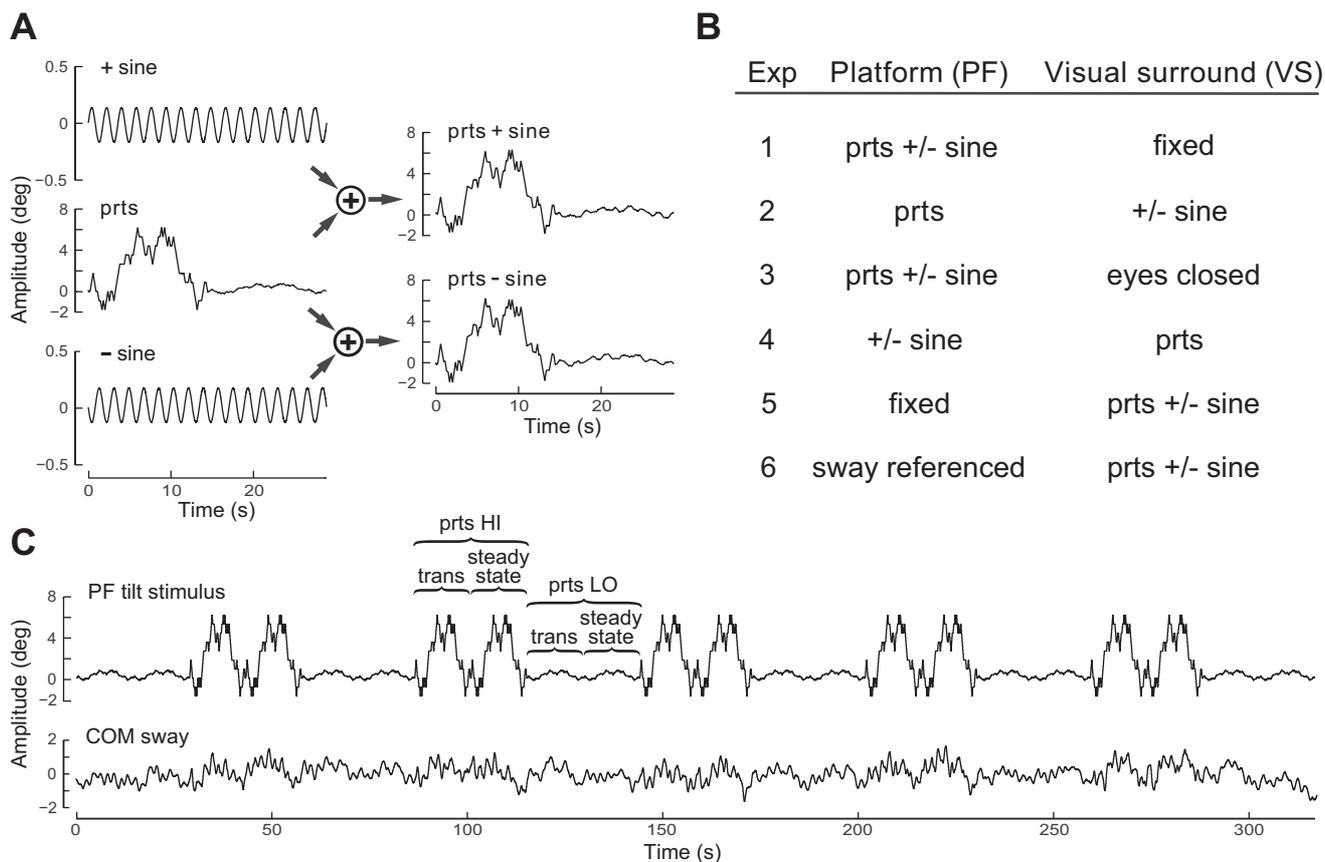


Fig. 1. A: sinusoidal and pseudorandom ternary sequence (prts) stimulus components (*left*) and combinations of sine and prts (*right*) that were applied to either the platform (PF) or the visual surround (VS) in the 6 experimental conditions. Note that the y-axis has different scales for the sine and prts components. B: description of the 6 experimental test conditions. Each test condition consisted of 2 separate trials, with the sine wave having opposite signs in the 2 trials. The 2 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 1 trial of *Exp. 2* (the VS sine stimulus is not shown) and the evoked center of mass (COM) sway response of 1 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.

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 intramodality 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 intramodality 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 "warm-up" trial consisting of a series of different stimuli from *Exps. 1–6* in order to familiarize subjects with the experiment. Then the 12 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 were exported to MATLAB (The MathWorks, Natick, MA) for further analysis. The first and last cycles 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*). Adding the two COM signals of each set (and dividing by 2) 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 2) 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

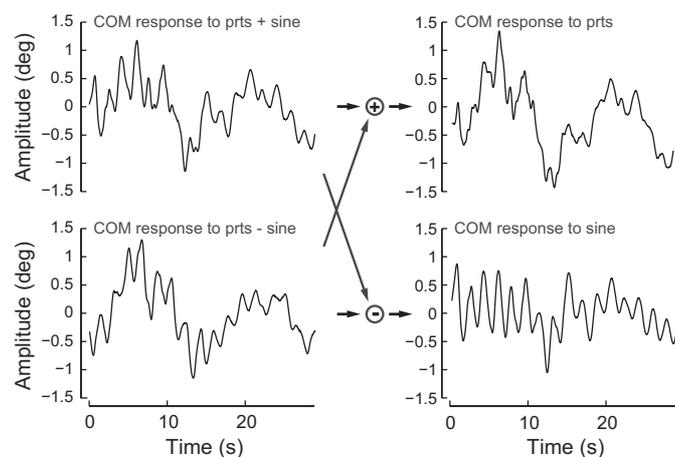


Fig. 2. Analysis scheme for the separation of responses to the prts and sine stimulus components. Adding the COM responses of a pair of trials (and dividing by 2) yields the COM response to the prts, while the response to the sign-opposed sine stimulus components are canceled out. Subtracting the COM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

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, with 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 with discrete Fourier transform methods that were appropriate for data collected with 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 (4-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 calculation of the mean gain and phase values; 95% confidence limits on the mean frequency response function gain and phase data were obtained with 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 eight 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, Hotelling's  $T^2$  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 test separately 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-to-HI and HI-to-LO transitions of the prts stimulus were obtained with 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 trade-off between reducing the fit error and adding parameters was considered. We used *F*-test statistics as described in Johansson (1993) to account for this trade-off 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 with bootstrap methods that resampled the mean COM responses of each of the 14

subjects 1,000 times (with replacement) and performed the fits to the mean of each resampled data set (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-to-HI and HI-to-LO transitions were fit with functions of the following form:

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

$$y(t) = a \cdot \sin(\omega t + \varphi) \quad \text{for } t < \Delta t \quad (2)$$

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 three sine cycles before the transition.

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

$$A(t) = a + b \left( 1 - e^{-\frac{(t-\Delta t)}{\tau_1}} \right) \quad (3)$$

$$\Phi(t) = \varphi + \Delta\varphi \left( 1 - e^{-\frac{(t-\Delta t)}{\tau_1}} \right) \quad (4)$$

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 three 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 Eq. 2 description). The parameter  $\Delta\varphi$  was similarly calculated as the difference between the phase value from the fit to the last three sine cycles and the value of  $\varphi$  (see Eq. 2 description).

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

$$A(t) = a + b \cdot \left( 1 - e^{-\frac{(t-\Delta t)}{\tau_1}} \right) + c \cdot \left( e^{-\frac{(t-\Delta t)}{\tau_2}} - e^{-\frac{(t-\Delta t)}{\tau_1}} \right) \quad (5)$$

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 0) 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 0) or  $\tau_1$ ,  $\tau_2$ ,  $c$ , and  $\Delta t$ . For all fits, the values of parameters  $a$ ,  $b$ ,  $\varphi$ , and  $\Delta\varphi$  were precalculated 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-to-LO and LO-to-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 with 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 intramodality modulation of the steady-state COM responses to the prts stimulus at LO and HI prts amplitudes as well as the associated intra- and intermodality 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 intermodality reweighting.* Steady-state COM sway responses to the prts PF and VS stimuli were analyzed by calculating frequency response functions with 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 (Fig. 3, *top*) and VS prts stimuli (Fig. 3, *bottom*). The general patterns 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  $\sim 0.2$  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 with HI-amplitude prts stimuli in each of the six experimental conditions. Thus the COM sway responses showed strong intramodality modulation of sensitivity for both PF and VS prts stimuli of different amplitudes.

Figure 3 also overlays the gain values derived from the COM responses to the constant-amplitude sinusoidal PF or VS stimuli. 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 intramodality modulation of the sine response sensitivity consistent with the intramodality 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 intermodality modulation of response sensitivity. For *Exp. 2* with PF prts amplitude changes, the gain value for the VS sine

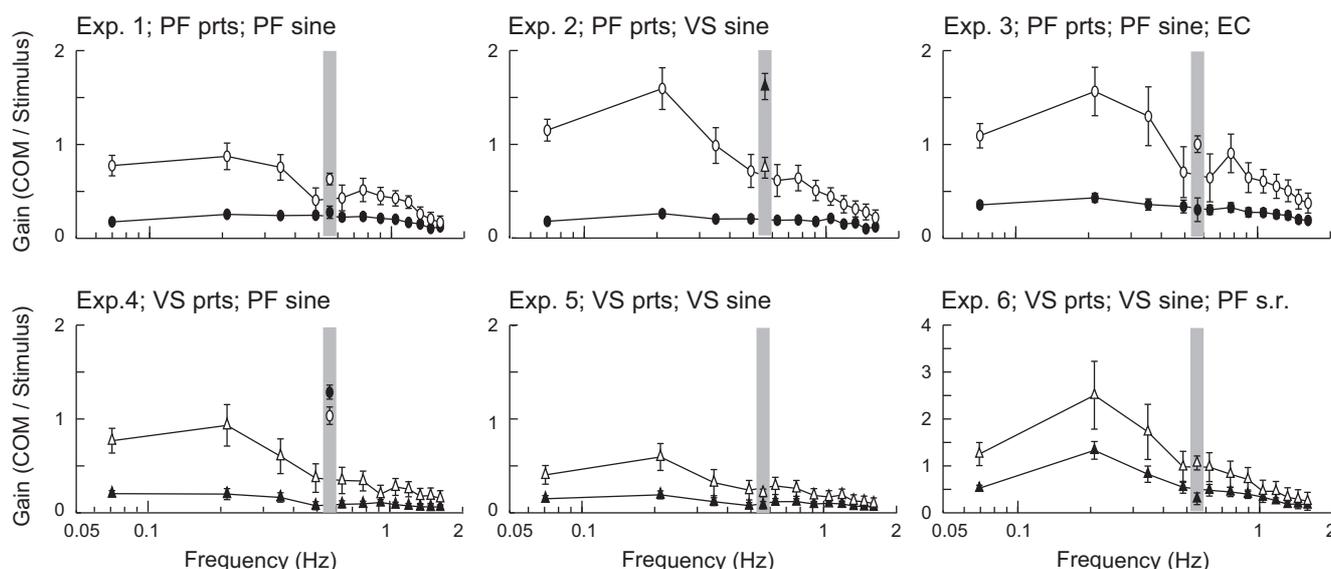


Fig. 3. Gain vs. stimulus frequency plots characterizing COM sway dynamics at the sine frequency (indicated by gray bar) and the prts frequencies. Gains were calculated from data during the steady-state cycles of prts LO conditions (open symbols) and prts HI conditions (filled symbols). Shown are mean gain values ( $\pm 95\%$  confidence limits) for PF prts (*top*; EC = eyes closed) and VS prts (*bottom*; s.r. = sway referenced) experimental conditions. Circles indicate response gains to PF stimuli; triangles indicate response gains to VS stimuli. Note the y-axis scale difference in *Exp. 6*.

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 given previous results using only PF prts stimuli (Peterka 2002), where results showed a quite uniform decline in gain with increasing frequency in this 0.3–0.8 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).

Figure 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 six 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, because of the low amplitude of stimulus-evoked sway compared with

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 intramodality conditions (*Exps. 5* and *6*). While these phase changes in *Exps. 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 (*Exps. 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.

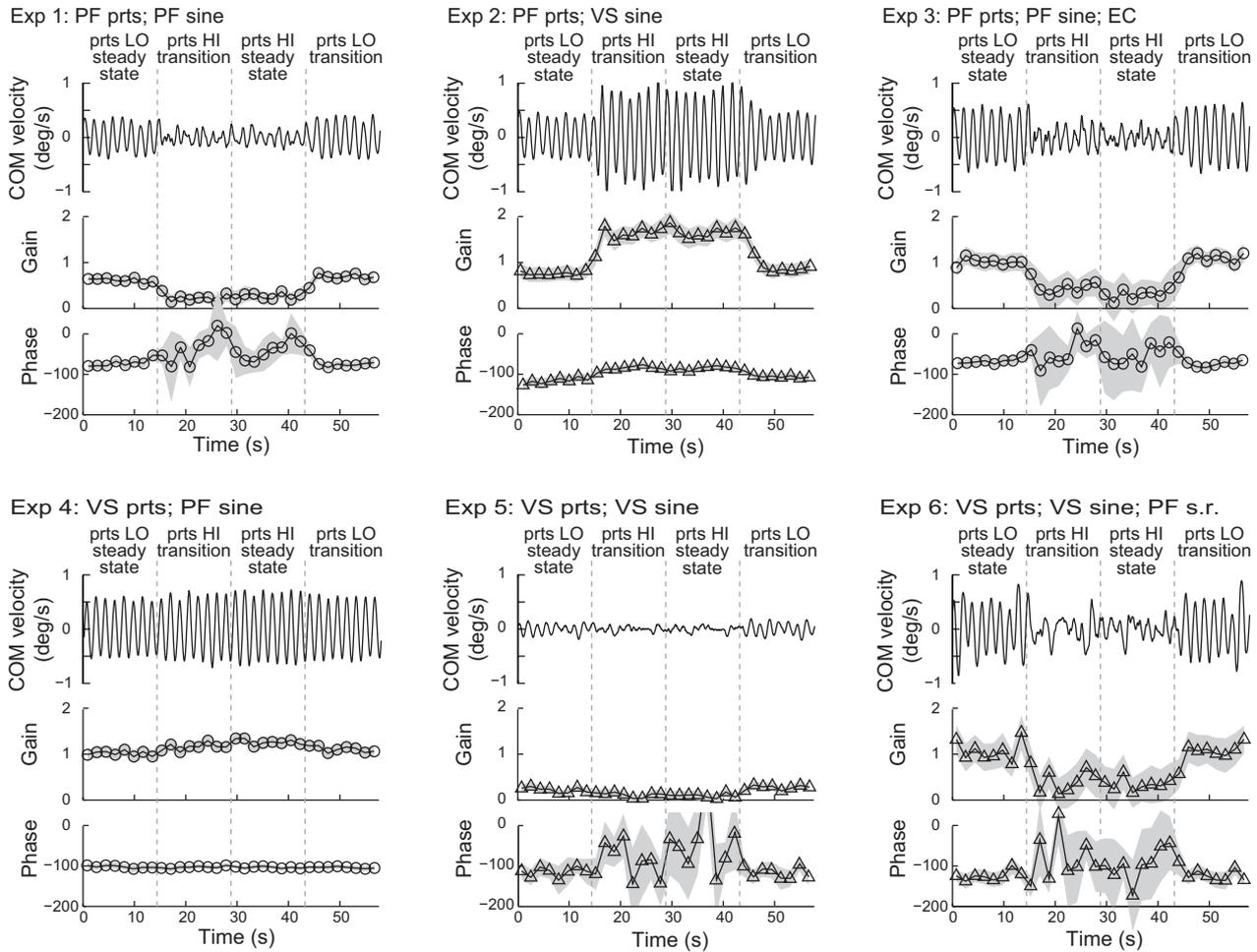


Fig. 4. Analysis of COM responses to the 0.56-Hz sinusoidal stimulus component in the 6 experimental conditions. Vertical dashed lines demarcate the steady-state and transition periods of the prts HI amplitude and LO amplitude conditions. *Top* plot in each experimental condition shows the mean COM velocity responses to the sine component. *Middle* and *bottom* 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. Gray shaded areas in gain and phase plots indicate 95% confidence limits.

During VS prts amplitude changes (*Exps. 4–6*; Fig. 4, *bottom*), gain differences were less pronounced compared with *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

Table 1. Statistical comparison of sine component responses during LO and HI steady-state conditions

Exp.	Experiment	Hotelling $T^2$ -Test	Steady-State Gain		$\Delta$ Gain Bootstrap Hypothesis Test	Steady-State Phase (°) Mean, 95% c.i		$\Delta$ Phase Bootstrap Hypothesis Test
			LO	HI		LO	HI	
1	PF prts PF sine	$P < 0.01$	0.62	0.25	$P < 0.01$	-69	-37	$P < 0.01$
			0.57/0.66	0.20/0.32		-73/-64	-45/-24	
2	PF prts VS sine	$P < 0.01$	0.75	1.63	$P < 0.01$	-118	-86	$P < 0.01$
			0.67/0.84	1.54/1.72		-125/-110	-91/-82	
3	PF prts PF sine, eyes closed	$P < 0.01$	1.01	0.28	$P < 0.01$	-69	-51	$P < 0.01$
			0.93/1.07	0.21/0.38		-74/-67	-68/-23	
4	VS prts PF sine	$P < 0.01$	1.02	1.27	$P < 0.01$	-102	-103	n.s.
			0.95/1.08	1.22/1.32		-106/-97	-107/-101	
5	VS prts VS sine	$P < 0.01$	0.20	0.05	$P < 0.01$	-114	-62	$P < 0.05$
			0.16/0.23	0.03/0.10		-124/-108	-86/-32	
6	VS prts VS sine, PF sway ref.	$P < 0.01$	1.06	0.29	$P < 0.01$	-124	-88	$P < 0.01$
			0.93/1.19	0.17/0.37		-130/-119	-108/-68	

Exp., experimental condition; PF, platform; VS, visual surround; prts, pseudorandom ternary sequence; c.i., confidence interval; n.s., not significant.

gain during VS prts LO (*Exp. 5*) were already quite low, indicating that 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 a 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 with LO condition (*Exp. 5*), 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  $\sim 5.5$  times higher in both the VS prts HI and LO conditions compared with 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-to-LO transitions were described by mathematical functions. Figure 5 displays the first three sine cycles of the best fit to the experimental COM velocity data following HI-to-LO and LO-to-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-to-LO or LO-to-HI prts transition are shown. In all experimental conditions, the fits closely resemble the experimental data following all HI-to-LO and LO-to-HI transitions (Fig. 5). Furthermore, the differences between the previous periods' steady-state responses (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 ( $\sim 1.25$  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 three cycles displayed in Fig. 5.

COM sway velocity following LO-to-HI transitions was best described by an exponential change of amplitude and phase

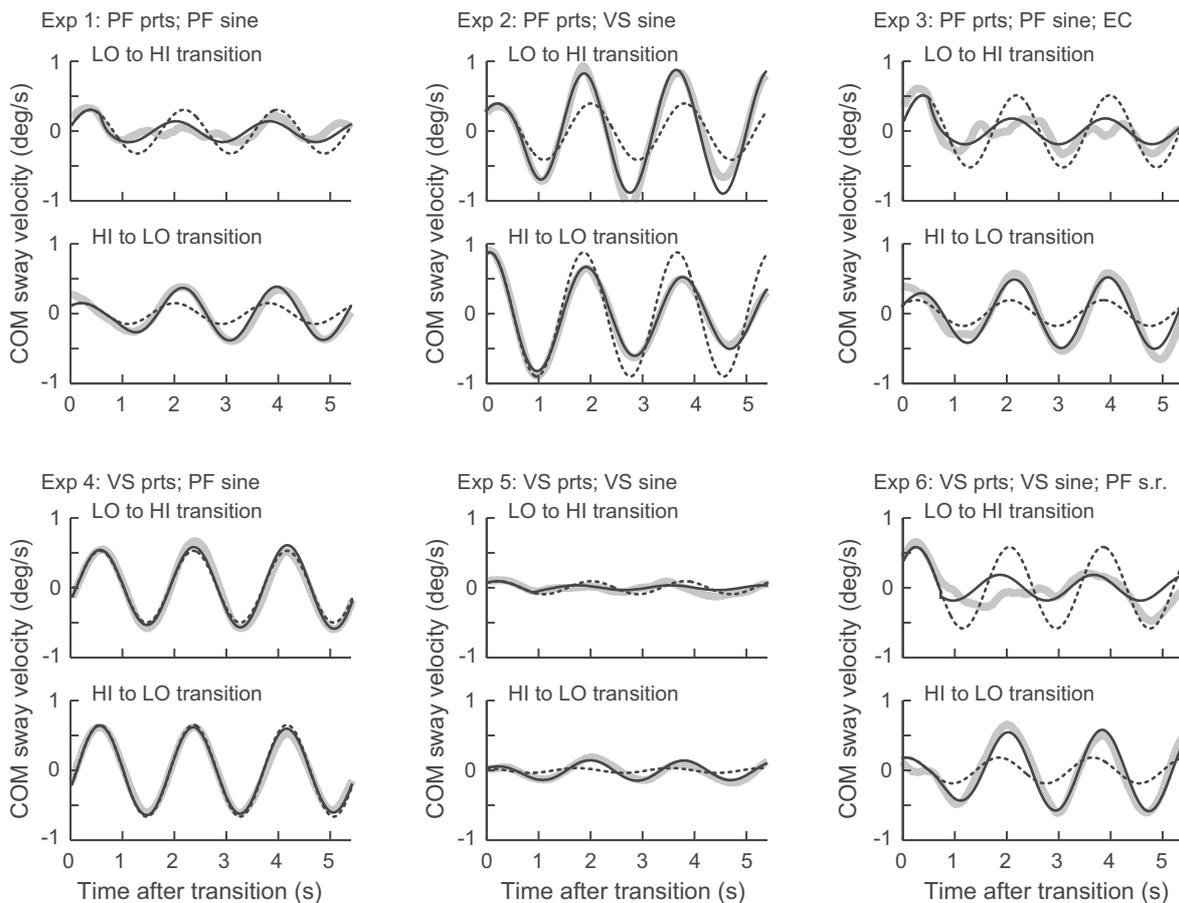


Fig. 5. Results for all 6 experimental conditions of mathematical fits to the COM sway velocity responses evoked by the 0.56-Hz sine stimulus following LO-to-HI (*top* plot in each experimental condition) and HI-to-LO (*bottom* plot in each experimental condition) transitions in the prts stimulus amplitude. 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. Gray 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); dashed 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.

Table 2. Parameters of fits to mean COM sway velocity responses to sine following transitions

Exp.	Experiment	$a$ , °/s	$b$ , °/s	$c$ , °/s	$\varphi$ , °	$\Delta\varphi$ , °	$\tau_1$ , s	$\tau_2$ , s	$\Delta t$ , s
<i>LO-to-HI transition</i>									
1	PF prts PF sine	0.31	-0.16		16	31	0.12		0.55
		0.28/0.36	-0.2/-0.12		10/22	23/40	0.01/0.18		0.46/0.86
2	PF prts VS sine	0.40	0.48		47	32	0.64		0.49
		0.33/0.48	0.41/0.56		35/57	25/38	0.33/1.6		0.07/0.67
3	PF prts PF sine, eyes closed	0.52	-0.33		16	17	0.13		0.49
		0.46/0.57	-0.41/-0.22		12/20	5/34	0.03/0.7		0.37/0.59
4	VS prts PF sine	0.51	0.14		-17	-2	4.9		
		0.46/0.57	0.10/0.19		-22/-10	-6/3	1.8/8.2		
5	VS prts VS sine	0.09	-0.06		50	52	0.13		0.80
		0.07/0.12	-0.07/-0.03		40/63	32/92	0.01/2.0		0.41/1.5
6	VS prts VS sine, PF sway ref.	0.58	-0.40		40	37	0.005		0.72
		0.49/0.68	-0.47/-0.29		34/47	21/54	0.005/0.25		0.61/0.86
<i>HI-to-LO transition</i>									
1	PF prts PF sine	0.15	0.16	0.10	47	-31	0.64	9.7	0.82
		0.12/0.2	0.12/0.2	0.057/0.19	40/57	-41/-23	0.44/0.85	2.0/15	0.66/1.2
2	PF prts VS sine	0.89	-0.48		78	-32	2.5		0.54
		0.82/0.97	-0.56/-0.41		69/86	-38/-25	1.5/3.9		0.16/0.99
3	PF prts PF sine, eyes closed	0.19	0.33		34	-17	0.96		
		0.12/0.3	0.21/0.41		19/52	-34/-5	0.39/1.5		
4	VS prts PF sine	0.66	-0.14		-19	2	9.3		
		0.63/0.69	-0.19/-0.10		-22/-16	-3/6	3.3/13		
5	VS prts VS sine	0.035	0.059	0.07	103	-52	0.54	11.7	
		0.028/0.064	0.028/0.073	0.04/0.096	80/143	-92/32	0.27/0.89	7.4/17	
6	VS prts VS sine, PF sway ref.	0.18	0.40		77	-37	0.63		0.49
		0.13/0.3	0.29/0.47		63/92	-54/-21	0.07/1.5		0.12/0.95

Values are mean and lower/upper limits of 95% c.i. COM, center of mass.

following a time delay for all experimental conditions except *Exp. 4* (Table 2, *top*). The fit statistics did not justify a time delay for *Exp. 4*, and the data were 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  $\sim 1$  s as identified on LO-to-HI transitions in all other experimental conditions. For all experimental conditions other than *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, *bottom*), the identified functions that best represented the experimental data were less consistent across experimental conditions compared with 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 (*Exps. 1 and 5*), a second exponential term was required to account for a small and slow decay in COM sway amplitude (decay amplitude  $c \approx 0.1^\circ/\text{s}$ ; 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 compared with 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 with 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 after HI-to-LO transitions.

For both LO-to-HI and HI-to-LO transitions, results from experimental conditions investigating intermodality reweighting had  $\sim 5$  times slower transitions compared with experimental conditions investigating intramodality reweighting for PF prts transitions (*Exp. 2* compared with *Exp. 1*) and  $>17$  times slower transitions for VS prts transitions (*Exp. 4* compared with *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 intramodality sensory reweighting of the human balance control system and the dynamic changes that follow sudden transitions in stimulus amplitude of PF and VS 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 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 are addressed, followed by a discussion of the temporal dynamics, with emphasis placed on differences of our findings compared with previous studies. Finally, we focus on some unexpected findings in the prts responses at frequencies close to the sine frequency.

*Influence of passive mechanics on sway responses.* 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 midfrequency 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 nonzero passive stiffness influences the midfrequency gain of responses to both PF and VS stimuli, but its influence is different for the two stimuli. Specifically, the midfrequency gain for PF stimuli,  $G_{PF}$ , is given by the equation

$$G_{PF} = \frac{K_{pas} + K_{act} \cdot W_{prop}}{K_{pas} + K_{act} - mgh} \quad (6)$$

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

$$G_{VS} = \frac{K_{act} \cdot W_{vis}}{K_{pas} + K_{act} - mgh} \quad (7)$$

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 that  $K_{act}$  was about 1/3 larger than  $mgh$ . If we define  $R$  as the ratio of  $K_{pas}$  to  $K_{act}$  and substitute  $K_{act} = (4/3) \times mgh$  into Eqs. 6 and 7, we get

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

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

For visual stimuli, Eq. 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 PF 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 PF 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 present study estimated that the passive stiffness contribution to balance control was  $\sim 10\%$  of the active contribution and thus  $R = 0.1$ . With this small  $R$  value, Eq. 8 predicts that the gain of the sway response to the PF 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, Eq. 8 predicts that the lowest possible midfrequency 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 intramodality reweighting effects.* The prts response gain values during steady-state cycles were greatly reduced during HI-amplitude prts conditions compared with 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 intermodality weights as they were influenced by changing PF and VS prts amplitudes. The results showed that in prts conditions where the intramodality gain was reduced the intermodality 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 (Maurer et al. 2006; Mergner et al. 2009a; Peterka 2002) and model simulations (e.g., Mergner et al. 2009b; Peterka 2002) have shown that the vestibular system contributes considerably during experimental conditions with a moving support surface (as in Exps. 3 and 6). Additionally, for frontal plane balance control, results consistent with sensory reweighting have been reported for proprioceptive-vestibular interactions by Cenciari and Peterka (2006) and for somatosensory (moving

touch plate)-visual interactions (Allison et al. 2006; Oie et al. 2002).

Our findings differed from those of Polastri et al. (2012), who did not find evidence for intermodality 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 intermodality reweighting effect was present after 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 complementary reweighting of sensory contributions for balance control. In contrast, our results (*Exp. 2*) showed intermodality-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 by 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 with 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 with the PF prts LO-to-HI transitions in both inter- and intramodality 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 with HI-to-LO transitions. Jeka et al. argued in favor of a functional reason for the different reweighting speeds following LO-to-HI compared with 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 intramodality reweighting (*Exp. 1*), the responsiveness to the PF sine after the PF prts HI-to-LO transition showed an initial rapid increase in gain, but this was followed by a slow decay in gain (time constant  $\tau_2 = 9.7$  s) by a small but significant amount ( $c =$

0.1°/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. After 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 after the PF prts LO-to-HI transition (*Exp. 2*: LO-to-HI  $\tau_1 = 0.64$  s) was five times slower compared with 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 compared with 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 intramodality changes in the visual contribution to balance (*Exps. 5 and 6*) showed asymmetries in response dynamics following LO-to-HI vs. 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) report 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 there being a delay in the increase in sway-response amplitude after the HI-to-LO transition while there was no delay after 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 with 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 intramodality 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) after the HI-to-LO transition in *Exp. 4*, but we did identify an  $\sim 0.5$ -s delay in *Exp. 6*. In fact, in many of our experimental conditions, we identified a delay of  $\sim 0.5$ – $0.8$  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 on the basis of previous results from 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 interaction effect on COM sway was not expected given the 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 intramodality experimental conditions would be expected to be similar across neighboring frequencies, as it was for the VS intramodality 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 (Carver et al. 2006; van der Kooij 2001; Kuo 2005; Oie et al. 2002; Peterka 2002). These mechanisms might be based on parallel,

frequency-selective channels as has been suggested as a mechanism for vestibuloocular 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 a nearly uniform distribution of the phases of neural responses in relation to the platform sine motion was found. 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; Mahboobin et al. 2009; Mergner 2010; Mergner et al. 2003; Peterka and Benolken 1995). 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 (Mahboobin et al. 2009; Mergner 2010; Mergner et al. 2003; Peterka and Benolken 1995). 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 intramodality 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 compared with time delays of 0.1–0.2 s found in previous studies (Maurer et al. 2006; Peterka 2002). 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, nonlinear, 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 multisegmental 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 intermodality sensory reweighting.

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## DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

## AUTHOR CONTRIBUTIONS

Author contributions: L.A. and R.J.P. conception and design of research; L.A. and R.J.P. performed experiments; L.A. and R.J.P. analyzed data; L.A. and R.J.P. interpreted results of experiments; L.A. and R.J.P. prepared figures; L.A. and R.J.P. drafted manuscript; L.A. and R.J.P. edited and revised manuscript; L.A. and R.J.P. approved final version of manuscript.

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