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Handedness and the Asymmetric Dynamics of Bimanual Rhythmic Coordination

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Human handedness was investigated in a 1:1 interlimb rhythmic coordination in which consistent and inconsistent left-handed and right-handed individuals oscillated hand-held pendulums. Mean phase difference (ϕ_{stable}) and its standard deviation ($SD\phi$) were evaluated as functions of mode of coordination (in-phase vs. anti-phase) and the symmetry conditions imposed by controlling the natural frequencies of the left and right pendulums. The dependencies of ϕ_{stable} and $SD\phi$ on coordination mode and imposed symmetry were found to be systematically affected by handedness. The data were consistent with an elaboration of the established order parameter dynamics of interlimb rhythmic coordination. The elaboration includes additional 2π periodic terms that break the symmetry of those dynamics when the natural frequencies of the component rhythmic units are identical.

The functional asymmetry of the upper limbs and of the cerebral mechanisms that subserve them is well-known (e.g., Corballis, 1991; Herron, 1980, Kinsbourne, 1978; Porac & Coren, 1981). For most people there is a bias toward using the right hand for manual tasks; although the two hands undoubtedly work together as a synergy (Guiard, 1987a), in both unimanual and bimanual tasks, performance distinctions between the upper limbs can be readily observed (e.g., Summers, 1990). Although few distinctions can be stated formally in strictly quantitative terms, it is apparent that left-handedness is not simply the converse of right-handedness and that, as a general rule, any asymmetry found in right-handed (RH) people tends to be smaller and in the opposite direction in left-handed (LH) people (Coren, 1990; Peters, 1990a; Peters & Durding, 1979; Springer & Deutsch, 1985).

The degree of laterality expressed is, however, a function of the particular task constraints. For example, musicians who play keyboard instruments (which necessarily permit greater independence of the hands), express a greater degree of handedness than do musicians who play strings and woodwinds (which necessarily require integrated movements; Christman, 1993). In a simple tapping task, intermanual differences depended on the degree of excursion of the fingers with smaller amplitudes entailing greater variability in force precision, especially of the left hand of RH participants (Peters, 1980). In addition, the rate at which a task is performed has been shown to influence expressed laterality with smaller intermanual differences produced by lower when compared with higher rates of performance (Rouselle & Wolff, 1991; Todor & Smiley, 1985; Wolff, Hurwitz, & Moss, 1977). It is also known that the hands can produce complex, nonisochronous rhythms (Treffner & Turvey, 1993), but performance is optimal provided the preferred hand implements the faster rhythm (Peters & Schwartz, 1989). This requirement has been interpreted in terms of the degree of attention that can be directed at the preferred or nonpreferred hand (Peters, 1981, 1985).

Others have investigated laterality from the perspective of dual-task paradigms in which both linguistic and manual activities are performed concurrently (Hammond, 1990a; Peters, 1990b). The interaction between tasks supposedly represented in the left hemisphere (thought to control both linguistic ability and movements of the right hand) led Kinsbourne and Hicks (1978) to adopt an account of laterality in terms of competition within a "functional cerebral space." However, although most left-handers are left-hemisphere-dominant for speech, the left-handers were subsequently shown to exhibit interference in the left hand rather than the right hand (Rey, Dellatolas, Baucard, & Talairach, 1988). This evidence indicates that the assumed competition may not take place where the motor commands to the left hand are issued (Peters, 1990b) but that such interference effects may be related to more general timing constraints as when both hands show increased variability under simultaneous, irregular speech (Todor & Smiley, 1985). In this article, we draw on these results in developing an account of handedness from the perspective of dynamics. That is, using the language of nonlinear dynamical systems, an alternative description may be developed that captures more precisely the intermanual cooperation and competition inherent in simple bimanual acts (Carson, 1993).

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Broken Symmetry and 1:1 Frequency Locking

Symmetries are formed and broken in dynamical systems (Stewart & Golubitsky, 1992). That is, the instability of a symmetric state (with a low degree of order) usually evolves in such a way that it leads to states of lesser symmetry but greater stability (and higher degree of order). Let the state of bilateral symmetry of the hands (H) be designated by $\Delta H = (L - R) = 0$; then left-handedness (L) is $\Delta H > 0$ and right-handedness (R) is $\Delta H < 0$. In strictly dynamical terms, the rarity of $\Delta H = 0$ in humans would reflect a fundamental instability in the bilateral symmetric pattern. The broken symmetries of $\Delta H > 0$ and $\Delta H < 0$ would reflect the stable solutions to the bifurcation from $\Delta H = 0$, with $\Delta H < 0$ being more accessible than $\Delta H > 0$. Therefore, if human handedness originated strictly in the nature of the dynamics of the human movement system, then questions of why $\Delta H = 0$ is unstable and why $\Delta H < 0$ is the most frequently observed broken symmetry would be legitimate questions. It is doubtful, however, that any left–right asymmetry exhibited by a biological system is understandable through dynamical instabilities at the scale at which it is manifest (Bock & Marsh, 1991). In the case of humans, for example, handedness is not likely to originate at the scale of unimanual or bimanual acts. If any consensus is to be found on the origin of handedness in its varied forms (as contrasted with its genetic propagation once it has originated), it is that handedness may be the outcome of nature repeatedly amplifying the tiny asymmetry of the weak interaction between elementary particles (Mason, 1991).

The focus of our research was on handedness in the most commonplace interlimb coordination, one that requires both limbs to execute the same spatiotemporal pattern. In ordinary human walking, for example, contralateral limbs exhibit 1:1 frequency locking as do ipsilateral limbs. Although stereotypic and apparently simple, 1:1 frequency locking of limbs and limb segments results from a complex of competitive and cooperative processes (Kelso & Jeka, 1992; Schmidt, Beek, Treffner, & Turvey, 1991; Schmidt, Treffner, Shaw, & Turvey, 1991). Because of their difference in size, an arm and a leg will differ in their uncoupled, natural frequencies (eigenfrequencies). The preferred frequency of the shorter and lighter arm is higher than that of the longer and heavier leg. For an arm and a leg to complete their respective cycles in the same amounts of time, that is, to exhibit a single coupled frequency, the competition between their natural frequencies must be overcome. In studies of the oscillating fins of the fish (*Labrus*) von Holst (1939/1973) referred to the coupling or cooperation between the two rhythmically moving fins as the "magnet effect" (i.e., each tries to align the other to its own frequency) and the competition between them as the "maintenance tendency" (i.e., each tries to continue oscillating at its preferred, uncoupled frequency). In this research, we studied human handedness in terms of similar competitive and cooperative processes.

Order Parameter Dynamics

The dynamics of interlimb rhythmic coordination have been modeled successfully by

$$\dot{\phi} = \Delta\omega - a\sin(\phi) - 2b\sin(2\phi) + \sqrt{Q}\,\xi_t, \tag{1}$$

an order parameter equation developed by Haken, Kelso, and Bunz (1985), Schöner, Haken, and Kelso (1986), and Kelso, DelColle, and Schöner (1990). In Equation 1, $\dot{\phi}$ is the time derivative of the phase difference, $\phi = (\theta_L - \theta_R)$, between the left (L) and right (R) oscillators. Because $\phi = (\theta_L - \theta_R)$ is a collective variable that captures the spatiotemporal organization of the rhythmically moving limbs, and because it changes more slowly than the variables characterizing the states of the rhythmically moving limbs (e.g., velocity, amplitude), it can be considered an order parameter for interlimb coordination (e.g., Haken, 1977, 1983; Haken et al., 1985; Kelso, Schöner, Scholz, & Haken, 1987). $\Delta\omega$ is the difference ($\omega_L - \omega_R$) in eigenfrequency between the two oscillators, a and b are coefficients that affect the interoscillator coupling, and ξ_t is a Gaussian white noise process (arising from the multiplicity of underlying subsystems) functioning as a stochastic force of strength Q.

In our research, the importance of Equation 1 lies in its predictions of the stationary states of interlimb coordination when the symmetry of the coordination dynamics is broken or lowered. The latter occurs when the individual biological oscillators are no longer equivalent, such as when the two rhythmically moving limb segments differ in their eigenfrequencies, that is, $\Delta\omega \neq 0$. Under such circumstances, a greater $\Delta\omega$ entails a lower degree of symmetry. The stationary states can be determined by solving Equation 1 numerically for $\dot{\phi} = 0$. Graphically, solutions to Equation 1 with $\dot{\phi} = 0$ can be obtained by plotting its right-hand side (excluding the stochastic force) against ϕ for various parameter values (Kelso et al., 1990). The stationary values, ϕ_{stable}, are given where $\dot{\phi}$ crosses the ϕ axis. These stationary states are stable if $d\dot{\phi}/d\phi$, the gradient at the zero-crossing, is negative and unstable if $d\dot{\phi}/d\phi$ at the zero-crossing is positive. The degree of stability is related to $|d\dot{\phi}/d\phi|$; that is for a constant Q, the steeper the (negative) slope at the zero-crossing, the more stable is the stationary state (Gilmore, 1981). For parameter values of $a > 0$ and $b > 0$ exceeding a critical value of b/a, negative zero-crossings occur in the vicinity of both $\phi = 0$ (in-phase) and $\phi = \pi$ (anti-phase).[1] Equation 1's predictions about stationary states in interlimb 1:1 frequency locking include the following:

1. When $\Delta\omega = 0$, ϕ_{stable} equals 0 and π, for any b/a.
2. When $\Delta\omega = 0$, $|d\dot{\phi}/d\phi|$ is greater at $\phi_{\text{stable}} = 0$ than at $\phi_{\text{stable}} = \pi$.

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[1] For $\Delta\omega = 0$, ϕ_{stable} in the vicinity of $\pm\pi$ (anti-phase coordination) is eliminated at $b/a = .25$, independently of the absolute values of a and b. For $\Delta\omega \neq 0$, the critical value of b/a differs from .25 and depends on the parameters' absolute values. The predictions that follow are for b/a values larger than the critical b/a values.

3. When $\Delta\omega \neq 0$, $\phi_{\text{stable}} \neq 0$ and $\phi_{\text{stable}} \neq \pi$.
4. When $\Delta\omega \neq 0$, the displacement of ϕ_{stable} from π is greater than that of ϕ_{stable} from 0.
5. When $\Delta\omega \neq 0$, $|d\dot{\phi}/d\phi|$ at ϕ_{stable} is smaller for larger $\Delta\omega$.
6. When $\Delta\omega \neq 0$, $|d\dot{\phi}/d\phi|$ at $\phi_{\text{stable}} \cong 0$ is greater than at $\phi_{\text{stable}} \cong \pi$.
7. For a constant b/a, larger values of $\Delta\omega \neq 0$ are associated with larger displacements of ϕ_{stable} from $\phi = 0$ and $\phi = \pi$. Similarly, for a given $\Delta\omega \neq 0$, the smaller the magnitude of b/a, the larger are the displacements of ϕ_{stable} from $\phi = 0$ and $\phi = \pi$.
8. For a constant b/a, the larger the magnitude of $\Delta\omega \neq 0$ the smaller is $|d\dot{\phi}/d\phi|$ at ϕ_{stable}. Similarly, for $\Delta\omega = 0$ and for a constant $\Delta\omega \neq 0$, the smaller the magnitude of b/a, the smaller is $|d\dot{\phi}/d\phi|$ at ϕ_{stable}.

Some of these predictions are visible in Equation 1 when it is restricted to the in-phase mode. Proximity to $\phi = 0$ means that Equation 1 may be linearized (ϕ is sufficiently small so that $\sin\phi = \phi$) (Haken, 1988; Schöner et al., 1986). Then, for $\dot{\phi} = 0$ and ignoring the noise term, Equation 1 becomes

$$\dot{\phi}_{\text{stable}} = \Delta\omega/(a + 4b). \tag{2}$$

Predictions similar in form to Predictions 1–8 are also derivable from the nonlinear coupled oscillator dynamics proposed by Cohen, Holmes, and Rand (1982), Rand, Cohen, and Holmes (1988), and Haken (1983):

$$\dot{\phi} = \Delta\omega - K\sin\phi \tag{3}$$

$$\phi_{\text{stable}} = \arcsin(\Delta\omega/K), \tag{4}$$

where K is the coupling strength (positive for in-phase and negative for anti-phase). To accommodate fluctuations in coordination, a stochastic force of the kind identified in Equation 1 can be added to Equation 3 (Schmidt & Turvey, 1994; Turvey, Schmidt, & Beek, 1993). The sine coupling function of Equation 3 is common to many formulations of linked biological oscillators (e.g., Niebur, Schuster, Kammen, & Koch, 1991; Daido, 1992; Strogatz & Mirollo, 1988). Equation 1, however, underscores that more complicated nonlinear forms are demanded by the experimental data on interlimb coordination.

Most of Predictions 1–8 have been evaluated and confirmed through experiments that manipulated ϕ_{ψ} (the intended coordination of 0 or π), $\Delta\omega$ (defined as $\omega_L - \omega_R$), and the coupled frequency of coordination, ω_c (which is inversely correlated with b/a). The quantities ϕ_{ψ}, $\Delta\omega$, and ω_c were manipulated within a procedure that involves a seated person oscillating hand-held pendulums parallel to the sagittal plane about an axis in the wrist (with other joints fixed; Kugler & Turvey, 1987). The pendulums can vary physically in length and mass (e.g., length of shaft, magnitude of attached weights). The eigenfrequency of an individual "wrist-pendulum system" can be estimated as the eigenfrequency of the equivalent simple gravitational pendulum, $\omega = (g/L)^{1/2}$, where L is the simple pendulum length and g is the constant acceleration attributable to gravity. In the experiments supporting Predictions 1–8, $\Delta\omega$ was controlled through differences in the lengths of the left and right pendulums, and ω_c was the comfort frequency freely chosen by the participant or controlled by a metronome (Schmidt, Beek, Treffner, & Turvey, 1991; Schmidt, Shaw, & Turvey, 1993; Schmidt & Turvey, 1994; Sternad, Turvey, & Schmidt, 1992; Turvey, Rosenblum, Schmidt, & Kugler, 1986).

New Observables for Studying Left–Right Asymmetry and Handedness

The order parameter dynamics identified earlier provide new measures (see Carson, 1993) by which the contribution of the body's functional asymmetry ΔH to interlimb rhythmic coordinations can be determined. In this research we focused on two primary observables:

1. ϕ_{stable}, particularly its deviation from the intended (ψ) phase $\phi_{\psi} = 0$ or $\phi_{\psi} = \pi$. Equation 1 predicts a systematic dependence of the magnitude of ϕ_{stable} on $\Delta\omega$ and, therefore, a systematic dependence of $|\phi_{\text{stable}} - \phi_{\psi}|$ on $\Delta\omega$. Given that the sign of $\Delta\omega = (\omega_L - \omega_R)$ reflects which hand-pendulum system has the higher frequency, the magnitude of $|\phi_{\text{stable}} - \phi_{\psi}|$ may depend not only on the absolute magnitude of $\Delta\omega$ but also on its sign if ΔH (the intrinsic functional asymmetry of the body) interacts with $\Delta\omega$ (the imposed asymmetry on the order parameter dynamics).
2. The standard deviation of ϕ. Equation 1 says that the degree of stability of ϕ_{stable}, indexed by $|d\dot{\phi}/d\phi|$, changes with $\Delta\omega$ and the coupling coefficients a and b. At issue in our research was whether ΔH, the difference between the hands, would affect the fluctuations of interlimb coordination and, if it did, to what extent the effect was exerted through $\Delta\omega$.

Method

Participants

Forty undergraduates (14 men and 26 women) at the University of Connecticut participated in the experiment in order to attain course credit. Twenty defined themselves as RH and 20 defined themselves as LH. In accordance with research by Peters (1990a, 1990c, 1991, 1992; Peters & Servos, 1989) indicating a strong performance distinction between the population of self-labeled left-handers who predominantly prefer the left hand for manual activities (consistent left-handers) and those who are less asymmetrical with respect to preference (inconsistent left-handers), the self-labeled left-handers were further subdivided on the basis of their response to a short questionnaire regarding which hand they preferred in certain tasks (i.e., holding a hammer, combing hair, holding a spoon, brushing teeth, writing and drawing, throwing a ball). Because throwing has been shown to be a strong predictor of consistency in LH individuals (Peters, 1990a, 1990c; Peters & Murphy, 1993), if an LH participant gave a response of "right hand or either" to the question regarding throwing a ball, and to at least one other question (excluding writing), then he or she was called an *inconsistent left-hander* (ILH); otherwise, the participant was called a *consistent left-hander* (CLH). There were 4 CLH and 6 ILH in the antiphase group and 6 CLH and 4 ILH in the in-phase group. The 20 RH participants were assigned to a group performing the in-phase mode or a group performing the anti-phase mode by order of appearance at the laboratory. A similar assignment was made for the 20 LH participants. Therefore, there were four groups of 10 participants each: RH in-phase, RH anti-phase, LH in-phase, and LH anti-phase.

Apparatus

A participant sat in a specially designed chair with arm rests that permitted comfortable support of both left and right wrists during oscillatory movements. The chair also provided leg rests that permitted raising the legs toward the horizontal in order to avoid interference with data collection. Kinematic data were collected using a three-dimensional sonic digitizer (SAC, Westport, CT) and associated MASS kinematic analysis software (Engineering Solutions, Columbus, OH). For collecting motion data on pendulums oscillated by hand, high-frequency sound emitters (30 mm long and 5 mm wide) were attached to the ends of the pendulums. The sounds emitted were detected by four microphones aligned parallel to the ground plane at a vertical distance of 60 cm below the participant's chair. The digitizer calculated the distances of the emitter from each microphone, using the three least noisy records to pinpoint the position of the emitter in 3-space at the time of the emission. The signal was sampled at 90 Hz, passed through an A-D converter, and stored on a PC computer's hard disk. Subsequent PC and Macintosh routines computed the continuous relative phase at intervals of 44 ms of the original time series of pendulum phase.

Materials

Each pendulum consisted of an aluminum rod of 1.2 cm diameter inserted 7.5 cm into a cylindrical wooden handle of 2.5 cm diameter and 12 cm length. Three pendulums were used: one for which the aluminum rod was 56 cm in length with a 500-g steel cylinder (outside radius = 2.5 cm, inside radius = 0.61 cm, height = 3.3 cm) attached at the end opposite the handle, one for which the aluminum rod was 45 cm in length with a 100-g attached steel cylinder (outside radius = 1.9 cm, inside radius = 0.6 cm, height = 1.1 cm), and one for which the aluminum rod was 26 cm in length with a 100-g attached steel cylinder (of the same dimensions as the preceding). As noted in the introduction, the eigenfrequency of an individual wrist-pendulum system can be estimated as the eigenfrequency (in rad/s) of the equivalent simple gravitational pendulum, $\omega = (g/L_S)^{1/2}$. The quantity L_S is calculable from the mass and spatial magnitudes of the aluminum rod, the wooden handle, the added steel cylinder, and the hand mass through the standard methods for calculating the first and second moments of any arbitrary rigid body oscillating about a fixed point and representing it as a simple pendulum oscillating about the same point (Kugler & Turvey, 1987). The ωs of the three wrist-pendulum systems were 5.72, 4.69, and 4.17 rad/s. Five coupled conditions were formed by combining the three systems according to $\Delta\omega = (\omega_L - \omega_R) = (4.17 - 5.72), (4.17 - 4.69), (4.17 - 4.17), (4.69 - 4.17)$, and $(5.72 - 4.17)$, yielding the five $\Delta\omega$ values of -1.55, -0.52, 0, 0.52, and 1.55.

The eigenfrequency of the coupled system was also estimated under the assumption that it would be the preferred time scale of the right and left wrist-pendulum systems coupled such that θ_R is always, at every instant, equal to θ_L or to $(\theta_L + \pi)$ (Kugler & Turvey, 1987; Sternad et al., 1992). The latter ideal would be achieved if the coupling between the two oscillators was functionally equivalent to that of a rigid connection (Kugler & Turvey, 1987). The simple pendulum equivalent L_v of a compound pendulum so composed (i.e., of two pendulums connected by a rigid bar) is given by

$$L_v = (m_1 l_1^2 + m_2 l_2^2)/(m_1 l_1 + m_2 l_2), \tag{5}$$

where m_i and l_i refer to the mass and the equivalent simple pendulum length, respectively, of an individual (compound) pendulum system. Through Equation 5, two coupled pendulums of lengths L_L and L_R can be interpreted as a virtual (v) pendulum of length L_v with an eigenfrequency $\omega_v = (g/L_v)^{1/2}$. The values of ω_v for the three values of $|\Delta\omega|$ were 4.48, 4.35, and 4.17 rad/s. These values expressed as periods (1.402, 1.444, and 1.509 s, respectively) defined the temporal units for setting the metronome tempos used to control the coupled frequencies. Although the frequency of coordination for the coupled system had been planned as being equal to ω_v, the coupled system's eigenfrequency, a computational error led to its marginal overestimation. Consequently, each coupled system was oscillated at a frequency marginally greater than its eigenfrequency: 1.07 ω_v. The purpose of equating the coupled frequency of each system in units of ω_v was to render them alike in terms of coupling strength, indexed in Equation 1 by b/a (see Sternad et al., 1992).

Procedure

The participant sat in a chair and placed his or her arms on the arm rests. He or she was given a pendulum in each hand and told to swing them from the wrist joints in the sagittal plane. Furthermore, the participant was told to look straight ahead rather than at the pendulums. Each participant was told to grasp the handles firmly throughout the oscillations prohibiting, thereby, motions of the pendulum relative to the hand. After receiving instructions from the experimenter, each participant was given practice swinging a pendulum pair. The participant was asked to begin swinging the pendulums at the tempo prescribed by an electronic auditory metronome (that emitted short duration blips) positioned 150 cm behind the participant's seat and to say "ready" when that goal had been achieved (usually in a matter of 5–10 s). The experimenter then started to record the trial for 20 s, during which the metronome remained on. At the end of the data collection, there was a short pause of 1 min while data were stored on disk and the experimenter replaced the pendulums with another pair for the next trial. Each condition had 4 trials and the order of the conditions was completely randomized across the 20 trials. Participants received no feedback about their performance. The overall experiment took about 30 min per participant.

Data Reduction

The data records were subjected to software analyses to determine the time series of the individual wrist-pendulum phase angles θ_L and θ_R, the time series of the relative phase angle ϕ between the two wrist-pendulum systems, and the means and standard deviations of these quantities. A peak picking algorithm was used to determine the time of maximum forward extension (ulna extension) and maximum backward extension (ulna flexion) of the wrist-pendulum trajectories. From the peak forward extension times, the mean frequency of oscillation for the nth cycle was calculated as

$$f_n = 1/(\textit{time of forward extension}_n - \textit{time of forward extension}_{n+1}). \tag{6}$$

The mean frequency of oscillation of a trial was calculated from these cycle frequencies.

The phase angle of each wrist-pendulum system (θ_i) was calculated for each sample (90/s) of the displacement time series to produce a time series of θ_i. The phase angles of wrist pendulum i at sample j (θ_{ij}) were calculated as

$$\theta_{ij} = \arctan(x_{ij}/\Delta x_{ij}), \tag{7}$$

where the numerator on the right-hand side is the velocity of the time series of wrist pendulum i at sample j divided by the mean angular frequency for the trial, and Δx_{ij} is the displacement of the time series at sample j minus the average displacement for the trial. The relative phase angle (ϕ) between the two coordinated wrist-pendulum systems was calculated for each sample as the magnitude of $\theta_L - \theta_R$. Equation 7 provides a reliable basis for determining ϕ because the waveforms of both left and right oscillators are of like kind (almost sinusoidal because of the constraints of pendular motion) and because the center of oscillation of each oscillator is fixed by the seating arrangement—the oscillations take place about the wrist joints, and the forearms and wrists of each upper limb maintain constant positions during the course of each trial. The ϕ that the participant intended to produce was 0 rad (in-phase) or π rad (anti-phase). The ϕ time series allows for an evaluation of how the participant satisfied these task demands. The mean ϕ (interpreted as ϕ_{stable}) and its standard deviation were calculated for each trial and condition.

Results and Discussion

1:1 Frequency Locking

A Handedness (LH vs. RH) × Mode (in-phase vs. anti-phase) analysis of variance (ANOVA) was performed on the ratio of the average frequency of the right wrist-pendulum oscillation to the average frequency of the left wrist pendulum. No main effects of handedness or mode were found, and there was no interaction (all $Fs < 1$). For in-phase and anti-phase, and for LH and RH participants, the frequency ratio did not differ from unity ($ps > .05$, two-tailed). That is, the required 1:1 frequency was, in the mean, reliably achieved.

Phase

Figure 1 shows the magnitudes of ϕ_{stable} for the two groups ($\phi_\psi = 0$, $\phi_\psi = \pi$) of RH participants and for the two groups of LH participants as a function of $\Delta\omega$. Inspection of Figure 1 suggests that participants in all four groups conformed to the general outcome expected from Equation 1, which is in agreement with the results of previous research (Schmidt et al., 1993; Schmidt & Turvey, 1994; Sternad et al., 1992; Turvey & Schmidt, 1994). Specifically, ϕ_{stable} was closest to 0 and π when $\Delta\omega = 0$, as expected from Prediction 1, and was increasingly displaced from 0 and π by increasing values of $\Delta\omega \neq 0$, as expected from Prediction 3. The analysis of ϕ_{stable} was conducted in terms of ($\phi_{\text{stable}} - \phi_\psi$) and proceeded in two steps. Step 1 focused on the symmetry condition $\Delta\omega = 0$. Step 2 focused on the four broken symmetry conditions: $\Delta\omega = -1.55$, $\Delta\omega = -0.53$, $\Delta\omega = 1.55$, and $\Delta\omega = 0.53$.

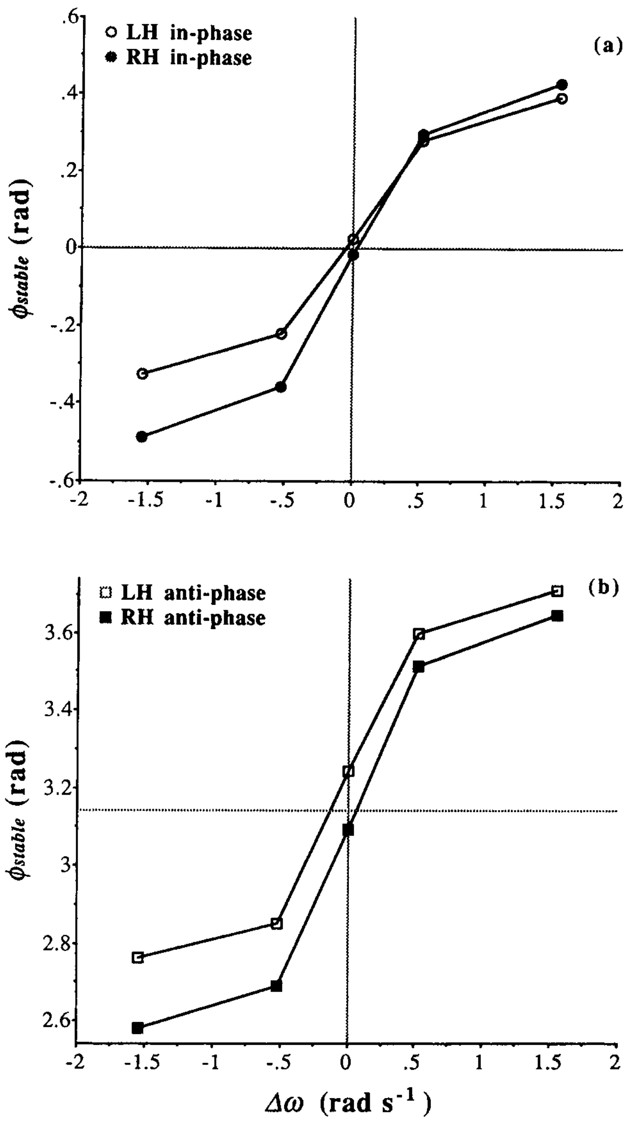

Figure 1. ϕ_{stable} as a function of $\Delta\omega$ and handedness for (a) in-phase ($\phi_\psi = 0$) and (b) anti-phase ($\phi_\psi = \pi$) coordination. RH = right-handed; LH = left-handed.

With respect to $\Delta\omega = 0$, the question of interest was whether ($\phi_{\text{stable}} - \phi_\psi$) departed significantly from zero under the in-phase and anti-phase conditions. As noted, such deviations would index the symmetry breaking of the coordination dynamics by the functional asymmetry of the limbs. Inspection of the data revealed that, of the RH participants, ($\phi_{\text{stable}} - \phi_\psi$) < 0 for 13 participants and ($\phi_{\text{stable}} - \phi_\psi$) > 0 for 7 participants. Of the LH participants, ($\phi_{\text{stable}} - \phi_\psi$) < 0 for 3 participants and ($\phi_{\text{stable}} - \phi_\psi$) $>$ 0 for 17 participants. For RH participants, the mean value of ($\phi_{\text{stable}} - \phi_\psi$) was -0.031 rad, but this was not significantly different from zero, $t(19) = -1.57$, $p > .05$. For the LH participants, the mean value of ($\phi_{\text{stable}} - \phi_\psi$) was 0.064 rad, and was significantly different from zero, $t(19) = 3.25$, $p < .001$.

Thus, compared with the LH participants, the RH participants were less uniform as a group because almost half of them had positive values of ($\phi_{\text{stable}} - \phi_{\psi}$). Given the convention $\phi = (\theta_L - \theta_R)$, the preceding pattern of departures from perfect in-phase and perfect anti-phase means that on average, for RH participants, the right hand led the left hand in 13 "Rr" participants (7 in the in-phase group and 6 in the anti-phase group) and that for LH participants, the right hand led the left hand in 3 "Lr" participants (2 in the in-phase group and 1 in the anti-phase group). Likewise, for LH participants, the left hand led the right hand in 17 "Ll" participants (8 in the in-phase group and 9 in the anti-phase group) and, for RH participants, the left hand led the right hand in 7 "Rl" participants (3 in the in-phase group and 4 in the anti-phase group). Chi-square tests were conducted to determine whether the LH and RH participants would exhibit leading-hand preferences that were different from what would be expected if there was no bias in the population toward one hand leading the other. Results indicated that the behavior of the left-leading LH participants was significantly different from expectation, $\chi^2(1, N = 20) = 9.8$, $p < .01$, whereas the RH participants were not distinguished with respect to leading hand, $\chi^2(1, N = 20) = 1.8$, $p > .05$.

An ANOVA performed on ($\phi_{\text{stable}} - \phi_{\psi}$) at $\Delta\omega = 0$ with handedness and mode as independent variables revealed a significant effect of handedness with values, as noted earlier, $F(1, 36) = 12.48$, $p < .001$, and a significant interaction (in-phase, LH = 0.025 rad vs. RH = −0.015 rad; anti-phase, LH = 0.103 rad vs. RH = −0.048 rad), $F(1, 36) = 4.24$, $p < .05$, indicating that the effect of handedness was greatest in anti-phase. Given the direction of the interaction, an ANOVA performed on $|\phi_{\text{stable}} - \phi_{\psi}|$ indicated that the coordination mode was significant, $F(1, 36) = 4.15$, $p < .05$, with anti-phase resulting in greater phase departure than in-phase coordination. The phase departure ($\phi_{\text{stable}} - \phi_{\psi}$) at $\Delta\omega = 0$ was converted into a temporal delay given the experimental angular frequency of 4.46 rad s^{-1}. The conversion revealed that the left hand led the right hand by 19.3 ms for the Ll participants and by 11.7 ms for the Rl participants. Similarly, the right hand led the left hand by 17.0 ms for the Rr participants and by 13.9 ms for the Lr participants. On the basis of the constituent subgroups' temporal delays, the LH participants considered as a single group exhibited a net left-hand lead of 5.4 ms, and the RH participants exhibited a net right-hand lead of precisely the same amount.

These results indicate that at $\Delta\omega = 0$, RH participants as a group were just as likely to lead with the right as with the left hand, whereas LH participants exhibited a consistent lead with the left hand. Additionally, handedness was more pronounced in anti-phase coordination than in in-phase coordination. In summary, performance under $\Delta\omega = 0$ revealed the presence of a functional asymmetry between the hands, ΔH. Interestingly, and perhaps importantly, this functional asymmetry in terms of the sign of ($\phi_{\text{stable}} - \phi_{\psi}$) did not comply with the more conventional RH versus LH distinction with the questionnaire-based measure of consistency taken at the outset for the LH participants.

Turning to the imposed broken symmetry conditions for which $\Delta\omega \neq 0$, and retaining the definition of handedness by self-designation, the results presented in Figure 1 are replotted in Figure 2 according to the sign of $\Delta\omega$ (i.e., ignoring its actual magnitude) and the absolute magnitude of phase deviation, $|\phi_{\text{stable}} - \phi_{\psi}|$. A three-way ANOVA (Handedness × Mode × Sign) revealed no main effect of either sign, $F(1, 36) = 2.72$, $p > .05$, or handedness, $F(1, 36) = 3.00$, $p > .05$, but a significant interaction between sign and handedness, $F(1, 36) = 30.11$, $p < .0001$. Whereas the magnitude of $|\phi_{\text{stable}} - \phi_{\psi}|$ was greater for $\Delta\omega < 0$ than for $\Delta\omega > 0$ in RH participants, it was greater for $\Delta\omega > 0$ than $\Delta\omega < 0$ in LH participants. Given the convention $\Delta\omega = (\omega_L - \omega_R)$, the preceding interaction means that the displacement of ϕ_{stable} from 0 and π was greater for RH participants when the right wrist-pendulum system had the higher eigenfrequency and greater for LH participants when the left wrist-pendulum system had the higher eigenfrequency. To define $\Delta\omega$ as a difference between left hand and right hand is to impose an extrinsic, geometrical, and arbitrary distinction on the system of coordinated limbs. An intrinsically based and therefore a potentially more meaningful distinction for the interlimb system is to use a functional categorization in terms of preferred (P) versus nonpreferred (NP) hand. Consequently, $\Delta\omega$ was redefined as $(\omega_P - \omega_{NP})$, where ω_P is now the eigenfrequency of the wrist-pendulum system in the preferred hand and likewise for ω_{NP}. Repeating the Handedness × Mode × Sign ANOVA yielded a main effect of sign, $F(1, 36) = 30.10$, $p < .0001$, no main effect of handedness, $F(1, 36) = 3.00$,

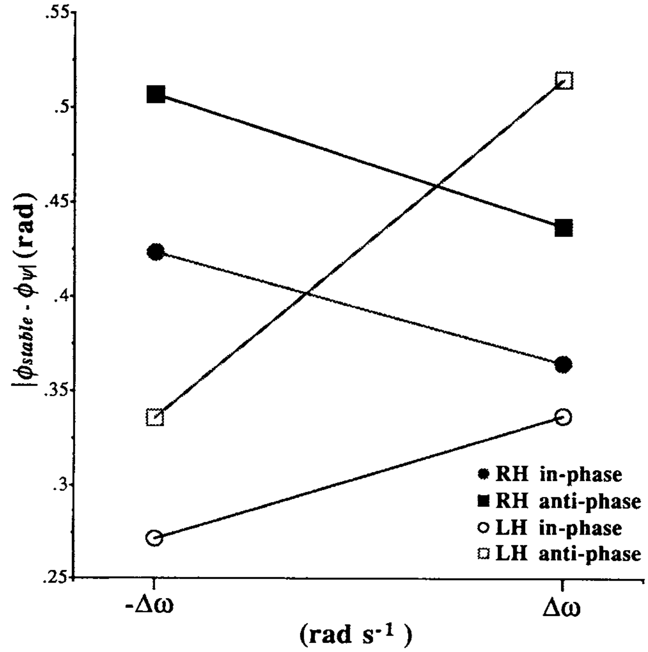

Figure 2. $|\phi_{\text{stable}} - \phi_{\psi}|$ for ±Δω (rad/s) as a function of handedness and mode. RH = right-handed; LH = left-handed.

$p > .05$, no interaction of sign and handedness, $F(1, 36) = 2.76$, $p > .05$, no interaction of sign and mode, $F(1, 36) = 3.31$, $p > .05$, and no three way interaction, $F(1, 36) = 2.32$, $p > .05$. Thus, under the convention $\Delta\omega = (\omega_P - \omega_{NP})$, $|\phi_{stable} - \phi_\psi|$ was greater for $\Delta\omega > 0$ than $\Delta\omega < 0$ and by the same amount in both RH and LH participants.

When the RH group was subdivided into the 13 right-leading (Rr) and 7 left-leading (Rl) participants, a Group (Rr vs. Rl) × Sign ANOVA revealed a similar interaction to that obtained when group was defined as RH versus LH participants (Rr, $-\Delta\omega = 0.496$ rad vs. $\Delta\omega = 0.395$ rad; Rl, $-\Delta\omega = 0.408$ rad vs. $\Delta\omega = 0.411$ rad), $F(1, 18) = 4.22$, $p < .05$. Given that this interaction verified the inhomogeneity of the RH group, the preceding ANOVAs were repeated with the RH and LH groups of participants defined by the 13 Rr participants and the 17 Ll participants. For the present task, it seemed as if a contrast between these two homogeneous groups would provide the most accurate measure of handedness. There was a main effect of group, with the Rr participants exhibiting a larger mean value of $|\phi_{stable} - \phi_\psi|$ than the Ll group, $F(1, 26) = 6.88$, $p < .01$. The interaction of this new group variable with the sign of $\Delta\omega = (\omega_L - \omega_R)$ was highly significant, $F(1, 26) = 36.46$, $p < .0001$. For the 13 Rr participants, $|\phi_{stable} - \phi_\psi|$ was greater for $\Delta\omega < 0$ than for $\Delta\omega > 0$; for the 17 Ll participants, $|\phi_{stable} - \phi_\psi|$ was greater for $\Delta\omega > 0$ than for $\Delta\omega < 0$. When the ANOVA was conducted on $\Delta\omega = (\omega_P - \omega_{NP})$, the main effect remained but the interaction disappeared, indicating that within the natural coordinate system provided by the dimension of preferred hand, the difference between $\Delta\omega > 0$ and $\Delta\omega < 0$ was the same for right-leading RH participants and left-leading LH participants.

An important feature of the data expressed in Figure 2 (but also in the comparison of Figures 1a and 1b and associated analyses at $\Delta\omega = 0$) is that $|\phi_{stable} - \phi_\psi|$ as a function of $\Delta\omega \neq 0$ was greater for $\phi_\psi = \pi$ than $\phi_\psi = 0$. The ANOVA on Handedness × Mode × Sign restricted to the $\Delta\omega \neq 0$ conditions confirmed the significantly greater magnitudes of $|\phi_{stable} - \phi_\psi|$ for anti-phase coordination, $F(1, 36) = 6.45$, $p < .02$; $F(1, 26) = 10.22$, $p < .01$, for the ANOVA using the Rr and Ll participants. This outcome concurs with Prediction 4 of Equation 1 regarding $|\phi_{stable} - \phi_\psi|$ under conditions in which $\Delta\omega \neq 0$. Previous research had not confirmed the prediction of a main effect of coordination mode on $|\phi_{stable} - \phi_\psi|$ under either $\Delta\omega = 0$ or $\Delta\omega \neq 0$, although numerical differences have been in evidence (e.g., Sternad et al., 1992).

Standard Deviation of Phase

Figure 3 shows the pattern of mean standard deviation (*SD*) of ϕ as a function of $\Delta\omega = (\omega_L - \omega_R)$ for the in-phase and anti-phase groups of RH and LH participants. As can be seen, the overall picture is that of minimal $SD\phi$ under the symmetry condition of $\Delta\omega = 0$ (with the exception of RH anti-phase) and increasingly larger $SD\phi$ with deviation of $\Delta\omega$ from 0. This outcome conforms to Prediction 5 of Equation 1 and has been observed in previous experiments (e.g., Schmidt, Beek, et al., 1991; Schmidt et al., 1993). Inspection of Figure 3 also suggests that, consistent with Prediction 6, larger $SD\phi$ occurred for $\phi_\psi = \pi$ than $\phi_\psi = 0$.

$SD\phi$ was analyzed as a function of the sign of $\Delta\omega = (\omega_L - \omega_R)$, ignoring the magnitude of $\Delta\omega$ and excluding $\Delta\omega = 0$. A Handedness × Mode × Sign ANOVA revealed that $SD\phi$ was less for LH participants (0.19 rad) than RH participants (0.25 rad), $F(1, 36) = 15.40$, $p < .001$, was less for $\phi_\psi = 0$ (0.20 rad) than $\phi_\psi = \pi$ (0.24), $F(1, 36) = 9.46$, $p < .001$, and was less for $\Delta\omega > 0$ (0.21 rad) than for $\Delta\omega < 0$ (0.23 rad), $F(1, 36) = 4.46$, $p < .05$. The significance of the three-way interaction, $F(1, 36) = 9.52$, $p < .01$, encouraged the separate analysis of RH and LH participants. For RH participants, there was significantly greater $SD\phi$ for $\phi_\psi = \pi$ than $\phi_\psi = 0$, $F(1, 18) = 6.08$, $p < .02$, significantly greater $SD\phi$ for $\Delta\omega < 0$ than for $\Delta\omega > 0$, $F(1, 18) = 6.42$, $p < .02$, and a significant Mode × Sign interaction, $F(1, 18) = 7.35$, $p < .01$. The interaction was produced by the mode difference at $-\Delta\omega$ ($p < .01$) and the sign difference at $\phi_\psi = \pi$ ($p < .01$). For LH participants, only the anti-phase ($\phi_\psi = \pi$) versus in-phase ($\phi_\psi = 0$) contrast was significant, $F(1, 18) = 4.54$, $p < .05$.

In summary, for both RH and LH participants, $\phi_\psi = \pi$ was associated with larger $SD\phi$, but only for RH participants was there an effect of the sign of $\Delta\omega$. Specifically, when $\phi_\psi = \pi$, RH participants exhibited greater $SD\phi$ under $\Delta\omega < 0$ than under $\Delta\omega > 0$. Stated differently, the anti-phase coordination of RH participants was less stable when the preferred hand had the higher gravitational eigenfrequency. For LH participants, mode stability was unaffected by the contrast of $\Delta\omega < 0$ and $\Delta\omega > 0$. Importantly, another ANOVA showed that the preceding statistical pattern of effects on $SD\phi$ held identically for the contrast between the homogeneous groups of 13 Rr and 17 Ll participants.

Phase and Its Standard Deviation for Inconsistent and Consistent LH Participants

An ANOVA on $|\phi_{stable} - \phi_\psi|$ for the LH participants with consistency (CLH vs. ILH), and $\Delta\omega$ as independent variables, revealed no main effects or interactions ($p > .05$). In contrast, an ANOVA on $SD\phi$ with consistency, mode, and $\Delta\omega$ as independent variables revealed a main effect of consistency, with ILH participants exhibiting larger $SD\phi$ than CLH participants (0.187 rad vs. 0.167 rad), $F(1, 16) = 4.18$, $p = .057$. There was also a significant interaction between consistency and mode (CLH, in-phase = 0.153 rad vs. anti-phase = 0.187 rad; ILH, in-phase = 0.188 rad vs. anti-phase = 0.186 rad), $F(1, 16) = 4.74$, $p < .05$. When the ANOVA was repeated under $\Delta\omega = 0$, the contrast in $SD\phi$ between ILH and CLH participants was especially pronounced (0.122 rad vs. 0.106 rad), $F(1, 16) = 7.69$, $p < .01$, as was the interaction between consistency and mode (CLH, in-phase = 0.096 rad vs. anti-phase = 0.120 rad; ILH, in-phase = 0.132 rad vs. anti-phase = 0.115 rad), $F(1, 16) = 13.83$, $p < .01$. A further ANOVA verified

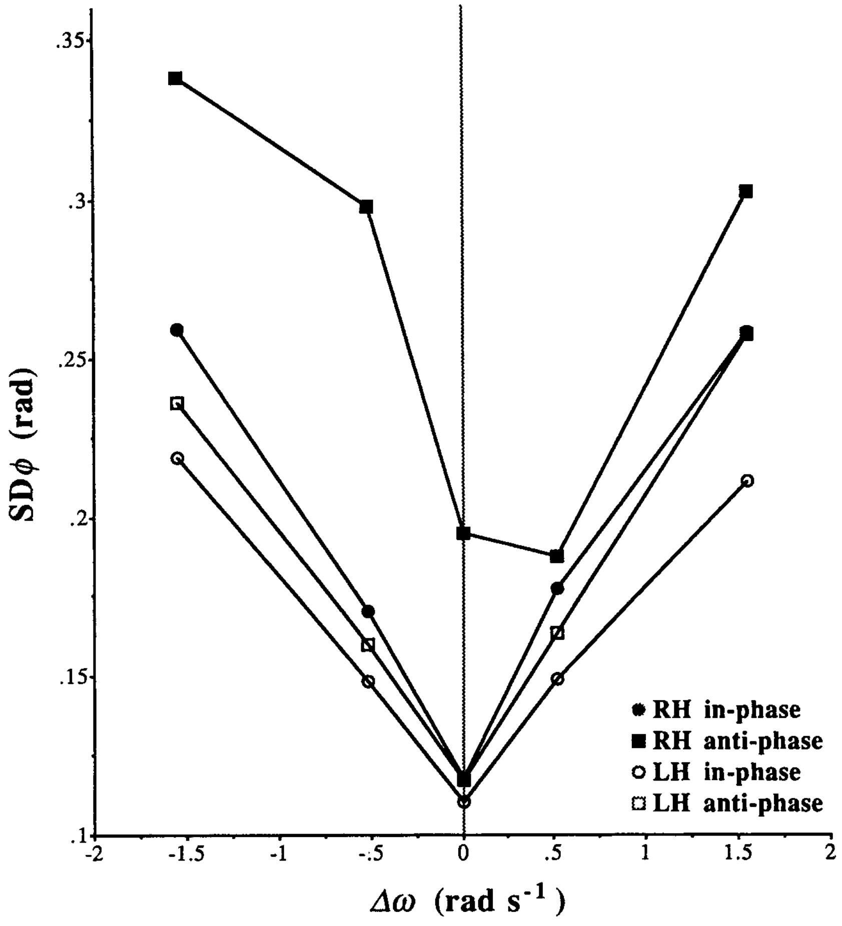

Figure 3. Standard deviations of ϕ as a function of $\Delta\omega$, handedness, and coordination mode (ϕ_ψ). RH = right-handed; LH = left-handed.

that only under in-phase were the ILH participants significantly more variable than the CLH participants, $F(1, 8) = 19.12, p < .01$.

General Discussion

It has been observed that some of the most pronounced manual asymmetries are evident in tasks that vary only the timing demands on each hand, that is, in the absence of contrasting spatial and manipulation requirements (Peters, 1985). In our experiment, participants had to achieve 1:1 frequency locking of two contralateral limb segments each constrained to oscillate in a plane parallel to the body's sagittal plane. The explicit task demands for the two hands were identical in all conditions of the experiment. The implicit task demands, however, were made nontrivially different for the two hands by loading them differentially. The manipulation of $\Delta\omega$ meant that the 1:1 frequency locking had to be achieved in the face of extrinsically imposed frequency competition. Given this competition, the temporal patterning of neuromuscular activity in the two limbs could not be identical. Congruent with Peters's (1985, 1987) observation, our experiment—involving the same overt spatial and manipulation demands on the two hands but different covert timing demands—revealed marked manual asymmetries. LH and RH participants in our experiment differed in several ways.

With respect to the eight predictions from Equation 1 listed in the introduction, we evaluated and confirmed Predictions 1–4. With respect to the contrast between LH and RH participants, the patterning of the predicted outcomes by the additional parameter of handedness revealed the following. The dependency of ϕ_{stable} on the sign of $\Delta\omega = (\omega_L - \omega_R)$ indicated that $\Delta\omega < 0$ produced larger $(\phi_{\text{stable}} - \phi_\psi)$ for RH participants and $\Delta\omega > 0$ produced larger $(\phi_{\text{stable}} - \phi_\psi)$ for LH participants. As measured by the average magnitude of $|\phi_{\text{stable}} - \phi_\psi|$, RH participants had greater departures from intended phase than did LH participants. The variability of bimanual coordination patterns as indexed by $SD\phi$ indicated that this was greater for RH than LH participants. There was also greater $SD\phi$ for ILH than for CLH participants. Importantly, although ILH participants were distinguished from CLH participants, ILH participants tended to be also distinguished from RH participants. Discussion follows of the implications of the preceding contrasts for understanding handedness in bimanual rhythmic coordination. The discussion is conducted in the context of two hypotheses about ΔH developed with respect to Equation 1.

Hypothesis 1: ΔH as a Differential Detuning

We consider first the departure of ϕ_{stable} from ϕ_ψ when $\Delta\omega = 0$. If the dynamics observed in the experiment followed from Equation 1, then the experimental observation of $(\phi_{\text{stable}} - \phi_\psi) \neq 0$ when $\Delta\omega = 0$ could not have arisen via the a and b coefficients. As is evident from Prediction 1 of Equation 1, if $\Delta\omega$ were equal to 0, then regardless of the value of b/a (see Footnote 1), $(\phi_{\text{stable}} - 0)$ and $(\phi_{\text{stable}} - \pi)$ would both be equal to 0. Accordingly, the fact that $(\phi_{\text{stable}} - \phi_\psi) \neq 0$ when $\Delta\omega = 0$ might be interpreted to mean that the functional asymmetry between the hands is a differential "detuning" of the wrist-pendulum systems. That is, the individual eigenfrequencies were each slightly modified or detuned rendering the nominal $\Delta\omega = 0$ as a functional $\Delta\omega \neq 0$. To conform to the observed patterning of $(\phi_{\text{stable}} - \phi_\psi)$, the right wrist-pendulum systems of the 13 right-leading RH participants and the 3 right-leading LH participants must have been of higher natural frequencies than the corresponding left wrist-pendulum systems. Likewise, the left wrist-pendulum systems of the 17 left-leading LH participants and 7 left-leading RH participants must have been of higher natural frequencies than the corresponding right wrist-pendulum systems. In more specific terms, the functional asymmetry is tantamount to two different scalar multiples, λ and ρ, of the left ω_L and right ω_R gravitational eigenfrequencies, respectively. With $\omega_L = \omega_R$, $(\lambda\omega_L - \rho\omega_R)$ is negative for right-leading participants because $\lambda < \rho$, and positive for left-leading participants because $\lambda > \rho$. From the perspective of a rhythmic movement unit as a self-sustained oscillator, differences in the detuning scalars λ and ρ would have to reflect differences in the oscillator's elastic and friction functions, considered singly or in combination (e.g., Beek & Beek, 1988; Kay, Kelso, Saltzman, & Schöner, 1987; Kay, Saltzman, & Kelso, 1991; Turvey, 1990). For example, a difference in elastic functions, such that the left stiffness is greater than the right stiffness for LH participants and vice versa for RH participants, would produce the observed handedness dependence of $(\phi_{\text{stable}} - \phi_\psi)$.

We now discuss how the detuning hypothesis addresses the interaction of $|\phi_{\text{stable}} - \phi_\psi|$ with the sign of $\Delta\omega$. The interpretation of detuning by λ and ρ speaks to the major result that for RH participants, $|\phi_{\text{stable}} - \phi_\psi|$ was greater for $\Delta\omega < 0$ than for $\Delta\omega > 0$, whereas for LH participants $|\phi_{\text{stable}} - \phi_\psi|$ was greater for $\Delta\omega > 0$ than for $\Delta\omega < 0$ and that this interaction dissolved when $\Delta\omega$ was redefined as $(\omega_P - \omega_{NP})$. The implication of the dissolution of the interaction is that the inequality $|\lambda\omega_{\text{higher}} - \rho\omega_{\text{lower}}| > |\lambda\omega_{\text{lower}} - \rho\omega_{\text{higher}}|$ for LH participants was of the same magnitude as the inequality $|\rho\omega_{\text{higher}} - \lambda\omega_{\text{lower}}| > |\rho\omega_{\text{lower}} - \lambda\omega_{\text{higher}}|$ for RH participants. These inequalities mean that $\Delta\omega$ was (a) amplified for both RH and LH participants when the wrist-pendulum system of higher eigenfrequency was in the preferred hand and (b) diminished for both RH and LH participants when the wrist-pendulum system of higher eigenfrequency was in the nonpreferred hand. By Equation 1, ceteris paribus, larger magnitudes of $\Delta\omega$ engender larger magnitudes of $|\phi_{\text{stable}} - \phi_\psi|$. Accordingly, over pairs of wrist-pendulum systems, the magnitudes of $|\phi_{\text{stable}} - \phi_\psi|$ associated with positive values of $(\omega_P - \omega_{NP})$ should be larger than the magnitudes of $|\phi_{\text{stable}} - \phi_\psi|$ associated with negative values of $(\omega_P - \omega_{NP})$.

An additional empirical fact suggests a difference between the LH and RH participants with respect to the control variables determining ϕ_{stable}. The fact in question was that, on the average, the departure of actual from intended phase, $|\phi_{\text{stable}} - \phi_\psi|$, was greater for RH participants than LH participants. From the perspective of Equation 1, this contrast could come about because the effective magnitude of $\Delta\omega$ (dictated by the values of λ and ρ in addition to the values of the eigenfrequencies ω_L and ω_R) was greater for RH than for LH participants, the magnitude of b/a was greater for LH participants than for RH participants, or both differences were at play simultaneously.

Finally, consider the dependence of $SD\phi$ on handedness from the perspective of the detuning hypothesis. Consistent with the greater average value of $|\phi_{\text{stable}} - \phi_\psi|$ for RH participants was the observation that $SD\phi$ was greater, on average, for RH participants. From Equation 1, the greater stability of interlimb coordination in the LH participants may be attributed either to smaller magnitudes of the effective $\Delta\omega$ or a larger average b/a relative to the RH participants. The condition largely responsible for the $SD\phi$ difference was $\phi_\psi = \pi$, $\Delta\omega < 0$, for RH participants. That is, RH participants found it particularly difficult to maintain the spatiotemporal pattern of anti-phase when the preferred hand had the higher eigenfrequency.

Hypothesis 2: ΔH as Nonisotropic Coupling

The departure point for the second hypothesis is that Equation 1 is incomplete. Equation 1 is a motion equation expressible as the negative of the phase derivative of a particular quantity $V(\phi)$ that functions like a potential, that is,

$$\dot{\phi} = -dV(\phi)/d\phi. \tag{8}$$

In approximating $V(\phi)$ for 1:1 frequency locking of two identical body segments, Haken et al. (1985) were constrained by the empirically demonstrated asymmetry of in-phase and anti-phase as the stable coordinated states of a dimensionally symmetrical system. The proposed equation

$$V(\phi) = -\Delta\omega\phi - a\cos(\phi) - b\cos(2\phi) \tag{9}$$

provides an "energy landscape" characterized for the condition of $\Delta\omega = 0$ by a global minimum at $\phi = 0$ and local minima at $\phi = \pm\pi$ as shown in Figure 4. This landscape is modulated by ω_c such that at a critical value ($a = 4b$ when

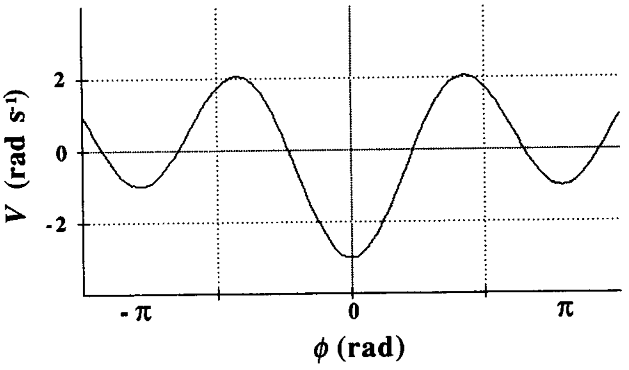

Figure 4. Equation 9 with $\Delta\omega = 0$.

$\Delta\omega = 0$), the local minima are annihilated and only the attractor at $\phi = 0$ remains (see Haken et al., 1985). When $\Delta\omega = 0$, $V(\phi)$ is symmetric, that is, $V(\phi) = V(-\phi)$. The hypothesis to be pursued here is that ΔH is interpretable as a quantity that, when added to Equation 9 under the condition of $\Delta\omega = 0$, breaks the equation's symmetry, that is, renders $V(\phi) \neq V(-\phi)$.

A potentially important insight into the form taken by the hypothesized symmetry breaking quantity comes from efforts to model the ("fictive") swimming action of the lamprey spinal cord. Evidence shows that within the spine of this primitive fish, oscillators of the same segment are in anti-phase and that a constant nonzero phase difference ($0 < \phi < \pi$) is maintained between ipsilateral oscillators of two neighboring segments (e.g., Cohen & Harris-Warrick, 1984; Cohen & Wallén, 1980). Equation 3 was advanced by Cohen et al. (1982) to model the intrasegmental and intersegmental coupling of two oscillators and, on extension, to model the chain of coupled segmental oscillators producing the uniform travelling wave that characterizes the lamprey's swimming. A "uniform travelling wave" means that the nonzero phase difference between neighboring oscillators is of (approximately) the same magnitude everywhere along the chain. According to Equation 3, phase differences other than 0 and π between two coupled oscillators can arise only when $\Delta\omega \neq 0$. Consequently, for there to be a nonzero phase difference between an oscillator in segment i and an ipsilateral oscillator in segment j, Equation 3 requires that oscillators i and j differ in their natural frequencies. The evidence suggests, however, that the natural frequencies of the oscillators at each segment of the chain are the same rather than different (Kopell, 1988; Kopell & Ermentrout, 1986). The phase differences between neighboring segments of the lamprey spine must arise, therefore, from anisotropy in the coupling rather than from a gradient of natural frequencies.

The kind of coupling behind the derivation of Equation 3 is referred to as *diffusive coupling,* which is defined formally as an interaction between two oscillators that goes to zero when $\phi = 0$ or $\phi = \pi$ (Cohen et al., 1982; Kopell, 1988; Murray, 1990; Rand et al., 1988). The coupling favored by Kopell (1988; Kopell & Ermentrout, 1986) is referred to as *synaptic coupling* and is formally defined as a two-oscillator interaction that is nonzero when $\phi = 0$ or $\phi = \pi$ (metaphorically, neurons associated with the two oscillators are always passing signals back and forth). Minimally, synaptic coupling requires another periodic term in Equation 3 that contrasts with the symmetry of the sine term (an odd function)—in brief, it requires a cosine term (an even function). The two-oscillator motion equation derived from synaptic coupling therefore includes Equation 3:

$$\dot{\phi} = \Delta\omega - K_1\sin(\phi) - K_2\cos(\phi) \qquad (10)$$

It is evident from Equation 10 that when $\phi = 0$ or $\phi = \pi$, the summed effect of the two coupling terms is not zero. A less apparent feature of Equation 10 is that when $\Delta\omega = 0$, neither $\phi = 0(K_1, K_2 > 0)$ nor $\phi = \pi(K_1, K_2 < 0)$ are stable solutions. This latter feature is the important one for accommodating the fact that there are phase differences between segments of the lamprey spinal cord in the absence of a natural frequency gradient. It is also the feature that is of special importance to our present concerns, namely, understanding the basis for systematic deviations in LH and RH participants from $\phi = 0$ and $\phi = \pi$ when $\Delta\omega = 0$. We can develop this important feature of Equation 10 most usefully in the context of potential functions.

The potential function for Equation 3 is

$$V(\phi) = -\Delta\omega\phi - K\cos(\phi) \qquad (11)$$

and that for Equation 10 is

$$V(\phi) = -\Delta\omega\phi - K_1\cos(\phi) + K_2\sin(\phi). \qquad (12)$$

Figure 5 shows the contrast between the two potential functions for in-phase coordination ($K > 0$ in Equation 11 and $K_1 > 0$ in Equation 12). Whereas Equation 11's minimum is at $\phi = 0$, the minimum of Equation 12 is at $\phi < 0$ when K_2 is positive and at $\phi > 0$ when K_2 is negative. From Figure 5 one might infer that the basic patterns of data

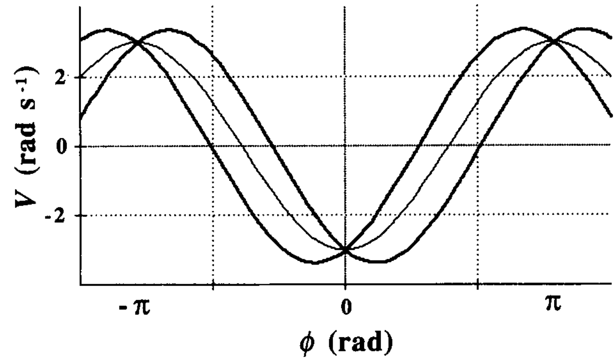

Figure 5. The potential functions for $\Delta\omega = 0$ under diffusive (Equation 11) and synaptic (Equation 12) coupling. The function with its minimum displaced to the left of $\phi = 0$ is Equation 12 with $K_2 > 0$ and the function with its minimum displaced to the right of $\phi = 0$ is Equation 12 with $K_2 < 0$. The function with its minimum at $\phi = 0$ is Equation 11.

associated with handedness that have been obtained in the current experiment follow from a symmetry-breaking term such as $K_2\sin\phi$ in Equation 12, with $K_2 > 0$ defining RH and $K_2 < 0$ defining LH. The data show immediately, however, that the requisite symmetry-breaking term cannot be identical to $K_2\sin\phi$. With $\Delta\omega = 0$, RH participants undershot both $\phi = 0$ and $\phi = \pi$ and LH participants overshot both $\phi = 0$ and $\phi = \pi$ (see Figure 1 and corresponding analyses). By contrast, numerical analyses of Equation 10 reveals that when $K_2 > 0$, ϕ_{stable} is to be found at $\phi < 0$ and $\phi > \pi$ and that when $K_2 < 0$, ϕ_{stable} is to be found at $\phi > 0$ and $\phi < \pi$. What is needed to produce either an overshoot of both attractors or an undershoot of both attractors depending on the sign of the coefficient is an additional sine term of the form $K_2\sin(2\phi)$.

Following from the preceding analyses and arguments, we propose that Equation 9, the potential function underlying Equation 1, be amended to read

$$V(\phi) = -\Delta\omega\phi - a\cos(\phi) - b\cos(2\phi) + c\sin(\phi) + d\sin(2\phi), \quad (13)$$

where the final two right-hand terms represent the symmetry breaking of interlimb dynamics by ΔH. That is, the proposed potential function for 1:1 frequency locking in human interlimb rhythmic coordination is simply the sum of the first three ($n = 0$, 1, and 2) even (cosine) and odd (sine) terms in the Fourier series (the 0th sine term is equal to zero). Figure 6 shows Equation 13 with $\Delta\omega = 0$ for $d > 0$ (by hypothesis, RH) and $d < 0$ (by hypothesis, LH) and with $a > 0$, $b > 0$, and $c = 0$. The minima of the potential wells are displaced from 0 and π in the negative direction by $d > 0$ and in the positive direction by $d < 0$. That is, Figure 6 shows a departure of ϕ_{stable} from ϕ_ψ when $\Delta\omega = 0$ whose direction depends on the sign of ΔH.

We now consider how the interpretation of ΔH as a symmetry breaking term in the governing potential function addresses the experimental facts evident in Figures 1, 2, and 3. Predictions about ϕ_{stable} and $SD\phi$ can be made from the amended form of Equation 1 that follows from Equation 13, that is,

$$\dot{\phi} = \Delta\omega - a\sin(\phi) - 2b\sin(2\phi) - c\cos(\phi) - 2d\cos(2\phi) + \sqrt{Q}\,\xi_t. \quad (14)$$

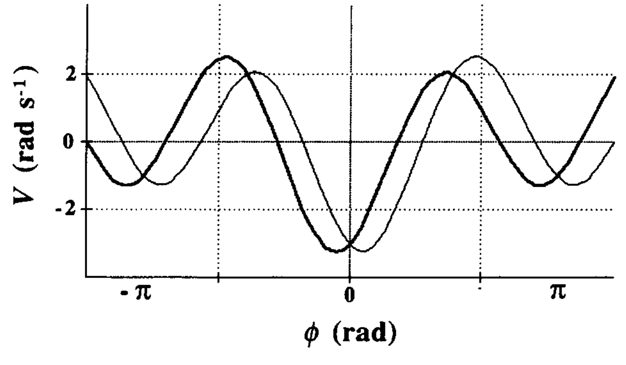

Figure 6. Equation 13 with $\Delta\omega = 0$ and $d = 1$ (dark curve) and $d = -1$ (light curve).

Recalling the methods applied to Equation 1, numerical solutions to Equation 14 (excluding the stochastic force) for $\dot{\phi} = 0$ yield the values of ϕ that are stationary for any given parameter values. If $d\dot{\phi}/d\phi$ is negative at a stationary state then that state is stable with degree of stability indexed by $|d\dot{\phi}/d\phi|$. $SD\phi$ is proportional to the inverse of $|d\dot{\phi}/d\phi|$ (Schöner & Kelso, 1988). A range of suitable parameter settings for a and b in Equation 14 are suggested by previous evaluations of Equation 1 as a model of human interlimb coordination (e.g., Schöner et al., 1986). With respect to c and d, their magnitudes are likely to be small relative to a and b. Whereas a and b are the coefficients of terms that determine the fundamental in-phase and anti-phase coordination dynamics, c and d are the coefficients of terms that break the symmetry of those dynamics but do not impair them. Because d is the more important handedness coefficient, producing the observed directions of fixed-point drift around both 0 and π, we can, for present purposes, set c to zero without any great loss of generality. Numerical analysis of Equation 14 reveals that when d is closely similar in absolute value to a and b, the effect of sign is such as to lead always to undershoot (when $d > 0$), or always to overshoot (when $d < 0$), of $\phi = 0$ and $\phi = \pi$ for all reasonable $\Delta\omega$ (e.g., $-3 \leq \Delta\omega \leq 3$). That is, the handedness term overrides $\Delta\omega$, contrary to the data presented in Figure 1. Numerical analyses reveals that to preserve the effect of the sign of $\Delta\omega$, $d < a$ and $d < b$. Further constraints on d are suggested by the facts that the overshoot by LH participants and the undershoot by RH participants of $\phi = 0$ and $\phi = \pi$ are systematic but small at $\Delta\omega = 0$, with the magnitude greatest for LH. The implication is that whereas d is small relative to a and b for both RH and LH, it is smaller for RH. Finally, the quantitative differences between LH and RH participants (evident in Figures 2 and 3) and the order and qualitative structure of $SD\phi$ (evident in Figure 3) suggest a further difference between RH and LH participants in the b/a ratio (see discussion of Equation 1).

Figure 7 depicts the values of $|\phi_{\text{stable}} - \phi_\psi|$ and $SD\phi$ ($\propto |d\dot{\phi}/d\phi|^{-1}$) generated by Equation 14 for the $\Delta\omega$ values of the current experiment with LH parameters of $a = 0.5$, $b = 1.45$, $c = 0$, and $d = -0.08$, and RH parameters of $a = 0.5$, $b = 1.15$, $c = 0$, and $d = 0.05$. That is, the contrast between LH and RH observed in our experiment can be drawn in the sign and magnitude of d and the magnitude of b/a. Inspection of Figure 7 reveals that the preceding parameterization of Equation 14 captures the qualitative characteristics of the data expressed in Figures 2 and 3. Not evident from inspection of Figure 7 is the fact that, so parameterized, the equation also predicts a larger effect of handedness for anti-phase (0.055 rad) than in-phase (0.043) when $\Delta\omega = 0$, consistent with observation in our experiment.

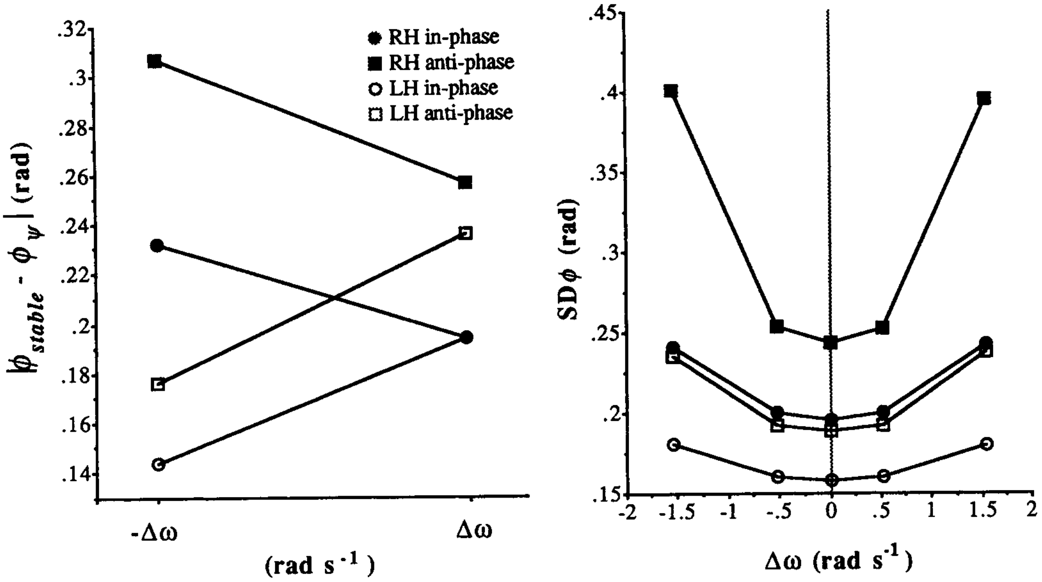

Figure 7. Predictions of Equation 14 with LH parameters of $a = 0.5$, $b = 1.45$, $c = 0$, and $d = -0.08$ and RH parameters of $a = 0.5$, $b = 1.15$, $c = 0$, and $d = 0.05$. Left panel corresponds to Figure 2. Right panel corresponds to Figure 3. RH = right-handed; LH = left-handed.

Relation Between Leading Hand and Handedness

Although estimates vary, a reasonable mean value for the incidence of right-handedness in the general population is approximately 88%, and of left-handedness it is approximately 12% (Porac & Coren, 1981). Given that there were, in the current experiment, 13 Rr and 7 Rl participants (classified as RH individuals), the implication is that 57.2% RH will exhibit a right-hand lead and 30.8% will exhibit a left-hand lead. Similarly, given that there were, in our experiment, 17 Ll and 3 Lr participants (classified as LH individuals), the implication is that 10.2% LH will exhibit a left-hand lead and 1.8% will exhibit a right-hand lead. Consequently, for the general population (regardless of prior classification), it can be argued that the overall bias toward the right hand is 59% and the overall bias toward the left hand is 41%. These relative proportions of the population exhibiting a left-lead or right-lead are clearly less disparate than the incidences of LH and RH typically reported. A test to determine whether the left-lead and right-lead proportions were different from what would be expected if there was no bias in the population toward a particular hand was insignificant, χ^2 (1, $N = 100$) = 3.24, $p = .07$). That is, by our analysis, a randomly sampled participant from the general population (RH plus LH participants) is equally likely to exhibit a left- or right-lead.

An argument of no bias in the general population toward either the left or right hand under simple task constraints of bimanual coordination finds support in experimental observations of a left-hand bias and in experimental results that are ambivalent regarding any particular bias. Thus, it has been suggested that there is a left-hand specialization for perceptually guided reaching, especially in some nonhuman primates (MacNeilage, Studdert-Kennedy, & Lindblom, 1987), that the left hand typically starts a bimanual gesture (Guiard, 1987b), that the left hand produces smaller constant error in reaching for a small target (Guiard, Diaz, & Beaubaton, 1983), and that the left hand is more forceful and variable in finger tapping than the right hand (Todor & Kyprie, 1980; Todor & Smiley, 1985). Coupled with the observations of a left-hand bias is the view that LH participants exhibit less of a contrast between the hands than RH participants (e.g., Hammond, 1990b; Peters & Durding, 1979), although this view was not corroborated by the current experiment or by a similar one with another 20 RH and 20 LH participants (Treffner, 1993).

Other inconsistencies across studies reinforce a cautious attitude to the standard view. Flowers (1975) found no differences between LH and RH participants on a ballistic tapping task using mean errors of unimanual tapping as a criterion, whereas Wolff et al. (1977) found that the left hand was more variable in timing than the right hand for both RH and LH participants. Relatedly, it has been found that tapping with the nonpreferred hand produces more variable timing than tapping with the preferred hand (Peters, 1980; Peters & Durding, 1978, 1979; Truman & Hammond, 1990). This hand asymmetry may be progressively accentuated under task constraints that require a participant to perform at increasingly greater rates (Truman & Hammond, 1990). In an investigation comparing normal and dyslexic individuals, normal RH participants led consistently with the right hand at each of three pacing frequencies in 1:1 finger tapping, but RH dyslexic participants led equally with both hands (Rouselle & Wolff, 1991). In anti-phase coordination, normal participants led with the right finger but only at the two higher frequencies; dyslexic participants showed no asymmetries under anti-phase, regardless of frequency.

The research on dyslexic individuals suggests complicated interactions between handedness and other factors and it underscores the understanding that the RH or LH designation does not necessarily define a homogeneous category. Other research is similarly suggestive. In 2:1 bimanual finger tapping, LH participants performed equally well in L1:R2 as in L2:R1, whereas RH participants performed better in L1:R2 (Peters, 1985, 1987; Peters & Servos, 1989; Webster, 1990). Conversely, between-hand asymmetries were reported for LH participants during the tapping of complex rhythms based on the self-reports of how the individual felt following performance (Ibbotson & Morton, 1981). In contrast to Ponton's (1987) conclusion that strongly RH and LH individuals perform less well than individuals without strong hand preferences (i.e., inconsistent participants), it has been found that CLH participants differ in neither speed nor quality of performance from ILH participants but that CLH and ILH exhibit differences in opposite directions that tend to cancel each other out under certain task conditions (Peters, 1990a, 1990c, 1991, 1992; Peters & Servos, 1989). Results of this latter kind suggest that CLH and RH participants may provide performance "mirror images" of each other. Furthermore, ILH participants performed much like RH participants in tasks requiring a dissociation between fine manipulative skill and gross movements requiring strength such as in throwing (Peters & Servos, 1989). Our results involved a similar division of the LH participants into CLH and ILH subgroups. In contrast to Peters and Servos's (1989) failure to reveal a difference between ILH and CLH participants, ILH participants in the current experiment exhibited greater $SD\phi$ than CLH participants under in-phase coordination indicating differential stability profiles for the two LH subgroups. In further contradiction of the mirror image hypothesis, and in contrast with the results of Peters and Servos (1989), RH participants were significantly different from CLH participants in $SD\phi$. These results therefore support the further subdivision of the LH population into those with either consistent or inconsistent left-hand preference and suggest that this division is associated with performance asymmetries in a basic form of motor coordination.

The primary lesson from the preceding review is that the manifestation of handedness is task and subject dependent. Consequently, the conditions responsible for the difference in d between LH and RH in the modeling of the current data by Equation 14 must be sought within the current experimental task and participants. Of possible relevance is the hypothesis that hand differences arise from hemispheric priming by attention or prior hemispheric activity (Kinsbourne, 1970). Consistent with this hypothesis, greater proficiency in bimanual coordination is found when the right hand is allocated the more demanding task (Peters, 1981, 1985) or when it leads the actions in a bimanual sequencing task (Hicks, Provenzani, & Rubstein, 1975; Oldfield, 1969; Peters, 1983; Summers & Sharp, 1979). The present 1:1 coordination task was sufficiently simple that participants may not have attended to any particular hand (by instruction, neither hand was attended to visually in the course of the experiment). As a consequence, there would have been no hemispheric priming. If 1:1 rhythmic coordination is an activity that draws predominantly on the right hemisphere's hypothesized manipulospatial capabilities (Bradshaw, Burden, & Nettleton, 1986; Haaland & Harrington, 1989), rather than the left hemisphere's hypothesized temporal sequencing capabilities, then it is feasible to imagine that the absence of priming countered a reliable right-hand-lead in the RH participants (left hemisphere dominance was canceled by right hemisphere use) and facilitated a predominant left-hand-lead in LH participants.

The foregoing interpretation of a bias toward a hand may be stated in terms of the temporal delay between hands given the inference that this delay may reflect interhemispheric transfer. In a bimanual task in which participants traced elliptical trajectories in the frontoparallel plane under either in-phase or anti-phase coordination, Stucchi and Viviani (1993) found a phase lag of the nondominant hand relative to the dominant hand of approximately 23 ms for both LH and RH participants.[2] They argued that lags of such magnitude could not have arisen solely from dynamical factors, such as a stiffness difference between the hands (Bingham, Schmidt, Turvey, & Rosenblum, 1991; our Hypothesis 1). A more plausible explanation, in their view, was that the 23-ms lag reflected the time scale of interhemispheric transfer of trajectory planning signals. In the current task, lag times were comparable in that the left hand led the right hand by 19.3 ms in the Ll participants and by 11.7 ms in the Rl participants, whereas the right hand led the left hand by 17.0 ms in the Rr participants and by 13.9 ms in the Lr participants. However, in contrast to Stucchi and Viviani's results, only within the LH group was there a predominant direction of lag. Thus, in the case of the RH participants, it is not clear how one would infer the direction in which trajectory planning signals are passed.[3]

The preceding analyses in terms of the priming and interhemispheric transfer hypotheses suggest ways in which the LH versus RH aspects of our data might be viewed. They do not, however, add substantially to the overall understanding of the asymmetry of interlimb dynamics provided by Equation 14. A deeper interpretation of the conditions dictating the sign and magnitude of d (and, presumably, of c) is more likely to follow from careful experimentation within the context of Equation 14 and its many specific predictions.

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[2] Stucchi and Viviani (1993) found that phase lags in the ellipse tracing task increased for anti-phase coordination as a function of ω_c. A dependency of $|\phi_{\text{stable}} - \phi_\psi|$ on ω_c is predicted from Equation 14.

[3] In Stucchi and Viviani (1993), each participant performed only a single trial in each condition. Therefore, it is possible that further trials would have revealed less consistency and possibly a different direction of phase lag.

Conclusion

In this research we have shown how a basic and easy-to-achieve interlimb rhythmic coordination—the 1:1 frequency locking that typifies locomotion patterns—can provide a medium for examining the functional asymmetry of the body. Left–right asymmetries in both left- and right-handers were plainly evident. Within the context of the dynamics expressing this interlimb rhythmic coordination, the functional asymmetry ΔH is tantamount to an asymmetry in either (a) the detuning parameter, if the dynamics abide by Equation 1, or (b) the governing potential, leading to anisotropic coupling, if the dynamics abide by Equation 14. For reasons of generality and precision of predictions, we lean toward the latter interpretation of ΔH. In combining the experimental and theoretical insights of Haken and colleagues (Haken et al., 1985; Kelso et al., 1990; Schöner et al., 1986) with those of Kopell and colleagues (Cohen et al., 1992; Ermentrout & Kopell, 1991; Kopell, 1988; Kopell & Ermentrout, 1986, 1990), Equation 14 provides a compact account of the functional broken symmetry of the body as an intrinsic and, one suspects, essential component in the assembling of interlimb coordination patterns.

The simplicity of our experimental task in conjunction with Equation 14 may provide a context for testing issues of concern to investigators of cognition in general rather than handedness in particular. For example, there are suggestions, noted earlier, that the differential sensitivity of the hands may involve attentional demands (e.g., Peters, 1985, 1987; Peters & Schwartz, 1989). It would be possible to have participants perform bimanual rhythmic coordination with varying degrees of attention under the maximally sensitive condition of imposed symmetry ($\Delta\omega = 0$) and to search for an interaction of attentional load with handedness. In addition, the sensitivity of the task in terms of fluctuation measures would seem to make it appropriate for investigating issues regarding the relation of manual specialization to the cerebral control of speech (Hammond, 1990a; Peters, 1990b; Shankweiler & Studdert-Kennedy, 1975). Under a dynamical systems perspective using finger-tapping tasks, major differences have been seen between normal individuals and left- and right-handed stutterers (Webster, 1990), dyslexic individuals (Rouselle & Wolff, 1991), and, in a continuous finger oscillation task, between normal and split-brain individuals (Tuller & Kelso, 1989). The distinct advantage of experimental manipulations within the context of a well-formulated dynamics of bimanual coordination is the promise that observed effects can be given precise interpretations in the vocabulary of competitive and cooperative dynamical processes.

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