Average phase difference theory and 1:1 phase entrainment in interlimb coordination

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Abstract. The dynamics of coupled biological oscillators can be modeled by averaging the effects of coupling over each oscillatory cycle so that the coupling depends on the phase difference \( \phi \) between the two oscillators and not on their specific states. Average phase difference theory claims that mode locking phenomena can be predicted by the average effects of the coupling influences. As a starting point for both empirical and theoretical investigations, Rand et al. (1988) have proposed \( d\phi/dt = \Delta \omega - K \sin \phi \), with phase-locked solutions \( \phi = \arcsin(\Delta \omega/K) \), where \( \Delta \omega \) is the difference between the uncoupled frequencies and \( K \) is the coupling strength. Phase-locking was evaluated in three experiments using an interlimb coordination paradigm in which a person oscillates hand-held pendulums. \( \Delta \omega \) was controlled through length differences in the left and right pendulums. The coupled frequency \( \omega_c \) was varied by a metronome, and scaled to the eigenfrequency \( \omega_e \) of the coupled system; \( K \) was assumed to vary inversely with \( \omega_e \). The results indicate that: (1) \( \Delta \omega \) and \( K \) contribute multiplicatively to \( \phi \); (2) \( \phi = 0 \) or \( \phi = \pi \) regardless of \( K \) when \( \Delta \omega = 0 \); (3) \( \phi \approx 0 \) or \( \phi \approx \pi \) regardless of \( \Delta \omega \) when \( K \) is large (relative to \( \Delta \omega \)); (4) results (1) to (3) hold identically for both in phase and antiphase coordination. The results also indicate that the relevant frequency is \( \omega_c/\omega_e \), rather than \( \omega_e \). Discussion highlighted the significance of confirming \( \phi = \arcsin(\Delta \omega/K) \) for more general treatments of phase-locking, such as circle map dynamics, and for the 1:1 phase-entrainment which characterizes biological movement systems.

1 Introduction

Von Holst (1937/1973) addressed the issue of movement coordination with medulla transected \( \textit{Larbus} \), a fish that swims with its main body axis immobile. Following surgery, the fins oscillate autonomously for hours. With this preparation von Holst observed the waxing and waning of phase-locking. Two different sized fins, with different uncoupled periods, would oscillate with a fixed phase relation and a common coupled frequency—a state von Holst referred to as \textit{absolute coordination}. Or they would oscillate without phase and frequency locking—a state von Holst referred to as \textit{relative coordination}. Both states would be seen intermittently, and whenever one dominated, signs of the other would be visible. Von Holst concluded that even when absolute coordination was achieved, the rhythmical interaction (each attempting to proceed at its own pace) remained, and even when relative coordination was occurring, interlim cooperation (each attempting to proceed at the pace of the other) was still in evidence. He referred to the competitive aspect as the “maintenance tendency” and the cooperative aspect as the “magnet effect.”

Von Holst’s research suggests four major requirements for an experimental paradigm directed at the dynamics of the interlimb rhythmic coordinations typifying locomotion. First, the studied movement pattern should be analogous to the locomotory pattern without engendering movement of the body relative to the environment—a fictive or mimed locomotion. Second, the eigenvalues of the individual rhythmic movement units should be manipulable and easily quantified. Third, the interlimb system should be easily prepared in one of the two basic patterns of in phase and antiphase. And fourth, the focus of measurement and dynamical modeling should be on the interactions of phase. An experimental paradigm satisfying the first three requirements has been developed by Kugler and Turvey (1987) and used to examine a variety of coordination phenomena (Bingham et al. 1991; Rosenblum and Turvey et al. 1989; Schmidt (submitted); Schmidt et al. (in press); Turvey et al. 1988 (in press). Dynamical models satisfying the fourth requirement have been developed most notably by Kopell (1988a), Rand et al. (1988); Murray (1990); Haken et al. (1985). Characteristic of these various models is the effort to reduce complicated (high dimensional) dynamics to simpler (lower dimensional)
describe the oscillators' motions, and an assumption of structural stability implies that for sufficiently weak coupling, stable oscillations will continue (Kopell 1988a; Murray 1990). Given the preceding, a first pass on the behavior of an individual oscillator under coupling yields

$$\dot{\theta}_i = \omega_i + H_{ij}(\theta_1, \theta_j)$$

(3)

Further developments require determination of the coupling function $H_{ij}$. Because $\theta_i$ is the single state variable of the individual oscillator, the coupling function $H_{ij}$ can depend only on $\theta_1$ and $\theta_2$ and cannot depend, by assumption, on factors such as the size of the limit cycle or the wave form of the oscillation. Further, in order for the motion expressed by (3) to be defined uniquely on $T^2$, $H_{ij}$ must be $2\pi$ periodic. This simply expresses the fact that the effect of the one oscillator on the same phase point of the other oscillator must always be the same. One move to resolve the form of $H_{ij}$ is to require that the coupling goes to zero when $\theta_1 = \theta_2$. This simplifying assumption defines what is known as diffusive coupling (Kopell 1988a; Murray 1990; Rand et al. 1988). It allows that

$$H_{12}(\theta_1, \theta_2) = H_{12}(\theta_2 - \theta_1) = H_{12}(\phi)$$

(4)

Armed with (4) and the understanding that $H_{ij}$ must be $2\pi$ periodic, the requisite coupling function can be approximated by taking the first terms of the Fourier series. Letting the coefficient on the cosine term be zero results in

$$H_{12}(\theta_1, \theta_2) = k_{12} \sin(\theta_2 - \theta_1)$$

(5)

Thus, for the two oscillators the motion equations take the form

$$\dot{\theta}_1 = \omega_1 + k_{12} \sin(\theta_2 - \theta_1)$$

$$\dot{\theta}_2 = \omega_2 + k_{21} \sin(\theta_1 - \theta_2)$$

(6)

Subtracting the motion equation for oscillator 2 from that of oscillator 1 provides us with a low dimensional dynamic in $\phi$

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

(7)

where $\Delta\omega = (\omega_1 - \omega_2)$ and $K = (k_{12} + k_{21})$. If $\Delta\omega = 0$, and if $K$ is positive in sign, then (7) exhibits a negative sinusoidal form with a negative second derivative (indexing a stable point) at the intercept points of 0 and $2\pi$ and a positive second derivative (indexing an unstable point) at $\pi$. These conditions characterize in-phase behavior (Rand et al. 1988; Schmidt et al. in press). Conversely, if the sign of $K$ is negative, then the sinusoidal form is positive with a negative second derivative at the intercept value of $\pi$ and a positive second derivative at 0 and $2\pi$. These conditions characterize antiphase behavior (Rand et al. 1988; Schmidt et al. in press). If $\Delta\omega \neq 0$, then the stable points will deviate from 0 and $\pi$ to a degree depending on the magnitude of $|\Delta\omega|$.

A general expression for the varied equilibria of (7) can be determined under the assumption that, at equilibrium, the time derivative of $\phi$ equals 0. Consequently, the equilibrium values of $\phi$ are given by

$$\phi = \arcsin(\Delta\omega/K)$$

(8)

Regardless of whether $K$ is positive or negative, the values of the arcsine function will be the same due to its symmetry. This means that (8) gives the same absolute values for in phase and antiphase.

1.3 Investigating APD theory

Schmidt et al. (in press) examined the validity of (7) for modeling the interlimb coordination of rhythmic movements using the wrist-pendulum paradigm. The measurable quantities relevant to evaluating the model are $\phi$, $\Delta\omega$, and $\omega_e$. The average value of $\phi$ over a dynamic run is $\bar{\phi}$ and the intended value is $\phi_e$ (with $\psi$ symbolizing "intended"). $\Delta\omega$ is a control parameter that governs the degree of competition between the oscillators (to comport with von Holst's intuitions about the nature of interlimb coordination). During a trial in the wrist-pendulum paradigm, the frequency competition between the rhythmic subsystems will be constant. The common or coupled frequency $\omega_c$ of the rhythmic units is another control parameter. It likewise can be held constant during a trial (by means of a pacing metronome).

Schmidt et al. (in press) found that (7) modeled equally the two modes $\phi_e = 0$ and $\phi_e = \pi$ and that $|\phi_{ave} - \phi_e|$ scaled to $\Delta\omega$ as interacted with $\Delta\omega$ in determining $|\phi_{ave} - \phi_e|$ and $\phi$ variability. The changes induced by increasing $\omega_e$ expected from (8). It was also demonstrated that $\omega_e$ were those expected from decreasing coupling strength $K$ in (7) and (8). The implication is that $K$ can be systematically manipulated by manipulating $\omega_e$. Equation (8) can be approximated, therefore, by

$$\phi = \arcsin(\Delta\omega)(\omega_e)$$

(9)

This latter relation is particularly useful because a decrease in coupling strength has been a major assumption in the modeling of transitions, observed at higher frequencies, from antiphase to in phase limb coordination (Haken et al. 1985; Kelso et al. 1986; Schmidt et al. 1990).

1.4 Significance of the eigenfrequency of the coupled system

When two pendular rhythmic units are mode locked, the system thus formed possesses, like the subsystems from which it is formed, an eigenfrequency. Kugler and Turvey (1987) presented arguments and data (see also Turvey et al. 1988) for characterizing a coupling of left and right wrist-pendulum systems as a single virtual system with an equivalent simple pendulum length. If the two wrist-pendulum systems were coupled such that $\theta_1$ was always, at every instant, identically equal to $\theta_2$, or to $(\theta_1 + \pi)$, then the two oscillators could be considered as rigidly connected. The simple pendulum equivalent $L_{\text{equivalent}}$ of a compound pendulum so composed (that is, of two pendulums connected by a rigid bar) is given by

$$L_{\text{equivalent}} = (m_1l_1^2 + m_2l_2^2)/(m_1l_1 + m_2l_2)$$

(10)
where \( m_i \) and \( l_i \) refer to the mass and the equivalent simple pendulum length, respectively, of an individual (compound) pendulum system. In words, the right-hand-side of the equation reads: sum of the individual moments of inertia divided by the sum of the corresponding individual static moments.) By the use of (10), two coupled pendulums of lengths \( l_i \) and \( l_j \) are expressed as a virtual (v) pendulum of length \( L_v \). Consequently, the eigenfrequency of the system of coupled pendulums considered as a virtual single pendulum is \( \omega_v = (g/L_v)^{1/2} \). In the same way that the eigenfrequencies \( \omega_i = (g/l_i)^{1/2} \) and \( \omega_j = (g/l_j)^{1/2} \) of the uncoupled wrist-pendulum systems can be taken as characterizing their respective maintenance tendencies, so it is the case that \( \omega_v \) can be taken as characterizing the maintenance tendency of the coupled wrist-pendulum system.

For present purposes, the importance of the preceding is that the operating frequency of the coupled system \( \omega_c \) should be expressed – by Kugler and Turvey’s (1987) hypothesis – in units of \( \omega_v \). That is, the control parameter is not purely \( \omega_c \), but \( \omega_c/\omega_v \). By this hypothesis, (9) becomes

\[
\phi = \arcsin(\Delta \omega)(\omega_c/\omega_v)
\]

(11)

### 1.5 Predictions

Three experiments on interlimb 1:1 frequency locking are reported in which \( \Delta \omega, \omega_c, \) and \( \omega_v/\omega_c \) are manipulated. They are directed at providing further substantiation of the Rand et al. equations. There are three major predictions: (a) that the frequency at which a 2-oscillator coupled system is running, and the difference between the eigenfrequencies of the two oscillators, relate multiplicatively in determining \( \phi_{ave} \), (b) that this relationship will hold for coordinates where \( \phi_0 = 0 \) and \( \phi_\pi = \pi \), and (c) that the physically relevant measure of the coupling frequency is \( \omega_c/\omega_v \). More specifically, it is predicted from (11) that, for both \( \phi_0 = 0 \) and \( \phi_\pi = \pi \), when \( \Delta \omega = 0 \), deviations of \( \phi_{ave} \) from \( \phi_0 \) will be zero independently of \( \omega_c/\omega_v \). Further, for both \( \phi_0 = 0 \) and \( \phi_\pi = \pi \), when \( |\Delta \omega| \neq 0 \), deviations of \( \phi_{ave} \) from \( \phi_0 \) will be inversely dependent on \( \omega_c/\omega_v \). Elaborating on the latter prediction, when \( \omega_c/\omega_v < 1 \) (the coupled system is oscillating slower than its eigenfrequency), deviations of \( \phi_{ave} \) from \( \phi_0 \) for a given \( |\Delta \omega| \neq 0 \) will be less than when \( \omega_c/\omega_v = 1 \) (the coupled system oscillating at its eigenfrequency), and when \( \omega_c/\omega_v > 1 \) (the coupled system is oscillating faster than its eigenfrequency), deviations of \( \phi_{ave} \) from \( \phi_\pi \) for a given \( |\Delta \omega| \neq 0 \) will be greater than when \( \omega_c/\omega_v = 1 \).

### 2 Experiment 1

Schmidt et al. (in press) investigated the predictions of APD theory for three values of \( \omega_c \) that at which the 1:1 frequency locking was most comfortable, \( \omega_c = \omega_v \), together with \( \omega_c = 5.84 \) (rad/s) and \( \omega_c = 7.22 \) (rad/s). In the Schmidt et al. experiment, \( \omega_c \) was not scaled to \( \omega_v \). Whereas the frequency condition \( \omega_c = \omega_v \) varied with \( \Delta \omega \), the frequency conditions \( \omega_c = 5.84 \) (rad/s), and \( \omega_c = 7.22 \) (rad/s) did not. It was the case, however, that the two frequency conditions \( \omega_c = 5.84 \) (rad/s), and \( \omega_c = 7.22 \) (rad/s) tended to be higher for all values of \( \Delta \omega \) than the frequency condition \( \omega_c = \omega_v \). In agreement with APD theory, Schmidt et al. found a significant interaction between \( \Delta \omega \) and \( \omega_c \), and no interactions with \( \phi_0 \), in the determination of \( \phi_{ave} \). The deviation of \( \phi_{ave} \) from \( \phi_0 \) increased with \( \Delta \omega \) and was increased further by \( \omega_c \).

The coupled frequency conditions examined by Schmidt et al. approximated \( \omega_c/\omega_v > 1 \). The present experiment manipulates \( \omega_c/\omega_v \) precisely and examines coupled frequency conditions satisfying \( \omega_c/\omega_v < 1 \) – conditions where the frequency of oscillation is slower than the eigenfrequency of the coupled pendulum system. It does so for \( \phi_0 \) with five values of \( \Delta \omega \). Where Schmidt et al. had found an amplification of \( |\phi_{ave} - \phi_0| \) for a given \( |\Delta \omega| \neq 0 \) in the domain of \( \omega_c/\omega_v > 1 \), it was expected that the present experiment should reveal a reduction of \( |\phi_{ave} - \phi_0| \) in the domain of \( \omega_c/\omega_v < 1 \).

### 2.1 Method

**Subjects.** One woman and four men participated. Two participants were faculty at the University of Connecticut, and three participants were graduate students. The age range was 28 years to 49 years. All participants were right handed.

**Apparatus.** The pendulums were constructed using the specifications described in Kugler and Turvey (1987). Each consisted of an ash dowel inserted into a bicycle hand grip. Weights were attached to a 10 cm long bolt that was drilled through the dowel at right angles 2 cm from the bottom. Four such pendulums were used, one of 74 cm, one of 48 cm, and two each of 31 cm. For all four pendulums the added mass was 200 g. There were five pairings that defined the coupled left-hand pendulum/right-hand pendulum systems: 74 cm/31 cm (Coupled System 1), 48 cm/31 cm (Coupled System 2), 31 cm/31 cm (Coupled System 3), 31 cm/48 cm (Coupled System 4), and 31 cm/74 cm (Coupled System 5).

The equivalent simple pendulum lengths \( l_i \) of the individual pendulums (consisting of the attached mass, the dowel, and the hand of the subject) were calculated according to procedures identified in Kugler and Turvey (1987), as was the equivalent simple pendulum length \( L_v \), of each of the five coupled systems (see (10)). The gravitational eigenfrequencies of the uncoupled systems, \( \omega_{left}, \omega_{right} \), the difference between time, \( \omega_{left} - \omega_{right} \), and the gravitational eigenfrequency of the coupled system, \( \omega_c \), are displayed in Table 1 for each Coupled System 1–5.

The subject sat in a specially designed chair with arm rests to support the forearms. The arm rests were designed to restrict oscillations to the wrist; the two forearms were kept in contact with the arm supports throughout a trial. The chair also provided a raised support for the subject’s legs so that they did not interfere with the ultrasonic acquisition of the data (see below).
Table 1. The gravitational eigenfrequencies (rad/s) of the uncoupled systems, \( \omega_{\text{left}} \), \( \omega_{\text{right}} \), the difference between them, \( \Delta \omega = \omega_{\text{left}} - \omega_{\text{right}} \), and the gravitational eigenfrequencies of the coupled systems, \( \omega_c \).

<table>
<thead>
<tr>
<th>Coupled System</th>
<th>( \omega_{\text{left}} )</th>
<th>( \omega_{\text{right}} )</th>
<th>( \Delta \omega )</th>
<th>( \omega_c )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4.002</td>
<td>6.509</td>
<td>-2.507</td>
<td>4.351</td>
</tr>
<tr>
<td>2</td>
<td>5.049</td>
<td>6.509</td>
<td>-1.450</td>
<td>5.468</td>
</tr>
<tr>
<td>3</td>
<td>6.509</td>
<td>6.509</td>
<td>0</td>
<td>6.509</td>
</tr>
<tr>
<td>4</td>
<td>6.509</td>
<td>5.049</td>
<td>1.450</td>
<td>5.468</td>
</tr>
<tr>
<td>5</td>
<td>6.509</td>
<td>4.002</td>
<td>2.507</td>
<td>4.351</td>
</tr>
</tbody>
</table>

Pendular trajectories were measured using an Ultrasonic 3-Space Digitizer (SAC Corporation, Westport, CT). An ultrasound emitter was affixed to the end of each pendulum. An ultrasound “spark” was issued from each emitter at 90 Hz. The digitizer operates by registering each emission using any of four microphones arranged to form a square grid. The digitizer calculates the distance of each emitter from each microphone, thereby pinpointing the position of the emitters in 3-space at the time of the emission. This slant range information was stored for later use on a 80286 based microcomputer using MASS digitizer software (Engineering Solutions, Columbus, Ohio). This software and analogous routines written on a Macintosh II use the slant range time series to calculate the primary angle of excursion of the pendulums and their respective phase angle \( \phi \). An electronic metronome was used to pace the pendulum oscillations at a preset frequency.

**Procedure and design.** On a given trial, the subject was instructed to move the two hand-held pendulums in antiphase \( (\phi = \pi) \) at a 1:1 frequency locking. The values of \( \omega_c \) at which a coupled system was 1:1 frequency locked were scaled to \( \omega_c \) according to \( \omega_c / \omega_c = 1 \), \( \omega_c / \omega_c = 0.77 \), \( \omega_c / \omega_c = 0.63 \). Coupled Systems 1–5 differed in \( \omega_c \) (see Table 1). Satisfying the preceding values of \( \omega_c \) meant, therefore, that the three \( \omega_c \)s differed for each coupled system. The 15 \( \omega_c \)s were determined beforehand, given the preceding calculations of the respective \( \omega_c \)s, and were controlled during a trial by means of a metronome. The design of the experiment, therefore, was a factorial consisting of three levels of \( \omega_c / \omega_c \) and five values of \( \Delta \omega \). There were two 32 s trials per condition for a total of 30 trials per subject. The experiment was divided into two blocks of 15 trials, each block including all conditions. To reduce the number of individual pendulum changes, the three coupled frequencies for a given coupled system were given in succession. In Block 1 the order was Coupled System 1 to Coupled System 5; in Block 2 the order was Coupled System 5 to Coupled System 1.

Each subject was given instructions and allowed to practice before the beginning of a session. He or she was told to place the forearms squarely on the arm rests, to gaze straight ahead without looking at the pendulums, and to swing the pendulums smoothly back and forth. The subject was instructed to hold the pendulums firmly in the hands so that rotation of the pendulum was generated about the wrist joint rather than about the finger joints. The motions of the pendulums were restricted to planes parallel to the subject’s sagittal plane. The subject was allowed to practice the task in the various conditions prior to the experiment proper. Prefatory to a trial, the metronome was started, ticking at the rate designated for the particular conditions tested on that trial. The subject was allowed as much time as needed to achieve the essential antiphase pattern at the prescribed metronome frequency. Data recording began after the subject indicated that he or she was ready, which was usually within about 10 s. An experimental session lasted between 60 and 80 min.

**Data reduction.** The digitized displacement time series of the pendulums were smoothed using a triangular moving average procedure with a window size of seven samples. Each trial was subjected to software analyses to determine the frequency of oscillation of each pendulum, the time series of the relative phase angle \( \phi \) between the two pendulum systems, the power spectra of this relative phase time series, and the total power associated with each of these spectra. A peak picking algorithm was employed to determine the time of maximum forward extension of the pendular trajectories. From the peak extension times, the frequency of oscillation for the \( n \)th cycle was calculated as \( f_j = 1/[(\text{time of peak extension}_{n+1}) - (\text{time of peak extension}_{n})] \).

The mean frequency of oscillation for a trial was calculated from these cycle frequencies. The phase angle of each pendulum \( \left( \theta_i \right) \) was calculated for each sample \( (90/\text{s}) \) of the displacement time series to produce a time series of \( \theta_i \). The phase angle was of wrist pendulum \( i \) at sample \( j(\theta_i) \) was calculated as

\[
\theta_{ij} = \arctan(\Delta x_{ij}/\Delta x_{ij})
\]

(12)

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 \( \Delta x_{ij} \) is the displacement of the time series at sample \( j \) minus the average displacement for the trial. The relative phase angle \( (\phi_i) \) between the two pendulums was calculated for each sample as \( \theta_{\text{right},i} - \theta_{\text{left},i} \). The \( \phi \) that the subject intended was \( \pi \). The mean of the \( \phi \) time series allows an evaluation of how the subjected satisfied this task demand.

**2.2 Results**

Three examples of the time series of \( \phi \) are shown in Fig. 2. Inspection reveals that \( \phi \) was not fixed but variable around \( \phi_{ave} \) in the manner of phase entrainment (Schmidt et al. in press) rather than phase locking; this is the usual observation for the interlimb coordination of pendular rhythmic movements (e.g., Schmidt et al. 1991). Comparison of actual \( \omega_c \) to the metronome-specified \( \omega_c \) revealed, across subjects and trials, a minimum average difference of the order of 1 ms and a maximum of the order of 6 ms (comparable values held for Experiments 2–3).
The expectation from (8), in the experimentally testable form of (11), is that average phase-locking behavior $\phi_{ave}$ is multiplicatively dependent on $\Delta \omega$ and $\omega_1/\omega_2$. The magnitude of $\phi_{ave}$ as a function of $\Delta \omega$ and $\omega_1/\omega_2$ is presented in Fig. 3, averaged over the five subjects. (The value of $\phi_{ave}$ was determined as the mean of the two values of $\phi_{ave}$ obtained from the two trials per condition.) Inspection reveals that the deviation of $\phi_{ave}$ from $\pi$ depended systematically on $\Delta \omega$ when $\omega_1/\omega_2 = 1$; this increase of $|\phi_{ave} - \pi|$ as a function of $|\Delta \omega|$ concurs with previous observations for conditions in which $\omega_1/\omega_2 = 1$ (Rosenblum and Turvey 1988; Schmidt et al. in press; Turvey et al. 1986). Importantly, inspection of Fig 3 reveals that there was no such dependency on $\Delta \omega$ for $\omega_1/\omega_2 = 0.77$ and $\omega_1/\omega_2 = 0.63$. Slowing the coupled frequency by approximately 20% and 30% below the 2-oscillator system eigenfrequency reduced $(\phi_{ave} - \pi)$ to near zero. This previously unobserved reduction in $|\phi_{ave} - \pi|$ for all $\Delta \omega$ as a result of slowing the frequency of the 2-oscillator coupled system was expected from APD theory as expressed in (8). Inspection of Fig. 3 also reveals that for $\Delta \omega = 0$, $\phi_{ave} = \pi$ regardless of $\omega_1/\omega_2$, an outcome similarly expected from APD theory. The observations
Table 2. Variance in $|\phi_{\text{ave}} - \phi_{\text{p}}|$ accounted for by $\omega_{p}/\omega_{e}$ and $\omega_{e}$ in Experiment 1

<table>
<thead>
<tr>
<th>Subject</th>
<th>$\omega_{p}/\omega_{e}$</th>
<th>$\omega_{e}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.465***</td>
<td>0.196*</td>
</tr>
<tr>
<td>2</td>
<td>0.242**</td>
<td>0.062</td>
</tr>
<tr>
<td>3</td>
<td>0.507***</td>
<td>0.077</td>
</tr>
<tr>
<td>4</td>
<td>0.226*</td>
<td>0.040</td>
</tr>
<tr>
<td>5</td>
<td>0.147*</td>
<td>0.006</td>
</tr>
</tbody>
</table>

* $p < 0.05$ ** $p < 0.001$ *** $p < 0.0001$

represented in Fig. 3 were subject to a 3 (values of $\omega_{p}/\omega_{e}$) by 5 (values of $\Delta \omega$) analysis of variance (ANOVA) with $\phi_{\text{ave}}$ as the dependent quantity. The ANOVA yielded a significant main effect of $\Delta \omega$, $F(4, 16) = 23.56$, $p < 0.0001$, but no main effect of $\omega_{p}/\omega_{e}$, $F(2, 8) = 2.11$, $p > 0.05$. The important interaction between $\Delta \omega$ and $\omega_{e}/\omega_{p}$ was highly significant, $F(8, 32) = 31.66$, $p < 0.0001$. A further ANOVA limited to the data of $\Delta \omega = 0$ found no effect of $\omega_{p}/\omega_{e}$, $F(2, 18) = 2.31$, $p > 0.05$. To check on the proximity of observed $\phi_{\text{ave}}$ to $\pi$ when $\Delta \omega = 0$, at $t$-test was conducted for each $\omega_{p}/\omega_{e}$: $t(9) = 2.40$, $p < 0.05$ for $\omega_{p}/\omega_{e} = 1$; $t(9) = 1.24$, $p > 0.05$ for $\omega_{p}/\omega_{e} = 0.77$; $t(9) = 1.40$, $p > 0.05$ for $\omega_{p}/\omega_{e} = 0.63$.

To evaluate the proposed contrast $\omega_{p}/\omega_{e}$ and $\omega_{e}$, simple linear regressions of $\phi_{\text{ave}}$ on $\omega_{p}/\omega_{e}$ and $\omega_{e}$ were conducted for each subject, with the values of $\omega_{e}$ in both independent measures the actually produced values rather than the metronome values. The results are summarized in Table 2. The relativized frequency accounted for significantly more of the variance in $\phi_{\text{ave}}$ than the absolute frequency.

In sum, the outcomes of Experiment 1 confirmed the major predictions of phase-locked behaviour derived from APD theory in the form of (8): the eigenfrequency difference between the component oscillators and the coupled frequency act multiplicatively in determining the phase equilibria; departures of phase difference from $\pi$ due to the eigenfrequency difference are less the slower the coupled frequency; when the eigenfrequency difference is zero, the phase equilibrium is at $\pi$ independently of the coupled frequency. Confirmation was also provided of the prediction that, in the determination of phase-locking, coupled frequency is a relative rather than an absolute quantity. It is expressed as a multiple of the coupled system's eigenfrequency.

3.1 Method

Subjects. The same five people who participated in Experiment 1 participated in the second experiment. Apparatus, procedure design, and data acquisition. These were identical to experiment 1 with the one exception that subjects were instructed to perform in phase.

3.2 Results

The magnitude of $\phi_{\text{ave}}$ as a function of $\Delta \omega$ and $\omega_{p}/\omega_{e}$ is presented in Fig. 3. Inspection reveals that the deviation of $\phi_{\text{ave}}$ from 0 depended systematically on $\Delta \omega$ when $\omega_{p}/\omega_{e} = 1$ but not when $\omega_{p}/\omega_{e} = 0.77$ and $\omega_{p}/\omega_{e} = 0.63$. For the latter two frequency conditions, $\phi_{\text{ave}}$ was approximately zero. This reduction of $|\phi_{\text{ave}}|$ under $\omega_{p}/\omega_{e} < 1$ was expected from APD theory. It is also evident from inspection of Fig. 3, in agreement with APD theory, that for $\Delta \omega = 0$, $\phi_{\text{ave}} = 0$ regardless of $\omega_{p}/\omega_{e}$. In confirmation of the preceding observations, ANOVA on $\phi_{\text{ave}}$ yielded a significant main effect of $\Delta \omega$, $F(4, 16) = 39.08$, $p < 0.0001$, no main effect of $\omega_{p}/\omega_{e}$, $F < 1$, and a significant interaction between $\Delta \omega$ and $\omega_{p}/\omega_{e}$, $F(8, 32) = 55.97$, $p < 0.0001$. An ANOVA on the data for $\Delta \omega = 0$ found no effect of $\omega_{p}/\omega_{e}$, $F < 1$. To check on the proximity of observed $\phi_{\text{ave}}$ to 0 when $\Delta \omega = 0$, a $t$-test was conducted for each $\omega_{p}/\omega_{e}$. All three were nonsignificant, $p > 0.05$.

Again, to evaluate the proposed contrast between $\omega_{p}/\omega_{e}$ and $\omega_{e}$, simple linear regressions of $|\phi_{\text{ave}}|$ on $\omega_{p}/\omega_{e}$ and $\omega_{e}$ were conducted. Relativized frequency accounted for significantly more of the variance in $\phi_{\text{ave}}$ than absolute frequency (Table 3). In sum, Experiment 2 corroborated and extended Experiment 1 in confirming the major predictions of APD theory under $\phi_{p} = 0$ and the role of the coupled system's eigenfrequency.

4 Experiment 3

The third experiment contrasts $\omega_{p}/\omega_{e} < 1$, $\omega_{p}/\omega_{e} = 1$, and $\omega_{p}/\omega_{e} > 1$ under antiphase coordination, that is, $\phi_{p} = \pi$. According to (8), in the form of (11), the dependency of $\phi_{\text{ave}}$ on $\Delta \omega$ should be steepest for $\omega_{p}/\omega_{e} > 1$ and shallowest for $\omega_{p}/\omega_{e} < 1$. For $\Delta \omega = 0$, $\phi_{\text{ave}}$ should equal $\pi$ for each of $\omega_{p}/\omega_{e} < 1$, $\omega_{p}/\omega_{e} = 1$, and $\omega_{p}/\omega_{e} > 1$. A lesson from Experiments 1 and 2, is that a coupled frequency approximately three-quar-

Table 3. Variance in $|\phi_{\text{ave}} - \phi_{\text{p}}|$ accounted for by $\omega_{p}/\omega_{e}$ and $\omega_{e}$ in Experiment 2

<table>
<thead>
<tr>
<th>Subject</th>
<th>$\omega_{p}/\omega_{e}$</th>
<th>$\omega_{e}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.462***</td>
<td>0.355***</td>
</tr>
<tr>
<td>2</td>
<td>0.292**</td>
<td>0.022</td>
</tr>
<tr>
<td>3</td>
<td>0.492***</td>
<td>0.084</td>
</tr>
<tr>
<td>4</td>
<td>0.419***</td>
<td>0.100</td>
</tr>
<tr>
<td>5</td>
<td>0.506***</td>
<td>0.165</td>
</tr>
</tbody>
</table>

* $p < 0.05$ ** $p < 0.001$ *** $p < 0.0001$
ters that of the 2-oscillator eigenfrequency suffices to render deviations of $\phi_{\text{ave}}$ from $\phi_{\omega}$ approximately zero. With respect to (8), this latter fact would have to be interpreted as indicating the $K$ was large relative to $\Delta\omega$ for $\omega_{c}/\omega_{e} = 0.77$ and $\omega_{c}/\omega_{e} = 0.63$, the two coupled frequency values satisfying $\omega_{c}/\omega_{e} < 1$ in Experiments 1 and 2. In Experiment 3, the requirement of $\omega_{c}/\omega_{e} < 1$ was satisfied with a value of 0.83 in the hope of producing $|\phi_{\text{ave}} - \phi_{\omega}|$ magnitudes under $\omega_{c}/\omega_{e} < 1$ that were less than the $|\phi_{\text{ave}} - \phi_{\omega}|$ magnitudes under $\omega_{c}/\omega_{e} = 1$ and greater than zero. A value of 1.25 was used to satisfy the requirement of $\omega_{c}/\omega_{e} > 1$.

5 General discussion

Coordinated patterns of rhythmic movements are ubiquitous. In locomotion, the commonplace interlimb patterns are antiphase 1:1 frequency locking (used by species as diverse as millipedes and humans), and in phase 1:1 frequency locking (as manifest by jumping frogs and quadrupeds at higher speeds). A general view of locomotion's neurobiology is that the patterns emerge from largely central interactions between networks controlling the individual appendages (Grillner, 1981). That they might be understood through the theory of coupled oscillators, and that the functional dependencies of interappendage phase differences might be the key to such understanding, has long been respected (Stein 1973, 1974; von Holst 1937/1973).

The present research evaluates a low-dimensional motion equation, due to Rand et al. (1988), intended to express the phase-locking behavior of two coupled biological oscillators. The derivation of this equation is founded on the assumption that mode locking phenomena can be predicted by analyzing the averaged effects of the coupling influences (Kopell 1988 a; Murray 1990; Rand et al. 1988); under some conditions, the dynamics of the averaged system should accomodate the phase locking behavior of the full system. Expressed strictly in the terms of (8), the present experiments (and Schmidt et al. in press) provide support for the following four general conclusions; (i) $\Delta\omega$ and $K$ contribute multiplicatively to $\phi$; (ii) $\phi = 0$ or $\phi = \pi$ regardless of $K$ when $\Delta\omega = 0$; (iii) $\phi = 0$ or $\phi = \pi$ regardless of $\Delta\omega$ when $K$ is large (relative to $\Delta\omega$); and (iv) results (i) to (iii) hold identically for in phase and antiphase coordination. These four conclusions are expected from (8) and suggest that (7) captures the essential form of the averaged dynamics of two coupled biological oscillators. A fifth conclusion from the present experiments, with implications for future developments in the analysis of biological coordination, is that coupled frequencies are scaled in units of the coupled system's eigenfrequency. Despite differences in $\omega_{e}$, systems of coupled biological oscillators were dynamically equivalent when equated for $\omega_{c}/\omega_{e}$.

The "success" of (7) is significant given that this equation bears an approximate relation to the structure present in the standard circle map

$$\theta_{n+1} = \theta_{n} + \Omega - (K/2\pi)\sin(2\pi\theta_{n}) \mod 1$$  \hspace{1cm} (13)
(where $\theta$ is a point on the unit circle and $\Omega$ is the ratio of uncoupled frequencies) studied by Arnold (1965) and used to provide a very general theory of phase-locking via nonlinear coupling (e.g., Baker and Gollub 1990; Glass and Mackey 1988; Jackson 1989), and to the structure present in the coupling dynamics

$$\dot{\phi} = \Delta \omega - a \sin(\phi) - b \sin(2\phi)$$

(14)

(where $a$ and $b$ vary with $\omega$, $\Delta$) advanced by Haken et al. (1985) to accommodate the non-equilibrium antiphase to in phase transition in biological movement patterns. Equation (7)’s success in predicting stable phase-locking in interlimb coordination underscores the claim that (13) and (14) relate closely to the dynamics of real biological systems and warrant careful study and elaboration (Kelso et al. 1990; Schmidt et al. 1991).

Finally, although (8) addresses stable phase-locking, the actual phase relation between the limbs evident in Experiments 1–3 is one of phase-entrainment (see Fig. 2). Phase-locking refers to a situation in which the phases of the two component oscillators are related linearly, that is, $\theta_2(t) = \theta_1(t) + \text{a constant}$. In contrast, phase-entrainment refers to a situation in which $\theta_2$ completes one full cycle in the same amount of time as $\theta_1$ completes one full cycle in the absence of a fixed magnitude of $\dot{\theta}_2 - \dot{\theta}_1$. It would seem that (7) and (8) are predictive of the stable mean phase difference in a 2-oscillator coupled system regardless of whether the coupling results in phase-locking or phase-entrainment. Given that phase-entrainment is the rule rather than the exception in biological movement systems (Kelso et al. 1990; Turvey et al. in press), this is a most welcome result.

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