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RESEARCH ARTICLE

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Symmetry, broken symmetry, and handedness in bimanual coordination dynamics

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Summary The symmetrical dynamics of 1:1 rhythmic bimanual coordination may be specified by an order parameter equation involving the relative phase between rhythmic components, and an interlimb coupling which determines the relative attractiveness of in-phase and anti-phase patterns. Symmetry breaking of these dynamics can occur via the difference in the natural frequencies, $\Delta\omega$, of the left and right rhythmic components, or by the intrinsic asymmetrical dynamics of the body. The latter is captured by additional terms that render the symmetrical coupling slightly anisotropic. A major prediction resulting from this step is that although $\Delta\omega = 0$, as the frequency of coordination is increased, the asymmetrical coupling will increase and the symmetrical coupling will decrease. This results in a greater left-limb bias in left-handers and right-limb bias in right-handers. This "increased handedness" prediction was confirmed in an experiment in which 20 left-handed and 20 right-handed individuals performed 1:1 coordination with hand-held rigid pendulums. Manipulations of left and right pendulum lengths controlled $\Delta\omega$, and the coupled frequency was determined by a metronome. Also confirmed was the prediction that the small shift in equilibria from in-phase and anti-phase due to the intrinsic asymmetry should be amplified in left-handers when $\Delta\omega > 0$ and in right-handers when $\Delta\omega < 0$. Further, the bias in left-handers was more consistent than the bias in right-handers, and a subgroup of right-handers was identified who performed similarly to left-handers. The coordination dynamics of functional asymmetry provides insights into the elementary synergy between the limbs, the dynamical mechanism that modulates it, and the nature of the asymmetry in left-handed and right-handed individuals.

Key words Handedness · Dynamics · Rhythmic movement · Synergies · Human

Introduction

The explanation of human functional asymmetry in general, and bimanual laterality in particular, remains an issue of considerable challenge. Although the existence of a bias toward a particular hand is undisputed, it has been argued that both hands work together as a single functional synergy or coordinative structure, for example, when writing with one hand and positioning the paper with the other (Guiard 1987a). That is, although attention may be directed towards a particular hand at a given time, the nonpreferred hand functions so as to prepare the behavioral context and thus complement and assist the preferred hand's duties. Any assessment of handedness will therefore be determined by the extent to which a task-specific, functional context constrains and induces either cooperation or competition between the hands. If a relative degree of attentional independence between the hands is permitted, for example in musicians who play keyboard instruments, then a greater degree of handedness is expressed than in musicians who play strings or wind instruments, which demand integrated movements (Christman 1993).

The neurophysiological mechanisms underlying human laterality may be approached via a review of several facts regarding the expression of handedness. When the hands produce nonisochronous rhythms that have timing demands more complex than simple 1:1 coordination (e.g., Kelso and DeGuzman 1988; Peper

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et al. 1991; Schmidt et al. 1992; Summers and Pressing 1994; Treffner and Turvey 1993), performance is optimal provided the preferred hand implements the faster of the two rhythms (Peters 1985). This is generally the case for both self-labelled right-handed (RH) and left-handed (LH) individuals, although a subset of self-labelled LH individuals exists who instead perform certain actions optimally, in particular, throwing, when executing the task in the manner of a right-hander [so-called inconsistent left-handers (Peters 1990a; Peters and Servos 1989)]. Further, under appropriate analyses, a well-defined subset of RH individuals emerges leading to a reconsideration that a right-hand bias exists in the population (Peters and Murphy 1992). Additional evidence indicates that handedness diminishes when attention is directed at the faster of two rhythmically moving hands and that attentional asymmetries may be instrumental to the expression of laterality (Peters 1995; Peters and Schwartz 1989).

Although these observations are well documented (e.g., Summers 1990), the issue remains as to why temporal constraints per se should influence the degree of handedness expressed. The corpus callosum may be considered crucial for the normal, smooth, coordinated trajectories exhibited by the limbs and for inhibiting the tendency towards gross bimanual synchrony (Swinnen et al. 1991; Tuller and Kelso 1989). However, interhemispheric transfer times are assumed independent of movement rate and have been estimated to be a constant factor of approximately 2–3 ms for simple reaction times to visual stimuli in unimanual movements, shorter for bimanual responses (Berlucchi et al. 1994), and approximately 23 ms for more complex bimanual rhythmic movements (Stucchi and Viviani 1993; see Discussion). Although callosotomized individuals have a reduced repertoire of movement patterns with in-phase coordination (homologous muscle group activation) more prevalent than anti-phase coordination (nonhomologous muscle group activation), they continue to exhibit coordinative abilities (Tuller and Kelso 1989). Hence, although higher cortical levels of motor organization subserved by the callosum may be necessary for performance asymmetries (Carson 1989), subcortical structures may suffice for basic bimanual coordination.

Evidence that temporal constraints influence manual laterality includes the observation that greater intermanual differences result when higher as opposed to lower rates of finger tapping are imposed (Todor and Kyprie 1980; Todor and Smiley 1985; Wolff et al. 1977), that increasing frequency can magnify the phase-lag between oscillating limbs (Sternad et al. 1992), thus instigating particular pattern transition pathways (Byblow et al. 1994; Jeka and Kelso 1995; Kelso and Jeka 1992). Further, the neurological organization of special populations may be different from normals under frequency constraints. In a study of dyslexic individuals performing a 1 : 1 finger tapping task, RH normals consistently led with the right hand under in-phase conditions at each of three different frequencies (Rouselle and Wolff 1991). Under anti-phase, the normals consistently led with the right finger but only at the two higher frequencies. In contrast, during in-phase coordination dyslexic individuals switched back and forth between whether the right hand or the left hand led, and showed no asymmetries under anti-phase, regardless of the frequency of performance.

It has also been recognized that any initial asymmetry found to exist between the hands often disappears when the task such as tapping is constrained by an external timing source [e.g., a pacing metronome (Carson et al. 1995; Todor and Smiley 1985; Truman and Hammond 1990; Wolff et al. 1977). In addition, the interaction between rate of tapping and hand employed results in greater difficulty of the non-preffered hand to tap the faster rhythm in a more complex timing task such as a 2 : 1 ratio (Peters 1985), and has been interpreted as due to constraints on the differential allocation of attention (Peters 1995), although nonlinear dynamical constraints also apply (Treffner and Turvey 1993).

In contrast to studies that employ complex activities, pronounced handedness effects were revealed in a simple 1 : 1 bimanual frequency-locking task under conditions whereby an external pacing signal provided the temporal constraint within which rhythmic movements were performed (Treffner and Turvey 1995). Any differential effects due to the rate of task execution were diminished by setting a metronome to a value determined by the natural frequency of coupled hand-held pendulums and was equal to the rate at which an individual elects to oscillate such objects (Kugler and Turvey 1987). The conclusion was that an account of bimanual coordination in terms of dynamics promises a more refined, accurate, and predictive account of the origin and nature of frequency effects on expressed handedness than does an account that ignores the organizational level of coordination dynamics (see also Carson 1993; Treffner and Turvey 1995).

Although rich and varied action patterns are common, the most conspicuous forms of interlimb coordination in humans are the rhythmicities typifying walking and running, in which limbs are 1 : 1 frequency-locked with phase angles differing by either π radians (anti-phase) or 0 radians (in-phase). These two patterns are expressions of an elementary rhythmic synergy that must have appeared early in the phylogeny or biological movement systems. In Bernstein's hierarchical division of the human movement system (Bernstein 1967; see also Latash and Turvey 1995), this elementary rhythmic coordination is the product of the *level of muscular-articular links or synergies*, a level involving the dynamical criteria of pattern stability and pattern reliability. The relation between the elementary rhythmic synergy between limbs, the mechanisms that modulate it, and the bimanual asymmetry characteristic of human actions has been highlighted by Peters's conjecture that: "The ability to interrupt the flow of bilateral coordinations, essential to locomotion in a world that offers obstacles and requires sudden changes in direction, forms the evolutionary basis for skilled bimanual coordination in humans. Supraspinal mechanisms have to be able to disrupt the spinal oscillatory network that underlies locomotion, so that asymmetry in movement can be achieved" (Peters 1994, p. 596). In the present article we address the nature of such supraspinal mechanisms by identifying sources of symmetry and symmetry-breaking within the dynamics of interlimb rhythmic coordination. In the following, the symmetrical and asymmetrical aspects of the coordination dynamics are elaborated in formal rather than strictly neurological terms for the reason that the same dynamics appear to govern various scales of biological organization and hence are not subservient to one particular neural structure (cf. Baldissera et al. 1991; Fuchs et al. 1992; Kelso 1995; Kelso et al. 1991; Swinnen et al. 1991; Turvey 1994), or to rhythmic movements in particular (Schöner 1990).

Symmetric coordination

The emergent behavior of any two contralateral limbs or limb segments in rhythmic motion has been captured by the change over time of relative phase (Haken et al. 1985; Kelso 1984), defined for present purposes as $\phi = (\theta_L - \theta_R)$, the difference between the left (L) and right (R) component oscillator's continuous phase angle. Quantities such as ϕ are relatively macroscopic variables that maintain invariant values under continual changes in the microscopic components. Further, such quantities index both the overall loss of stability of a pattern preceding a qualitative transition and the new pattern's subsequent stabilization. Hence, such quantities that specify the relevant pattern dynamics of a given coordinative system (Schöner and Kelso 1988a) have been termed *order parameters* (Haken 1977).

For simplicity, the important changes in ϕ can be assumed to be of first order, that is, no time derivatives of ϕ other than the first need be considered. Further, the rate at which ϕ changes (its "velocity" $d\phi/dt$) can be assumed to depend on ϕ and on certain parameters κ that remain unchanged during the rhythmic motion. That is,

$$\dot{\phi} = F(\phi, \kappa) \tag{1}$$

where the dot signifies the time derivative. Equation 1 is the equation of a *gradient system,* meaning that it can be put into the form

$$\dot{\phi} = -dV/d\phi \tag{2}$$

where d signifies derivative (here with respect to ϕ) and $V = V(\phi, \kappa)$ is a potential function (Gilmore 1981; Haken 1977; Jackson 1989). V is a "potential" because it is always decreasing along the solution curves of Eq. 1, attaining a minimum when the time-derivative of ϕ goes to zero.

Particular experimental investigations of interlimb rhythmic coordination have suggested the form of V. As noted at the outset, 1 : 1 frequency-locking tends to occur in two patterns, in-phase ($\phi = 0$, or homologous muscle group activation) and anti-phase ($\phi = \pi$, or nonhomologous muscle group activation). The particular experiments in question revealed that the two patterns are not equivalent: $\phi = 0$ is more persistent over frequency scaling than $\phi = \pi$. In these experiments a person was required to oscillate the two index fingers (or two hands) at the coupled frequency ω_c, where ω_c was varied by a metronome that the person tracked (Kelso 1984). With increasing ω_c, a person's fingers "prepared" in anti-phase switched suddenly to in-phase. The transition from anti-phase to in-phase was not reversed, however, by a reduction in ω_c, and if the fingers were prepared in in-phase, the increase in ω_c did not bring about a transition to anti-phase. Constrained by the preceding pattern of results, Haken et al. (1985) postulated that (a) V was periodic, that is, $V(\phi + 2\pi) = V(\phi)$, (b) the roles of the two limb segments were symmetrical, meaning that V was identical under the transformation $\phi \rightarrow -\phi$, and (c) given these postulates of periodicity and symmetry, V may be developed as the Fourier series in even (cosine) terms. Because of the inequality in stability of $\phi = 0$ and $\phi = \pi$, and the implication of the data that the two attractors coexisted, the series must include, minimally, the first two even terms. Further, because $\phi = 0$ and $\phi = \pi$ must be the minima of V, the coefficients on these two terms must be negative. Hence,

$$V = -a\,cos(\phi) - b\,cos(2\phi)\,. \tag{3}$$

The ratio of coefficients, b/a, identifies a control parameter, inversely dependent on ω_c, that dictates qualitative changes in V and, thereby, coordination changes in the fundamental interlimb rhythmic synergy.

By Eq. 2, the form of the motion equation, Eq. 1, can be derived as the negative gradient (with respect to ϕ) of V (Haken et al. 1985), that is,

$$\dot{\phi} = -a\,sin(\phi) - 2b\,sin(2\phi)\,. \tag{4}$$

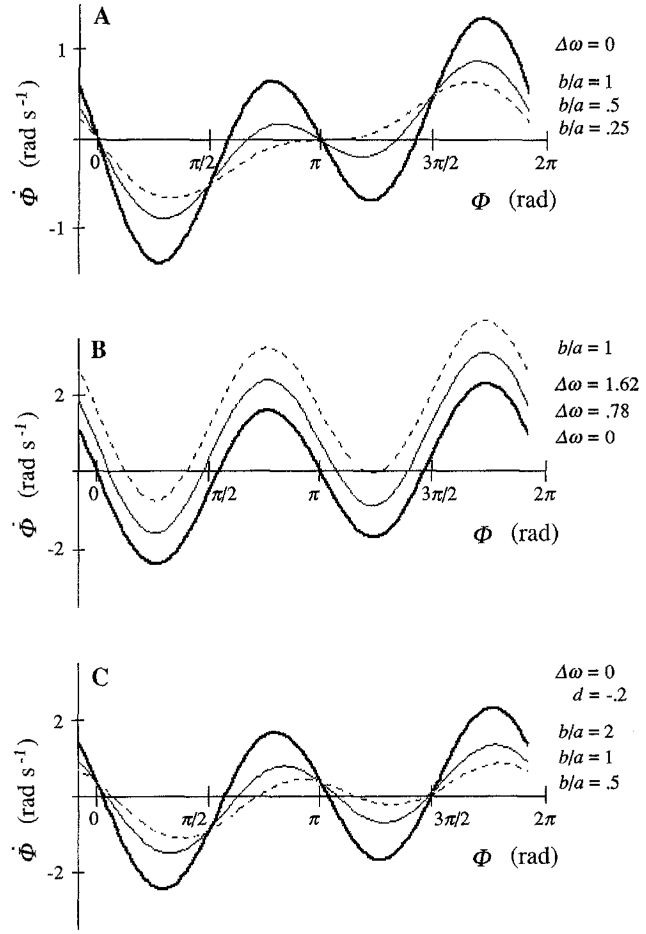
This equation of motion can be referred to as the deterministic part of the *symmetric coordination law* (Kelso 1994). It applies to rhythmic coordination between segments that assume identical roles in the coordination. It identifies the equilibria of the coordination for any given parameter values and the changes in number and kind (stable, unstable) of equilibria that occur as the parameter values are scaled – changes that are commonly referred to as *bifurcations.* The equilibria can be found by solving numerically for $\dot{\phi} = 0$. If Eq. 4's right-hand side is plotted against ϕ, then the equilibria are those values of ϕ, designated by ϕ_0, at which the obtained curve crosses the zero line (see Fig. 1).

An equilibrium point can be either a stable equilibrium (an attractor) or an unstable equilibrium (a repeller). The kind of equilibrium point is determined by the derivative of $\dot{\phi}$ with respect to ϕ evaluated at ϕ_0 (see e.g. Hilborn 1994; Strogatz 1994)

$$\lambda = \left.\frac{d\dot{\phi}}{d\phi}\right|_{\phi=\phi_0} . \tag{5}$$

Equation 5 is negative ($\lambda < 0$) for an attractor and positive ($\lambda > 0$) for a repeller. The value of λ is called the *characteristic value* of the equilibrium or the *Lyapunov exponent* for the region near the equilibrium (e.g., Abraham and Shaw 1992; Haken 1983; Hilborn 1994). The larger the value of $\lambda < 0$, the more attractive is the equilibrium. With respect to Eq. 3, the rate of descent to a potential minimum, the steepness of a potential well, is measured by λ (e.g., Gilmore 1981; Schöner et al. 1986).

Fig. 1 Comparative dynamics of Eq. 4 for $\Delta\omega = 0$ and b/a decreasing (**A**), $b/a = 1$ and $\Delta\omega$ decreasing (**B**), and of Eq. 8, $d \neq 0$, $\Delta\omega = 0$, and b/a decreasing (**C**). Fixed-point shift occurs under conditions of either frequency detuning (**B**), or asymmetrical coupling (**C**). Shift of ϕ_{stable} under anti-phase ($\psi = \pi$) coordination is greater than under in-phase ($\psi = 0$) coordination. The gradient at the zero-crossing is less under anti-phase than under in-phase



A stochastic force

Because the collective dynamics of the elementary rhythmic synergy between limbs is a projection in larger space and time scales of the behavior and interactions of many subsystems taking place at much smaller scales, fluctuations in ϕ are expected. Equation 1 should, in fact, include a noise term in the parentheses. The noise welling up from the interior of the elementary rhythmic synergy will function as a stochastic force influencing the collective variable. It can be identified with $Q^{1/2}\zeta_t$, where ζ_t is gaussian white noise and $Q > 0$ is its strength (Schöner et al. 1986). The symmetric coordination law, Eq. 4, must be elaborated, therefore, to include this essential random element (Schöner et al. 1986). The effect of this stochastic force on the behavior of ϕ will depend on the magnitude of λ. The presence of noise means that ϕ is displaced continuously from the bottom of a potential well by a random sequence of kicks. The standard deviation of ϕ (SDϕ) around an equilibrium point is given by (e.g., Gilmore 1981):

$$\mathrm{SD}\phi = \sqrt{\frac{Q}{2\lambda}} . \tag{6}$$

In sum, a steeper negative slope at a zero crossing means a larger λ, a smaller variance in ϕ, and an equilibrium point, therefore, that is more readily retained against perturbations of strength Q.

Symmetry breaking through frequency competition

For the more general case, two segments will not be physically identical and, therefore, will not contribute identically to interlimb rhythmic coordination (von Holst 1973). Physical differences break the symmetry of the coordination dynamics. To accommodate this broken symmetry, a detuning term must be introduced to Eq. 4. Such a detuning term was introduced to capture purely functional differences, as in the frequency difference between an oscillating limb and an auditory metronome (Kelso et al. 1990). In the present case, the detuning term is equated with the difference between the uncoupled frequencies of the bimanual rhythmic components themselves, i.e. $\Delta\omega = (\omega_L - \omega_R)$ (e.g., Cohen et al. 1982; Jeka and Kelso 1995; Kelso and Jeka 1992; Kopell 1988; Rand et al. 1988; Sternad et al. 1992; Treffner and Turvey 1995). Hence,

$$\dot{\phi} = \Delta\omega - a\,sin(\phi) - 2b\,sin(2\phi) + \sqrt{Q}\zeta_t . \tag{7}$$

The kinds of predictions that follow from Eq. 7 regarding the equilibria and fluctuations (SD$\phi \propto \lambda^{-1}$) of interlimb 1:1 frequency locking are depicted in Fig. 1A, B.

They have been confirmed through experiments that manipulated ψ (the required 1:1 coordination of 0 or π), $\Delta\omega$, and ω_c (see summaries in Kelso 1994; Schmidt and Turvey 1995; Treffner and Turvey 1995).

Symmetry breaking through coupling

The interlimb rhythmic coordination abstractly defined by Eq. 4 has no left-right asymmetry. Because the coupling is symmetrical (the two rhythmically moving limb segments affect each other identically), any right lead ($\phi < 0$, $\phi < \pi$), or right lag ($\phi > 0$, $\phi > \pi$), will be strictly due to the sign of $\Delta\omega$ in Eq. 7. For two homologous body segments (e.g., two hands, two index fingers), the probable identity of uncoupled frequencies means $\Delta\omega = 0$, with no tendency for either segment to lead, ($\phi = 0$, $\phi = \pi$); for nonhomologous body segments, $\Delta\omega \neq 0$, the segment of higher uncoupled frequency will lead the other (Jeka and Kelso 1995; Kelso and Jeka 1992). If the fundamental interlimb rhythmic coordination is truly left-right symmetric, however, then the question arises of how the needed biases to a left or right limb – identified in the quotation from Peters (1994) in the Introduction – might be imposed in tailoring locomotion to environmental conditions. Perhaps the left-right asymmetry is manifest in the elementary rhythmic synergy, albeit subtly.

An experiment by Treffner and Turvey (1995) examining the simple task of 1 : 1 frequency locking (using the procedure depicted in Fig. 3 and described in the Methods section), revealed that for $\Delta\omega = 0$, RH individuals tended to exhibit a small but reliable right lead ($\phi < 0$, $\phi < \pi$) and LH individuals tended to exhibit a small but reliable left lead ($\phi > 0$, $\phi > \pi$). Further, for RH individuals the shifts of equilibria from 0 and π were greater under $\Delta\omega < 0$ (right oscillator was of higher frequency) than $\Delta\omega > 0$. For LH, the equilibria were displaced more by $\Delta\omega > 0$ than $\Delta\omega < 0$. In sum, handedness interacted with the sign of $\Delta\omega$.

Two hypotheses about the incorporation of handedness in the elementary coordination dynamics of Eq. 7 have been advanced (Treffner and Turvey 1995). One hypothesis assumes that the body's functional asymmetry is expressed in the detuning term $\Delta\omega$, for example, homologous but contralateral limb segments are not identical in uncoupled frequency – the preferred limb's natural frequency is higher. The other hypothesis assumes that the body's functional asymmetry is in the coupling term, specifically, the coupling between contralateral limb segments is not isotropic. Against the detuning hypothesis is the evidence from Kugler and Turvey (1987, Table 6.2), in the very procedure used by Treffner and Turvey (1995), that oscillations of hand-held pendulums by the right and left hands exhibit statistically identical uncoupled frequencies. In favor of the anisotropic coupling hypothesis is (a) the necessity of such coupling in the extensive modeling of swimming by the primitive lamprey eel (e.g., Ermentrout and Kopell 1991), and (b) the general strategy of expanding the potential function to accommodate the "vector field" (the plot of $\dot{\phi}$ against ϕ for all parameter values) implicated by experimental data (e.g., Schöner and Kelso 1988a, 1988b).

Pursuing (b), the symmetric potential (Eq. 3) underlying the symmetric coordination law (Eq. 4) must be broken by handedness. V can no longer be invariant over the transformation $\phi \rightarrow -\phi$. Adding the first two odd (sine) terms of the Fourier series, namely, $c\,sin(\phi)$ and $d\,sin(2\phi)$, to Eq. 3 deflects the minima of V from $\phi = 0$ and $\phi = \pi$ (see Treffner and Turvey 1995). Both c and d are coefficients, whose signs and magnitudes determine the degree and direction of asymmetry, respectively. Treffner and Turvey's (1995) results suggest, therefore, that the emergent elementary rhythmic synergy between limbs or limb segments is governed by a *slightly* asymmetric potential. That is, in the determination of the full potential V for interlimb coordination with functional asymmetry, c and d are small relative to a and b. The collective dynamics of intersegmental rhythmic coordination reflecting the full complement of symmetric and asymmetric influences is given by

$$\underset{\substack{\text{coordination}\\\text{change}}}{\dot{\phi}} = \underset{\substack{\text{frequency}\\\text{competition}}}{\Delta\omega} - \underset{\substack{\text{symmetric coupling}\\\text{attractors: } 0,\ \pm\pi}}{[a\,sin(\phi) + 2b\,sin(2\phi)]} - \underset{\text{asymmetric coupling}}{[c\,cos(\phi) + 2d\,cos(2\phi)]} + \underset{\substack{\text{stochastic}\\\text{force}}}{\sqrt{Q}\,\xi_t} \qquad (8)$$

$$\swarrow \qquad \searrow$$

$$\underset{\text{(for c and d > 0)}}{\text{attractors: } \frac{-\pi}{4}, \frac{-5\pi}{4}, \frac{3\pi}{4}} \qquad \underset{\text{(for c and d < 0)}}{\text{attractors: } \frac{\pi}{4}, \frac{5\pi}{4}, \frac{-3\pi}{4}}$$

The symmetric and asymmetric periodic components of Eq. 8 assume different roles, consonant with the intuition expressed by Peters (1994). Whereas b/a determines the relative strengths of the fundamental in-phase and anti-phase equilibria, small values of c and d break the symmetry of the elementary coordination dynamics while leaving their essential characteristics unaltered (see Fig. 1C). In exploring Eq. 8, Treffner and Turvey (1995) showed that d is the more important handedness coefficient, producing the empirically observed directions of shift in the equilibrium around both 0 and π, and thus c can be set to zero without loss of generality. They were able to successfully model the observed equilibria and fluctuations of their experiment with $d = -0.08$ for LH individuals and $d = 0.05$ for RH individuals.

Handedness and frequency scaling: predictions from the coordination dynamics of equation 8

There is an implied division of labor in Eq. 8. The experimental control parameter ω_c is linked (inversely) to b/a. When bimanual 1 : 1 rhythmic coordination is performed at different coupled frequencies, the symmetric coupling coefficients change. An increase in ω_c means a decrease in the relative strengths of the attractors at 0 and π, as depicted in Fig. 1A for the limiting case of $\Delta\omega = 0$. What should be expected of the coefficients of the asymmetric coupling when bimanual 1 : 1 rhythmic coordination under $\Delta\omega = 0$ is performed at different coupled frequencies? Because the task assigns an equal status to the movements of the two hands, the weight of the experimental evidence on handedness in bimanual coordination (see Peters 1994) favors the hypothesis that the coefficients of asymmetric coupling will be invariant over ω_c. If so, then with $\Delta\omega = 0$ and increasing ω_c, the attractors at $\pm\ \pi/4$, $\pm\ 3\pi/4$, and $\pm\ 5\pi/4$ identified for the asymmetric part of Eq. 8 will remain at constant relative strength as the attractors near to 0 and π weaken. Stated differently, the contribution of the asymmetric coupling to the coordination dynamics under $\Delta\omega = 0$ will increase in relative influence as ω_c increases and b/a decreases – that is, the difference between LH individuals and RH individuals will increase with frequency. This prediction is shown in Fig. 2 (left). Following the simulations of Treffner and Turvey (1995), we set $c = 0$, $d = -0.08$ for LH individuals, $d = 0.05$ for RH individuals, and b/a equal to 1.0, 0.7, and 0.5, reflecting increase in ω_c. Numerical analysis of Eq. 8 for these parameter settings and $\Delta\omega = 0$ reveals that $(\phi_{stable} - \psi)$ becomes increasingly positive for LH individuals and increasingly negative for RH individuals as ω_c increases (where ψ is the required phase of 0 or π).

A similar prediction can be made for the dependence of the absolute magnitude of $(\phi_{stable} - \psi)$ on the sign of $\Delta\omega$ when $\Delta\omega \neq 0$, as shown in Fig. 2 (right). The magnitudes of the displacement in equilibria from ψ, in either the positive or negative direction, should be larger for RH individuals when $\Delta\omega$ is negative (the shorter, right-hand pendulum has the higher eigenfrequency) than when $\Delta\omega$ is positive, and they should be larger for LH individuals when $\Delta\omega$ is positive (the shorter, left-hand pendulum has the higher frequency) than when $\Delta\omega$ is negative. The latter pattern was observed in the original data of Treffner and Turvey (1995), as noted above. The new expectations that arise from Eq. 8, and the assumption of invariant asymmetric coupling parameters in 1 : 1 frequency locking, are that the absolute magnitudes of $(\phi_{stable} - \psi)$ should increase with ω_c at approximately the same rate for both LH and RH individuals and that the form of the interaction between the sign of $\Delta\omega$ and handedness should, therefore, persist over increases in ω_c. The following experiment was designed to evaluate this.

Methods

Participants

Forty undergraduates (17 women and 23 men) at the University of Connecticut participated in the study in partial fulfillment of requirements for the introductory psychology course. Twenty defined themselves as RH and 20 as LH. Both the 20 LH individuals and the 20 RH individuals were assigned to an in-phase or anti-phase group by order of appearance at the laboratory. Thus, there were four groups of 10 participants each: LH in-phase, LH anti-phase, RH in-phase, RH anti-phase.

Apparatus

A special purpose chair with arm rests was utilized permitting the support of both left and right forearms and wrists during oscilla-

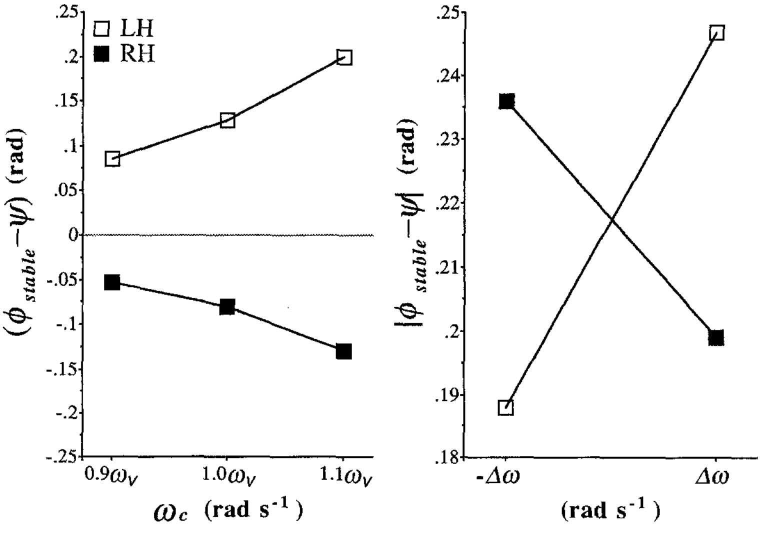


Fig. 2 *Left* Predictions from Eq. 8 for $\Delta\omega = 0$ and increasing ω_c. *LH parameters* are $d = -0.08$, $c = 0$, $a = 0.5$, and $b = 0.5$, 0.35, and 0.25 for $b/a = 1.0$, 0.7, and 0.5, respectively. *RH parameters* as for LH but with $d = 0.05$. *Right* predictions for $\Delta\omega \neq 0$ with constant $b/a = 0.7$. Parameters are $a = 2.5$, $b = 1.75$, $c = 0$, and either $d = -0.08$ (LH) or $d = 0.05$ (RH)

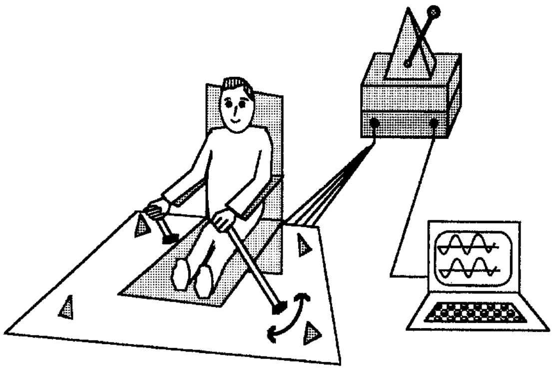


Fig. 3 Front view of the experimental arrangement in which an individual oscillates two hand-held pendulums at a frequency specified by an electronic metronome. The schematic depicts the four microphones of a sonic 3D digitizer arranged at the corners of a horizontal square grid beneath the participant. A sound emitter is attached to the lower end of each pendulum. The time-varying positions of the emitters are recorded by computer

tory movements (see Fig. 3). Attached to the seat were leg rests which allowed the legs to be raised toward the horizontal in order to avoid interference with sonic data collection. Kinematic data were collected using a three-dimensional sonic digitizer (SAC, Westport, CONN.) and associated MASS kinematic analysis software (Engineering Solutions, Columbus, Ohio). In order to collect motion data from the pendulums, high frequency sound emitters (30 mm long and 5 mm wide) were attached to the tip of each pendulum. 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 sonic digitizer calculated the distances of the emitter from each microphone, using the three least noisy records to pinpoint the position of the emitter in three dimensions at the time of emission. The signal was sampled at 90 Hz, passed through an A-D converter and stored on a PC's hard disk. Subsequent PC and Macintosh routines were used for additional computations related to the continuous relative phase.

Materials

Each pendulum was composed 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. Coupled systems were composed of two of the following three pendulums: (1) 56 cm in length with a 500-g steel disk attached at the lower end, (2) 45 cm in length with a 50-g steel disk attached at the lower end, and (3) 26 cm in length with a 100-g steel disk attached at the lower end. As noted, 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 standard methods of calculating the first and second moments of a rigid body oscillating about a fixed point and representing it as a simple pendulum oscillating about the same point (Kugler and Turvey 1987). The ω values of the three individual wrist-pendulums were 5.72, 4.88, and 4.10 rad/s. Five coupled conditions were formed by combining these three systems according to $\Delta\omega = (\omega_{left} - \omega_{right}) = (4.10 - 5.72), (4.10 - 4.88), (4.10 - 4.10), (4.88 - 4.10)$, and $(5.72 - 4.10)$, yielding five $\Delta\omega$ values of -1.62, -0.78, 0, 0.78, and 1.62 rad/s.

The eigen frequency of the coupled system was computed under the assumption that it would be the preferred time scale of the right (R) and left (L) wrist-pendulum systems coupled such that θ_R is always, at every instant, equal to θ_L, or to $(\theta_L + \pi)$ (Kugler and Turvey 1987; Sternad et al. 1992). Such a situation occurs when the coupling between the two oscillators is functionally equivalent to that of a rigid connection (Kugler and Turvey 1987). The simple pendulum equivalent L_v of such a compound pendulum is given by

$$L_v = (m_1 l_1^2 + m_2 l_2^2)/(m_1 l_1 + m_2 l_2) \tag{9}$$

where m_i and l_i refer to the mass and the equivalent simple pendulum length, respectively, of an individual (compound) pendulum system. Using Eq. 9, 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 4.35, 4.29, and 4.10 rad/s with corresponding periods of 1.444, 1.464, and 1.532 s which defined the metronome tempos used to control the coupled frequencies. The three coupled frequencies of oscillation chosen were related to the coupled system's eigenfrequency, ω_v, as follows: $\omega_c = 0.9\omega_v$ (lower than eigenfrequency), $\omega_c = 1.0\omega_v$ (equal to the eigenfrequency), and $\omega_c = 1.1\omega_v$ (higher than eigenfrequency).

Procedure

The participant sat in the chair with his or her arms placed comfortably on the arm rests. A pendulum was placed in each hand and he or she was asked to swing them from the wrist joints in the saggittal plane while looking straight ahead rather than at the pendulums, although peripheral vision of the hands was not restricted. The participant was told to grasp the handles firmly throughout the oscillations preventing slippage of the pendulum relative to the hand. After receiving instructions from the experimenter, each individual was given practice swinging a pendulum pair. The participant was asked to begin swinging the pendulums at the tempo prescribed by an auditory metronome (that emitted short duration beeps) positioned 150 cm behind the participant's seat and to say "Ready" when synchronous coordination had been achieved (usually in a matter of 5–10 s). The experimenter then started to record the trial for 30 s during which the metronome remained on. At the end of each trial's data collection, the experimenter replaced the pendulums with another pair for the next trial. Each of the 15 conditions (five coupled pendulum systems and three ω_c) was repeated twice. The order of the 30 experimental trials was completely randomized. Participants received no feedback about their performance. The session took approximately 45 min per individual.

Data reduction

The data records were subjected to software analyses to compute the time series of the individual wrist-pendulum phase angles θ_L and θ_R, the time series of the relative phase angle $\phi = (\theta_L - \theta_R)$, and the means and standard deviations of these quantities. The time of maximum forward extension (ulna extension) and maximum backward extension (ulna flexion) of the wrist-pendulum trajectories was determined by a peak picking algorithm. From the peak forward extension times, the mean frequency of oscillation for the nth cycle was calculated as

$$f_n = 1/(\text{time of forward extension}_n - \text{time of forward extension}_{n+1}) \tag{10}$$

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

$$\theta_{ij} = \arctan(\dot{x}_{ij}/\Delta x_{ij}) \tag{11}$$

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. ϕ between the two coordinated wrist-pendulum systems was calculated for each sample as $\theta_L - \theta_R$. Equation 11 is a reliable basis for determining ϕ given that (a) the waveforms of both left and right oscillators are essentially sinusoidal due to the constraints of pendular motion, and (b) the center of oscillation of each oscillator is fixed because the oscillations take place about the wrist joints, and the forearms and wrists of each upper limb maintain constant positions during each trial. The required relative phase ψ was either 0 rad (in-phase) or π rad (anti-phase). The ϕ time series allows for an evaluation of how well task requirements were satisfied. The mean ϕ (interpreted as ϕ_{stable}) and its standard deviation (SDϕ) were calculated for each trial.

Results

1:1 Frequency locking

The ratio of the average frequency of the right wrist-pendulum oscillation to the average frequency of the left wrist-pendulum oscillation did not differ from unity (two-tailed t-test, $P > 0.05$ in all cases) for both in-phase and anti-phase, both LH and RH individuals, for all three ω_c, and for all five $\Delta\omega$ values. Thus, 1:1 frequency locking was reliably achieved in all conditions.

Overall patterning of relative phase

The magnitudes of ϕ_{stable} for RH and LH individuals in in-phase and anti-phase coordination at each ω_c, are presented in Fig. 4. Ignoring handedness differences for the time being, and recalling that b/a varies inversely with ω_c (see Haken et al. 1985; Schmidt et al. 1993), the data pattern of Fig. 4 conform to major expectations from Eq. 7: $\Delta\omega$ and ω_c interact in determining ϕ_{stable}, and that when $\Delta\omega = 0$, $\phi_{stable} = 0$ (for $\psi = 0$) and $\phi_{stable} = \pi$ (for $\psi = \pi$) regardless of ω_c.

Evaluating the handedness prediction for $\Delta\omega = 0$

Turning to expectations unique to Eq. 8, did the data parametrized by handedness conform to Fig. 2? Figure 5 (left) presents mean ($\phi_{stable} - \psi$) under $\Delta\omega = 0$ for the 20 LH individuals and the 20 RH individuals as a function of ω_c. Inspection of Fig. 5 (left) suggests that, in rough agreement with the aforementioned prediction (see Introduction), ($\phi_{stable} - \psi$) became increasingly positive with ω_c for LH individuals and became decreasingly positive with ω_c for RH individuals. A handedness $\times\ \psi \times \omega_c$ analysis of variance (ANOVA) performed on ($\phi_{stable} - \psi$) at $\Delta\omega = 0$ revealed a significant effect of handedness [LH = 0.080 rad vs RH = -0.004 rad; $F(1, 36) = 10.08$, $P < 0.01$] indicating that overall, the LH individuals were left-leading (of the right by the left hand), and the RH individuals were right-leading (of the left by the right hand). Although there was no interaction between handedness, ω_c and ψ, there was an interaction between handedness and ω_c [$F(2, 72) = 3.06$, $P < 0.05$], indicating that as ω_c increased, LH individuals became increasingly left-leading and RH individuals became increasingly right-leading. To evaluate the influence of ω_c, a handedness $\times\ \psi \times \omega_c$ ANOVA on the mean absolute magnitude of phase deviation, $|\phi_{stable} - \psi|$, revealed a significant effect of ω_c, 0.07, 0.09, and 0.13 rad for $\omega_c = 0.9\omega_v$, $1.0\omega_v$, and $1.1\omega_v$, respectively [$F(2, 72) = 10.03$, $P < 0.0001$]. No other significant effects were found.

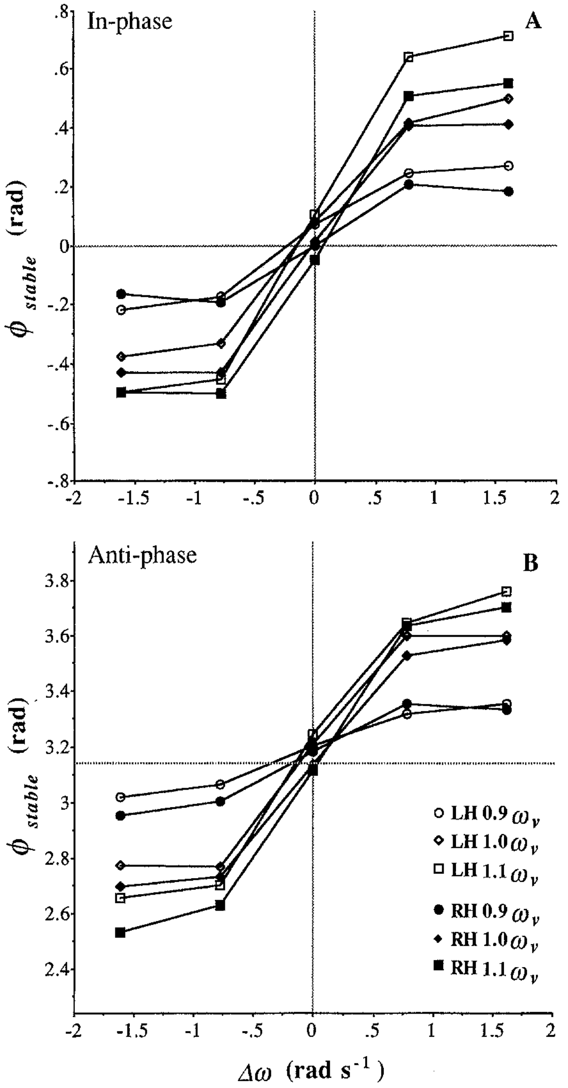


Fig. 4 Observed ϕ_{stable} as a function of $\Delta\omega$, handedness, and ω_c for in-phase (**A**), and anti-phase (**B**) coordination. Values of ϕ_{stable} above the horizontal midline indicate a left-hand lead, and values below indicate a right-hand lead

According to Eq. 8, a functional asymmetry of the limbs in 1:1 frequency coordination would be revealed as a mean value of ($\phi_{stable} - \psi$) different from zero in different directions for RH and LH individuals when $\Delta\omega = 0$. The preceding ANOVA confirmed the functional asymmetry. In further evaluation, t-tests

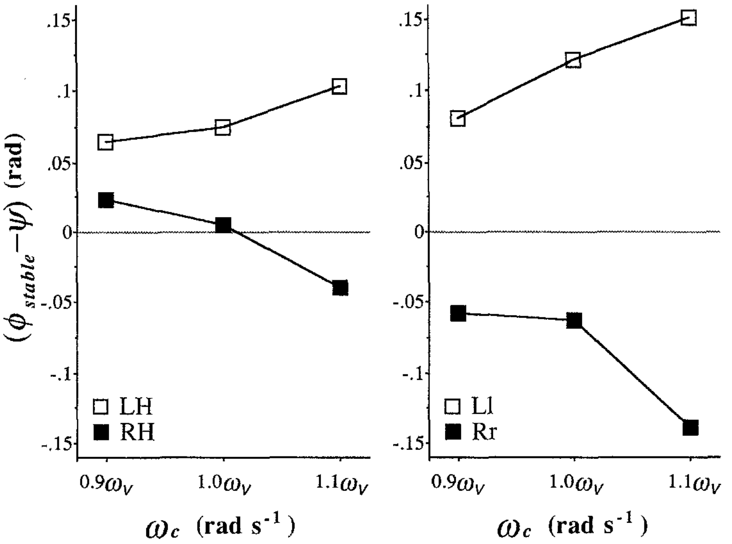


Fig. 5 Performance as measured by $(\phi_{stable}-\psi)$ for $\Delta\omega = 0$ and increasing ω_c for conventionally defined LH and RH individuals (*left*), and functionally defined Ll and Rr individuals (*right*)

were conducted to determine whether $(\phi_{stable}-\psi)$ departed significantly from zero in all cases. For the 20 LH individuals, the mean values of $(\phi_{stable}-\psi)$ for $\omega_c = 0.9\omega_v$, $1.0\omega_v$, and $1.1\omega_v$ were 0.065, 0.075, and 0.103 rad, respectively. Each was significantly different from zero $t(19) = 3.57$, 3.24, and 3.56 ($P < 0.01$). For the 20 RH individuals, the mean values of $(\phi_{stable}-\psi)$ were 0.023, 0.005, and -0.039 rad for $\omega_c = 0.9\omega_v$, $1.0\omega_v$, and $1.1\omega_v$, respectively, and none were significantly different from zero ($P > 0.05$). Chi-square tests were conducted to determine whether the participants exhibited leading-hand preferences at $\Delta\omega = 0$ that were different from what would be expected if there was no bias in the population toward one hand leading the other. The left-hand lead of the LH individuals was significantly different from expectation: χ^2 (1, N = 20) = 9.8 ($P < 0.01$), 5.0 ($P < 0.05$), and 7.2 ($P < 0.01$), for $\omega_c = 0.9\omega_v$, $1.0\omega_v$, and $1.1\omega_v$, respectively. RH individuals, in contrast, were not distinguished with respect to leading hand ($P > 0.05$ for all ω_c). In brief, RH individuals were just as likely to lead with the left as with the right hand but LH individuals tended to lead with the left hand.

In order to further examine the effect of ω_c on handedness (i.e., the degree to which the left-hand lead in LH individuals and the right-hand lead in RH individuals was magnified by ω_c), functional handedness groups were defined as composed of only those participants that consistently led with the preferred hand at a particular frequency. Table 1 presents the number of left-leading LH individuals (Ll individuals), the number of right-leading RH individuals (Rr individuals), and the associated values of mean $(\phi_{stable}-\psi)$ for both $\psi = 0$ and $\psi = \pi$ at a given ω_c. It can be seen that the magnification of mean $(\phi_{stable}-\psi)$ with increasing ω_c was in opposite directions for Ll and Rr individuals implying that "handedness" was amplified, in precise accordance with prediction – compare Fig. 5 (right) with Fig. 2 (left). Further inspection of the values of $(\phi_{stable}-\psi)$ at $\Delta\omega = 0$ revealed that although 13 out of 20 LH individuals produced a mean $(\phi_{stable}-\psi) > 0$ (left hand leading) for all three ω_c, only 5 out of 20 RH individuals produced a mean $(\phi_{stable}-\psi) < 0$ (right hand leading) for all three ω_c. This suggests that the RH individuals were less homogeneous as a group with respect to leading hand. The relative heterogeneity of the groups (especially the RH individuals) with regard to leading hand suggested that further analyses incorporate the partitioning of the 40 participants on the basis of leading hand, as was done in Treffner and Turvey (1995).

Evaluating the handedness prediction for $|\Delta\omega| > 0$

The $\Delta\omega \neq 0$ manipulations were collapsed over the two individual negative values of $\Delta\omega$ and the two individual positive values of $\Delta\omega$ thus yielding a new independent variable of the sign of $\Delta\omega$. A handedness × ψ × sign × ω_c ANOVA was conducted on mean $\phi_{stable}-\psi$

Table 1 Number (out of 10) of right-leading RH individuals, left-leading LH individuals, and mean $(\phi_{stable}-\psi)$, at $\Delta\omega = 0$ as a function of ω_c/ω_v and ψ

	ω_c/ω_v		
ψ	0.9	1.0	1.1
LH individuals			
In-phase			
Number of participants	8	7	8
Mean $(\phi_{stable}-\psi)$	0.087	0.149	0.163
Anti-phase			
Number of participants	9	8	8
Mean $(\phi_{stable}-\psi)$	0.075	0.094	0.139
RH individuals			
In-phase			
Number of participants	5	5	7
Mean $(\phi_{stable}-\psi)$	−0.047	−0.065	−0.138
Anti-phase			
Number of participants	3	7	5
Mean $(\phi_{stable}-\psi)$	−0.069	−0.060	−0.140

for the 20 LH individuals and 20 RH individuals. At issue was whether handedness and the sign of $\Delta\omega$ interacted, and whether this interaction occurred in the same form at all three ω_c. That is, did the data conform to the predictions from Eq. 8 as captured in Fig. 2 (right)? Inspection of Fig. 6 (left) suggests that they did. There were significant effects of ω_c [$F(2, 72) = 167.50$, $P < 0.0001$] of sign [$F(1, 36) = 8.90$, $P < 0.01$], and of the interaction between handedness and sign [$F(1, 36) = 8.40$, $P < 0.01$], but there was no significant three-way interaction between handedness, sign, and ω_c.

Separate handedness × ψ × sign ANOVAs were performed on mean $|\phi_{stable} - \psi|$ for each ω_c separately. The handedness groups were defined to consist of either Ll individuals or Rr individuals according to performance at $\Delta\omega = 0$ for each ω_c. For $\omega_c = 1.1\omega_v$, there was a significant main effect of sign [$F(1, 24) = 4.12$, $P < 0.05$], and importantly, a significant interaction between handedness and sign [$F(1, 24) = 19.40$, $P < 0.001$]. There was also an interaction between ψ and sign [in-phase: $-\Delta\omega = 0.51$ rad vs $\Delta\omega = 0.63$ rad; anti-phase: $-\Delta\omega = 0.48$ rad vs $\Delta\omega = 0.50$ rad; $F(1, 24) = 4.22$, $P < 0.05$]. For the two lower frequencies, both interactions between handedness and sign were significant [$F(1, 23) = 5.73$, $P < 0.05$, and $F(1, 21) = 8.99$, $P < 0.01$, for $\omega_c = 1.0\omega_v$ and $\omega_c = 0.9\omega_v$, respectively]. No other significant effects were found. In sum, the results with Rr and Ll groups shown in Fig. 6 (right) buttressed the conclusion that handedness and the sign of $\Delta\omega$ related in the manner expected from Eq. 8.

Analyses within RH individuals

A separate ANOVA was performed on Rr individuals vs left-leading, RH (Rl) individuals. As observed in the experiment of Treffner and Turvey (1995), Rr and Rl individuals contrasted in the same way as Rr and Ll individuals. Although there were no significant results for $\omega_c = 1.1\omega_v$, ($Fs < 1$), the interaction of group and sign occurred for $\omega_c = 1.0\omega_v$ [Rl: $-\Delta\omega = 0.40$ rad vs $\Delta\omega = 0.46$ rad; Rr: $-\Delta\omega = 0.45$ rad vs $\Delta\omega = 0.37$ rad; $F(1, 18) = 4.42$, $P < 0.05$], and at $\omega_c = 0.9\omega_v$, [Rl: $-\Delta\omega = 0.13$ rad vs $\Delta\omega = 0.22$ rad; Rr: $-\Delta\omega = 0.21$ rad vs $\Delta\omega = 0.18$ rad; $F(1, 18) = 5.89$, $P < 0.05$]. These results indicated that the subgroup of Rl individuals embedded within the self-designated group of RH individuals, exhibited a pattern of coordination functionally similar to that shown by the LH individuals.

A natural coordinate system

Since defining $\Delta\omega$ as a difference between left and right hand is to impose an extrinsic, geometrical and possibly arbitrary distinction on the coupled component limbs, an intrinsically based and potentially more meaningful distinction for the interlimb system is to use a functional categorization in terms of preferred hand (*P*) vs nonpreferred hand (*NP*) (Treffner and Turvey 1995). Such a categorization is relatively blind to the left-right distinction regardless of the handedness of the participants. The handedness × ψ × sign ANOVA on $|\phi_{stable} - \psi|$ was repeated with $\Delta\omega = (\omega_L - \omega_R)$ replaced by the intrinsic sign metric of $\Delta\omega = (\omega_P - \omega_{NP})$ and conducted for each individual ω_c.

At $\omega_c = 1.1\omega_v$, there was a significant main effect of sign [$-\Delta\omega = 0.47$ rad, $\Delta\omega = 0.59$ rad; $F(1, 24) = 19.40$, $P < 0.001$], indicating that ϕ_{stable} departed from ψ to a greater degree when the preferred hand oscillated the pendulum of higher frequency. Significant interactions remained, however, between sign and handedness [$F(1, 24) = 4.12$, $P < 0.05$], and between handedness, ψ and sign [$F(1, 24) = 4.22$, $P < 0.05$]. Separate ANOVAs for each handedness group indicated that the latter interaction was primarily due to the ψ × sign interaction of the Ll individuals [in-phase: $-\Delta\omega = 0.45$ rad vs $\Delta\omega = 0.70$ rad; anti-phase: $-\Delta\omega = 0.41$ rad vs $\Delta\omega = 0.53$ rad; $F(1, 14) = 4.76$, $P < 0.05$]. In addition, the Ll

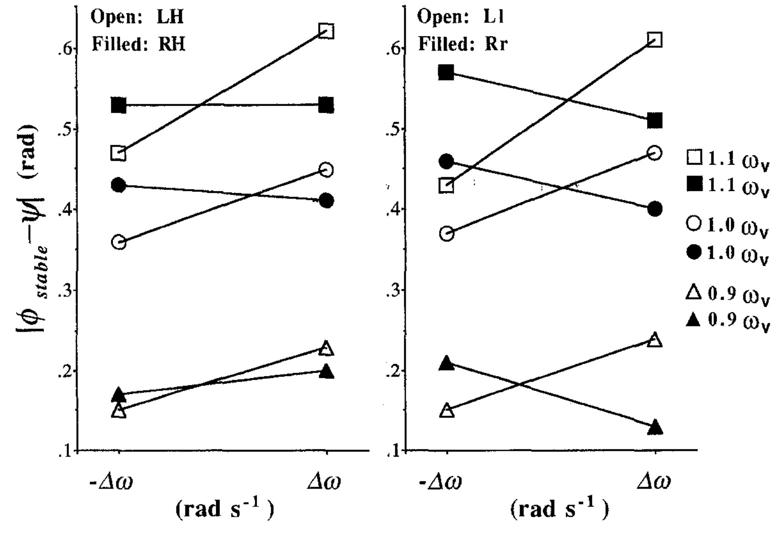
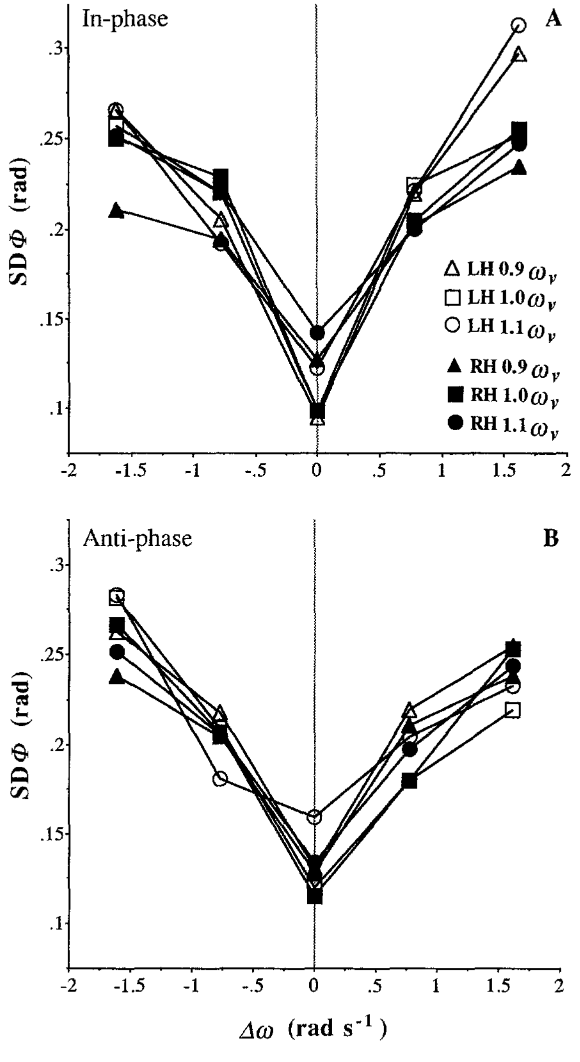


Fig. 6 Performance as measured by $|\phi_{stable} - \psi|$ for $\Delta\omega \neq 0$ as a function of ω_c for conventionally defined groups (*left*) and functionally defined groups (*right*)

individuals exhibited a main effect of sign, indicating that $|\phi_{stable} - \psi|$ was greater for $\Delta\omega$ (0.61 rad) than $-\Delta\omega$ (0.45 rad) [$F(1, 14) = 39.31$, $P < 0.0001$]. In contrast to the Ll individuals, there were no significant effects for the Rr individuals.

For $\omega_c = 1.0\omega_v$, there was a significant main effect of sign [$-\Delta\omega = 0.39$ rad, $\Delta\omega = 0.46$ rad; $F(1, 23) = 5.73$, $P < 0.05$], but, as expected, the interaction between handedness and sign disappeared in the natural coordinate system. That is, the difference between $\Delta\omega$ and $-\Delta\omega$ was the same for Ll and Rr individuals. Finally, for $\omega_c = 0.9\omega_v$, there was a significant main effect of sign [$-\Delta\omega = 0.15$ rad vs $\Delta\omega = 0.23$ rad; $F(1, 21) = 8.99$, $P < 0.01$], and again, no interaction between handedness and sign. These results confirm an expectation from Eq. 8 witnessed previously (Treffner and Turvey 1995): for both LH and RH individuals, departures in ϕ_{stable} from ψ are amplified when the *P* hand, as opposed to the *NP* hand, is modulated by an oscillatory system of higher eigenfrequency. In terms of Eq. 8, when the signs of $\Delta\omega$ and *d* agree displacements of ϕ_{stable} from ψ are greater than when the signs of $\Delta\omega$ and *d* disagree.

Fig. 7 Standard deviations of ϕ as a function of $\Delta\omega$, handedness, and ω_c for in-phase (**A**) and anti-phase (**B**)



Standard deviation of phase

Mean SDϕ as a function of the experimental manipulations is summarized in Fig. 7 (top, in-phase; bottom, anti-phase). A handedness (conventional LH and RH individuals) × ψ × $\Delta\omega$ (conventional, $\omega_L - \omega_R$) × ω_c ANOVA was preformed. There was no main effect of handedness ($F < 1$), and handedness did not enter into any significant interactions, although the interaction of handedness and ω_c approached significance [$F(2, 72) = 2.77$, $P = 0.07$]. In agreement with Eq. 7 (see Treffner and Turvey 1995), there was a significant effect of $\Delta\omega$, with SDϕ smallest for $\Delta\omega = 0$ and largest for $\Delta\omega = \pm 1.61$ [specifically, SDϕ was 0.26, 0.21, 0.12, 0.21, and 0.25 rad for $\Delta\omega = -1.61, -0.78, 0, 0.78$, and 1.61 rad/s, respectively; $F(4, 144) = 109.74$, $P < 0.0001$]. Contrary to what Eq. 7 predicts, however, SDϕ was not larger for anti-phase than in-phase ($F < 1$), and SDϕ did not increase with ω_c [0.208, 0.206, and 0.213 for 0.9, 1.0, and $1.1\omega_v$, respectively; $F(2, 72) = 2.06$, $P > 0.05$]. There were significant interactions between $\Delta\omega$ and ω_c, [$F(8, 288) = 2.63$, $P < 0.01$] and between $\Delta\omega$ and ψ [$F(4, 144) = 3.04$, $P < 0.05$], but neither was strictly consistent with expectations. The same pattern of statistical outcomes was obtained with the functional handedness groups Ll and Rr, and additional analyses using the non-normalized ω_c underscored the insignificance of coupled frequency to variability in ϕ.

Discussion

Validity of the collective symmetric and asymmetric dynamics of Eq. 8

The experiment was directed at the equilibrium predictions from Eq. 8 expressed in Fig. 2. The predicted amplification by ω_c of the difference in equilibria of LH and RH individuals at $\Delta\omega = 0$ was confirmed. As predicted, the tendency was for the equilibria to become increasingly more positive for LH individuals (the left hand leads) and increasingly more negative for RH individuals (the right hand leads) (see Fig. 5). As the present model now stands, the influence of coupled frequency on ϕ_{stable} (Fig. 4) may be understood as a decrease in the effect of the symmetric coupling (via *b*/*a*), with a consequent increase in the effect of the asymmetrical terms, either $\Delta\omega$, the *d* term, or both. Thus, although the effect on the overall dynamics due to $\Delta\omega$ or the *d* term is magnified by increasing ω_c, we do not conceive of the value of $\Delta\omega$ itself changing with changes in ω_c. The latter interpretation might be drawn from the discussion in Jeka and Kelso (1995) of an arm-leg coordination task whereby the phase-lag between the limbs was magnified (to the point of continual phase-drift) as the frequency of coordination was increased (see also Kelso and Jeka 1992).

Other major predictions of Eq. 8 expressed through Fig. 2 were similarly confirmed: the sign of $\Delta\omega$ interacted with handedness, with the interaction persisting in the same form over the magnitude scaling induced by increases in ω_c (see Fig. 6). These predictions were based on the following assumptions: (a) d retains the same sign and magnitude across variations in ω_c, (b) d retains the same sign and magnitude over ψ (in-phase vs anti-phase), (c) c is negligible and fixed. The data concurred overall with these assumptions. They did not, however, concur in all respects. Contrary to assumption (a), only five participants in the RH group were consistently negative on the measure of handedness ($\phi_{stable} - \psi$) at $\Delta\omega = 0$, meaning that only these five participants maintained a positively signed d across ω_c. For the remaining RH individuals, it would have to be conjectured that d was variable over the ω_c conditions, assuming either positive or negative values.

Predictions of Eq. 8 with respect to variability in ϕ were also evaluated. For comparatively small values of the asymmetric coefficients relative to the symmetric coefficients, Eq. 8 is predictively similar to Eq. 7. The two most significant predictions concern the influences of ψ and $\Delta\omega$ on variability in ϕ: the variability should be greater for anti-phase than in-phase, and it should increase with $|\Delta\omega|$ from a minimum at $\Delta\omega = 0$. The confirmation of the $\Delta\omega$ prediction is portrayed in Fig. 7 and is in agreement with previous research. The prediction regarding anti-phase however, was not confirmed, contrary to previous research (e.g., Schmidt et al. 1993; Sternad et al. 1995; Treffner and Turvey 1995; Turvey et al. 1986). Coupled with the statistically negligible effects of ω_c on variability, the failed anti-phase prediction brings into question the assumption that Q (noise strength) was constant over the experimental manipulations. By Eq. 7 and 8 as parametrized above, λ is smaller for anti-phase and decreases with ω_c. Consequently, an equating of SDϕ across coordination modes and coupled frequencies would implicate (formally) a compensatory reduction in Q (see Eq. 6). The more basic implication, however, is that the dynamics of interlimb 1 : 1 frequency locking remain only approximately controllable within the experimental system of Fig. 3, and experimental sources of noise (which are likely to be subtle) await identification.

The partitioning of RH and LH individuals according to leading hand

In the related experiment of Treffner and Turvey (1995), the 20 RH individuals divided into 13 Rr individuals and 7 Rl individuals for $\omega_c \approx 1.0\ \omega_v$. The corresponding partitioning for the LH individuals was 17 Ll and 3 Lr. In the present experiment, the division of the 20 RH individuals by leading hand was 8 Rr and 12 Rl at $\omega_c = 0.9\omega_v$, 12 Rr and 8 Rl at $\omega_c = 1.0\omega_v$, and 12 Rr and 8 Rl at $\omega_c = 1.1\omega_v$. The corresponding division of the LH individuals in the present experiment was 17 Ll and 3 Lr, 15 Ll and 5 Lr, and 16 Ll and 4 Lr, respectively. Clearly, RH and LH individuals partitioned similarly in the present and previous experiment.

Simple calculations from the present data (averaging over ω_c), based upon the estimates 88% RH and 12% LH in the general population (Porac and Coren 1981), imply an overall population bias, regardless of handedness, toward leading with the right hand of 49.3% and an overall population bias toward leading with the left hand of 50.7%. 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 leading hand confirmed the lack of a directional bias in the general population (χ^2 (1, N = 40) = 0.02, $P > 0.05$). In short, for a randomly sampled individual from the general population (RH plus LH individuals), leading with the left hand in bimanual 1 : 1 frequency locking would be just as probable as leading with the right. Although at odds with the widespread acceptance that a right hand bias exists in the general population, the preceding is nonetheless consistent with the conclusion that an observed manual bias is sensitive to the task used in its expression (Treffner and Turvey 1995).

Of significance to the division into left-leading and right-leading individuals was the observation for Rr and Rl individuals of a group × handedness interaction in respect to $|\phi_{stable} - \psi|$. This interaction had also been observed by Treffner and Turvey (1995). In both the present and previous experiment, the RH individuals (conventionally defined) subdivided into two self-consistent subgroups (Rr and Rl individuals) whereas the LH individuals remained more homogeneous as a group (they consisted of mostly Ll individuals). The Rl individuals performed similarly to the LH individuals in that $|\phi_{stable} - \psi|$ was greater when $\Delta\omega > 0$ than when $\Delta\omega < 0$ (compare with Fig. 6). This may indicate the existence of a subpopulation of "inconsistent" RH individuals analogous to the subpopulation of "inconsistent" LH individuals. Members of the latter group prefer the "nondominant" right hand for tasks requiring gross movements or strength (Peters 1990a, b, 1991, 1992; Peters and Servos 1989). Indeed, it has been shown that there may exist up to three different subgroups of LH individuals and, importantly, at least two of RH individuals (Peters and Murphy 1992).

The preceding results encourage questioning the common belief that there is a population bias for humans toward the right hand. Other research suggests that there is a smaller population bias toward the right hand than typically assumed. Thus, it has been shown that the left hand tends to lead the right hand during bimanual gestures (deSchonen 1977; Guiard 1987b; Peters 1994), that there is a left hand advantage, especially with regard to movement initiation, under conditions of single aiming movements both with and without visual feedback (Bradshaw et al. 1990; Flowers 1975; Guiard et al. 1987; Haaland and Harrington 1989; Oldfield 1969; Watson and Kimura 1989), and that the left hand may be more accurate in reaching (Kimura and Vanderwolf 1978; Roy and McKenzie 1978). Although it has been shown that there is, under certain conditions, less of a contrast between the two hands in LH individuals than in RH individuals (e.g., Emmerik 1992; Hammond 1990; Peters and Durding 1979), our experimental results support the conclusion that, at the level of a particular handedness group, there is a greater bias toward the preferred hand in LH individuals than in RH individuals. However, when generalized to the overall human population, a bias toward the preferred hand disappears.

The result of a tendency for LH but not RH individuals to lead with the preferred hand may be approached from the perspective of hemispheric priming (Kinsbourne 1970). If the present task was sufficiently simple that an individual may not have attended to a particular hand, then there would have been no hemispheric priming. Further, if 1 : 1 rhythmic coordination is considered an activity that exploits hypothesized manipulo-spatial mechanisms of the right hemisphere (Bradshaw et al. 1986; Haaland and Harrington 1989) which result in left hand superiority for certain tasks (LeDoux et al. 1977), then in the absence of priming, an expected right hand lead in the RH individuals due to left cerebral dominance would be diminished by right hemispheric activity. In contrast, the reliable left hand lead in LH individuals would result from an amplification of the right hemispheric activity associated with the left hand by the manipulo-spatial mechanisms of the right hemisphere. Given that the same result was found in Treffner and Turvey (1995) with a different group of LH and RH individuals, this result supports the hypothesized predisposition of the right hemisphere and left hand toward certain manipulo-spatial actions.

The proposed right hemispheric predisposition may have implications for the reported lack of a population-level lateral bias (and hence inferred cerebral specialization) in non-human species (Corballis 1989). Recent counter-arguments show that a population bias may exist in non-human primates under conditions of low task complexity (Fagot and Vauclair 1991), in particular for left-handed, visually guided reaching (MacNeilage et al. 1987), and for picking up baby monkeys with the left hand (Hatta and Koike 1991). Such a left hand (right hemisphere) bias in nonhuman primates would find support in the present results under the foregoing cerebral cancellation hypothesis.

The cerebral lag hypothesis

The role of the callosum in bimanual coordination was addressed in an experiment in which individuals bimanually traced elliptical trajectories in the frontoparallel plane under either in-phase or anti-phase conditions (Stucchi and Viviani 1993). It was found that the average temporal lead of the left over the right hand was 21.64 ms for LH individuals and the average temporal lead of the right over the left hand was 24.53 ms for RH individuals. In addition, an effect of movement frequency was found on phase lag for one of four possible patterns (counterclockwise anti-phase). In correspondence with the current model's predictions, Treffner and Turvey (1995) found that anti-phase motion resulted in greater phase lags than in-phase motion. Further support for this model comes from Stucchi and Viviani (1993) who found anti-phase produced greater lags (30.72 ms) than in-phase coordination (15.45 ms). The temporal lag between the hands was interpreted by Stucchi and Viviani as evidence for delays in interhemispheric transfer. It was argued that a lag of approximately 23 ms could not have arisen solely from biomechanical factors alone (e.g., differential stiffness between the hands) but instead reflected a time scale whereby trajectory planning signals are elaborated in the dominant hemisphere and transmitted contralaterally.

To compare the present results with those of Stucchi and Viviani (1993), the corresponding temporal value for each phase-lag was derived. That is, the values of mean $(\phi_{stable} - \psi)$ presented in Table 1 were converted into a temporal delay given the experimental angular frequencies (at $\Delta\omega = 0$) of 3.778, 4.155, and 4.616 rad/s for $\omega_c = 0.9\omega_v$, $1.0\omega_v$, and $1.1\omega_v$, respectively. For the L1 individuals, under in-phase, the left hand led the right hand by 23.03, 35.86, and 35.31 ms for $\omega_c = 0.9\omega_v$, $1.0\omega_v$, and $1.1\omega_v$, respectively. Under anti-phase, the left hand led the right hand by 19.85, 22.62, and 30.11 ms for $\omega_c = 0.9\omega_v$, $1.0\omega_v$, and $1.1\omega_v$, respectively. For the Rr individuals, under in-phase, the right hand led the left hand by 12.44, 15.64, and 29.90 ms for $\omega_c = 0.9\omega_v$, $1.0\omega_v$, and $1.1\omega_v$, respectively. Under anti-phase, the right hand led the left hand by 18.26, 14.44 and 30.33 ms for $\omega_c = 0.9\omega_v$, $1.0\omega_v$, and $1.1\omega_v$, respectively. In the present experiment, ω_c had an overall significant effect on lag times, whereas Stucchi and Viviani (1993) found a frequency effect for only one particular pattern (counterclockwise antiphase), although this may have been due to task idiosyncrasies. The present data are also in agreement with Stucchi and Viviani's (1993) estimates of the magnitude of the temporal lag – in the present data the means were 27.80 ms for L1 individuals and 20.17 ms for Rr individuals.

As the proposal of Stucchi and Viviani (1993) now stands, the cerebral lag is a neural constant and is presumably independent of the frequency at which the hands are rhythmically coordinated. Their observed frequency effect on lag times was used as evidence against biomechanical asymmetries. We concur, but maintain that the interlimb coupling should be examined for an understanding of how and why asymmetry is expressed via dynamics. In sum, the distinct advantage of the collective dynamics captured by Eq. 8 over a cerebral lag hypothesis is that they accommodate both the essential character of bimanual rhythmic coordination (see predictions in Treffner and Turvey 1995; Table 1 of Kelso 1994) and its asymmetries (e.g., Figs. 5 and 6).

Concluding remarks

Reiterating points made in the Introduction, Eq. 8 may be considered as a particular form of the elementary dynamics of interlimb rhythmic coordination. The symmetric and asymmetric periodic components assume different roles, in keeping with the intuition expressed by Peters (1994) about the interface between cortical mechanisms and the fundamental rhythmic synergies governing the body's appendages. Whereas the coefficients of symmetric periodic components (a and b) determine the relative strengths of the fundamental in-phase and anti-phase equilibria, small coefficients of the asymmetric periodic components (c and d) break the symmetry of the elementary coordination dynamics while leaving their essential features invariant. The asymmetric potential constitutes an inherent predisposition towards lateralized behavior that an individual brings to a task, i.e., the intrinsic dynamics (Zanone and Kelso 1992), and its effects can be either amplified or diminished depending on imposed constraints such as $\Delta\omega$ or ω_c. A major hypo-thesis of left-right differences in bimanual coordination is that they are the consequences of asymmetrically directed attention (Peters 1987, 1994; Peters and Schwartz 1989). In the collective dynamics of Eq. 8, attentional differences would be manifest as differences in the signs and magnitudes of the asymmetric coefficients. It is evident from inspection of Eq. 8 that for fixed symmetric coefficients, increases in the asymmetric coefficients will deflect the order parameter in the direction of attractors at odd multiples of $\pi/4$, that is, in the direction of more asymmetric coordinations. Less evident from inspection, but readily determined by numerical means, is that such deflections would be accompanied by increases in λ, and hence, stability. Specific expectations about equilibria and their variability would follow, therefore, from Eq. 8 for 1 : 1 frequency-locking tasks in which the focussing of attention and the allocation of intention (e.g., required movement accuracy) are differentiated across the two hands as ways of manipulating the asymmetric coefficients. Such experiments would contribute to the formalizing of the differential attention hypothesis, and to the understanding of how Bernstein's level of synergies (Latash and Turvey, 1995) is modulated by higher levels in the course of adjusting rhythmic intersegmental behavior to environmental and intentional exigencies.

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