

Effects of Temporal Scaling and Attention on the Asymmetrical Dynamics of Bimanual Coordination

*Michael A. Riley, Eric L. Amazeen, Polemnia G. Amazeen,
Paul J. Treffner, and Michael T. Turvey*

Handedness and attentional asymmetries in bimanual rhythmic coordination were examined as a function of movement speed. In an in-phase 1:1 frequency locking task, left-handed and right-handed subjects controlled the oscillations of either the right or the left hand so as to contact spatial targets. The task was performed at three frequencies of coupled movement. Coordination dynamics incorporating the body's functional asymmetry predicted that left-handers and right-handers would deviate from zero relative phase in opposite directions, that the deviation would be greater for preferred-hand targeting, and that this deviation would be greater at higher movement frequencies. The results confirmed the major predictions and suggested that asymmetry due to handedness is magnified by attention.

Peters (1994) recently observed that investigations of human bimanual coordination seem to have two different foci. One focus is the different roles of the left and right hands in performing everyday tasks that are characterized more by intermittency than rhythmical repetition and that involve specific behavioral and environmental goals. The other focus is the dynamic modeling of the two hands in bimanual in-phase and anti-phase rhythmic coordination where the performance goal is simply temporal stability, the roles of the hands are considered equivalent, and there is no meaning to counterbalancing hand task assignments. These experimental foci remain distinct, Peters (1994) suggested, because functional asymmetry is manifest only when the two hands differ in either the attention or effort allocated to them. Asymmetry of bimanual movements is neither expected nor typically found when the two hands perform movements of equal status or when their movements satisfy a shared timing constraint. Accordingly, Peters (1994) emphasized that handedness is an important aspect of bimanual coordination and that we can expect the skilled bimanual coordinations of humans to be very different from the rhythmic activities that characterize human locomotory behaviors.

Michael A. Riley and Michael T. Turvey are with the Center for the Ecological Study of Perception and Action, Department of Psychology, U-20, University of Connecticut, 406 Babbidge Road, Storrs, CT 06269. Eric L. Amazeen and Polemnia G. Amazeen are with Free University, Amsterdam, The Netherlands. Paul J. Treffner is with the University of Southern Queensland, Toowoomba, Queensland, Australia.

Recent research suggests, however, that with respect to handedness, there may not be a qualitative difference between 1:1 frequency locking of the two hands and intermittent, goal-oriented bimanual coordinations. Treffner and Turvey (1995) found that when the hands perform the same rhythmic movements at the same tempo, the relative phase relation between them is sensitive to handedness. With relative phase defined as $\phi = (\theta_L - \theta_R)$, the difference between the left (L) and right (R) phase angles (θ_i), left-handed (LH) participants tended to lead in phase with the left hand ($\phi > 0$) and right-handed (RH) participants tended to lead in phase with the right hand ($\phi < 0$). This effect of handedness in a simple bimanual rhythmic coordination may be of considerable significance to the experimental investigation of functional asymmetry (Amazeen, Amazeen, Treffner, & Turvey, in press). It means that issues centered on the differential allocation of attention and effort to the hands can be studied in the context of experimental settings that have been used to formulate and examine coordination from a dynamics perspective (e.g., Kelso, 1995; Schöner, 1994; Sternad, Amazeen, & Turvey, 1996). In the present article, we report an experiment that extends investigations (cited and described below) showing that bilateral asymmetry and attentional asymmetry can be expressed in formal terms and the resultant predictions evaluated experimentally through the elementary rhythmic synergy of 1:1 frequency locking. To set the stage for the present experiment we will discuss the ideas behind a dynamic interpretation of the body's functional asymmetry.

Near Decomposability of the Elementary Rhythmic Synergy

Oscillation of two or more body segments at the same frequency is a common feature of most animals' movement patterns. It is an expression of an apparently fundamental rhythmic synergy that seems to underlie all forms of animal locomotion (by limb, by fin, by wing, and by undulation) (Bernstein, 1996). In humans, this rhythmic synergy is apparent in walking, running, and swimming and in everyday tasks requiring synchronization of the motions of the two hands. Despite its elementary nature, each instance of 1:1 frequency locking involves a large number of subsystems at very many levels (e.g., Stein, 1995). The subsystems differ in type and size and function at different rates. As often noted, at each functional level of this complex organization there is the issue of which of the many measurable differences within and between the subsystems are significant (e.g., Kopell, 1993). For one who would hope to model the elementary rhythmic synergy and, in particular, its expression in bimanual coordination, there is the overwhelming question, How should the multiplicity and diversity of the subsystems and their interactions be addressed?

Despite the complexity and uncertainty evident in the componential structure of two limbs sharing a temporally repeating pattern, it is hard to avoid the impression that, at their own level, they follow a relatively uncomplicated coordination law (Kelso, 1994a). Although the individual dynamics of the many (muscular, neural, vascular) subsystems are difficult to comprehend, the collective dynamics of the limbs seem to be relatively simple. In this regard, Amazeen, Sternad, and Turvey (1996) recently recalled Simon's (1962) central argument from the chapter "Architecture of Complexity," namely, that the emergence of simplicity in complex systems is due to that fact that such systems are *nearly decomposable*. At each stratification of a complex system, the interactions within an individual subsystem are strong but the interactions between subsystems are weak. Consequently,

the high-frequency dynamics associated with the processes internal to the subsystems are separated from the low-frequency dynamics associated with the interactions among the subsystems. The short-run processes occurring within a subsystem do not depend on the details of the short-run processes occurring within the other subsystems, and a subsystem's long-run behavior depends only on the sum total of the behaviors of the other subsystems. Because of this feature of being nearly decomposable, a complex system's collective dynamics are relatively independent of the specific details of internal and external interactions of its component subsystems. In short, the collective dynamics (in this case, of biological intersegmental coordination) can be usefully modeled in relative ignorance of the constituent dynamics.

Symmetrical Coordination Dynamics

Consonant with the postulate of nearly decomposable systems, a number of contemporary strategies for modeling intersegmental coordination make no assumptions about the internal neuromuscular details of individual segments and their interactions. The modeling refers only to the "observables" (measurable variables) of the segments in oscillation, so that the scope of the dynamic study of rhythmic intersegmental coordination is limited to specifying the observables that describe the coordination and characterizing the manner in which these observables are linked (e.g., Kopell, 1993; Rand, Cohen, & Holmes, 1988; Murray, 1990; Schöner, 1994).

With respect to human bimanual coordination, the foregoing strategy has resulted in a motion equation in relative phase governing the temporal stabilities of the in-phase and anti-phase bimanual patterns (Haken, Kelso, & Bunz, 1985; Schöner, Haken, & Kelso, 1986):

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

where $\dot{\phi}$ is the first time derivative of relative phase. The ratio of the coefficients b/a determines the relative strengths of the attractors in the equation, $\phi = 0$ and $\phi = \pi$, corresponding to in-phase and anti-phase coordination patterns. Experiments support the interpretation of b/a as inversely related to movement frequency (e.g., Collins & Turvey, 1997; Schmidt et al., 1993; Treffner & Turvey, 1996). The last right-hand term is a stochastic force arising from the multiplicity of interactions among the underlying subsystems.

The fixed points or equilibria of Equation 1, for given values of b/a , are determined by solving for $\dot{\phi} = 0$. At a zero-crossing, $d\dot{\phi}/d\phi < 0$ defines a stable fixed point or attractor, and $d\dot{\phi}/d\phi > 0$ defines an unstable fixed point or repeller. The degree of variability expected for a fixed point is given by

$$SD\phi = (Q/2|\lambda|)^{1/2}, \quad (2)$$

(see Gilmore, 1981; Schöner et al., 1986) where Q is the strength of the stochastic force in Equation 1 and $\lambda = d\dot{\phi}/d\phi$ is the Lyapunov exponent of the fixed point (e.g., Haken, 1977; Hilborn, 1994). Equation 2 states that a steeper negative slope at a zero crossing of Equation 1 means a larger absolute λ , a smaller variance in ϕ , and an equilibrium point that is more readily retained against perturbations of strength Q .

Equation 1 is symmetrical: It is invariant under the transformation $\phi \rightarrow -\phi$. The symmetry exists because the components, the two hands and their neuromuscular support, are taken to be identical in their contributions to the 1:1 frequency locking (Haken & Wunderlin, 1990; Haken et al., 1985). If the two hands contribute nonidentically, then the perfect symmetry between ϕ and $-\phi$ would no longer exist. An imperfection in the bimanual system, such as an asymmetry of the hands, would mean that the observed dynamics of 1:1 frequency locking would be less symmetrical than predicted by Equation 1. The symmetrical states of Equation 1, $\phi = 0$ and $\phi = \pi$, would no longer be stable; in their place would be states close to but distinct from 0 and π . Stated differently, the symmetry of Equation 1 would be broken. The terms *broken symmetry* and *symmetry breaking* refer to either an effect (as when a system's behavior has less symmetry than the governing equations) or a cause (as in noting the tiny imperfections that reduce the original symmetry) (see Stewart & Golubitsky, 1992, for examples of both usages). Following Strogatz (1994, p. 69) and Kelso (1994a, 1995; Kelso, DeGuzman, & Holroyd, 1991; Kelso & Ding, 1993; Kelso & Jeka, 1992), we will focus on the causes or sources of symmetry breaking with respect to the coordination dynamics of Equation 1.

The Imperfection Parameter

As noted above, Treffner and Turvey (1995) found that handedness affected the stable states of 1:1 frequency locking. Rather than producing the perfect in-phase and anti-phase coordinations expected from Equation 1, RH subjects produced relative phase relations less than 0 and π and LH subjects produced relative phase relations greater than 0 and π . Accommodating the results of Treffner and Turvey (1995) requires a modification to Equation 1. The simplest way to break the symmetry of Equation 1 is to introduce an additive term—an imperfection parameter (Strogatz, 1994). As suggested by Kelso, Delcolle, and Schöner (1990), the coordination dynamics for asymmetrical components can be expressed as

$$\dot{\phi} = \bar{\nu} - a \sin(\phi) - 2b \sin(2\phi) + \sqrt{Q} \xi_t \quad (3)$$

where $\bar{\nu}$ is the imperfection parameter (a symmetry-breaking parameter; see Strogatz, 1994). For values of $\bar{\nu} \neq 0$, the stable states of Equation 3 are shifted from 0 and π in direction and magnitude, depending on the sign and size of $\bar{\nu}$. How should $\bar{\nu}$ be interpreted? In the neurobiological modeling of Cohen, Holmes, and Rand (1982), Rand et al. (1988), and Kopell (1988) (see also Murray, 1990), $\bar{\nu}$ is interpreted as the uncoupled frequency (ω) difference between individual oscillators; for left and right hands, $\bar{\nu} = (\omega_{\text{left}} - \omega_{\text{right}})$. This interpretation of $\bar{\nu}$ follows from summing the separate motion equations in phase angle for the two individual oscillators and modeling the coupling between them as a perturbation on their respective uncoupled or eigenfrequencies (see, for example, Rand et al., 1988). A similar interpretation is to be expected from the synergetic approach of Haken, Kelso, and Schöner, inasmuch as the general strategy is to relate the collective dynamics to the dynamics of the individual subsystems (see Haken et al., 1985). Accordingly, experimental investigations of Equation 3 have tended to interpret $\bar{\nu}$ as $(\omega_{\text{left}} - \omega_{\text{right}})$ (e.g., Amazeen et al., 1996; Fitzpatrick, Schmidt, & Carello, 1996;

Jeka & Kelso, 1995; Jeka, Kelso, & Kiemel, 1993; Kelso & Jeka, 1992; Schmidt et al., 1993; Sternad et al., 1996).¹

The predictions about fixed points and their corresponding variability that follow from Equation 3 under manipulations of b/a and ∂ so interpreted have been confirmed experimentally. Detailed listings of the predictions and the relevant experiments can be found in the reviews by Kelso (1994a) and Schmidt and Turvey (1995). Among the nonobvious predictions are (a) invariance of relative coordination over variations in movement rate when $\partial = 0$ but not when $\partial \neq 0$, (b) increased variability in relative phase ($SD \phi$) with increased movement rate when $\partial = 0$ despite the indifference of the mean value of relative phase to movement rate, (c) greater change in stable relative phase per change in ∂ for coordinations prepared in anti-phase than coordinations prepared in in-phase, and (d) a discontinuous transition from anti-phase to in-phase at high movement rates (a pitchfork bifurcation) when $\partial = 0$ but a gradual transition (a saddle-node bifurcation) when $\partial \neq 0$.

The success of Equation 3 has important implications for understanding motor timing, particularly the account given in terms of a generalized motor program with proportional scaling. According to this account, a person able to produce a particular movement pattern has relative durations stored in motor memory together with a single rate parameter that generates the specific, absolute durations which characterize a given execution of the pattern (Heuer & Schmidt, 1988; Schmidt, 1985; Viviani & Terzuolo, 1980). A frequent observation, however, is that the perfect proportional scaling predicted by this account for different rates of execution does not occur (Abbs & Connor, 1990; Gentner, 1987; Wann & Nimmo-Smith, 1990; Zelaznik, Schmidt, & Gielen, 1986), leading some to suggest that the proportionality is compromised by nonmultiplicative transformations subsequent to the central mechanism for timing (e.g., Heuer, 1988). If coordination dynamics of the form given by Equation 3 characterize a person's skill, rather than a temporal pattern of relative durations, then it is not surprising that temporal rescaling leads to different timings among the components. Temporal stability under different conditions dictates different timing relations among the components for the same fundamental pattern.

Equation 3 predicts changes in bimanual timing due to the relation between component oscillators and required temporal rescaling. The precision with which such predictions can be made was well expressed by the experiment of Amazeen et al. (1996), in which movement rate was either held constant or decreased over increased detuning. The confirmed predictions were of shifts in the equilibria of relative phase that followed one particular nonlinear function of ∂ when movement rate was fixed and another particular nonlinear function of ∂ when movement rate varied inversely with detuning. Highly specific, falsifiable predictions distinguish investigations involving coordination dynamics from investigations involving the generalized motor program with proportional scaling. As Heuer and Schmidt (1988) noted, the evidence for the latter account has only been confirmatory.

¹Experiments directed specifically at the interpretation of ∂ as an arithmetic difference in the uncoupled frequencies have shown that the imperfection parameter is a more complicated quantity. The proper form of ∂ is determined, additionally, by the ratio of uncoupled frequencies. For a given arithmetic difference, the degree of shift in stable relative phase depends on the ratio of the component uncoupled frequencies; different ratios, different degrees of shift (Collins, Sternad, & Turvey, 1996; Sternad, Collins, & Turvey, 1995).

Although the imperfection parameter for bimanual rhythmic coordination has typically been characterized by the frequency difference identified above, this characterization is not exclusive. Any imperfection—any source of asymmetry in any form—can be captured in principle by the additive term $\dot{\delta}$. However, without an explicit derivation of $\dot{\delta}$ appropriate to an expressed asymmetry, the utility of this more general interpretation within experimental investigations of bimanual coordination is limited. With respect to handedness, Treffner and Turvey (1995) suggested that the imperfection parameter referred to the fact that for homologous but contralateral limbs, the frequency of the preferred limb is higher. Their experiment was conducted using the hand-held pendulums procedure (Kugler & Turvey, 1987) in which two pendulums of identical or different uncoupled frequencies are oscillated, one by the left hand and one by the right hand. Treffner and Turvey (1995) argued that functional asymmetry within the hand-held pendulums task is due to two different scalar multiples, λ and ρ , of the left ω_{left} and right ω_{right} uncoupled pendulum frequencies, respectively. With $\omega_{eff} = \omega_{right}$, $\dot{\delta} = (\lambda \omega_{left} - \rho \omega_{right})$ is negative for RH participants, as $\lambda < \rho$, and positive for LH participants, as $\lambda > \rho$.

From the perspective of a rhythmic movement unit as a self-sustained oscillator, differences in the detuning scalars λ and ρ would need to reflect differences in the oscillator's elastic and friction functions, considered singly or in combination (e.g., Beek, Schmidt, Morris, Sim, & Turvey, 1996). For example, a difference in elastic functions, such that the left stiffness is greater than the right stiffness for LH participants ($\dot{\delta} > 0$) and vice versa for RH participants ($\dot{\delta} < 0$), was shown to model successfully the handedness dependence of relative phase seen by Treffner and Turvey (1995). However, as noted by Treffner and Turvey (1996), equating handedness with $\dot{\delta} = (\lambda \omega_{left} - \rho \omega_{right})$ is opposed by evidence indicating that frequency measures of uncoupled left-hand and right-hand oscillations do not differ. If $\dot{\delta}$ is not interpretable as $(\lambda \omega_{left} - \rho \omega_{right})$, then efforts to model handedness effects through the imperfection parameter are limited to assuming nonzero values of the additive constant $\dot{\delta}$ ($\dot{\delta} > 0$ for LH, $\dot{\delta} < 0$ for RH) when the uncoupled component frequencies are equal. As will be shown below, however, further modeling and experimentation are inconsistent with the hypothesis that handedness is captured by the imperfection parameter.

Is Functional Asymmetry in the Imperfection Parameter or the Coupling?

Treffner and Turvey (1995) considered another possibility for how the body's functional asymmetry is reflected in bimanual coordination dynamics. They hypothesized that the symmetry of Equation 1 might be broken by additional 2π periodic terms that represent the body's functional asymmetry. Specifically, they proposed the following elaboration of Equation 1:

$$\ddot{\phi} = -a \sin(\phi) - 2b \sin(2\phi) - c \cos(\phi) - 2d \cos(2\phi) + \sqrt{Q} \xi_j. \quad (4)$$

Equation 4, like Equation 1, is derived from a potential function $V(\phi)$ according to $\ddot{\phi} = -dV(\phi)/d\phi$. Roughly interpreted, $V(\phi)$ is an "energy landscape" with minima corresponding to the attractors and maxima corresponding to the repellers. For symmetrical dynamics, $V(\phi)$ is defined by the first two cosine (or even) terms of the Fourier series (Haken et al., 1985). The expansion of $V(\phi)$ to capture the body's

functional asymmetry requires adding the first two sine (or odd) terms of the Fourier series (Treffner & Turvey, 1995).

The symmetrical and asymmetrical periodic components of Equation 4 assume different roles. Whereas a and b (symmetrical components) determine the relative strengths of the fundamental in-phase and anti-phase equilibria, small values of c and d (asymmetrical components) break the symmetry of the elementary coordination dynamics while leaving their essential characteristics unaltered. In exploring Equation 4, Treffner and Turvey (1995) showed that d is the more important handedness coefficient, producing the empirically observed directions of equilibrium drift around both 0 and π ; thus, c can be set to zero without loss of generality. Treffner and Turvey (1995) modeled both the observed equilibria and the observed variability associated with them by setting $d < 0$ for LH participants and $d > 0$ for RH participants.

The Treffner and Turvey (1996) Experiment

Whether handedness is interpreted by the imperfection parameter δ as in Equation 3 or by the inclusion of asymmetrical coupling terms as in Equation 4, the resultant coordination dynamics make a nonobvious prediction: For a fixed asymmetry (imperfection parameter $\delta > 0$ for LH and $\delta < 0$ for RH, or asymmetrical coupling coefficient $d < 0$ for LH and $d > 0$ for RH), an increase in movement rate corresponding to a decrease in b/a should magnify the handedness seen in simple 1:1 frequency locking. At higher coupled frequencies or movement rates, LH participants should amplify their left-hand lead and RH participants should amplify their right-hand lead. From the perspective of Equation 3, a weakening of the coupling relative to the constant imperfection parameter would magnify the effects of handedness as movement frequency is scaled upward. From the perspective of Equation 4, a weakening of the symmetrical coupling relative to the asymmetrical coupling would similarly magnify the effects of handedness with an upward scaling of movement frequency. Treffner and Turvey (1996) confirmed the prediction that with hand-held pendulums of equal uncoupled frequencies, the left-hand lead observed in LH individuals ($\phi > 0$) and the right-hand lead observed in RH individuals ($\phi < 0$) increased as movement frequency increased.

The Amazeen, Amazeen, Treffner, and Turvey (in press) Experiment

Equating handedness with attentional asymmetry has played a prominent role in analyses of bimanual coordination (e.g., Peters, 1981, 1994). It is nonetheless plausible to consider that any biasing of attention and effort to one or the other hand during 1:1 frequency locking is tantamount to either a change in the imperfection parameter of Equation 3 or a change in the parameters of the asymmetrical coupling terms of Equation 4.

By the analyses of Treffner and Turvey (1995, 1996), the asymmetrical coupling parameter $d < 0$ defines left-handedness and $d > 0$ defines right-handedness, with $c = 0$ in both cases. If LH participants are required to attend more to the left hand than to the right hand, then d might become more negative as the left-handedness of the participants is magnified. In contrast, when LH participants are required to attend more to the right hand, d might become less negative as the left-handedness of the participants is reduced. For RH participants, attending to the

left and right hands would have the opposite effect. Attending left would decrease the positive size of d (reducing their right-handedness) and attending right would increase the positive size of d (increasing their right-handedness).

Consider a simple task in which two identical hand-held pendulums are oscillated in 1:1 frequency locking with $\phi = 0$. Attention can be differentiated across the two hands by superimposing an additional task to be conducted by one hand but not by the other. For example, a spatial target can be placed in the plane of motion of the right pendulum with the participant's task to control the right pendular motion so that the right pendulum just makes contact with the target. The parameter d can be manipulated systematically by having LH and RH participants perform this task with left and right hands. The expected outcome can be derived from Equation 4 under very simple assumptions about parameter values. Let $a = 1$, $b = 1$, for both LH and RH participants; that is, assume identical symmetrical coupling. Let intrinsic (i) handedness be defined by d_i , with $d_i = -0.1$ for LH participants and $d_i = 0.1$ for RH participants, and $c = 0$ in both cases. Then assume that the act of attending (a) to a spatial target of a given size at a given distance, specifically controlling the pendular motion to that target, is associated with $d_a = -0.08$ when attending left and $d_a = 0.08$ when attending right. The effective magnitude of the parameter d is then the algebraic sum of d_i and d_a . With respect to attending left, for example, this sum will be -0.18 for LH participants and 0.02 for RH participants. When attending right, the value of $d_i + d_a$ is -0.02 and 0.18 for LH and RH, respectively.

The expected pattern of equilibria of 1:1 rhythmic coordination and their corresponding degrees of stability (indexed by $1/|\lambda|$) as determined numerically from Equations 4 and 2 can be determined using the preceding parameter values. For LH participants, the expected equilibrium drift from $\phi = 0$ is in the direction $\phi > 0$ and is greater when attention is to the left; for RH participants, the expected equilibrium drift from $\phi = 0$ is in the direction $\phi < 0$ and is greater when attention is to the right. Further, for LH participants, the expected stability is greater ($1/|\lambda|$ and, by inference, $SD\phi$ is smaller) when attending left, and for RH participants, the expected stability is greater ($1/|\lambda|$ and, by inference, $SD\phi$ is smaller) for attending right. This expected pattern of stability means that the greater the equilibrium shift (i.e., the greater the departure from $\phi = 0$), the more stable is the coordination.

What are the corresponding predictions from Equation 3? In order to parallel the modeling of the coupling hypothesis embodied in Equation 4, let the intrinsic values of the imperfection parameter be $(\partial)_i = 0.1$ for LH and $(\partial)_i = -0.1$ for RH. Further, let attention to the left pendular motion in controlling its contact with the given spatial target correspond to $(\partial)_a = 0.08$, and let attention to the right pendular motion to achieve target contact correspond to $(\partial)_a = -0.08$. Numerical analysis of Equations 3 and 2 using the preceding parameter values duplicates the pattern of equilibria for Equation 4 but, importantly, not the pattern of stabilities (predicted $SD\phi$ magnitudes). In the general case, with handedness manipulations restricted to the imperfection parameter, a larger shift in equilibrium (greater departure from $\phi = 0$) is necessarily associated with a less stable coordination. Accordingly, Amazeen et al. (in press) argued that if stability increases experimentally with the shift in equilibrium engendered by attention, then the hypothesis that handedness is an anisotropic coupling (see also Byblow, Chua, & Goodman, 1995; Carson, 1993), as expressed in Equation 4, will be favored over the hypothesis that handedness is incorporated in the imperfection parameter (however interpreted), as

expressed in Equation 3. The experimental results confirmed the predictions of Equation 4: Equilibrium shift was greater when attention was directed at the preferred hand; stability was greater ($SD \phi$ was smaller) when attention was directed at the preferred hand and it was greater for larger deviations from $\phi = 0$.

The Present Experiment: Handedness, Attentional Asymmetry, and Movement Frequency

In the present research, we combine the temporal scaling studied by Treffner and Turvey (1996) with the attentional asymmetry studied by Amazeen et al. (in press). Treffner and Turvey manipulated the symmetrical coupling terms by manipulating movement frequency and held the asymmetrical coupling terms constant (RH and LH subjects were used, but no attentional asymmetry was introduced). In comparison, Amazeen et al. held movement frequency constant, keeping the symmetrical coupling of Equation 4 constant, and varied attentional requirements to manipulate asymmetrical coupling. In the present experiment, we manipulated both the symmetrical and asymmetrical coupling functions by manipulating both movement frequency and direction of attention. The focus of the experiment was on the coordination equilibria as predicted by Equation 4 under the dual manipulations of attention and movement frequency.

Combining the two manipulations in one experiment was not expected to be straightforward. Participants had to track a metronome precisely in order to satisfy the movement rate for a given trial and had to control carefully the contact with a left or right spatial target to satisfy the attentional requirement for that trial. The robustness of the handedness effect in 1:1 frequency locking demonstrated in previous experiments suggested that a successful combination of the two manipulations might be achievable. The average relative phase ϕ_{ave} as a function of handedness, attention, and movement frequency was expected to conform to the predictions from Equation 4: that left-handers and right-handers would deviate from zero relative phase in opposite directions, that the deviation would be greater for preferred-hand targeting, and that this deviation would be greater at higher frequencies. These predictions are depicted in Figure 1.

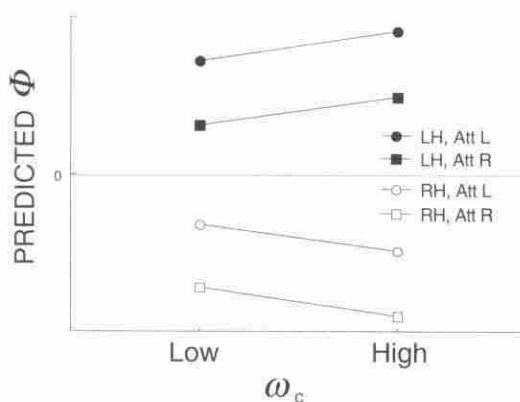


Figure 1 — Predicted effects of handedness, direction of attention, and frequency of movement on ϕ (from numerical simulation of Equation 4).

Method

Subjects

Twenty students (8 men and 12 women) from the University of Connecticut participated in the experiment. Eighteen of the subjects were undergraduate students who participated in partial fulfillment of requirements for an introductory psychology course; the other 2 subjects were graduate student volunteers. Ten subjects were LH and 10 were RH. Handedness classifications were based upon subjects' reports of their own handedness preferences for writing and throwing a ball (Treffner & Turvey, 1995).

Apparatus

Two pendulums were constructed out of wooden rods and 200-g metal rings. The rods had a mass of 85 g, were 1 m in length, and were 1.2 cm in diameter. The ring weights were positioned 30 cm from the bottom of the rods. Subjects grasped the rod at a point 60 cm from the bottom. They performed the task while sitting in a specially designed chair (see Figure 2). The chair had armrests on which participants positioned their wrists, allowing for free movement of the wrist joint while keeping the rest of the arm fixed. The chair also allowed a subject's legs to be raised above the hanging pendulums so that the legs would not obstruct data collection.

Two 35.5 cm long and 5.7 cm wide white paper strips served as targets. They were suspended above the hand by hooks attached to dowels that were suspended parallel to and 60 cm above the armrests. The targets were equidistant from the hand-held pendulum when the pendulum was held in the vertical position (one target 15 cm in front of the hand and one target 15 cm behind the hand). Participants were to touch the targets with the upper portion of the pendulum (40 cm of the 1-m pendulum extended vertically above the hand, as the pendulums were held 60 cm from the bottom). The targets served as end points of the cycle trajectories, thus specifying a movement amplitude of 0.77 rad. Previous research provided the

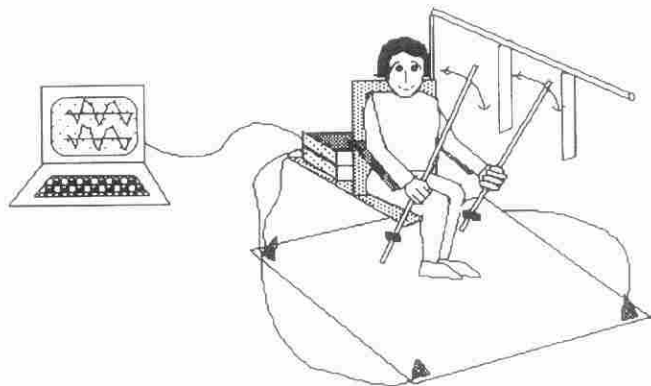


Figure 2 — Apparatus used in the experiment. The figure shows a participant touching strips of paper with the top of the pendulum.

basis for the motion amplitude defined by the intertarget distance. Preferably, the freely elected amplitude of movement without spatially directed attention (i.e., without the spatial targets) should be similar to the amplitude under the attention constraint. The movement amplitude of 0.77 rad was the average amplitude produced freely by participants in a study by Sternad et al. (1996) for the hand-held pendulums used in the present experiment.

Procedure

Subjects gripped the pendulums firmly to ensure that oscillation occurred about the axis of the wrist joint rather than about the finger joints. The wrists were positioned at the end of the armrests of the chair to allow free movement of the wrist joint while supporting the rest of the forearm. Pendular motion was restricted to the plane of movement parallel to the sagittal plane. Subjects were asked to swing the pendulums smoothly and continuously while maintaining an in-phase relationship between the two pendulums. A pacing metronome was set to beep once per cycle at one of three coupled frequencies, $\omega_c = 5.70 \text{ rad} \cdot \text{s}^{-1}$, $7.60 \text{ rad} \cdot \text{s}^{-1}$, and $9.50 \text{ rad} \cdot \text{s}^{-1}$, corresponding to periods of 1,102, 826, and 661 ms, respectively. Subjects were instructed to coordinate the peak forward extension of each swing with the beeping of the metronome.

Each of the 9 conditions (3 directions of attention as operationalized by target conditions \times 3 frequency conditions) was repeated 3 times; thus, an experimental session consisted of 27 trials and lasted approximately 45 min. Order of direction of attention (neither side, R, or L) and pacing frequency were randomized. During the first 10 s of each 40-s trial, subjects achieved the appropriate frequency of oscillation determined by the metronome prior to data collection. Subjects were instructed to follow the pace of the metronome while maintaining an in-phase coordination. During trials when a target was present, participants were additionally instructed to direct their attention to the target by looking at it and to touch the target as lightly as possible with the top of the pendulum (the instruction to touch the target lightly was given to encourage precise control). During trials without a target, subjects were told to maintain in-phase coordination at the frequency specified by the metronome and not to direct attention to any particular side of the body (participants looked straight ahead). Amplitude of movement was not controlled in the nontarget trials. Subjects were allowed 2-min rest breaks as needed.

Data Collection and Reduction

Movement trajectories of the hand-held pendulums were obtained using a Sonic 3-Space Digitizer (SAC Corporation, Stratford, CT). Sonic emitters, which produce sonic sparks at a rate of 90 Hz, were attached to the end of the pendulums. Microphones positioned in the four corners of the experimental chamber registered the position of each emitter by computing the distance of each emitter from the three microphones that showed the fewest errors (due to reflection of the sonic sparks from walls and apparatus) for that trial. The recorded movement trajectories yielded for each trial a slant-range time series of each individual wrist-pendulum phase angle, θ_{left} and θ_{right} . The slant-range time series were stored on a 80486-based microcomputer using MASS digitizer software (ESI Technologies, OH). The MASS

software was used to calculate the mean frequency of oscillation of each pendulum, the primary angle of excursion for each pendulum, and the relative phase angle between the two pendulums $\phi = \theta_{left} - \theta_{right}$.

For each trial, mean relative phase, ϕ_{ave} , was computed. The time of maximum forward extension (ulnar extension) and maximum backward extension (ulnar flexion) was determined by a peak-picking algorithm. Using the peak forward extension time, the mean frequency of oscillation for the n th cycle was calculated as

$$f_n = 1/(\text{time of forward extension}_n - \text{time of forward extension}_{n-1}), \quad (5)$$

and the mean frequency of oscillation for each trial was calculated from the cycle frequencies. A time series of the phase angle θ_i was produced from the computations of the phase angle at each sample. The phase angle of pendulum i at sample j was calculated as

$$\theta_{ij} = \arctan(\dot{x}_{ij}/\Delta x_{ij}), \quad (6)$$

where the numerator on the right-hand side is the velocity of the time series of pendulum i at sample j divided by the mean angular frequency for that trial, and the denominator is the displacement at sample j minus the average displacement for that trial. Relative phase $\phi = \theta_{left} - \theta_{right}$ was calculated for each sample, yielding a ϕ time series, and ϕ_{ave} was calculated for each trial. The repeated conditions were averaged to obtain one ϕ_{ave} per condition per participant.

Results

Frequency Locking. To determine whether subjects maintained a 1:1 frequency-locked relation between the two hand-held pendulums, the ratio of the frequency of the left to the frequency of the right pendulum was calculated. The observed ratio of .999 did not differ significantly from the required ratio of 1.0, indicating that 1:1 frequency locking was achieved, $t(19) = -1.72$, $p > .05$ (two-tailed).

ϕ_{ave} and Handedness. ϕ_{ave} for RH and LH participants in the condition involving no direction of attention (collapsed across ω_i) was tested to determine whether ϕ_{ave} differed significantly from zero. For LH ($\phi_{ave} = 0.068$ rad), $t(20) = 5.00$, $p < .01$ (two-tailed), and for RH ($\phi_{ave} = -0.023$ rad), $t(20) = -2.13$, $p < .05$ (two-tailed).

ϕ_{ave} Under Variations in ω_i and Direction of Attention. An analysis of variance (ANOVA) was conducted on ϕ_{ave} as a function of handedness, direction of attention, and ω_i . There was a main effect of handedness, with LH showing $\phi_{ave} = 0.056$ rad and RH showing $\phi_{ave} = -0.027$ rad, $F(1, 18) = 5.00$, $p < .05$. There was also a main effect of direction of attention, $\phi_{ave} = 0.017$ rad for no direction, $\phi_{ave} = 0.072$ rad for left attention, and $\phi_{ave} = -0.045$ rad for right attention, $F(2, 36) = 21.27$, $p < .0001$. There was no interaction between handedness and direction of attention, $F < 1$. Figure 3 shows that as direction of attention was manipulated, ϕ_{ave} always changed according to the direction of attention, regardless of handedness (ϕ_{ave} changed consistently for LH and RH).

There was a significant interaction between direction of attention and ω_i , $F(4, 72) = 3.76$, $p < .01$; as ω_i increased, deviation from in-phase varied in the direction to which attention was focused. Figure 4 reveals this interaction.

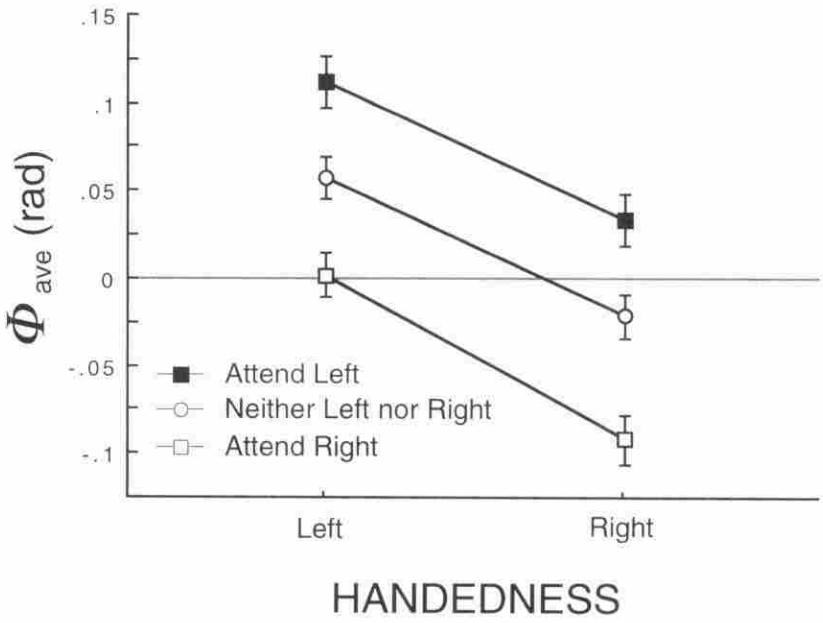


Figure 3 — Results for ϕ as a function of handedness and direction of attention. Bars indicate standard error of the mean.

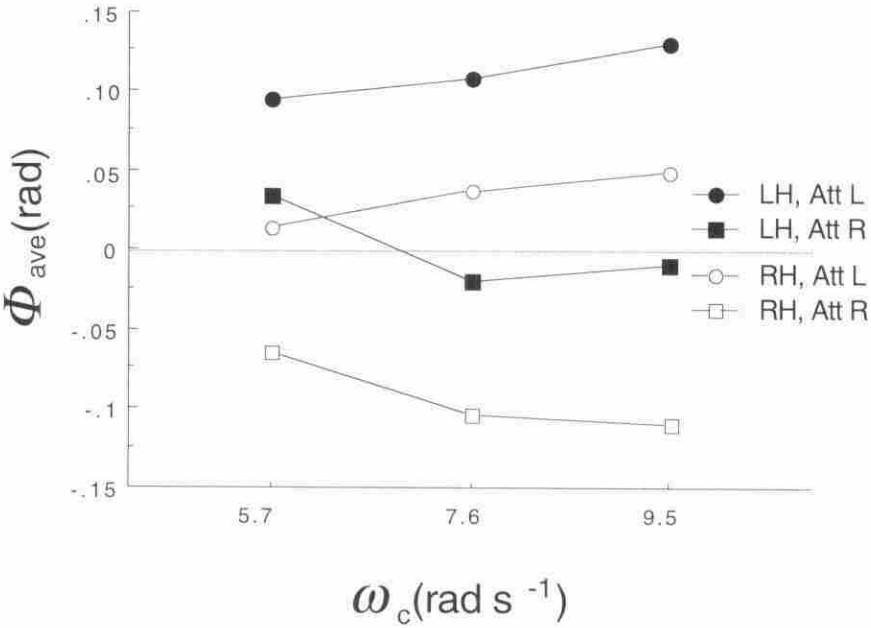


Figure 4 — Results for ϕ as a function of handedness, direction of attention, and ω_c .

Simple effects analyses performed subsequent to the significant interaction of direction of attention and ω_i revealed that the effect of direction of attention was significantly different at each level of ω_i : For $\omega_i = 5.70 \text{ rad} \cdot \text{s}^{-1}$, $F(2, 38) = 6.91$, $p < .01$; for $\omega_i = 7.60 \text{ rad} \cdot \text{s}^{-1}$, $F(2, 38) = 18.73$, $p < .001$; and for $\omega_i = 9.50 \text{ rad} \cdot \text{s}^{-1}$, $F(2, 38) = 17.869$, $p < .001$. The effect of ω_i was significant when attention was directed to the right hand, $F(2, 38) = 3.36$, $p < .05$, but not when attention was directed to the left hand, $F(2, 38) = 1.165$, $p = .32$. The effect of ω_i was not significant when attention was directed to neither side in particular (when no targets were present), $F < 1$. In order to evaluate the effect of ω_i uncontaminated by the sign difference for ϕ_{ave} due to handedness, the ANOVA was repeated with the absolute value of ϕ_{ave} . The main effect of ω_i approached but did not reach significance ($p = .06$).

Discussion

The present research strengthens the finding by Treffner and Turvey (1995, 1996) and Amazeen et al. (in press) that functional asymmetry is reliably evident in a task that requires no spatial or temporal distinctions in the behaviors of the two hands. Until very recently, handedness in such tasks was considered unlikely (e.g., Peters, 1994). As Figure 3 shows, LH and RH participants exhibited different coordination equilibria and did so even when overt attention was undirected. Relative phase shifted from the stable state of $\phi = 0$ to a more positive ϕ_{ave} for LH and a more negative ϕ_{ave} for RH. Additionally, the present results confirm the observation by Treffner and Turvey (1996) that deviations from an intended phase of $\phi = 0$ due to handedness asymmetries increase with movement frequency, and the present results also confirm the observation by Amazeen et al. (in press) that handedness effects are magnified by directing attention to the preferred hand and reduced by directing attention to the nonpreferred hand.

The predictions based upon numerical solutions of Equation 4 were generally supported, as can be seen by comparing Figure 1 (predicted patterning of ϕ_{ave}) and Figure 4 (observed patterning of ϕ_{ave}). The additional 2π periodic asymmetrical coupling terms in Equation 4 deflect the coordination equilibria away from the equilibria of $\phi = 0$ and $\phi = \pi$ (although the latter was not studied in the present research) determined by the symmetrical coupling terms of Equation 1. The special feature of the present experiment was the co-manipulation of Equation 4's asymmetrical and symmetrical coupling; specifically, the d coefficient and the ratio of the a and b coefficients were manipulated. The predicted consequence of an increase in the absolute magnitude of d (through manipulations of attention) is an increase in phase shift in the direction of attention. The predicted consequence of an accompanying decrease in b/a (brought about through an increase in ω_i) is a further increase in phase shift in the direction toward which attention is focused. As observed, LH subjects became "more left-handed" (ϕ_{ave} became more positive) when focusing attention to the left side of the body and "less left-handed" when focusing attention to the right side of the body. At the two highest frequencies in the latter condition, LH subjects performed more like RH subjects: ϕ_{ave} changed from positive to negative. RH subjects performed the task in a more right-handed manner (ϕ_{ave} became more negative) when focusing attention to the right side and performed similarly to LH subjects when focusing attention to the left side (at all three ω_i conditions, ϕ_{ave} was positive). The model

predictions presented in Figure 1 do not account for this finding. These predictions were based upon the assumption that d is a fixed parameter under manipulations of ω_c and that an increase in ω_c would shift ϕ from 0 due to the increased relative influence of asymmetrical coupling as the magnitude of symmetrical coupling decreases.

The results suggest, however, that d did not remain fixed as ω_c was increased. The asymmetrical coefficient d can be thought of as consisting of (at least) two components: asymmetries arising both from handedness and from direction of attention. It is reasonable to assume that the functional asymmetry of the body remains invariant under manipulations of ω_c . It is also reasonable to assume that as ω_c increases, the asymmetries stemming from direction of attention might vary. This notion has a certain intuitive appeal; as ω_c increases, higher levels of attention might be necessary to perform a given task at a desired level of competence. Assuming that the asymmetrical coupling coefficient d consists of one component that remains invariant under ω_c manipulations (handedness) and another component whose absolute magnitude increases with increasing ω_c (direction of attention), and using d values that correspond to these assumptions and to the appropriate experimental conditions, Equation 4 can account for the observed patterning of relative phase in the present experiment.

For example, the attentional component of d for an RH participant attending right becomes increasingly positive with increasing ω_c , while the handedness component remains constant. But for an RH participant attending left, the d component corresponding to attentional asymmetries increases in magnitude in the negative direction with increasing ω_c , while the handedness component remains constant. Equation 4, therefore, captures the symmetrical and asymmetrical coupling dynamics of bimanual coordination. To summarize, increasing ω_c decreases the relative influence of symmetrical coupling (as b/a decreases) and increases the relative influence of asymmetrical coupling (as the attentional component of d changes with ω_c , while the handedness component remains constant).

It is worth underscoring that formulations such as Equation 4 constitute a preferred modeling strategy for addressing the cyclic interactions composing rhythmic organizations at many scales and in many different complex biological, chemical, and physical systems (e.g., Koppel, 1993; Murray, 1990; Strogatz & Mirollo, 1988). To reiterate remarks made in the introduction, models of the kind expressed by Equations 1, 3, and 4 are very general, requiring knowledge of the observed oscillations of the system but not the particulars of the processes producing the oscillations. The models do not aim to capture the internal structure of the oscillators involved and are not meant to address the issues of how oscillations originate (e.g., the work of Selverston, 1988). The utility of these models is with respect to studying the collective behavior of a system of oscillators whose substrates (e.g., neuronal, muscular) and modes of interaction (e.g., forcing functions) are either largely unknown or poorly understood. Specifically, Equation 4 is directed at the coordination dynamics of the functionally asymmetrical left and right hands, not their physical dynamics (although the latter may affect the former; see Kelso, 1994b, Schöner, 1994). As the present and previous results reveal, Equation 4 strongly supports Simon's (1962) "nearly decomposable" argument: The equation expresses the time-evolution of the collective states of the central nervous system in producing bimanual rhythmic coordinations under restraints of selective attention and specified movement frequencies.

Turning to the hypothesis that handedness is a direct result of asymmetrical direction of attention to the hands (e.g., Peters, 1994), it is noteworthy that in the condition involving no direction of visual attention, LH subjects showed left-leading behavior and RH subjects showed right-leading behavior. Directing overt attention to a particular side of the body increased the phase shift in the direction of attention. Thus, handedness asymmetries seem to exist independent of overt attentional asymmetries but may indeed be modified by attentional asymmetries (Amazeen et al., in press).

Also, whereas Carson, Byblow, and Goodman (1994) noted that intrinsic asymmetries may interact with informational and mechanical constraints near transition points in interlimb coordination, the results of the present experiment, and the results of Treffner and Turvey (1995, 1996) and Amazeen et al. (in press), suggest that a dynamic explanation of human bimanual coordination can account for the handedness asymmetry and attentional asymmetries in stable patterns of coordination. Moreover, these results contrast with those of Wuyts, Summers, Carson, Bylow, and Semjen (1996), who found (for a bimanual circle drawing task) no effects of overtly directing attention to the dominant hand and that the effects of directed attention are prominent only at the level of the individual hands rather than at the relational level.

Outside of the present line of research, data on the interaction of handedness with movement speed and attention are somewhat equivocal (Peters, 1994, 1995). Intermanual differences in timing accuracy and variability of finger tapping have been shown to increase with tapping rate (Rouselle & Wolff, 1991; Todor & Kyprie, 1980; Todor & Smiley, 1985; Wolff, Hurwitz, & Moss, 1977), but in experiments in which the rate is systematically constrained by a metronome, differences in these measures of tapping performance become less apparent (e.g., Truman & Hammond, 1990). It has been suggested that when the two hands perform rhythms of different frequencies concurrently, performance is best if the preferred hand executes the faster rhythm, presumably because attention is free to control the nonpreferred hand (Peters, 1985).

The results of Peper, Beek, and van Wieringen (1995) suggest that, in bimanual multifrequency coordination, the relation of the faster moving hand to the slower moving hand is like that of a forcing oscillator to a forced oscillator. An asymmetrical influence, suggesting asymmetrical coupling, is evident in several multifrequency tapping studies in which timing of the slower hand depends on timing of the faster hand (Peters & Schwartz, 1989; Summers, Ford, & Todd, 1993; Summers & Kennedy, 1992; Summers, Rosenbaum, Burns, & Ford, 1993). When the nondominant hand is required to take the faster role, interruptions in the smooth performance of an intentionally continuous 1:2 coordination became magnified (Byblow, Carson, & Goodman, 1994; Byblow & Goodman, 1994; Sternad, 1995). However, for the more general case of polyrhythmic performance and transitions among $n:m$ coordinations, Peper et al. (1995) found no evidence for a hands effect and little support for an influence of the body's asymmetry on the coupling asymmetry favoring the faster hand. Extending the coordination dynamics perspective to bimanual multifrequency behavior may clarify the roles of handedness and attention and the relation between them (Peper, 1995; Sternad, 1995).

The directed-attention aspects of the present results should be viewed in light of Allport's (1990) argument that attention is best interpreted with respect to the selectivity of the control of action rather than the selectivity of processing. According to Allport, whereas selectivity for action is a clear idea that can be

studied behaviorally, the conventional notion of selectivity of processing is ill-defined and difficult to operationalize. On the questions that need to be raised about visual attention, Allport said,

These questions are not about processing limitations or "bottlenecks" but about the mechanisms of attentional *control*: questions about the—multiform—computational mechanisms by which attentional engagement is established, coordinated, maintained, interrupted, and redirected, both in spatial and nonspatial terms, in the preparation of action. (1990, pp. 662–663)

In the present research, and that of Amazeen et al. (in press), directing attention overtly to one hand in bimanual 1:1 coordination shifted the equilibrium further from in-phase when the attended hand was the preferred hand than when it was the nonpreferred hand. According to Equation 4, this result means that establishing attention to a hand in bimanual rhythmic coordination and maintaining that attention is understandable as setting and preserving a particular parameterization of the function that couples the two hands. In Allport's (1990) terms, the parameterization is a mechanism of visual attentional control for the present experimental task. Patently, selection-for-action in the context of the body's functional asymmetry can be pursued further within bimanual 1:1 frequency locking and the coordination dynamics by which it is modeled. Issues of the precision of attentional control, together with questions about interrupting and redirecting attention, can be addressed experimentally. Perhaps such research could provide a useful departure point for the newer, action-oriented approach to attention.

References

- Abbs, J.H., & Connor, N.P. (1990). Motor coordination for functional human behaviors: Perspectives from a speech-motor data base. In S.A. Wallace (Ed.), *Perspectives on the coordination of movement* (pp. 123–156). Amsterdam: North Holland Press.
- Allport, A. (1990). Visual attention. In M. Posner (Ed.), *Foundations of cognitive science* (pp. 631–682). Cambridge, MA: MIT Press.
- Amazeen, E.L., Amazeen, P.G., Treffner, P.J., & Turvey, M.T. (in press). Attention and handedness in bimanual coordination dynamics. *Journal of Experimental Psychology: Human Perception and Performance*.
- Amazeen, E.L., Sternad, D., & Turvey, M.T. (1996). Predicting the nonlinear shift of stable equilibria in interlimb rhythmic coordination. *Human Movement Science*, **15**, 521–542.
- Beek, P., Schmidt, R.C., Morris, A., Sim, M., & Turvey, M.T. (1996). Linear and nonlinear stiffness and friction functions in biological rhythmic movements. *Biological Cybernetics*, **73**, 499–507.
- Bernstein, N. (1996). On dexterity and its development. In M. Latash & M.T. Turvey (Eds.), *Dexterity and its development* (pp. 3–244). Hillsdale, NJ: Erlbaum.
- Byblow, W.D., Chua, R., & Goodman, D. (1995). Asymmetries in coupling dynamics of perception and action. *Journal of Motor Behavior*, **27**, 123–138.
- Byblow, W.D., & Goodman, D. (1994). Performance asymmetries in multifrequency coordination. *Human Movement Science*, **13**, 147–174.
- Byblow, W.D., Carson, R.G., & Goodman, D. (1994). Expressions of asymmetries and anchoring in bimanual coordination. *Human Movement Science*, **13**, 3–28.
- Carson, R. (1993). Manual asymmetries: Old problems and new directions. *Human Movement Science*, **21**, 157–162.

- Carson, R., Byblow, W., & Goodman, D. (1994). The dynamical substructure of bimanual coordination. In S. Swinnen, H. Heuer, J. Massion, & P. Casaer (Eds.), *Interlimb coordination: Neural, dynamical, and cognitive constraints* (pp. 319–337). San Diego, CA: Academic Press.
- Cohen, A.H., Holmes, P.J., & Rand, R.H. (1982). The nature of the coupling between segmental oscillators of the lamprey spinal generator for locomotion: A mathematical model. *Journal of Mathematical Biology*, **13**, 345–369.
- Collins, D., Sternad, D., & Turvey, M.T. (1996). An experimental note on defining frequency competition in intersegmental coordination dynamics. *Journal of Motor Behavior*, **28**, 299–303.
- Collins, D.R., & Turvey, M.T. (1997). A stochastic analysis of superposed rhythmic synergies. *Human Movement Science*, **16**, 33–80.
- Fitzpatrick, P., Schmidt, R.C., & Carello, C. (1996). Dynamical patterns in clapping behavior. *Journal of Experimental Psychology: Human Perception and Performance*, **22**, 707–724.
- Gentner, D.R. (1987). Timing of skilled motor performance: Tests of the proportional duration model. *Psychological Review*, **94**, 255–276.
- Gilmore, R. (1981). *Catastrophe theory for scientists and engineers*. New York: Wiley.
- Haken, H. (1977). *Synergetics*. Berlin: Springer Verlag.
- Haken, H., Kelso, J.A.S., & Bunz, H. (1985). A theoretical model of phase transitions in human hand movements. *Biological Cybernetics*, **51**, 347–356.
- Haken, H., & Wunderlin, A. (1990). Synergetics and its paradigm of self-organization in biological systems. In H.T.A. Whiting, O.G. Meijer, & P.C.W. van Wieringen (Eds.), *The natural-physical approach to movement control* (pp. 1–36). Amsterdam: VU University Press.
- Heuer, H. (1988). Testing the invariance of relative timing: Comment on Gentner (1987). *Psychological Review*, **95**, 552–557.
- Heuer, H., & Schmidt, R.A. (1988). Transfer of learning among motor patterns with different relative timing. *Journal of Experimental Psychology: Human Perception and Performance*, **14**, 241–252.
- Hilborn, R.C. (1994). *Chaos and nonlinear dynamics*. New York: Oxford University Press.
- Jeka, J.J., & Kelso, J.A.S. (1995). Manipulating symmetry in the coordination dynamics of human movement. *Journal of Experimental Psychology: Human Perception and Performance*, **21**, 360–374.
- Jeka, J.J., Kelso, J.A.S., & Kiemel, T. (1993). Pattern switching in human interlimb coordination dynamics. *Bulletin of Mathematical Biology*, **55**, 829–845.
- Kelso, J.A.S. (1994a). Elementary coordination dynamics. In S. Swinnen, H. Heuer, J. Massion, & P. Casaer (Eds.), *Interlimb coordination: Neural, dynamical, and cognitive constraints* (pp. 301–318). San Diego, CA: Academic Press.
- Kelso, J.A.S. (1994b). The informational character of self-organized coordination dynamics. *Human Movement Science*, **13**, 393–414.
- Kelso, J.A.S. (1995). *Dynamic patterns: The self-organization of brain and behavior*. Cambridge, MA: MIT Press.
- Kelso, J.A.S., & Ding, M. (1993). Fluctuations, intermittency, and controllable chaos in biological coordination. In K.M. Newell & D.M. Corcos (Eds.), *Variability and motor control* (pp. 139–169). Champaign, IL: Human Kinetics.
- Kelso, J.A.S., Delcolle, J.D., & Schöner, G. (1990). Action-perception as a pattern formation process. In M. Jeannerod (Ed.), *Attention and performance XIII*. Hillsdale, NJ: Erlbaum.

- Kelso, J.A.S., deGuzman, G.C., & Holroyd, T. (1991). The self-organized phase attractive dynamics of coordination. In A. Babloyantz (Ed.), *Self organization, emerging properties, and learning* (pp. 41–62). New York: Plenum Press.
- Kelso, J.A.S., & Jeka, J.J. (1992). Symmetry breaking dynamics of human limb coordination. *Journal of Experimental Psychology: Human Perception and Performance*, **18**, 645–668.
- Kopell, N. (1988). Toward a theory of modelling central pattern generators. In A.H. Cohen, S. Rossignol, & S. Grillner (Eds.), *Neural control of rhythmic movements in vertebrates* (pp. 369–413). New York: Wiley.
- Kopell, N. (1993). *Rhythms and clues: Mechanisms of self-organization in nature*. University lecture, Boston University, October 18.
- Kugler, P.N., & Turvey, M.T. (1987). *Information, natural law, and the self-assembly of rhythmic movement*. Hillsdale, NJ: Erlbaum.
- Murray, J.D. (1990). *Mathematical biology*. Berlin: Springer Verlag.
- Peper, C.E. (1995). *Tapping dynamics*. Unpublished doctoral dissertation, Free University, Amsterdam.
- Peper, C.E., Beek, P.J., & van Wieringen, P.C.W. (1995). Multifrequency coordination in bimanual tapping: Asymmetrical coupling and signs of supercriticality. *Journal of Experimental Psychology: Human Perception and Performance*, **21**, 1117–1138.
- Peters, M. (1981). Attentional asymmetries during concurrent bimanual performance. *Quarterly Journal of Psychology*, **33A**, 95–103.
- Peters, M. (1985). Constraints in the performance of bimanual tasks and their expression in unskilled and skilled participants. *Quarterly Journal of Experimental Psychology*, **37A**, 171–196.
- Peters, M. (1994). Does handedness play a role in the coordination of bimanual movement? In S. Swinnen, H. Heuer, J. Massion, & P. Casaer (Eds.), *Interlimb coordination: Neural, dynamical, and cognitive constraints* (pp. 595–612). San Diego, CA: Academic Press.
- Peters, M. (1995). Handedness and its relation to other indices of cerebral lateralization. In R.J. Davidson & K. Hugdahl (Eds.), *Brain asymmetry* (pp. 183–214). Cambridge, MA: MIT Press.
- Peters, M., & Schwartz, S. (1989). Coordination of the two hands and effects of attentional manipulation in the production of a bimanual 2:3 polyrhythm. *Australian Journal of Psychology*, **41**, 215–224.
- Rand, R.H., Cohen, A.H., & Holmes, P.J. (1988). Systems of coupled oscillators as models of central pattern generators. In A.H. Cohen, S. Rossignol, & S. Grillner (Eds.), *Neural control of rhythmic movements in vertebrates* (pp. 333–367). New York: Wiley.
- Rouselle, C., & Wolff, P.H. (1991). The dynamics of bimanual coordination in developmental dyslexia. *Neuropsychologia*, **29**, 907–924.
- Schmidt, R.A. (1985). The search for invariance in skilled movement behavior. *Research Quarterly for Exercise and Sport*, **56**, 188–200.
- Schmidt, R.C., Shaw, B.K., & Turvey, M.T. (1993). Coupling dynamics in interlimb coordination. *Journal of Experimental Psychology: Human Perception and Performance*, **19**, 397–415.
- Schmidt, R.C., & Turvey, M.T. (1995). Models of interlimb coordination: Equilibria, local analyses, and spectral patterning. *Journal of Experimental Psychology: Human Perception and Performance*, **21**, 432–443.
- Schöner, G. (1994). From interlimb coordination to trajectory formation: Common dynamical

- principles. In S. Swinnen, H. Heuer, J. Massion, & P. Cisek (Eds.), *Interlimb coordination: Neural, dynamical, and cognitive constraints* (pp. 339–368). San Diego, CA: Academic Press.
- Schöner, G., Haken, H., & Kelso, J.A.S. (1986). A stochastic theory of phase transitions in human hand movement. *Biological Cybernetics*, **53**, 442–452.
- Silverston, A.I. (1988). Invertebrate central pattern generators as computational data bases. In J.A.S. Kelso, A.J. Mandel, & M.F. Shlesinger (Eds.), *Dynamic patterns in complex systems* (pp. 137–142). Singapore: World Scientific.
- Simon, H.A. (1962). *The sciences of the artificial*. Cambridge, MA: MIT Press.
- Stein, P.S.G. (1995). A multiple level approach to motor pattern generation. In W.R. Ferrell & U. Proske (Eds.), *Neural control of movement* (pp. 159–165). New York: Plenum Press.
- Sternad, D. (1995). *Dynamics of 1:2 coordination in rhythmic interlimb movement*. Unpublished doctoral dissertation, The University of Connecticut.
- Sternad, D., Amazeen, E.L., & Turvey, M.T. (1996). Diffusive, synaptic and synergetic coupling: An evaluation through inphase and antiphase rhythmic movements. *Journal of Motor Behavior*, **28**, 255–270.
- Sternad, D., Collins, D., Turvey, M.T. (1995). The detuning factor in the dynamics of interlimb rhythmic coordination. *Biological Cybernetics*, **73**, 27–35.
- Stewart, I., & Golubitsky, M. (1992). *Fearful symmetry: Is God a geometer?* Cambridge, MA: Blackwell.
- Strogatz, S.H. (1994). *Nonlinear dynamics and chaos*. Reading, MA: Addison Wesley.
- Strogatz, S.H., & Mirollo, R.E. (1988). Phase-locking and critical phenomena in lattices of coupled nonlinear oscillators with random intrinsic frequencies. *Physica*, **31D**, 143–168.
- Summers, J.J., Ford, S.K., & Todd, J.A. (1993). Practice effects on the coordination of the two hands in a bimanual tapping task. *Human Movement Science*, **12**, 111–133.
- Summers, J.J., & Kennedy, T.M. (1992). Strategies in the production of a 5:3 polyrhythm. *Human Movement Science*, **11**, 101–112.
- Summers, J.J., Rosenbaum, D.A., Burns, B.D., & Ford, S.K. (1993). Production of polyrhythms. *Journal of Experimental Psychology: Human Perception and Performance*, **19**, 416–428.
- Todor, J.L., & Kyprie, P.M. (1980). Hand differences in the rate and variability of rapid tapping. *Journal of Motor Behavior*, **12**, 57–60.
- Todor, J.L., & Smiley, A.L. (1985). Performance differences between the hands: Implications for studying disruption to limb praxis. In E.A. Roy (Ed.), *Neuropsychological studies of apraxia and related disorders* (pp. 309–344). Amsterdam: Elsevier.
- Treffner, P.J., & Turvey, M.T. (1995). Handedness and the asymmetric dynamics of bimanual rhythmic coordination. *Journal of Experimental Psychology: Human Perception and Performance*, **21**, 318–333.
- Treffner, P.J., & Turvey, M.T. (1996). Symmetry, broken symmetry, and handedness in bimanual coordination dynamics. *Experimental Brain Research*, **107**, 463–478.
- Truman, G., & Hammond, G.R. (1990). Temporal regularity by the left and right hands in timed and untimed finger tapping. *Journal of Motor Behavior*, **22**, 521–535.
- Viviani, P., & Terzuolo, C. (1980). Space-time invariance in learned motor skills. In G.E. Stelmach & J. Requin (Eds.), *Tutorials in motor behavior* (pp. 525–533). Amsterdam: North Holland.

- Wann, J.P., & Nimmo-Smith, I. (1990). Evidence against relative invariance of timing in handwriting. *Quarterly Journal of Experimental Psychology*, **42A**, 105-119.
- Wolff, P.H., Hurwitz, I., & Moss, H. (1977). Serial organization of motor skills in left- and right-handed adults. *Neuropsychologia*, **15**, 539-546.
- Wuyts, I.J., Summers, J.J., Carson, R.G., Byblow, W.D., & Semjen, A. (1996). Attention as a mediating variable in the dynamics of bimanual coordination. *Human Movement Science*, **15**, 877-898.
- Zelaznik, H., Schmidt, R.A., & Gielen, S.C.A.M. (1986). Kinematic properties of rapid aimed hand movements. *Journal of Motor Behavior*, **18**, 353-372.

Author Notes

This research was supported in part by NSF Grant SBR 94-22650, awarded to the fifth author. We wish to thank C. Carello and R.C. Schmidt.

Manuscript submitted: September 9, 1996

Accepted for publication: March 27, 1997