ABSTRACT. We investigated the patterns of coordination between the left and right legs that support the task of maintaining an upright standing posture. We used cross-wavelet analyses to assess coordination between the centers of pressure under the left and right feet. We recruited participants with a lateralized functional preference for their right leg, and we manipulated whether these participants stood with symmetric/asymmetric stances and whether their eyes were open or closed. Our hypotheses were derived from the Haken-Kelso-Bunz (HKB) model of interlimb coordination dynamics. Consistent with HKB model predictions, we observed (1) coordination taking the form of metastable, transient epochs of stable phase relations, (2) preferences for in-phase and anti-phase coordination patterns, and (3) changes in pattern stability and phase leads associated with both stance asymmetry and right-side lateral preference. The form and stability of observed coordination patterns were mediated by the availability of visual information. Our findings confirm the existence of a metastable coordination dynamic associated with the task of maintaining upright stance. We discuss the implications of these findings in the context of evaluating the utility of the HKB model for understanding the functional organization of the posture system.

Keywords: coordination dynamics, detuning, HKB dynamics, laterality, postural control, quiet standing

Introduction

Upright stance is considered a special and costly human skill in comparison to the movement repertoires of other mammals and the apes (Pontzer et al., 2009; Ward, 2002). Standing tall is associated with improved capacities for seeing great distances and for reaching further. It is also associated with increased risks of being seen by others and of greater risk of injury from falls. Effective human actions are frequently predicated upon an ability to organize the body in an upright standing posture that is robust to variations in super-postural task demands and performance context (Duarte et al., 2000; Woollacott et al., 1986). The ability to organize the body in an upright standing posture requires that neuromusculoskeletal degrees of freedom become functionally organized (Bernstein, 1967; Turvey, 2007). In this context, a system is functional to the extent that it can (1) produce organizations of degrees of freedom that reconcile the demands of the task, the demands of the internal physiological/biomechanical context of the body, and the external context of the environment (Gelfand et al., 1971; Riley et al., 2011; Tuller et al., 1982), and (2) flexibly switch between such organizations (Harrison & Stergiou, 2015).

Laboratory studies of upright standing reveal concinnities of muscle activations (Nashner, 1977), joint motions (Creath et al., 2005), and locations of centers of pressures under the feet (Winter et al., 1996). Various analysis and modeling approaches have yielded interpretations of such concinnities as postural control strategies (Day et al., 1993; Horak & Nashner, 1986), neuro-muscular synergies (Berniker et al., 2009; Hof, 2007; Torres-Oviedo & Ting, 2007), preferred states on uncontrolled manifolds (Hsu et al., 2007; Krishnamoorthy et al., 2003; Kuznetsov & Riley, 2012), network topologies (Boonstra et al., 2016), and stable states or attractors of dynamical systems (Bonnet et al., 2009; Kinsella-Shaw et al., 2011; Ting et al., 2009; Wang et al., 2014). Taking the last of these approaches as our starting point, in this paper we examine the possibility that the Haken-Kelso-Bunz model (a simple dynamical systems model) can capture important aspects of the functional organization of upright stance when stance symmetry and the availability of vision are varied. Note, stance symmetry is investigated here by compelling participants in some conditions to adopt an asymmetrical stance when the surfaces of support under the two feet are of different elevations, a challenge that must be met regularly in natural settings. Though the HKB model was originally proposed as a model for the dynamics of interlimb coordination (“open” kinetic-chain movements generated on opposite sides of the body – see Haken et al., 1985), there are three reasons the HKB model merits investigation as a potential model for whole body dynamics during upright standing:

First, while it has been reported that task of maintaining a steady upright posture is not characterized by oscillatory patterns possessing a stable limit cycle dynamics except in cases of pathology (see analyses of net center of pressure fluctuations by Chagdes et al., 2016a; 2016b). There is ample evidence of rich patterns of
recurrence in center of pressure fluctuations consistent with the nonrandom outputs of a nonlinear dynamical system. Patterns of recurrence consistent with at least transiently stable attractor dynamics have been found in the center of pressure excursions trajectories of each foot in isolation (Kinsella-Shaw et al., 2013), between the centers of pressure under the left and right feet (Kinsella-Shaw et al., 2011; Wang & Newell, 2012a) and in the patterns of the net (algebraic sum) center of pressure generated by both feet (Kinsella-Shaw et al., 2006; Riley et al., 1999). Moreover, in all the aforementioned studies, the recurrence associated with the potential attractor dynamics has been observed to be systematically responsive to performance context (e.g., visual support).

Second, the major predictions of the HKB model have been empirically confirmed for varied human coordinated actions, so arguing from the perspective of simple parsimony, evaluating the model’s applicability to the coordination of upright standing seems warranted. Exemplars of coordinated actions whose dynamics are consistent with predictions of the HKB model include rhythmic coordination between left and right fingers (Haken et al., 1985; Kelso, 1984), left and right forearms (Torre, 2010), swung pendulums held in the left and right hands (Amazeen et al., 1996; Fink et al., 2000), arms and legs (Kelso & Jeka, 1992), arms and oscillating stimuli in the environment (Byblow et al., 1995; Wimmers et al., 1992), and between the leg movements of two visually or mechanically coupled people (Harrison & Richardson, 2009; Schmidt et al., 1990). The predictions of the HKB model have also been found to generalize to patterns of coordination between joints during arm movements (Kelso et al., 1991), locomotion (Diedrich & Warren, 1995), and, most significantly in the current context, postural control during visual tracking (Bardy et al., 1999).

Third, our choice of the HKB model was also motivated by the fact that the Haken-Kelso-Bunz (HKB) model supports multiple empirically testable predictions. The HKB model makes predictions about the form and dynamics of coordination between two coupled oscillatory subsystems. Coordination is captured via the collective variable of relative phase ($\phi$), where $\phi$ is simply the difference in phase of the two oscillatory subsystems. (Haken et al. (1985); Kelso, 1995; Kelso, 2008). Three specific predictions derived from the HKB model are of interest and are explicated subsequently. In this paper we subject the time-series of the center of pressure displacements to cross-wavelet analysis. Using this methodology, we evaluate the degree to which the center of pressure trajectories generated during upright standing with either symmetric or asymmetric stance, and with or without visual support, are consistent with the following predictions of HKB model:

**Prediction 1.** A system of two coupled oscillatory subsystems will be drawn into one of two coordination patterns (i.e., stable states) with relative phases of 0° and 180°, and with 0° being the most stable and therefore most reliably observed and least variable pattern (Kelso, 2012). Thus, in the current study we evaluate whether on average the prevalent relative phase of the excursions of the left and right centers of pressure are in fact 0° and 180°.

**Prediction 2.** When certain relevant asymmetries, referred to as imperfection parameters (Park & Turvey, 2008), are present, the observed mean relative phase will shift away from the otherwise preferred states of $\phi = 0°$ and $\phi = 180°$, and the stability of solutions will be reduced. Identified imperfection parameters include neuromuscular, biomechanical, spatial, functional, and attentional asymmetries. Biomechanical asymmetry arises when the two oscillatory subsystems differ in their intrinsic dynamical tendencies to oscillate at a certain frequency or amplitude (de Poel et al., 2009; Sternad et al., 1995). For example, when two hand-held pendulums of differing lengths, and therefore possessing distinct natural frequencies, are coordinated, the shorter of the pendulums possessing the faster natural frequency is observed to phase-lead the longer pendulum (Sternad et al., 1995). Spatial asymmetry arises from differences in the spatial configuration of oscillatory subsystems (Park et al., 2001; Park & Turvey, 2008). For example, in the case of coordinating the oscillations of hand-held pendulums, where one pendulum is oriented downwards and the other pendulum is oriented upwards (Park & Turvey, 2008). Neuromechanical asymmetry arises from differences in the neuromechanical degrees of freedom recruited in the coordinated effectors (Carson et al., 2000). Functional asymmetries arise from lateralized physiological differences such as handedness. Handedness has been shown to produce a shift in relative phase away from $\phi = 0°$ and $\phi = 180°$, with the dominant hand leading the non-dominant hand (Treffner & Turvey, 1996). Lastly, attentional asymmetries arise from asymmetries in focus, such as in the case of paying specific attention to the actions of the right hand when two pendulums are manually coordinated (Amazeen et al., 1997). In this example, the attended to effector phase leads the non-attended effector. Consider that in the current study all participants demonstrated a consistent right-side bias for lower-limb use in tasks dependent on balance, and were required to assemble coordination dynamics that would support upright standing with surfaces of support that differed in elevation between the two legs, and to do so in some trials without visual information to support their actions. In this manner, one or more imperfection parameters were imposed by our experimental manipulations, providing opportunities under the cross-wavelet analysis to evaluate how any resultant
changes in coordination patterns compared with those predictable from the HKB model.

*Prediction 3:* Under certain conditions the coordination dynamics of two coupled oscillatory subsystems is *metastable* rather than stable (Kelso, 2012). In contrast to the phase locking that is characteristic of stable states of coordination, in a metastable state, all possible states of coordination are visited, expressed as phase wandering, but certain phase values are visited preferentially and maintained for longer, expressed as *phase trapping*. Phase trapping manifests as dwellings near potentially stable states, called *ghost attractors*. Metastability arises when asymmetries exist across the intrinsic dynamics of coupled the subsystems, when the subsystems possess weak intrinsic oscillatory dynamics, when the coupling between the subsystems is weak, and/or when significant biological noise is present in the system (Kelso, 2012). Any or all the aforementioned challenges to ideal dynamic stability may arise intrinsically in the postural control system, and may be amplified, or diminished in influence with changes in postural task constraints. In fact, metastability may in fact be preferable to simple stability in relatively high-dimensional systems when metabolically cost-effective adaptability must be available to better ensure viability, as with the human action system (Bressler & Kelso, 2001; Dotov, 2014; Harrison & Stergiou, 2015; Kelso, 2012; van Leeuwen et al., 1997). In the current study, the observation of metastability that approximates for any significant period the expected stable states (relative phase relations of $\phi = 0^\circ$ and $\phi = 180^\circ$ between left and right centers of pressure) would be consistent with the HKB. This is especially the case if Prediction 2 supports the tempering of expectations for simple stability in the presence of the imperfection parameters carried by our experimental manipulations.

Our proposal that the task of maintaining a stable upright standing posture is characterizable in terms of a metastable coordination dynamics that are consistent with the HKB model (and therefore testable via predictions 1–3), is well motivated in the literature. James (2013) observed epochs of both phase trapping and phase wandering in the coordination of head and center of mass accelerations. Examination of relative phase distribution plots revealed that phase trapping occurred around specific phase relations. These preferences were observed in both anterior-posterior and medial-lateral directions of body segment motions. The existence of these preferred states changed in accord with the availability of visual information (i.e., eyes open vs. eyes closed), and the biomechanics of posture (i.e., one leg vs. two leg stance). Creath et al. (2005) similarly observed coherent patterns of coordination between trunk and leg body segments during quiet standing. They observed co-existing in-phase and anti-phase patterns.

Wang and Newell (Wang et al., 2012; Wang & Newell, 2012a, 2012b) used a system of two force plates to record the trajectories of center of pressure (COP) locations under the left and right foot during quiet standing. They separately analyzed anterior-posterior and medial-lateral directions of COP motion under each foot. They observed epochs of phase trapping and phase wandering in the relative phase of these measures. The form and stability of observed coordination patterns were found to depend upon the relative positioning of the feet, with preferences for either in-phase and anti-phase patterns varying as a function of adopting a staggered, side-by-side, or tandem stance (Wang & Newell, 2012a). In side-by-side stance, left and right COPs were coordinated in-phase in the anterior-posterior direction and anti-phase in the medial-lateral direction. Note that Wang and Newell used medial-lateral to refer to left-right motion in the frame of reference of the environment, counter to our use of the frame of reference of the body depicted in Figure 1. In staggered stance, left and right COPs were coordinated in-phase in the both directions. In tandem stance, left and right COPs were coordinated in-phase in the medial-lateral direction, and no clear coordination pattern preferences were observed in the anterior-posterior direction. Wang et al. (2012) further observed that the stability of observed metastable coordination patterns depended upon the availability of visual information (i.e., eyes-open vs. eyes closed). Wang and Newell (2012a) observed that the form and stability of coordination patterns across left and right COPs was mediated by the proportion of body weight loading across the two feet. Loading was manipulated by having participants intentionally bear weight across the left and right limbs in either a 50:50, 70:30, or 30:70 distribution. In the case of tandem stance, the manipulation of weight bearing percentage affected whether an in-phase or anti-phase coordination pattern was observed. For side-by-side and staggered stance, changes between in-phase or anti-phase patterns were not observed as a function of weight bearing. Although Wang and Newell (2012a) did not report statistical analyses of mean relative phase values, the means and standard deviations presented in Table 2 of their paper suggests that weight bearing asymmetries produce systematic shifts in mean relative phase away from preferred in-phase and anti-phase patterns. Thus, the manipulation of weight bearing may be introducing an imperfection parameter into the dynamics. In the case of anterior-posterior direction coordination in the side-by-side stance condition, a phase lead of the less-loaded foot was observed in the 70:30 and 30:70 conditions, and a mean relative phase of close to zero was observed for 50:50 condition.

To summarize, in this paper we examine the form and stability of coordination patterns during the task of quietly maintaining upright standing posture. We use two
force plates to analyze coordination between independently measured center of pressure (COP) locations under the left and right feet during side-by-side stance (see also, Kinsella-Shaw et al., 2011; 2013; Wang & Newell, 2012a; 2012b; Winter et al., 1996). We manipulate the relative heights of the support surface under the two feet (Figure 1A), and the availability of visual information via eyes-open and eye-closed conditions.

Motivated by predictions 1–3 drawn from the HKB model and the findings of Wang and Newell, we can make the following specific hypotheses. First, coordination patterns will be observed as phase gatherings around either $\phi = 0^\circ$ (in-phase) or $\phi = 180^\circ$ (anti-phase). Second, functional asymmetry arising from a functional preference for one leg (Peters, 1988; Sadeghi et al., 2000) will result in systematic deviations away from $\phi = 0^\circ$ and $\phi = 180^\circ$, with the dominant leg phase-leading the non-dominant leg. Third, biomechanical asymmetry (i.e., uneven support surface heights under the feet) will reduce the stability of coordination patterns and will also result in systematic deviations away from $\phi = 0^\circ$ and $\phi = 180^\circ$, with the less-loaded raised leg phase-leading the more-loaded non-raised leg. Thus, in testing this hypothesis we are aiming to confirm the pattern of results suggested by the means and standard deviations reported in Table 2 of Wang and Newell (2012a). Our manipulation of stance asymmetry differs from that of Wang and Newell (2012a). Rather than manipulating loading asymmetry by training participants to assume and maintain specific weight distributions, participants in our study always assume self-selected comfortable postures, and our manipulation of loading asymmetry arises from how participants adapt their posture to various the support surface conditions. Following Swaminathan et al. (2014), we expected support surface height asymmetries to produce weight bearing asymmetries, with participants loading the lowered limb to a greater degree. We also expected participants to adapt the posture of the raised limb to the elevated surface, via flexion at the hip, knee, and ankle. Such a change effectively shortens the raised limb and may therefore introduce an additional biomechanical asymmetry. Speculatively, differences in leg length in the task of coordinating upright stance may be analogous to differences in pendulum lengths in the task manually wielded pendulums (Kugler & Turvey, 1987; Sternad et al., 1995). From this analogy, we would again predict systematic deviations away from $\phi = 0^\circ$ and $\phi = 180^\circ$, with the shorter raised leg phase-leading the longer non-raised leg. Lastly, we predict that the stability of coordination patterns will be affected by the availability of visual information. This prediction is motivated by both the above referenced relative phase analyses (Buchanan & Horak, 1999; James, 2013; Wang et al., 2012), as well as cross-recurrence quantification analyses of the reconstructed phase spaces of center of pressure outputs (Kinsella-Shaw et al., 2011; 2013).

Methods

Participants

Ten participants (seven male, three female), taking a course in Psychology at University of Connecticut, participated in the experiment for credit. All participants gave their consent to participate. The consent process and study procedures were approved by the University of Connecticut’s Institutional Review Board. This study complied with the Declaration of Helsinki. Participants were all young healthy adults, aged between 18 and

FIGURE 1. Participants stood in initially self-selected symmetric and asymmetric stances. (A) Risers placed under the feet produced left-riser (LR) and right-riser (RR) asymmetric stances. The symmetric stance involved no riser. (B) Data averaged across right-footed participants for mean locations of foot anatomical landmarks (black dots) and centers of pressure under the left foot (COP$_L$), right foot (COP$_R$), and across the two feet (COP$_{net}$). COP is measured in a global coordinate system with anterior-posterior and medial-lateral axes shown as vertical and horizontal gray arrows respectively. Mean position of the wooden block (i.e., riser) placement are depicted (black lines).
23 years old, who reported no known neurological or movement disorders, and had normal or corrected-to-normal vision.

Materials

Time series of the vertical component of ground reaction force (GRF) fluctuations and center of pressure (COP) excursions under the left and right feet were obtained at a sampling rate of 100 Hz using two side-by-side Advanced Mechanical Technology Incorporated OR6-7 force plates and a Run Technologies Datapac 2000 Analog-to-Digital Collection System. The plates were embedded in the floor and separated by a 4 mm gap. A 342.5 mm × 143 mm × 37.5 mm block of pressure-treated hardwood, placed either under the right foot or the left foot, was used as a riser to impose a biomechanical stance asymmetry (Figure 1A). A block was placed under the left foot to produce the left-side riser (LR) condition. A separate but identical block was placed under the right foot to produce the right-side riser (RR) condition. No block was used in the no-riser (NR) condition.

Procedure

After providing information regarding the nature and procedure of the experiment, a licensed physical therapist obtained consent, established the participant’s medical history relevant to the inclusion/exclusion criteria, and performed a simple test of leg functional preference. A “kicking a ball” test was selected as a gross measure of footedness (Peters, 1988). This test was chosen as it is a simple, commonly used, and a reasonably reliable indicator of overall functional preference (Kalaycoglu et al., 2008). This measure also closely corresponds to nominated dominant footedness (Schneiders et al., 2010). The “kicking a ball” test used a 22 cm diameter lightweight inflated rubber ball. The test involved the experimenter placing a ball 4 meters in front of the participant and the participant walking up to the ball and kicking it with whichever foot was preferred. Participants were instructed to kick the ball to a target 2 meters in front of the ball. This test was run three times. Kick accuracy was not evaluated.

For the main part of the experiment, participants removed their shoes and were asked to stand with one foot on each force plate, in a side-by-side stance (Figure 1A, center), using a self-selected foot separation that they believed would allow them to stand comfortably for an extended period of time while facing and looking forwards (i.e., anteriorly). Feet outlines of adopted comfortable stances were drawn on the sheets of paper taped to each force plate. Alignment markings, made at points adjacent to the tips of the great toes, the heel, and the first and fifth metatarsals heads (see black dots in Figure 1B), were drawn on the paper covering the force plate and were also marked with tape on the participant’s feet/socks. The wooden risers for the RR and LR conditions were placed over the outlines of the feet and the position of the riser was marked on the paper covering the force plates. Lastly, foot alignment markings were transferred from the force plate to the surface of the riser using tracing paper. Given this procedure the presence of a riser acted to vertically translate the position of the foot by 37.5 mm, while maintaining a fixed base of support width across conditions. Participants were asked to stand with feet inside the foot alignment markings in each of the three studied stances (Figure 1A). This approach of studying the upright stance in self-selected comfortable stances is motivated by adoption of similar methods by Wang and Newell (2012a). Once participants were standing comfortably, joint angles were measured using a hand-held goniometer. For the NR stance posture leg lengths were additionally recorded using a cloth tape to measure the distance between the anterior superior iliac spine and the medial malleolus.

Before beginning the main experiment, a second lower limb functional preference test was conducted. Since functional lower-limb preference has been found to depend upon the specifics of the task being performed (Hart & Gabbard, 1997), we selected a functional test that bore similarity to the investigated behavior of quietly maintaining upright stance. Participants were asked to assume in turn each of the three stances to be investigated (Figure 1A). Once settled in each stance (i.e., after a couple of seconds) participants were then asked to raise one of their feet off the ground and to hold a single-leg posture for 10 seconds. The primary goal of this simple single-leg stance task is postural stabilization. By contrast, the primary goal of more skilled tasks commonly used in tests of footedness, such as kicking a ball, is object manipulation or leading out (Kalaycoglu et al., 2008; Peters, 1988). Participants that (1) used their right foot to kick the ball back to the target on all trials, and (2) selected their right leg as their stance leg in the NR condition, were designated as right-footed, and were included in our analysis of a group of right-footed participants. Non-right footed participants were excused from participation.

Presentation of experimental conditions was fully randomized. Participants received a total of five presentations of each of the three stance (LR, NR, RR) and two vision (eyes-open, eyes-closed) conditions. Each participant completed a total of 30 trials of the task of quietly maintaining upright stance. Each trial lasted 35 seconds and commenced a few seconds after participants reported that they were standing comfortably. At the start of each trial participants placed their feet inside the foot alignment markings, aligning taped markers on each sock/foot with those on the force plate or the riser.
In asymmetric stance conditions, participants placed and aligned the non-elevated foot first, and then placed the elevated foot. In eyes closed conditions participants closed their eyes after reporting standing comfortably in either symmetric or asymmetric stance, as required. Once positioned participants were asked to report when they were standing comfortably. Data recording commenced within 2-3 seconds of this report. Participants were instructed to stand comfortably during the recording and not change their foot placement or the posture of their arms from the instructed posture of hanging their arms comfortably by their sides.

Data Analysis

Voltage data recorded from the force plates was transformed to produce time series of forces and moments and then filtered using a 4th order low-pass Butterworth filter with a cutoff frequency of 18 Hz. The time series of forces and moments were used to calculate the center of pressure (i.e., the centroid of the pressure distribution) under the left (COP\textsubscript{L}) and right (COP\textsubscript{R}) feet, as well as the ground reaction forces for the left (GRF\textsubscript{L}) and right (GRF\textsubscript{R}) feet. Using the equations presented in Winter et al. (1996), we also calculated the locus of the centroid of the pressure distribution across the two force plates (COP\textsubscript{net}). COP\textsubscript{L}, COP\textsubscript{R}, and COP\textsubscript{net} coordinates were transformed into a common global coordinate system (gray arrows in Figure 1B).

The orientation of COP\textsubscript{L} and COP\textsubscript{R} trajectories were evaluated by performing Principal Component Analyses (PCA) on all of the anterior-posterior and medial-lateral coordinates recorded over the duration of a trial (Figure 3A). The orientation of the trajectory is found from the eigenvalues of the first and second principle components and was measured in relation to the direction of the anterior-posterior axis (Duarte & Zatsiorsky, 2002). Figure 3A visually depicts this analysis, with the trajectory of COP\textsubscript{R} shown overlaid with an ellipse whose long axis is aligned to the direction of the first principle component. Orientation was measured as the angle between the direction of the anterior-posterior axis and the direction of the first principle component. Matlab code for this analysis is available as an appendix in Duarte and Zatsiorsky (2002).

The analysis of COP coordination adopted one non-standard convention. The respective coordinate systems used to measure COP\textsubscript{L} and COP\textsubscript{R} were rotated out of the conventional ap and ml axes to be aligned to the orientation of each foot in the self-selected comfortable stances adopted by participants (see Figure 4A). The realigned COP\textsubscript{L} and COP\textsubscript{R} trajectories yielded X and Y coordinates under each foot, with the Y axis defined by a line drawn between a point behind the heel and a point in front of the great toe. The X axis was defined to be orthogonal to the Y axis in the ground plane and was oriented such that the positive direction was away from the center of the body, that is lateral (see Figure 4A). This choice of a foot-aligned COP coordinate system allowed to (1) account for the individual differences in foot orientation across the self-selected stances, and (2) increase the possibility that the potentially distinct influences of the action of plantarflexors/dorsiflexors and ankle invertors/evertors might be picked out in our analysis of the coordination of upright stance. The action of plantarflexors/dorsiflexors was assumed to affect the COP motion in the direction of the Y axis to a greater degree than the X axis; the action of ankle invertors/evertors was assumed to affect COP motion in the direction of the X axis to a greater degree than the Y axis. Time series of X and Y for the left and right side were standardized via z-score, and coordination between the resulting four standardized time series X\textsubscript{L}, X\textsubscript{R}, Y\textsubscript{L}, and Y\textsubscript{R}, was investigated. Following Wang and Newell (2012b), we restricted our analysis of coordination to be

\begin{figure}
\centering
\includegraphics[width=\textwidth]{figure2.png}
\caption{Effects of stance and vision on (A) the proportion of loading (i.e., ground reaction force, GRF) of the right-limb, and (B) the length of the center of pressure trajectories measured over the 35 s trial duration.}
\end{figure}
focused upon the two pairings of outputs that were matched for direction, X_R X_L and Y_R Y_L.

Coordination between the outputs in each studied output pair was quantified via cross-wavelet analysis (CWA). CWA was performed with a Matlab (MathWorks, Inc.) wavelet coherence package developed by A. Grinsted (Grinsted et al., 2004). CWA is a time-frequency analysis method built off the wavelet transform. Contrasting the Fourier transform, the wavelet transform expands time series into time-frequency space and can therefore find localized intermittent periodicities. This wavelet approach was adopted for two reasons. Firstly, it is relatively unbiased by the non-stationary time series obtained from measures of upright stance (Carroll & Freedman, 1993), and secondly it allows for the identification of transient regions of coherent coordination hypothesized to underlie the metastable coordination of upright stance.

The wavelet transform (W_u) of the time series u with respect to the wavelet ψ is defined as:

$$W_u = W_{u,ψ}(s, t) = u(t) ψ^*_s(t),$$

where t is time and s is the wavelet at the scale s (which is linearly related to the characteristic period of the
wavelet). Following Varoqui et al. (2010) we adopted a Morlet wavelet as the wavelet mother function. The order 6 Morlet mother function adopted in this paper has been demonstrated to have good time and frequency resolution (Grinsted et al., 2004). For this wavelet, the scale approximates the Fourier period.

For analysis of the covariation of two time series the cross-wavelet spectrum of two time series \( U \) and \( V \) with wavelet transforms \( W_U \) and \( W_V \) was calculated as

\[
W_{UV}(s, t) = W_U(s, t)W_V^*(s, t) \quad [2]
\]

where * denotes complex conjugation. Cross-wavelet Coherence (C), a measure of the intensity of the covariance of the two series in time-frequency space was calculated from the cross-wavelet spectrum as follows,

\[
C(s, t) = \frac{|S(s^{-1}W_{UV}(s, t))|^2}{\left(|S(s^{-1}W_U(s, t))|^2\right) \cdot \left(|S(s^{-1}W_V(s, t))|^2\right)} \quad [3]
\]

where \( S \) is a smoothing operator. Intuitively, cross-wavelet coherence is a localized correlation coefficient in time frequency space, and as such provides a measure of frequency coordination. Following Jevrejeva et al. (2003), obtained values of \( C \) were tested against a null hypothesis of chance coherence. We employed a Monte Carlo method to determine a 5% statistical significance level for each scale using only values outside the cone of influence (COI), where the COI captures regions of the analysis where edge artifacts may affect the results. The estimate for chance level coherence was derived from 10000 surrogate data set pairs of randomly generated red noise. The choice of red background noise (i.e., Brownian motion) was one of convenience (given that it is already integrated into Grinsted’s wavelet coherence package). While a nice refinement of this method would be to utilize a noise spectrum tuned to the specific spectrum of the measures collected, the color of the noise has been found to have little impact on the significance levels yielded from the Monte Carlo method (Grinsted et al., 2004), and a red noise spectrum would seem to provide a reasonable approximation of COP variability (e.g., Kinsella-Shaw et al., 2006). The cross-wavelet spectrum has edge artifacts because the wavelet is not completely localized in time. Consequently, all variables used in the analysis were calculated outside of the COIs, thus adjusting for scale specific edge effects in the cross-wavelet analysis. In addition to the calculation of cross-wavelet coherence, the wavelet relative phase (\( \phi \)) was calculated at the phase angle of \( W_{UV} \), describing the phase relationship between \( u \) and \( v \) in time-frequency space. In the analysis of an output pairing (e.g., \( X_LX_R \)), \( \phi \) identifies the phase angle of first output in the variable name relative to the second output in the variable name.

Thus, for \( X_LX_R \), if \( \phi = 10^\circ \), then \( X_L \) is the reference limb, and \( X_R \) is leading \( X_L \) by \( 10^\circ \).

The scales were selected according to two constraints, (1) the amount of data loss at a given scale due to the removal of edge artifacts (i.e., COI), which for a fixed trial length increases with the wavelet scale (an upper bound constraint), and (2) the frequencies taken to be behaviorally relevant and not obscured by measurement noise (a lower bound constraint). For our data, sampled at 100 Hz and low pass filtered at 18 Hz, wavelet sample periods of 32, 64, 128, and 256 samples, with equivalent Fourier frequencies of 3.03, 1.51, 0.76, and 0.38 Hz formed the major scales at which our analysis was conducted. The analysis of each scale consisted of the wavelet coherence and relative phase data for the major scale averaged together with the data from five minor (sub-scales) above and below the major scale. Each of the scales above and below the major scale were proportionally bigger or smaller than the major scale, with each successive smaller sub-scale scaled by 0.94 the major scale period, and each successive larger sub-scale scaled by 1.06 the major scale period. This resulted in four frequency bands covering an overall frequency range from 0.28 Hz to 4.04 Hz, with the two upper and two lower bands being approximately above and below 1 Hz.

The primary measures derived from the CWA employed in our analysis were the percentage of each trial exhibiting above chance coherence (PTC), and the mean relative phase (\( \phi \)). PTC provides a measure of the stability of coordination. \( \phi \) provides a measure of phase-shifts.

All statistical analyses were performed using IBM SPSS software version 25.0. For each Analysis of Variance (ANOVA) a Mauchly’s Test of Sphericity was employed to test for violations of the assumption of sphericity. All ANOVAs included only repeated measures factors. Greenhouse-Geisser corrections were used to adjust the degrees of freedom of the ANOVAs when violations of the assumption of sphericity were discovered. In the presentation of our results, the degrees of freedom in each ANOVA are reported to two decimal points in cases when Greenhouse-Geisser corrections were made.

**Results and Discussion**

**Self-Selected Side-by-Side Posture**

Prior to the start of the main experiment—during which force plate outputs were measured—participants were asked to assume a comfortable side-by-side stance with feet placed on either side of the visible line created by the 4 mm separation of the two force plates. Feet placements in this self-selected stance were measured by finding the positions of foot anatomical landmarks and marking them on paper covering the force plates. Feet
placements did not show systematic asymmetries. The splay of the left and right feet was measured as the degree of external rotation of the foot direction vector (a line between the participant’s heel and toe) out of the anterior-posterior axis (see Figure 1B). Splay showed no left-right asymmetry ($F < 1$). Mean and standard errors of foot splay angles are shown as a solid gray lines and dashed lines respectively in Figure 1C. No lateral asymmetry in the length of participants’ left and right limbs was observed, $F < 1$. The positions of the feet—indexed by the location of the heel—did not differ in the mediolateral direction (i.e., in the lateral distances between the heels and the center of the two force plates), $F < 1$. A numerically small but significant difference was observed between the anterior-posterior coordinates of the left ($-136.8 \text{ mm} \pm 17.8 \text{ mm}$) and right ($-132.0 \text{ mm} \pm 17.3 \text{ mm}$) heels, $F(1, 9) = 5.16, p < .05, \eta^2_p = .36$. Mean foot positions are shown in Figure 1B as black dots on the edges of the illustrative gray foot silhouettes. Stance width (measured as the mediolateral distance between the anatomical landmarks for the heels) was $28.2 \pm 5.5 \text{ cm}$ (range: 20.9–36.7 cm).

Goniometric measurements of joint angles were taken for each participant while they stood in their self-selected symmetric (NR) and asymmetric (LR and RR) stances. In the symmetric NR stance, knee flexion and ankle dorsiflexion showed no significant lateral asymmetry. Left and right leg knee flexion angles were $4.3^\circ \pm 1.0^\circ$ and $4.5^\circ \pm 1.6^\circ$, $F < 1$. Left and right leg ankle dorsiflexion angles were $3.0^\circ \pm 2.3^\circ$ and $2.3^\circ \pm 1.0^\circ$, $F < 1$. These measurements changed systematically as a function of stance symmetry. Knee flexion angles of elevated limbs in asymmetric (LR and RR) stances ($17.2^\circ \pm 5.7^\circ$) were increased compared to the NR stance ($4.4^\circ \pm 1.2^\circ$), $F(1, 9) = 35.20, p < .001, \eta^2_p = .80$. Ankle dorsiflexion of the elevated limbs ($8.5^\circ \pm 5.0^\circ$) was increased compared to the NR stance ($2.7^\circ \pm 1.4^\circ$), $F(1, 9) = 13.30, p < .05, \eta^2_p = .60$. Across RR and LR stances, no differences in either knee flexion, $F(1, 9) = 2.19, p = .17, \eta^2_p = .20$, or ankle dorsiflexion angles, $F < 1$, of the elevated limbs were observed. Since the experimenters did not observe any obvious changes relative to the initial form of each participant’s self-selected NR, LR, and RR stances, we assumed that these pre-experiment measurements can be used to understand the form that was typical to the self-selected postures of participants throughout the experiment. These results reveal that elevated limbs were flexed and therefore effectively shortened.

Ground Reaction Forces (GRFs) and Centers of Pressure (COPs)

In the main experiment, force plate recordings were analyzed across manipulations of both stance and vision. In the symmetrical stance (NR) condition, GRF under the right foot (GRF$_L$) expressed as a proportion of total GRF (GRF$_L$ + GRF$_R$) was $0.497 \pm 0.025$ (Figure 2A). This proportion did not differ from a state of symmetrical limb loading (i.e., .5), $t(9) = -0.36, p = .72$, and did not vary as a function of vision, $F < 1$. In the asymmetrical stance conditions (LR and RR), the proportion of GRF$_R$ was lower when the right root was elevated, $F(1, 9) = 29.88, p < .001, \eta^2_p = .77$, and this was unaffected by vision, $F(1, 9) = 4.61, p = .06, \eta^2_p = .34$. The effect of stance upon limb loading asymmetry observed here is comparable in magnitude to that observed by Wang and Newell (2012b). In that study loading was manipulated by intentional weight bearing, rather than unintentionally via a block placed under one foot.

COP$_{net}$ quantifies the centroid of the pressure distributions formed by the combined contact of the left and right feet with the surface of support. The mediolateral coordinate of COP$_{net}$ was affected by stance, $F(1, 9) = 24.51, p < .001, \eta^2_p = .73$, but not vision, $F(1, 9) = 3.81, p = .083, \eta^2_p = .30$. Post hoc pairwise comparisons with Bonferroni corrections revealed that the mediolateral coordinates of COP$_{net}$ in the LR, NR, and RR stances all differed from one another ($p’s < .01$). As revealed in Figure 1B, the mediolateral location of COP$_{net}$ shifts toward the more loaded limb in asymmetrical stances. The anterior-posterior coordinate of COP$_{net}$ was also affected by stance, $F(2, 18) = 3.84, p < .05, \eta^2_p = .30$, but not by vision, $F < 1$. Post hoc pairwise comparisons with Bonferroni corrections revealed no differences between LR, NR, and RR stances.

COP$_L$ and COP$_R$ quantify the centroids of the pressure distributions formed by the left and right foot’s contact with the surface of support. These COP locations are shown as a function of stance in Figure 1B. In the symmetrical stance condition, no difference in the anterior-posterior coordinates of COP$_L$ ($-27.15 \text{ mm} \pm 22.99 \text{ mm}$) and COP$_R$ ($-16.72 \text{ mm} \pm 19.81 \text{ mm}$) was observed, $F(1, 9) = 3.94, p = .08, \eta^2_p = .30$. These coordinates were unaffected by vision, $F(1, 9) = 1.52, p = .25, \eta^2_p = .14$. In the asymmetric stance conditions, coordinates of COP$_L$ and COP$_R$ in the anterior-posterior direction were affected by the relative elevation of the limbs, $F(1, 9) = 11.94, p < .001, \eta^2_p = .57$, but not by the particular limb that was elevated, $F < 1$, or vision, $F(1, 9) = 1.26, p = .29, \eta^2_p = .12$. Measured relative to the center of the two force plates, COPs were on average located more anteriorly for raised limbs ($-11.63 \text{ mm} \pm 17.61 \text{ mm}$) than for the lowered limbs ($-32.48 \text{ mm} \pm 22.58 \text{ mm}$). In the symmetrical stance condition, mediolateral axis coordinates of COP$_L$ ($119.93 \text{ mm} \pm 37.27 \text{ mm}$) and COP$_R$ ($129.39 \text{ mm} \pm 32.64 \text{ mm}$) differed in their lateral displacement from the center of the force plates, $F(1, 9) = 5.72, p < .05, \eta^2_p = .39$. This lateral displacement was unaffected by vision, $F < 1$. In the asymmetric stances, mediolateral axis coordinates of
COP_L and COP_R were affected by the relative elevation of the limbs, $F(1, 9) = 6.04, p < .05, \eta^2_p = .40$. COP_L and COP_R on were on average located more medially for raised limbs (154.2 mm ± 36.3 mm) than for lowered limbs (160.2 mm ± 33.8 mm). This lateral displacement was unaffected by the side of the limb, $F(1, 9) = 3.94, p = .08, \eta^2_p = .30$, or by vision, $F(1, 9) = 2.27, p = .17, \eta^2_p = .20$.

The magnitudes of COP_L and COP_R variability were evaluated as the COP trajectory path lengths. In the symmetrical stance condition, path length was larger in the eyes-closed condition, $F(1, 9) = 15.26, p < .001, \eta^2_p = .63$, but did not differ across right and left limbs, $F < 1$ (Figure 2B). In the asymmetric stance conditions, path length increased for elevated limbs, $F(1, 9) = 23.61, p < .001, \eta^2_p = .72$. Path length also increased in the eyes-closed condition, $F(1, 9) = 37.48, p < .001, \eta^2_p = .81$. The effect of vision depended upon side, $F(1, 9) = 8.25, p < .05, \eta^2_p = .48$ (Figure 2B), with the effect of vision more pronounced for the right limb. This laterality effect is consistent with results reported in Kinsella-Shaw et al. (2013). Employing the same dual force platform configuration as in the current study, cross-recurrence quantification of the anterior-posterior and medio-lateral coordinates of COP_L and COP_R for right-footed older and younger adults, revealed that right-leg coordination was more responsive to changes in the degree of visible structure. In combination with the current study, these results suggest that a functional preference for the right leg is associated with greater susceptibility of that limb for being modulated by visual information.

The distributions of COP_L and COP_R locations in the transverse plane exhibited a tendency, indexed by PCA eigenvector orientation (Figure 3A), to be externally rotated relative to the anterior-posterior axis (i.e., 0°), $t(9) = 7.43, p < .001$ (Figure 3B). In the symmetrical stance condition the degree of external rotation did not observably differ between COP_L and COP_R trajectories, $F(1, 9) = 1.06, p = .33, \eta^2_p = .11$, or between eyes-open and eyes-closed conditions, $F(1, 9) = 1.07, p = .33, \eta^2_p = .11$. In the asymmetric stance conditions, PCA eigenvector external rotation did not observably differ as a function of relative limb elevation, $F(1, 9) = 1.43, p = .26, \eta^2_p = .14$, the particular limb that was elevated, $F < 1$, or vision, $F < 1$.

**Stability of Coordination**

Frequency coordination between foot-aligned COP outputs (Figure 4A) was observed in the form of regions of above chance coherence in the cross-wavelet analysis (Figure 4B). Regions of frequency coordination for X_RX_L and Y_RY_L lasted on average 2.25 s and 3.38 s respectively. Figure 5A shows the distributions of observed region durations. These results suggest that states of frequency coordination were typically not long lasting (i.e., they rarely persisted throughout the trial), and were therefore, intermittently occurring, and were not very stable.

Phase coordination was investigated via the analysis of cross-wavelet relative phase ($\phi$) values evaluated within determined regions of frequency coordination. Figure 5B presents relative phase histograms for $X_RX_L$ and $Y_RY_L$, as a function of both frequency band and stance condition. Multiple one-tailed t-tests were performed to highlight in each of these relative phase histograms whether relative phases close to hypothesized preferred states of $\phi = 0^\circ$ (range 330° to 30°) and $\phi = 180^\circ$ (range 150° to 210°) occurred more frequently than relative phases distal from $\phi = 0^\circ$ (ranges 270° to 330° and 30° to 90°) and $\phi = 180^\circ$ (ranges 90° to 150° and 210° to 270°). The results of these tests are displayed in the relative phase histograms (Figure 5) with a * symbol. When placed close to either $\phi = 0^\circ$ or $\phi = 180^\circ$, the * denotes a greater frequency of observed relative phase values close to that phase mode. This analysis reveals a reliable preference for relative phase values close to $\phi = 0^\circ$ and $\phi = 180^\circ$. It suggests that in-phase ($\phi = 0^\circ$) and anti-phase ($\phi = 180^\circ$) coordination modes exist across stance conditions and frequency bands, and that the existence and stability of those modes changed with stance condition.

A measure of percent trial coherent (PTC) was used to capture the percentage of each trial exhibiting coherent frequency coordination. PTC was calculated for $X_RX_L$ and $Y_RY_L$ at the four selected frequency bands. PTC was used to evaluate the stability of coordination patterns, with greater stability assumed to be related to greater proportion of trial exhibiting coordination. The systematic pattern of preferences for relative phase values close to either $\phi = 0^\circ$ and $\phi = 180^\circ$ evident across the relative phase histograms (Figure 5B) motivated the inclusion of an additional independent variable in our analysis of PTC, phase mode. This variable was used to pull apart in-phase PTC (PTC_{IP}, $\phi = 0^\circ ± 90^\circ$) and anti-phase PTC (PTC_{AP}, $\phi = 180^\circ ± 90^\circ$). Thus, in the following analyses we assume that each output pair has two potential modes (IP and AP).

The percentage of each trial exhibiting coherent frequency coordination in the X-axis was 19.44%. In-phase was seen to be the dominant mode of coordination PTC_{IP} = 16.35%, PTC_{AP} = 3.09%, $F(1, 9) = 11.77, p < .05, \eta^2_p = .57$. Analyses of the effects of stance, vision, and frequency band were performed separately for each mode. PTC_{IP} depended upon stance, $F(1.15, 10.34) = 14.97, p < .05, \eta^2_p = .62$, frequency band, $F(1.41, 12.73) = 15.07, p < .001, \eta^2_p = .63$, and vision, $F(1, 9) = 14.12, p < .05, \eta^2_p = .61$. Post hoc pairwise comparisons with Bonferroni corrections revealed greater PTC_{IP} in the symmetrical stance condition compared to
asymmetric stance conditions ($p's < .05$), and revealed that the 0.38 Hz and 0.76 Hz frequency bands were different from the 1.51 Hz and 3.03 Hz frequency bands. The effect of stance was more pronounced in the lower frequency bands $F(2.56, 22.12) = 8.27, p < .001, \eta_p^2 = .48$ (Figure 6A, left panel). In the case of the non-dominant (anti-phase) mode of coordination for $X_RX_L$, PTC$_{AP}$ depended upon stance, $F(2, 18) = 8.61, p < .05, \eta_p^2 = .49$ (Figure 6B, left panel). Post hoc pairwise comparisons revealed greater PTC$_{AP}$ in asymmetric stances compared to the symmetric stance, and greater PTC$_{AP}$ in the RR condition compared to the LR condition ($p's < .05$).

For the $Y_RY_L$ output pair, the percentage of each trial exhibiting coherent frequency coordination was 42.95%. In-phase was seen to be the dominant mode of coordination PTC$_{IP} = 41.73\%$, PTC$_{AP} = 1.22\%$, $F(1, 9) = 225.53, p<.001, \eta_p^2 = .96$. Analyses of the effects of stance, vision, and frequency band were performed separately for each mode. PTC$_{IP}$ depended upon stance, $F(2, 18) = 38.76, p < .001, \eta_p^2 = .81$, vision, $F(1, 9) = 71.88, p < .001, \eta_p^2 = .89$, and frequency band, $F(3, 27) = 114.32, p < .001, \eta_p^2 = .93$ (Figure 6A, right). Greater PTC$_{IP}$ was observed in the absence of visual information. Post hoc pairwise comparisons with Bonferroni corrections revealed greater PTC$_{IP}$ in the symmetric compared to asymmetric stance conditions ($p's < .05$). Other comparisons revealed 0.38 Hz and 0.76 Hz frequency bands to each differ from the 1.51 Hz and 3.03 Hz frequency bands ($p's < .05$). The effect of stance was more pronounced in the lower frequency bands $F(6, 54) = 3.46, p < .05, \eta_p^2 = .28$. The effect of vision was more pronounced in the lower frequency bands $F(3, 27) = 3.52, p < .05, \eta_p^2 = .28$.

In the case of the non-dominant (anti-phase) mode of coordination for $Y_RY_L$, PTC$_{AP}$ depended upon frequency band, $F(1.55, 13.98) = 6.34, p < .05, \eta_p^2 = .41$. Post hoc pairwise comparisons with Bonferroni corrections revealed greater PTC$_{AP}$ in the 0.38 Hz band.
compared to the 0.76 Hz band \((p < .05)\). Interaction effects of stance and frequency band, \(F(2.78, 33.33) = 3.57, p < .05, \eta^2_p = .23\), and frequency band and vision, \(F(3, 36) = 6.69, p < .01, \eta^2_p = .32\), were observed (Figure 6B, right). These interactions reveal that the effects of both stance and vision were most pronounced for the 3.02 Hz band.

The similar pattern of effects of stance and visual information upon the PTC measure of both \(X_R X_L\) and \(Y_R Y_L\) raises the possibility that these measures are picking out a single underlying coordination pattern. Given previous claims of the independence of control mechanisms in anterior-posterior versus medial-lateral directions during side-by-side stance (Rosenblum et al., 1998; Winter et al., 1993; 1996) we hypothesized that observed regions of coordination of \(X_R X_L\) and \(Y_R Y_L\) would not significantly overlap in time. Consistent with this hypothesis, the overlap of in-phase coordinated regions of \(X_R X_L\) and \(Y_R Y_L\) was not greater than the chance level overlap of 23.44\% \((M = 19.79\%, SD = 13.09\%), \eta(9) = −0.88, p = .40\).

The pattern of results observed for the PTC measure is consistent with the comparison of side-by-side and staggered stances performed by Wang et al. (2012). In both their results and ours, in-phase (as defined in our coordinate system) is the preferred state of coordination during side-by-side stance, and the introduction of a biomechanical stance asymmetry (either staggered stance or a riser) reduces the stability of in-phase and increases the stability of anti-phase. In contrast to the results of Wang et al. (2012) we observe reliably coexisting in-phase and anti-phase modes in some conditions. This is likely due to a lower degree of biomechanical asymmetry in our stance manipulation.

**Mean \(\phi\) as a Function of Biomechanical Asymmetry**

As with PTC, mean relative phase \((\phi)\) for each output pairing was analyzed in separate modes for in-phase \((\phi_{IP} = 0^\circ \pm 90^\circ)\) and anti-phase \((\phi_{AP} = 180^\circ \pm 90^\circ)\). For \(X_R X_L\), the analysis of mean relative phase in the dominant in-phase mode \((\phi_{IP})\) revealed an interaction of stance and vision, \(F(2, 18) = 4.12, p < .05, \eta^2_p = .31\) (Figure 7A and B, left subpanels). \(\phi_{IP}\) was also affected by frequency band, \(F(3, 27) = 6.45, p < .05, \eta^2_p = .42\). For \(Y_R Y_L\), \(\phi_{IP}\) was affected by stance, \(F(2, 18) = 11.76,\)
$p < .001, \eta_p^2 = .57$, with post hoc pairwise comparisons with Bonferroni corrections revealing differences between LR and NR, and LR and RR conditions. These results suggest a phase lag associated with the LR condition, and phase leads associated with NR and RR conditions. An interaction of stance, frequency band, and vision, $F(6, 54) = 2.66, p < .05, \eta_p^2 = .23$, was observed (Figure 7A and B, right subpanels), revealing that in the eyes open condition, the phase lead/lags associated with stance asymmetries were no longer evident in the lower frequency bands of the analysis. For $X_RX_L$, analysis of the mean relative phase in the non-dominant anti-phase mode ($\phi_{AP}$), was affected by stance, $F(2, 18) = 5.66, p < .05, \eta_p^2 = .37$ (Figure 7C and D, left subpanels). Post hoc pairwise comparisons with Bonferroni corrections revealed a difference between RR and NR and LR conditions ($p$'s $< .05$). For $Y_RY_L$, $\phi_{AP}$ was affected by stance, $F(2, 18) = 6.33, p < .05, \eta_p^2 = .41$. Post hoc pairwise comparisons with Bonferroni corrections revealed a difference between LR and NR, and LR and RR conditions (Figure 7C and D, right subpanels).

We expected that a biomechanical asymmetry introduced by the manipulation of blocks placed under the feet would produce systematic phase shifts away from $\phi = 0^\circ$ and $\phi = 180^\circ$. This prediction was consistently borne out. We also tentatively hypothesized that the elevated limb would phase-lead the lowered limb. This prediction held in the case of the in-phase coordination mode of the $Y_RY_L$ output pair (which was the most stable coordination mode observed; an
analagous effect of direction on interleg coordination sta-

Within-trial Metastability

From the above analysis of PTC, we can conclude that manipulations of stance and vision produced changes in the stability of specific coordination modes. The PTC analysis sums over potentially multiple regions of in-phase and anti-phase coordination observed over a trial (see Figure 4B), and as such, the analysis is blind to the nature of within trial coordination. It is possible that only single states of coordination are observed in the context created by a specific participant, standing at a specific moment in time, in the situation of a specific manipulation of stance and vision. Alternatively, examples of switching between regions of on-average in-phase and on-average anti-phase coordination may exist within a trial. The latter of these possibilities would suggest that even in the seemingly steady state context of a specific trial, the potential exists for flexibly switching between transiently stable modes of coordination, called metastability. To provide context for an analysis of within-trial mode switching we must look at the average number of regions exhibiting coordination across a trial. For X_R X_L, this number was 1.29, 2.06, 3.25, and 4.27 per trial, within the 0.38 Hz, 0.76 Hz, 1.51 Hz, and 3.03 Hz frequency bands respectively. For Y_R Y_L, the average number of regions in a trial was 1.56, 2.69, 4.79, and 7.14, within the 0.38 Hz, 0.76 Hz, 1.51 Hz, and 3.03 Hz frequency bands respectively. The percentage of within trial mode switching was examined by determining the number of switches that occurred between in-phase regions with mean $\phi = 0^\circ \pm 45^\circ$ and anti-phase regions with mean $\phi = 180^\circ \pm 45^\circ$, scaled to the number of possible switches that could have occurred in a trial, and multiplied by 100. Note that the range of mean phases used evaluate coordination as either in-phase or anti-phase was narrowed in this analysis to $\pm 45^\circ$. This was done to avoid spurious detections of switching due to trivial fluctuations around the quadrant boundaries at $\phi = 90^\circ$ and $\phi = 270^\circ$.

For X_R X_L, the percentage of within-trial mode switching was 1.30%, 2.35%, 5.94%, and 16.68%, within the 0.38 Hz, 0.76 Hz, 1.51 Hz, and 3.03 Hz frequency bands respectively. For Y_R Y_L, the percentage of within trial mode switching was 1.56%, 2.69%, 4.79%, and 7.14%, within the 0.38 Hz, 0.76 Hz, 1.51 Hz, and 3.03 Hz frequency bands respectively. For X_R X_L, an analysis of percentage of within trial mode switching revealed a main effect of frequency band, $F(3, 27) = 95.79, p < .001, \eta_p^2 = .91$. Post hoc pairwise comparisons with Bonferroni corrections revealed differences in all frequency band comparisons ($p$’s < .05), except for 0.38 Hz and 0.76 Hz. For Y_R Y_L, an analysis of percentage of within trial mode switching revealed a main effect of frequency band, $F(1,28, 11.49) = 31.09, p < .0001, \eta_p^2 = .78$. Post hoc pairwise comparisons with Bonferroni corrections revealed differences between all frequency band

Mean $\phi$ as a Function of Functional Asymmetry

Given the demonstrated reliable preference of all study participants for using their right foot to kick a ball, and for selecting their right-leg as a support leg in single-leg stance we predicted a functional asymmetry would exist in participants’ symmetrical side-by-side stance standing postures (i.e., the NR condition). We predicted that this asymmetry would be revealed as a shift in mean phase away from $\phi_{IP} = 0^\circ$ and $\phi_{AP} = 180^\circ$, consistent with the effect of a detuning parameter in the HKB model. We further predicted a right-side phase lead, motivated by handedness biases observed in manual rhythmic coordination tasks (Treffner & Turvey, 1996). For the dominant in-phase mode, this prediction was supported in the analysis of Y_R Y_L, with a one-tailed t-test, testing for $\phi_{IP} > 0^\circ$, revealing a phase lead for Y_R (M = 5.51°, SD = 3.34°), $t(9) = 5.22, p < .001$. The prediction was not supported in the analysis of X_R X_L, (M = 2.98°, SD = 6.90°), $t(9) = 1.36, p = .10$, although the direction of the mean was consistent with the prediction. Figure 7 reveals phase lags of the right limb instead of the expected phase leads in the analysis of the anti-phase mode (i.e., NR conditions in panels C and D). For X_R Y_L, a phase lag was confirmed with a one-tailed $t$-test, testing for $\phi_{AP} < 180^\circ$, (M = 171.64°, SD = 7.23°), $t(9) = -3.66, p < .001$. For X_R X_L, a phase lag also was confirmed for $\phi_{AP} < 180^\circ$, (M = 172.26°, SD = 11.90°), $t(9) = -2.06, p < .05$, one-tailed. Paralleling the analysis of biomechanical asymmetry in the previous section, we observe an inverting of the direction of phase lead/lag as a function of the phase mode.

In sum, a right-sided functional asymmetry was associated with phase shifts away from $\phi_{IP} = 0^\circ$ and $\phi_{AP} = 180^\circ$ in the NR stance condition. A right-side phase-lead, matching the direction of previously observed phase-lead effects, was observed for $\phi_{IP}$.
comparisons (p’s < .05), except for 0.38-1.51 Hz, and 0.76-1.51 Hz. From these results, we can conclude that switching between modes occurs within a trial, albeit infrequently. The analysis of $Y_R Y_L$, additionally revealed a main effect of vision, $F(1, 9) = 15.45$, $p < .01$, $\eta^2 = .63$ and an interaction of vision and stance $F(1.17, 10.58) = 5.46$, $p < .05$, $\eta^2 = .38$. These results suggest that instances of mode switching were most frequent in the eyes open condition when standing in an asymmetry stance (Figure 8B). The interpretation of these results, in conjunction with the findings for PTC findings (Figure 6A), is that switching between modes is most frequent when the stability of coordination is lowest.

General Discussion

The ability to maintain an upright standing posture is thought to rely upon distinct means of postural stabilization, variously described as strategies, solutions, or synergies, and the ability to adaptively switch between such means with changes in context (Riley et al., 2011; Ting et al., 2009). Understanding this ability requires uncovering the principles of constraint that prescribe how neuromusculoskeletal degrees of freedom become functionally organized. Motivated by the dynamical systems approach (Chiel & Beer, 1997; Haken, 1977; Harrison & Stergiou, 2015; Kelso, 1995; Newell, 1986; Turvey, 1990; Warren, 2006), we conjectured that the HKB model captures basic principles of constraint underlying the dynamics of upright stance. Specifically, we tested hypotheses motivated by three specific predictions of the HKB model. Across trials, we manipulated stance via changes in the symmetry of support surface elevation, and the availability of visual information.

In overview, the HKB model predicts the existence of preferred modes of coordination (Prediction 1), and consistent with this prediction we observed preferences for in-phase and anti-phase coordination patterns. The HKB model also predicts the existence of imperfection parameters (Prediction 2), and consistent with this prediction we observed phase leads associated with both biomechanical and functional asymmetries. Lastly, the HKB model predicts the possibility of metastable coordination dynamics (Prediction 3). Consistent with this prediction we found that observed coordination patterns took the form of transient epochs of stable phase relations, and that observed patterns of coordination were neither highly stable (i.e., persisting throughout the trial) nor completely unstable (i.e., an absence of coordination).

Imperfection Parameters of the Dynamics of Upright Stance

We predicted the existence of imperfection parameters in the dynamics of upright stance (Prediction 2). In general terms, an imperfection parameter introduces a difference between coupled oscillatory subsystems that breaks (or redistributes) the symmetry of the coordination dynamics (Kelso, 1994; Park & Turvey, 2008). In the HKB model, the predicted “characteristic” effects of an imperfection parameter are a shift in mean relative phase away from the otherwise preferred states of $\phi = 0^\circ$ and $\phi = 180^\circ$, and a reduction in the stability of solutions. We hypothesized that a manipulation of biomechanical asymmetry (i.e., standing with asymmetric limb loading and limb lengths) and the existence of a functional asymmetry (i.e., right sided functional preference for kicking a ball and standing on one leg) would each produce the characteristic effects of imperfection parameters.
Our hypothesis that functional asymmetry acts as an imperfection parameter in the dynamics of upright stance is supported by our finding that the studied group of “right footed” participants exhibited a righted-side phase lead in both dominant coordination patterns. By comparison, Wang and Newell (2012a), who did not selectively recruit participants based upon footedness, reported relative phase values that were close to zero under similar experimental conditions. A stronger test of this hypothesis would be achieved by testing whether a left-side phase lead is observed in groups of “left footed” participants. Our hypothesis that biomechanical stance asymmetry acts as an imperfection parameter in the dynamics of upright stance was supported with our observation of shifts in phase away from zero in the asymmetric stance conditions. For the dominant (i.e., most frequently observed) coordination mode of $Y_R Y_L$ we observe a phase lead in the less-loaded/shortened/raised leg. For the dominant in-phase coordination mode of $X_R X_L$, this direction of effect is reversed. For the dominant coordination modes of both $Y_R Y_L$ and $X_R X_L$, we also observed the expected decrease in the stability of coordination associated with biomechanical asymmetry.

It is clear from our results that right footedness and asymmetric limb loading are both associated with systematic phase leads. It is not presently clear whether these results should be interpreted as being caused by two distinct imperfection parameters, or only one. When two distinct imperfection parameters are simultaneously introduced into the task of coordinating two hand-held pendulums the effects of the effects of imperfection parameters have been shown to be approximately additive (Park & Turvey, 2008). If this finding generalizes to the dynamics of upright stance, we would have expected the effect of right footedness to combine additively with the effect of riser condition. For example, in the case of the mean $\phi_{IP}$ for the $Y_R Y_L$ output pair (Figure 7A and B), we would have expected the magnitude of the phase deviation evident in the NR condition to add to the magnitude of the phase deviation in the RR condition, and to subtract from the magnitude of the phase deviation in the LR condition. Contrary to this expectation, we found a reliable difference between the LR and NR conditions, but no difference between the RR and NR conditions. Our results are markedly mixed on this issue. For a contrary example we can look at the case of mean $\phi_{AP}$ for the $Y_R Y_L$ output pair in the eyes-closed condition (Figure 7D). Here, the pattern of results appears to align with an assumption of additivity. Gaining clarity on this issue in future research studies will provide insight into what counts as an imperfection parameter in the dynamics of upright stance. If we assume that two imperfection parameters are implicated in our results, then it is reasonable to conclude that they are interpretable as functional and biomechanical asymmetries. If in contrast, we assume that only one imperfection parameter exists, we would need to identify a common underlying asymmetry. One possibility is attentional asymmetry, where both right-footedness and a raised right foot may similarly lead participants to preferentially attending to their right limb.

The predicted effects of phase leads and reduced pattern stability were reliably observed in our analysis of the in-phase coordination in $Y_R Y_L$ (i.e., the most frequently observed pattern in our analysis), and were mostly observed in our analysis of in-phase coordination in $X_R X_L$ (the next most frequently observed pattern). In sharp contrast, the pattern of results observed in our analysis of anti-phase coordination (i.e., the less frequently observed non-dominant patterns) was the exact opposite of what was predicted. This systematic flipping of effects indicates to us that a higher-order dynamic is operating to constrain the form and stability of the four coordination patterns that we have observed. We would expect that the symmetries in our results to be revealing of the symmetries of this higher-order dynamic, and the imperfection parameters of that system to be the cause of breaks or redistributions in that symmetry.

We use the term higher-order dynamic here to mean some dynamical process that is operating upon and acting to organize the various states of coordination we have studied here. We conjecture that such a dynamical process could act as a basis for self-organized switching between coordination states (e.g., from the in-phase mode of $Y_R Y_L$ to the anti-phase mode of $Y_R Y_L$). In general terms such a process would entail some form of parameter or graph dynamics (Saltzman et al., 2006). From the theoretical perspective of coordination dynamics, we would want to identify a specific higher order collective variable, such that changes in this variable would capture the switching between the lower-order states of coordination we have studied here. One potential candidate has been identified by Wang et al. (2014). They demonstrated that COP – COM (i.e., the difference between the center of pressure and the center of mass) is a higher-order collective variable for the dynamics of human standing posture.

**Understanding Upright Stance as a Metastable Dynamical System**

We observed coordination patterns between the limbs taking the form of transient epochs of stable phase relations. This observation was consistent with our prediction (Prediction 3) that coordination between the limbs should exhibit the properties of a metastable dynamics. Kibele et al. (2015) proposes that the biomechanics of upright stance is more adequately characterized through the concept of metastability than it is through concepts such as static stability, instability, and equilibrium, which are better suited for the mechanics of rigid bodies. In
their proposal, the concept of metastability is needed for capturing the complementary macro constraints of stability and mobility and the spatial interplay between the base of support and the projection of center of mass. We suggest that metastability is also needed for adequately characterizing the functional organization ongoing at the deeper level of coordinating neuromuscular degrees of freedom.

Metastable coordination has been interpreted to be a functional state of system organization, as opposed to simply being an impoverished or noisy form of stable coordination (Haken, 1977; Harrison & Stergiou, 2015; Kelso, 2012). The functionality of metastability is assumed to lay in the flexibility it affords. Metastable dynamics are thought to underlie the rapid and flexible reorganizations of brain states supporting effective perception and action (Bressler & Kelso, 2001; Dotov, 2014; Harrison & Stergiou, 2015; Kelso, 2012; van Leeuwen et al., 1997).

Our finding of metastability (see also Creath et al., 2005; James, 2013; Wang et al., 2012; Wang & Newell, 2012a; 2012b) and confirmations of predictions drawn from a simple dynamical model of coordination suggest that the task of maintaining an upright stance can be understood as a metastable dynamical system. Interpreted as such, the task of maintaining an upright standing posture can be understood to be supported by multiple coexisting transiently stable dynamical solutions, called metastable modes. Each metastable mode captures a coordination of neuromusculoskeletal degrees of freedom that can potentially support effective balance. Metastable systems balance qualities of stability and flexibility. Applied to upright stance, stability results from the transient stability of a context-relevant metastable mode of inter-limb coordination. The property of flexibility results from the coexistence of other metastable modes that are adapted to other contexts. Understood in this manner, metastability affords the exploration of varied and redundant means of postural stabilization and a basis for uncovering those means that are best adapted to the constantly evolving demands of the task and the situation. In our results, the nature of flexibility is revealed in two ways: firstly, in the changing relative stabilities of dynamic modes across trials as a function of the manipulation of stance and vision, and secondly, in the transient stability of modes within a trial. Taken together, these two types of flexibility suggest that the context defined by a specific manipulation of stance and vision constrains, but does not determine, the metastable modes observed. We assume that these dependencies reflect functional adaptations to context. Given this assumption we might interpret the destabilization of the dominant in-phase modes of $X_RX_L$ and $Y_RY_L$ in the asymmetric stance conditions as being associated with a decrease in the effectiveness of symmetrically coupling these degrees of freedom in this context. Following this logic, we might expect to see that the coordination asymmetric degrees of freedom, such as $X_RY_L$ and $Y_RX_L$, is contrastingly stabilized in asymmetric stance conditions.

The existence of mode switching within a trial suggests that other contextual factors, beyond the experimental manipulations of stance and vision, may be at play. Changes in the internal physiological context of upright stance, resulting from factors such as mild fatigue and discomfort (e.g., venous pooling) resulting from prolonged bouts of standing, are thought to produce intermittent changes in posture, such as shifts in body weight support, drifts, and fidgets (Duarte et al., 2000).

With respect to visual information, we found reduced stability (i.e., lower PTC) and greater coordinative flexibility (i.e., more frequency mode switching) in the eyes open condition. We suggest that the availability of visual information in the eyes open condition produced a situation in which visual information could modulate the dynamics. Specifically, with vision, more possibilities become available for the perceptual regulation of quiet standing posture, both in terms of the relative contributions of different perceptual systems (Peterka, 2002) and in terms of the frames of reference utilized by a specific perceptual system (Stoffregen et al., 2000). We speculate that with more informational support available, the postural control system is better positioned or “poised” to make transitions to other biomechanical configurations, and correspondingly different coordinative dynamics, that are potentially better context adapted. Thus, the availability of vision may offer greater adaptive flexibility and make it more likely newly selected affordances are successfully exploited in a timely manner. This is potentially suggested in the PTC and mode switching results that show that the effect of asymmetric stance is enhanced in the eyes open condition.

Can metastable Modes be Related to Postural Control Strategies?

We predicted the existence of preferred states in the coordination of the left and right legs (i.e., relative phases of $0^\circ$ and $180^\circ$) (Prediction 1). As predicted, we observed metastable coordination states with mean relative phase values close to $0^\circ$ and $180^\circ$, in our analysis of both $X_RX_L$ and $Y_RY_L$. Having identified these states, it is important to consider what these metastable states mean? One possibility is that the observed metastable states can be directly interpreted distinct means of maintaining upright stance.

The idea that distinct means of maintaining upright stance (e.g., strategies, synergies, solutions) exist, has been used to understand both quiet and perturbed stance. The distinction between quiet and perturbed stance picks out a difference between the basic task of maintaining a postural configuration against the destabilizing forces of
gravity (quiet stance), and the task of maintaining upright stance against externally imposed forces (other than gravity) or internally generated forces related to satisfying the demands of super-postural tasks (perturbed stance). Studies of coordinated postural responses to imposed perturbations such as physical pushes and pulls reveal clearly distinct means of maintaining upright stance (Horak & Nashner, 1986; Maki et al., 2003; McIlroy & Maki, 1993; Nashner, 1977). In these studies, ankle, hip, stepping, and reaching strategies exhibit distinct intersegmental kinematics and muscle recruitment patterns. In the case of quiet stance, distinct mechanisms have also been distinguished via analysis of centers of pressure and ground reaction forces under the two feet. These mechanisms include ankle, hip, and hip load/unload strategies (Day et al., 1993; Winter et al., 1996). The metastable coordination patterns in the kinematics of quiet standing, observed by James (2013) and Creath et al. (2005), were interpreted as transiently stable instances of hip and ankle postural control strategies. The fact that we did not see any evidence of a switch in preference for in-phase versus anti-phase modes above and below 1 Hz in our frequency band analysis (c.f. Creath et al., 2005) suggests that the observed coordination patterns may not correspond to hip and ankle strategies. Given the medial-laterally oriented coordination patterns ($X_R X_L$) it is possible that the observed coordination patterns correspond to postural control strategies involving ankle inverters/evertors and/or hip abductor/adductors (Winter et al., 1996). The implication of the former of these strategies would be consistent with the observed increase in stability of the anti-phase modes of $X_R X_L$ and $Y_R Y_L$ with stance asymmetry (Winter et al., 1996).

Direct tests of these possibilities will require concurrent analyses of coordination patterns in COP trajectories and joint kinematics, and net COP and center of mass trajectories. At this juncture we can form some conjectures regarding the gross biomechanical functions associated with each of the four observed metastable modes. The in-phase mode of $Y_R Y_L$ is likely associated with synchronized shifts in COP$_L$ and COP$_R$ that are coordinated with anterior-posterior fluctuations of the center of mass. The anti-phase mode of $Y_R Y_L$ is likely associated with rotations and torques of the body about its vertical axis. The in-phase mode of $X_R X_L$ is likely associated with widening and narrowing of the functional base of support via changes in the lateral separation of COP$_L$ and COP$_R$. Lastly, the anti-phase mode of $X_R X_L$ is likely associated with medial-lateral weight shifts. The fact that in the present study both stance and vision produced more pronounced effects in the lower frequency bands suggests that distinct functional organizations of posture may be implicated across these time scales. This is consistent with recent claims that distinct functional networks for postural control exist, and that these distinct networks have distinct characteristic timescales (Kerkman et al., 2018).

**HKB as a General Model of the Dynamics of Upright Stance**

It has been suggested that a unified framework exists for understanding upright standing posture under both quiet (i.e., unperturbed) and perturbed stance conditions (Creath et al., 2005). On this issue, our findings contribute to a growing body of evidence that shows that dynamics of the HKB model exist in the dynamics of both quiet and perturbed stance. The evidence for the HKB model applying to perturbed stance is as follows: When participants stand on a rhythmically oscillating support surface distinct stable coordination patterns between ankle, hip, and knee reliably emerge from intersegmental interactions (Ko et al., 2001). Consistent with HKB model predictions, spontaneous transitions between stable in-phase ($\phi \approx 0^\circ$) and stable anti-phase ($\phi \approx 180^\circ$) coordination patterns are observed when the frequency of platform oscillation is increased (Buchanan & Horak, 1999; Ko et al., 2003). HKB model predictions have also been borne out in studies in which participants intentionally track the oscillatory movements of a seen target with coordinated anterior-posterior body sway (Bardy et al., 1999, 2002). The confirmed theoretical predictions of the HKB model include the existence of stable in-phase and anti-phase hip-ankle coordination patterns, frequency induced transitions from in-phase and anti-phase patterns, and critical fluctuations observed near the transition region. Paralleling our findings, the stability of the postural coordination patterns emerging during rhythmic platform oscillation has been found to depend upon the availability of visual information (i.e., eyes-open vs. eyes closed) (Buchanan & Horak, 1999). In sum the HKB model appears to apply to both quiet and perturbed standing posture, and the principal difference between the dynamics observed in our results (for quiet stance), and the dynamics observed in the above-mentioned studies of perturbed stance, appears simply to be the stability of the HKB dynamics.

**Future Directions**

A question that needs to be forefront of future research into the HKB dynamics of upright standing posture is “How is upright standing posture usefully understood as a system with stable/metastable HKB dynamics?” An effective way to evaluate whether the task of maintaining upright stance is usefully understood in terms of HKB dynamics, will be to attempt to reconcile our analysis with others in the literature. For example, how do the dynamics of metastable modes relate to patterns of body sway, net COP adjustments, and muscle recruitments? Particularly pertinent analyses
include mapping the dynamics of metastable modes onto (1) fidgets, shifts, and drifts in net COP trajectories (Duarte et al., 2000), (2) intermittencies of ballistic control (Loram et al., 2005; Loram & Lakie, 2002; Stins & Roerdink, 2018), (3) onsets of informationally guided control relative to boundaries of stability (Haddad et al., 2006; Martin, 1990; Pai et al., 1998), and (4) the coordination dynamics between the center of mass and the center of pressure (Wang et al., 2014). One of the most powerful features of the HKB model is the ability to produce self-organized switching between different coordination patterns. A key question, regarding the efficacy of postural control, is whether the self-organized switching dynamics of the of HKB model plays an important role in supporting adaptive balance. On a similar vein, we might also ask whether imperfection parameters can provide a useful means adaptively tuning the dynamics of upright stance to the demands of the current situation.

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DISCLOSURE STATEMENT

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