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The detuning factor in the dynamics of interlimb rhythmic coordination

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Abstract. Dynamical models of two coupled biological oscillators interpret the detuning term as an arithmetic difference between the uncoupled frequencies, $\Delta\omega = (\omega_1 - \omega_2)$. This $\Delta\omega$ interpretation of detuning was addressed in four experiments in which human subjects oscillated pendulums in their right and left hands in 1:1 frequency locking in antiphase (Experiments 1–3) or inphase (Experiment 4). Differences between the uncoupled frequencies were manipulated through differences in the equivalent simple pendulum lengths, and the effects of this manipulation on the detuning of relative phase from π or 0 and the standard deviation of relative phase SDϕ were measured. In Experiment 1, the same values of ω_i were satisfied by several different physical configurations. The experiment confirmed that the detuning term is related strictly to the uncoupled frequencies rather than to other physical characteristics of the oscillators. Experiments 2, 3 and 4 showed, however, that the particular dependency of fixed point drift and SDϕ on $\Delta\omega$ depends on the particulars of ω_1 and ω_2. With variations in $\Delta\omega$ brought about by different ω_1 and ω_2 that always formed a constant ratio, fixed point drift related inversely to $\Delta\omega$, and SDϕ varied with $\Delta\omega$ in ways that depended on the magnitude of the constant ratio. These outcomes do not conform to expectations from models of coordination dynamics that interpret detuning as $(\omega_1 - \omega_2)$.

1 Introduction

Recent research on interlimb rhythmic coordination has shown that the dynamics of two coordinated limbs or limb segments is captured by relative phase ϕ, which is defined as the difference between the phases of two individual oscillating units. In the stable rhythmic performance of two limb segments, such as the index fingers or hands, two stable patterns are observed: inphase, $\phi = 0$, and antiphase, $\phi = \pi$. Following the modeling strategy of synergetics (Haken 1977, 1983), this prototypical observation can be formalized in the following equation of motion for ϕ (Haken et al. 1985; Schöner et al. 1986):

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

a and b are such that their ratio governs the relative stability of the inphase and antiphase patterns, and ξ_t is a gaussian white-noise process (arising from the multiplicity of underlying subsystems) functioning as a stochastic force of strength Q (see Haken 1977, 1983). Within the theoretical context motivating (1), attempts have been made to identify the particular form of the component nonlinear oscillators. For example, a 'hybrid' oscillator consisting of Rayleigh and van der Pol terms has been proposed (Kay et al. 1987; Kelso et al. 1987). Other work, however, has questioned the generality of this characterization of rhythmic limb movements (e.g., Kadar et al. 1993; Kay et al. 1991). Fortunately for the modeling of coordination dynamics, (1) is valid regardless of the precise nature of the individual oscillators as long as they display stable limit cycles without strong relaxational behavior.

The synergetic coupling (1) evolved to provide a mathematically accurate description of the main qualitative features of phase transitions in interlimb rhythmic coordination. Transitions are observed typically in an experimental procedure in which a person is required to oscillate the two index fingers (or two hands) at the coupled frequency ω_c, where ω_c is varied by a metronome that the person tracks (e.g., Kelso 1984; Kelso et al. 1987). The experimental results show that with increasing ω_c, $\phi = \pi$ switches abruptly to $\phi = 0$, but $\phi = 0$ does not switch to $\phi = \pi$, and the transition to π is not reversed by a reduction in ω_c. Further, ϕ around π exhibits increases in relaxation time and increases in its fluctuations as the transition point is approached. Such spontaneous jumps in coordination accompanied by critical fluctuations also occur when two limbs are connected optically between two people rather than anatomically within a person (Schmidt et al. 1990).

Under the operation $\phi \rightarrow -\phi$, the relative phase dynamics expressed by (1) are invariant. Model predictions derived from this functional form are therefore confined to this symmetry, which also implies a symmetry between the two coordinated rhythmic components, i.e., identity of the two uncoupled frequencies and physical dimensions

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the simple pendulum length and g is the constant acceleration due to gravity (see Sect. 2.1). In the experiments, $\Delta\omega$ was controlled through differences in the lengths of the left and right pendulums, and ω_c was either the freely elected frequency for a given pair of pendulums or another frequency determined by a metronome.

1.3 Goals of the present research

Two questions are raised about $\Delta\omega$. One question is in respect to the two oscillators ω_i and ω_j composing a particular value of $\Delta\omega$. From the vantage points of (2), (5), and (6), given constant coupling coefficients, the equilibria of the coordination dynamics are dictated by the sign and magnitude of $\Delta\omega$ and are independent of the particular values of ω_i and ω_j satisfying $\Delta\omega$. In the case of $\Delta\omega = 0$, where $\omega_i = \omega_j$, very many differently composed oscillators can equal ω_i, meaning that $\Delta\omega = 0$ can be satisfied by very many pairs of oscillators that differ in their physical dimensions. More concretely, in the wrist-pendulum method, the physical lengths of the pendulums and their added masses can be different across two wrist-pendulum systems but so chosen as to yield identical magnitudes of L and, therefore, identical eigenfrequencies. According to the above models of coordination dynamics, when $\Delta\omega = 0$, the equilibria or fixed points should be the same for the many different possible pairings of physically identical and nonidentical wrist-pendulum systems comprising $\Delta\omega = 0$. This expectation is addressed by Experiment 1.

The second question is with respect to the scope of the proposed equation between detuning and $\Delta\omega$. According to the coordination dynamics expressed by (2), (5), and (6), if $\Delta\omega = (\omega_{Left} - \omega_{Right})$, then for two or more different $\Delta\omega_i$ values ($i = 1, 2, 3, \ldots$) satisfying $(\Delta\omega)_1 < (\Delta\omega)_2 < (\Delta\omega)_3 \ldots$, the fixed point drift (from 0 or π) should increase from the smallest to the largest $\Delta\omega$. In Experiments 2–4, the mean value of $\phi = (\theta_{Left} - \theta_{Right})$ as a consequence of $\Delta\omega = (\omega_{Left} - \omega_{Right})$ is examined for particular values of $\Delta\omega$ satisfied by different combinations of ω_{Left} and ω_{Right}. Because of the prominence of the ratio of uncoupled frequencies, e.g., $\Omega = (\omega_{Left}/\omega_{Right})$, in certain formulations of phase-locked behavior (e.g., Jackson 1989), the values of ω_{Left} and ω_{Right} comprising a given $\Delta\omega$ were chosen in Experiments 2–4 according to the requirement that they always formed the same ratio. If $\Delta\omega = (\omega_{Left} - \omega_{Right})$ is the proper form of the detuning term, then the preceding constraint on the formation of $\Delta\omega$ should not affect the expected dependency of fixed-point drift on $\Delta\omega$.

2 Experiment 1

The focal manipulation of Experiment 1 is the pendulum configurations comprising the symmetry condition $\Delta\omega = 0$. The manipulation takes two forms. The particular values of ω_{Left} and ω_{Right} satisfying $\Delta\omega = 0$ are varied. Also varied is whether or not the physical dimensions of the right and left oscillators are identical. According to (2), (5), and (6), the equilibria of the coordination dynamics should depend only on the 0 value of $\Delta\omega$ and not on the details of the oscillators composing $\Delta\omega$. Consequently, mean ϕ under instructions to perform antiphase coordination (as is the case in Experiment 1) should be unaffected by either form of manipulation.

2.1 Method

Subjects. Two women and three men participated. All were students (undergraduate or graduate) at the University of Connecticut. The age range was 21–34 years. All participants were right handed.

Apparatus. Each pendulum was composed of an aluminum rod of 1 cm diameter which was attached to a cylindrical wooden grip 2.5 cm in diameter and 12 cm in length. Steel cylinders could be attached at the end of the aluminum rods by means of a set screw. There were seven pairs of pendulums, each pair satisfying $\Delta\omega = 0$. The pendulums in two pairs were identical in rod length and mass; in the other five pairs, the pendulums comprising a pair were nonidentical in rod length and mass. The physical dimensions of these 'identical' and 'nonidentical' pairs are given in Table 1.

The equivalent simple pendulum lengths l_i of the individual wrist-pendulum systems (consisting of attached cylinders, the rod, and the average hand mass calculated as $0.006 \times$ average body mass) were calculated according to procedures identified in Kugler and Turvey (1987), as was the equivalent simple pendulum length L_v, of each of the seven pairings of pendulums. If the right and left wrist-pendulum systems are coupled such that θ_{Right} is always, at every instant, identically equal to θ_{Left}, or to $(\theta_{Left} + \pi)$ (Kugler and Turvey 1987), then the coupling between the two oscillators would be functionally equivalent to that of a rigid connection (Kugler and Turvey 1987). The simple pendulum equivalent L_v of a compound pendulum so composed (that is, of two pendulums connected by a rigid bar) is given by

$$L_v = (m_1 l_1^2 + m_2 l_2^2)/(m_1 l_1 + m_2 l_2) \qquad (7)$$

where m_i and l_i refer to the mass and the equivalent simple pendulum length, respectively, of an individual (compound) pendulum system. Through (6), two coupled pendulums of lengths l_{Right} and l_{Left} can be interpreted as a virtual (v) pendulum of length L_v with an eigenfrequency $\omega_v = (g/L_v)^{1/2}$. The mean component eigenfrequencies ω_{Left}, ω_{Right} and the mean virtual eigenfrequency ω_v of each of the seven pairs are displayed in Table 1.

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 sonic acquisition of the data (for a schematic of the apparatus, see Sternad et al. 1992). Pendular trajectories were measured using a Sonic 3-Space Digitizer (SAC Corporation, Westport, Cann.). An emitter was affixed to the end of each pendulum, set at 90 Hz.

and Schmidt et al. (1993). Linear stability analysis of (2) for $a > 0$ and $b > 0$ and $b/a > 0.25$ (see Schöner et al. 1986) indicates that variations in b/a do not induce an equilibrium shift from π for $\delta = \Delta\omega = 0$ (confirmed by Sternad et al. 1992; Schmidt et al. 1993; and by the data of the present experiment), but they do affect the attractiveness of π. The inverse of $|d\dot{\phi}/d\phi|$ evaluated at a stable fixed point defines a time, specifically, the relaxation time τ_{rel}, which is the time to return to the fixed point following a perturbation (Gilmore 1981; Schöner et al. 1986). Analysis reveals that τ_{rel} increases as b/a decreases. Given noise of strength Q, variability in ϕ is related to τ_{rel} through

$$\mathrm{SD}\phi = \sqrt{(Q\tau_{rel})}/2 \qquad (9)$$

(see Gilmore 1981; Schöner et al. 1986). For $\delta = \Delta\omega = 0$, Schmidt et al. (1993) found that although ϕ was unchanged over increases in ω_c, SDϕ increased systematically. The data depicted in Fig. 1 are further confirmation of this prediction from (2). They also confirm (5) and (6) under the similar understanding that k and K_1/K_2 relate inversely to ω_c (Schmidt et al. 1993). These confirmations aside, the main lesson from Experiment 1 seems plain: The degrees of freedom for capturing the detuning parameter are strictly the uncoupled eigenfrequencies of the component oscillators.

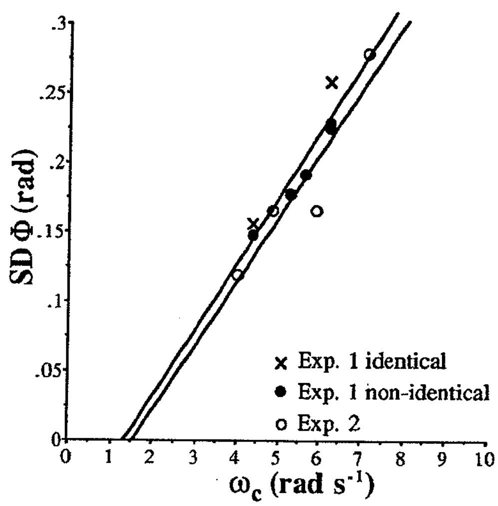

Fig. 1. Linear variation of SDϕ as a function of ω_c in Experiment 1 (SD$\phi = 0.05\,\omega_c - 0.06$) and Experiment 2 (SD$\phi = 0.05\,\omega_c - 0.07$) for the condition $\delta = \Delta\omega = 0$

Table 2. Subject mean ϕ (rad) and SDϕ (rad) for the conditions of Experiment 1

Subjects	Conditions						
	1	2	3	4	5	6	7
1	3.23[a] 0.12[b]	3.31 0.23	3.29 0.12	3.25 0.17	3.32 0.23	3.24 0.24	3.23 0.26
2	3.23 0.09	3.17 0.10	3.23 0.12	3.26 0.14	3.12 0.16	3.24 0.15	3.20 0.16
3	3.19 0.16	3.21 0.16	3.12 0.17	3.13 0.19	3.18 0.23	3.14 0.25	3.13 0.23
4	3.30 0.26	3.25 0.21	3.36 0.28	3.41 0.31	3.20 0.30	3.32 0.31	3.20 0.39
5	3.23 0.14	3.16 0.15	3.33 0.20	3.15 0.15	3.11 0.20	3.19 0.19	3.13 0.25
Mean	3.24	3.22	3.27	3.24	3.19	3.23	3.18

[a] ϕ (rad)
[b] SDϕ (rad)

3 Experiment 2

Ω is used to define the conditions for phase-locked behavior in the circle map (e.g., Arnold 1965; Jackson 1989). Because Ω is a ratio (e.g., $\omega_{Left}/\omega_{Right}$), Ω and $\Delta\omega$ as the two ways of quantifying the symmetry of a 2-coupled oscillator system do not covary: a constant Ω can be defined over different $\Delta\omega$. At issue in Experiment 2 is how ϕ and SDϕ vary as a function of $\Delta\omega$ and the correlated quantity ω_c when Ω is fixed. According to diffusive and synaptic coupling and the common interpretation of synergetic coupling, the relevant expression for detuning is $\Delta\omega$. Consequently, holding Ω constant over different magnitudes of $\Delta\omega$ should not affect the predicted influence of $\Delta\omega$ on fixed point drift: That is, the larger the deviation of $\Delta\omega$ from 0, the greater should be the fixed point drift. Similarly, holding Ω constant should not affect the predicted influence of $\Delta\omega$ on SDϕ: That is, the larger the deviation of $\Delta\omega$ from 0, the greater should be SDϕ. Exploration of these issues requires, necessarily, the consideration of both symmetrical ($\Omega = 1$, $\Delta\omega = 0$) and asymmetrical ($\Omega \neq 1$, $\Delta\omega \neq 0$) conditions.

3.1 Method

Subjects. Four women and six men between 20 and 34 years of age participated. All were students (undergraduate or graduate) at the University of Connecticut, and all were right handed.

Apparatus. Pendulums were of the same basic design as in Experiment 1. Four Ω quantities were selected: 1.0, 0.825, 0.65, and 1.54, with the latter two identifying simply a reversal of which hand held which pendulum. There were four instances of each Ω. For $\Omega = 1.0$, each of these instances was $\Delta\omega = 0$; for each of $\Omega = 0.825$, 0.65, and 1.54, these four instances amounted to four different values of $\Delta\omega$. The selection of these four values was dictated by the requirements that the spacing between the four values and their range be comparable for each $\Omega \neq 1$. The 16 experimental conditions are given in Table 3.

Procedure and data acquisition. These were essentially the same as in Experiment 1. There were two trials per condition with the 16 conditions randomized individually for each subject. The experiment lasted 60–80 min.

3.2 Results

With respect to the task requirement of 1:1 frequency locking, the mean frequency ratios for five subjects were

Ω: Deviation from the intended antiphase increased from larger arithmetic differences to smaller arithmetic differences between the ω_{Left} and ω_{Right} magnitudes comprising a constant Ω.

Figure 2B reports the mean SDϕ for the 16 conditions. Inspection suggests a different dependency of SDϕ on Ω and $\Delta\omega$ than that observed for ϕ. The quadratic function of Fig. 2B, with a minimum at $\Omega = 1$ and $\Delta\omega = 0$, was significant at $P < 0.0001$. As was expected from (2), (5), and (6), the lower the symmetry of the coordination dynamics, the greater was SDϕ. However, the patterning of SDϕ was not uniformly consistent with

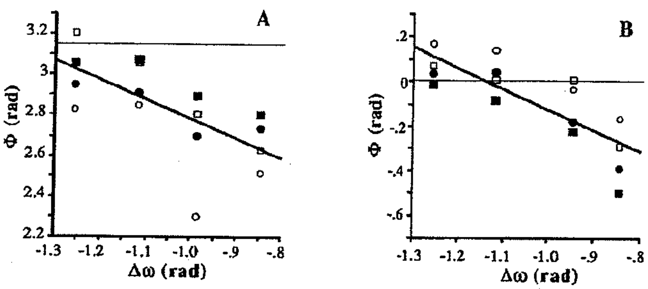

Fig. 4. A Mean ϕ for each subject at each value of $\Delta\omega$ satisfying $\Omega = 0.825$ in Experiment 3. Required coordination was antiphase, and ω_c was self-selected. **B** Mean ϕ of each subject for each value of $\Delta\omega$ satisfying $\Omega = 0.825$ in Experiment 4. Required coordination was inphase, with ω_c held constant across conditions at 5.24 rad s^{-1}

Table 4. Multiple regression of $|\phi - \pi|$ (rad) on Ω (rad) $\in [0, 1]$ and $|\Delta\omega|$ (rad s^{-1}) for individual subject data of Experiment 2

Subject	r^2	Intercept	Ω coefficient	P	$\lvert\Delta\omega\rvert$ coefficient	P
1	0.89	2.48	−2.40	0.001	−0.26	0.01
2	0.75	4.29	−4.32	0.001	−0.54	0.01
3	0.31	2.79	−2.69	0.07	−0.36	0.10
4	0.47	4.69	−4.55	0.05	−0.57	0.07
5	0.81	5.48	−5.42	0.001	−0.69	0.001
6	0.13	1.45	−1.29	0.62	−0.12	0.76
7	0.08	2.17	−1.92	0.50	−0.24	0.58
8	0.70	3.90	−3.87	0.01	−0.46	0.05
9	0.84	2.09	−2.05	0.0001	−0.28	0.0001
10	0.68	1.90	−1.87	0.01	−0.24	0.01

(5) and (6) and the interpretation of δ in (2) as $\Delta\omega$. Under the condition $\Omega = 0.825$, the trend for 9 of the 10 subjects was for SDϕ to increase with $\Delta\omega$, whereas under the condition $\Omega = 0.65$, the trend for 8 of the 10 subjects was for SDϕ to decrease with $\Delta\omega$.

The pattern of SDϕ at the symmetry $\Omega = 1$, $\Delta\omega = 0$ replicates that observed in Experiment 1 and in Schmidt et al. (1993). SDϕ was a positively linear function [$r^2(39) = 0.44$, $P < 0.0001$, SD$\phi = 0.05\omega_c - 0.07$] of ω_c, as shown in Fig. 1. The overall dependencies of SDϕ on Ω and ω_c are revealed most usefully in the multiple regression of SDϕ on $\Omega \in [0, 1]$ and ω_c. The consistency across the individual subject regressions reported in Table 5 is captured by the highly significant ($P < 0.0001$) analysis using the 160 means: SDϕ (rad) $= 0.26 - 0.28\Omega + 0.04\omega_c$.

4 Experiment 3

A partial replication of Experiment 2 was conducted on four new subjects (right-handed male undergraduates at the University of Connecticut). The coupled oscillator conditions were those of $\Omega = 0.825$ in Table 3. Unlike Experiment 2, the subjects were not paced by a metronome but rather were instructed to achieve 1:1 frequency in antiphase at the most comfortable tempo (the freely chosen ω_c ordered as the ω_v of the four conditions). Each of the four subjects attained a frequency ratio of 1.00 ± 0.001. ϕ for the four $\Delta\omega$ values satisfying $\Omega = 0.825$ is shown in Fig. 4A. In agreement with Experiment 2, the drift of mean ϕ from π was a decreasing function of $\Delta\omega$, $r^2(15) = 0.44$, $P < 0.01$, and SDϕ was an increasing function of ω_c (means of 0.155, 0.147, 0.196, 0.208, respectively), $r^2(15) = 0.37$, $P < 0.05$.

5 Experiment 4

A fourth experiment was conducted to test the generality of the results of Experiments 2 and 3. The coupled oscillator conditions were again those of $\Omega = 0.825$ in Table 3. Unlike Experiments 2 and 3, the coordination was inphase rather than antiphase, and ω_c was fixed by a single metronome frequency of 5.24 rad s^{-1} across the

Table 5. Multiple regression of SDϕ on Ω (rad) $\in [0, 1]$ and ω_c (rad s^{-1}) for individual subject data of Experiment 2

Subject	r^2	Intercept	Ω coefficient	P	ω_c coefficient	P
1	0.85	0.28	−0.37	0.001	0.04	0.0001
2	0.68	0.22	−0.28	0.001	0.04	0.01
3	0.50	0.28	−0.28	0.01	0.03	0.05
4	0.82	0.27	−0.31	0.0001	0.04	0.001
5	0.64	0.36	−0.26	0.001	0.03	0.05
6	0.66	0.36	−0.40	0.001	0.04	0.05
7	0.25	0.18	−0.11	0.16	0.36	0.06
8	0.54	0.23	−0.28	0.01	0.05	0.01
9	0.62	0.20	−0.24	0.001	0.04	0.01
10	0.75	0.24	−0.24	0.0001	0.03	0.001

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