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Interlimb coupling in a simple serial behavior: A task dynamic approach

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Abstract

Whereas rhythmic interlimb actions are characterized by an invariant spatio-temporal relation between the oscillating limbs, in serially coordinated movements the individual components' motions are discrete or intermittent, with little or no temporal overlap with other components' motions. An experimental and modeling framework is presented that systematically extends purely parallel rhythmic coordination towards serial rhythmic coordination. In two experiments subjects rhythmically moved a pendulum with the right hand in continuous fashion and performed a single, discrete cycle with a pendulum in the left hand every *n*th right-hand cycle. This pattern was rhythmic but not homogeneous in that it consisted of a globally repetitive sequence of unimanual and bimanual cycles. In Experiment 1, the two wrist-pendula's eigenfrequencies were identical, and the task involved a discrete cycle every fourth and fifth unit. The major results of the kinematic analyses were: (1) coupling during the bimanual cycle affected the amplitude, not the period of the continuous oscillations; (2) the discrete hand's movement showed characteristics of a damped oscillator displaying a "ringing" after its task-specified cycle; (3) the relative phase measures demonstrated immediate synchronization of the "discrete" event. Experiment 2 additionally manipulated the eigenfrequency difference δ between the two hands in the same task. The results from Experiment 1 were generalized with the additional findings: (4) While the amplitude magnification during the

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coupled cycle was indifferent to δ, the periods during the coupled cycle were affected by the discrete event; (5) relative phase at the coupled cycle was a function of δ in accordance with results in parallel interlimb coordination. These results were simulated by a three-layered task-dynamic network of coupled oscillators. This stratification allows for the assembly of a time-invariant dynamic regime that gives rise to seemingly discrete consequences on the level of the endeffector movements.

PsycINFO classification: 2330

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1. Introduction

In the interlimb coordination patterns characterizing human walking, running, and swimming, the limbs tend to be 1:1 frequency locked with an invariant phase difference of 0 rad (in-phase) or π rad (antiphase). Such rhythmic interlimb motions in which both limbs move continuously in parallel within a common time frame are instances of *parallel coordination*. In other examples of human interlimb coordination there is little or no temporal overlap – the movements of the two limbs occur in sequence. These latter movement patterns are instances of *serial coordination*. Serially coordinated motions display spatio-temporal relations between the limbs in which the motions of a given limb may be discrete or intermittent in nature. A simple example of serial coordination is one in which one limb or limb segment oscillates for so many cycles and stops, then another limb or limb segment oscillates for so many cycles and stops, with the first limb then renewing its oscillatory behavior, and so on.

Bimanual limb movements have been studied extensively under conditions of parallel coordination. In particular, bimanual rhythmic behaviors have been studied under conditions of 1:1 frequency locking in both in-phase and antiphase modes (see summaries in Kelso, 1994; Schmidt and Turvey, 1995) as well as under conditions of small, non-1:1 frequency ratios such as 1:2 and 2:3 (e.g., Byblow et al., 1994; Peper et al., 1995a, 1995b; Sternad et al., in press, submitted a, submitted b). Progress in understanding these coordination patterns has resulted from conceptualizing them as dynamical systems: A rhythmically moving limb is treated as a limit cycle oscillator coupled nonlinearly to the other limb, similarly conceptualized as a limit cycle oscillator (e.g., Beek and Beek, 1988; Haken et al., 1985; Kay et al., 1987;

Rand et al., 1988; Sternad et al., 1996). The research reported in the present article is based on the premise that serial coordinations can be viewed in much the same framework as parallel coordinations, viz., as the behaviors displayed by dynamic systems of coupled (nonlinear) components.

Consider the following task: A person is asked to produce oscillations at the same tempo with the left and right hands. If both hands were oscillating continuously in synchrony this would be an instance of parallel coordination. Now imagine that same person is asked to produce one single, discrete oscillation of the left hand that must occur simultaneously with every fourth oscillation of the continuously moving right hand. This latter task would be an example of serial coordination: The person must time the onset of a discrete cyclic motion relative to an ongoing cyclic process in the contralateral limb segment and to limit the duration of this single cycle to the duration of the target cycle of the continuous limb. This sequence is then repeated and, thereby, forms another global cycle. As such, the task could be considered as consisting of a sequence of three unimanual cycles followed by one bimanual cycle.

At first sight, our serial task might also be understood as an instance of polyrhythmic coordination with a 1:4 frequency ratio. However, it is worth clarifying that in multifrequency coordination the rhythmic units have to be performed during the same time interval and, hence, the period of the single cycle should have the same period as the four cycles together (for an investigation of 1:2 multifrequency coordination see Sternad et al., submitted a, submitted b, in press). In contrast to this more complex instance of parallel coordination, in our task all individual cycles in both left and right hand should have the same period. Therefore, the discrete hand had to start from rest to perform a movement cycle and had to be stopped again after one cycle. This highlights an essential feature which is inherent in every serial task: there are transients from one movement pattern to another.

The second important aspect of our bimanual serial task is that the single discrete cycle may be influenced, or perturbed by the concurrent cycle of the continuous oscillation. As Abbs and Connor (1992) underscore, in typical serial behaviors the co-dependencies and mutual influences of overlapping units are inseparable from the correct sequential order. The effect of a voluntary discrete action of one hand on the contralateral hand performing alternating flexion and extension in the wrist was studied by Cohen (1970). In experiments where the discrete cycles' onsets of one hand were triggered by a metronome, Cohen (1970) found that the rhythmic hand's period was indeed altered by the discrete hand and induced a phase shift in the flexion–extension pattern of the continuous oscillation. In a similar vein, Yamanishi et al. (1979, 1980) studied a bimanual rhythmic task where external perturbations were applied to one hand and then analyzed the phase resetting behavior of the perturbed hand. This method proved a useful analytic tool to characterize the nature of the coupled oscillatory behavior. While in the present Experiments 1 and 2 our subjects self-initiated the discrete cycle to be synchronized with the ongoing cycle, the aspect of crossmanual perturbation remains the second important issue.

As the literature on rhythmic interlimb coordination shows, bimanual patterns in a steady state – in parallel coordination – have successfully been captured by models of coupled oscillators and predictions based on stability analyses of these motion equations could be empirically verified. While stability analysis of dynamical systems in a steady state is a well developed analytic procedure in nonlinear dynamics, the application of analytic tools for serial coordination is no longer as straightforward. The question how to incorporate the sequencing aspect into a dynamic system formulation is a resilient problem. The challenge is to account for (a) the serial order of movement parts, i.e., how to determine the onset and offset of given movement segments in a parsimonious fashion, (b) the anticipatory and hereditary aspects, i.e., the transients in the trajectory that are elicited by the onset and those that follow the offset of one segment's motion, and (c) the mutual influences between the units during this transient activity. One route to address these phenomena is to adopt a layered approach as we will develop in this study.

From a dynamic systems perspective Saltzman and Munhall (1992) have proposed a framework for understanding behavioral sequences and transitions which is based on a distinction among state-, parameter- and graph-dynamics as three levels of a dynamical system (Farmer, 1990). They argue that behavioral change and specifically bifurcations in action patterns can be understood as an instance of a dynamic process originating on the level of the parameters. While state-dynamics capture the time evolution of the state variables described by the equations of motion with the parameters assumed to be invariant, the second level of parameter-dynamics refers to the case where it is these coefficients of the equations of motion that undergo a dynamic process. Therefore, an additional level of change can be specified on the level of the parameter dynamics. Saltzman and Munhall (1992) argue that continuous as well as discontinuous changes occurring in learning and development are likely candidates for parameter dynamic processes. The third and topmost layer of graph-dynamics refers to the case where the entire "architecture" of the system such as the size and connectivity of the set of equations of motion is not stationary. While this latter level of a dynamic system has not yet been empirically addressed, Saltzman and Munhall (1992) encourage the exploration of parameter-dynamics as a possible mechanism accounting for discontinuous changes in behavior. This theoretical perspective will motivate the modeling suggested in the present work. In our specific task, the serial aspect will be governed by a dynamic change on the level of the parameters. The aspect of crossmanual interaction or perturbations across hands will be dealt with in terms of coupling at the level of state variable dynamics.

From this departure we raised the following questions for our simple serial task: Of what nature should the model be in order to distinguish a state from a parameter level? What kind of parameter dynamics has to be introduced to minimally induce for the sequential order? How can the transient effects be brought about? What kind of state parameter dynamics need to be assumed to account for the interactions between hands? Specifically, how are the oscillations of the continuously moving hand affected by the effects of coupling with the left, discretely rhythmic unit? Given bimanual coupling, is the discrete cycle truly discrete in the sense that, as specified by the task instructions, it begins and ends in exact coincidence with the coupled cycle of the right, continuously rhythmic unit?

We will investigate these questions in two experiments where we analyze the kinematic characteristics of the two hands' trajectories. We will first report Experiment 1, then we will introduce our model following the task dynamic strategy by Saltzman and Munhall (1992). The model's simulations will be evaluated by comparing them to the results of Experiment 1. In Experiment 2, the task is extended by having participants swing different pendula in their two hands. With the help of these results we will further examine the adequacy of the model.

2. Experiment 1

In Experiment 1, the left and right hands held equally-sized pendula. The focus was upon the left-hand and right-hand dynamics as a function of a single oscillation of the left hand every fourth or fifth oscillation of the right hand.

2.1. Method

2.1.1. Participants

There were six participants. All were right-handed students at the University of Connecticut with no known neurological or muscular impairments.

2.1.2. Apparatus

Two hand-held pendula were used. Each pendulum consisted of an aluminum rod with an attached hand grip at the proximal end, and an attached annular metal disc at the distal end. Each rod was 46 cm long with an added mass of 200 g. The eigenfrequency of a hand-plus-wrist-pendulum was 5.15 rad/s (for details of calculation, see Amazeen et al., 1996; Sternad et al., 1996)

The experimental arrangement is schematized in Fig. 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. Pendulum trajectories were measured in 3 dimensions using a Sonic Digitizer (SAC Corporation, Westport, CT) digitizing data at 90 Hz. Details of this data collection apparatus can be found in Sternad et al. (1996). This software (Virtual Images, Columbus, OH) and analogous routines written on a Macintosh use the kinematic time series of angular displacement of the tip of the pendulum to calculate the cycle amplitudes and cycle periods.

2.1.3. Design

There were three types of movement patterns: (1) Serial, or discontinuous coordination (SC), in which the task was to oscillate the right-hand pendulum continuously, and only move the left-hand pendulum in phase with

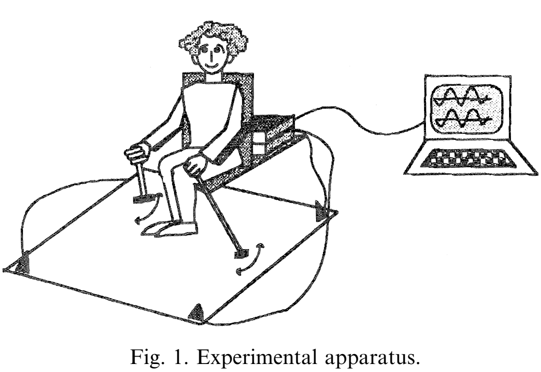

Fig. 1. Experimental apparatus.

the right hand on each *n*th cycle of the right hand. During the other cycles of the continuously rhythmic right hand, the discontinuously rhythmic left hand was to be motionless, pointing vertically downward. There were two SC conditions. In the one condition, the *n*th cycle was the fourth cycle, in the other condition the *n*th cycle was the fifth cycle. These two conditions are referred to as SC4 and SC5, respectively. (2) Parallel, or continuous coordination (PC), in which the task was to oscillate continuously both right-hand and left-hand pendula in-phase at the same (mutually comfortable) frequency. (3) Isolated, or single-handed coordination (IC), in which the right-hand pendulum was oscillated continuously, with the left-hand pendulum remaining in the equilibrium position (downward vertical) throughout. The PC and IC movement patterns were controls for the two SC movement patterns. All four conditions (SC4, SC5, CP, and IC) were run in one block of trials in a completely randomized order. Five trials per condition were performed.

2.1.4. Procedure

Each trial lasted 60 s. Prior to each trial the subject was instructed as to whether it was SC4, SC5, PC or IC. If the trial was an SC trial, the subject was instructed to swing the right pendulum continuously at a comfortable frequency, and to swing the left pendulum for one full cycle (the "serial cycle") in-phase with every fourth (SC4) or fifth (SC5) cycle of the continuously rhythmic right hand. The subject's instructions for performing the serial cycle were to start from the vertical rest position, swing the pendulum forward, then backward through the rest position, then forward again to the rest position, and to keep the pendulum motionless during the next three (SC4) or four (SC5) cycles of the continuous right hand. There were no restraints on how participants controlled the sequencing. The participants could count the continuous cycles explicitly or implicitly, introducing the left-hand discrete cycle after the appropriate number of right-hand continuous cycles. If it was a PC trial, the subject was instructed to swing the two pendula at the most comfortable common frequency and to do so in-phase. If the trial was an IC trial, the subject was instructed to swing the right pendulum continuously at the most comfortable frequency with the left pendulum immobile.

Each recorded 60 s trial was preceded by an interval following the trial instructions in which the subject settled into the requisite movement pattern. When the subject felt that the pattern was satisfactory, the subject signalled to the experimenter who then initiated the recording.

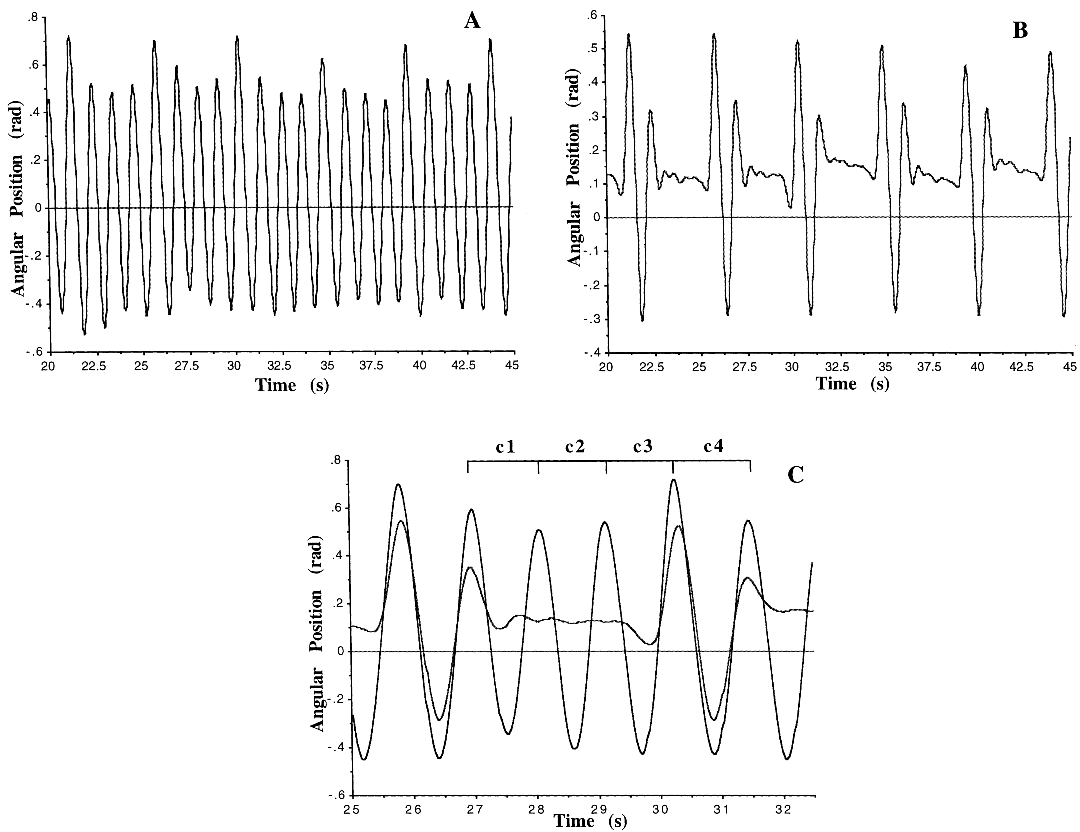

Fig. 2. (A) Time series of a subsection of the right continuous unit in a SC4 trial of Experiment 1. (B) Time series of the discrete hand's movement over the same interval. (C) Superposed time series during a sequence of four cycles which is the global period of the bimanual pattern ci denotes the ith cycle of the continuous hand.

2.2. Results

Fig. 2(A) presents a typical time series for the right, continuously rhythmic unit in an SC4 movement pattern, in which positive/negative angular displacement corresponds to forward/backward swinging motion of the pendulum in the sagittal plane, and zero displacement denotes a downward vertical orientation of the pendulum. In this example the subject did not oscillate symmetrically around the vertical position but centered his oscillations around 0.13 rad which is indicated by the approximately constant positive offset. Fig. 3(A) shows the phase plane trajectory for the same continuous unit shown in Fig. 2(A) over the same time interval. (The data were adjusted

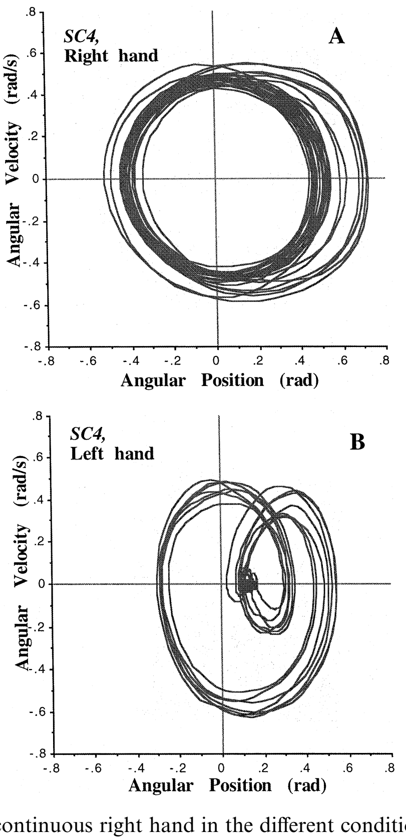

Fig. 3. Phase portraits of the continuous right hand in the different conditions of Experiment 1: (A) limit cycle of the same trial in the SC4 condition as shown in Fig. 2(A); (B) corresponding phase portrait of the coupled discrete unit.

for this mean offset of 0.13 rad.) This phase portrait displays limit cycle behavior with the same characteristically thick band of orbits as was observed by Kay (1988), Kay et al. (1991) and Mitra et al. (1997). Figs. 2(B) and 3(B) show the time series and phase portrait, respectively, for the left, discretely rhythmic unit during the same SC4 trial displayed in Fig. 2(A). The relative phasing of the serial and rhythmic motions in Fig. 2(A) and (B) is highlighted on an expanded time scale by the superposed time series shown in Fig. 2(C). This figure also illustrates the manner in which the *global period* of the continuous movement pattern was defined and partitioned: Each global period began at the continuous peak closest in time to the second positive peak of a discrete *bout* of activity and ended at the corresponding peak of the next discrete bout. Additionally, a series of *i*-cycles of the continuous hand was defined within each global period ($i = 1$ to 4 or 5 for SC4 or SC5, respectively). Cycle 4 (c4) in SC4 and cycle 5 (c5) in SC5 were defined as the *coupled cycles* of the continuous hand, since they co-occurred with the largest excursions of the discrete hand's bout of activity. Finally, the continuous unit in the PC and IC movement patterns show typical limit cycles with similar broad bands.

The following analyses report period and amplitude characteristics of the within-hand and between-hand movements in the four conditions. The results are presented around five empirical issues: (1) Comparison of the kinematic characteristics of the continuous right rhythmic unit when engaged in PC and SC; (2) Detailed quantification of the kinematic characteristics of the discrete left unit in the two SC conditions; (3) Comparison of the mutual spatiotemporal influences of the continuous and discrete units during the coupled cycle; (4) Relative phasing between the right and left units in PC and SC conditions; (5) Comparison of the right, continuous unit in SC, PC and IC.

2.2.1. Serial coordination: Continuous right rhythmic unit

Detailed kinematic analyses of the continuous unit in the two SC movement patterns are summarized in Fig. 4. Averages across subjects for cycle periods and amplitudes are plotted in Fig. 4 against cycle number for both SC4 (top) and SC5 (bottom). The mean periods (in s) and mean amplitudes (in rad) for cycles 1–4 of SC4 were 1.038/1.07, 1.032/1.05, 1.036/1.09, and 1.077/1.13, respectively (amplitudes were defined as the sum of A_1 and A_2 in Fig. 5). The mean periods and mean amplitudes for cycles 1–5 of SC5 were 1.059/1.13, 1.062/1.09, 1.060/1.10, 1.064/1.10, and 1.068/1.21, respectively. One-way ANOVAs were conducted for the SC4 and SC5 conditions, com-

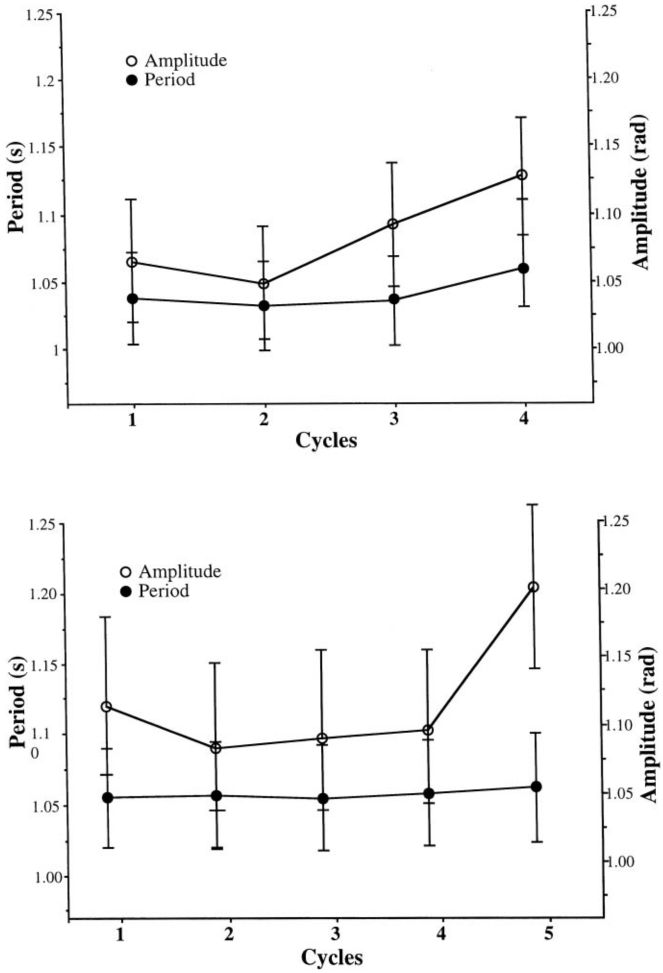

Fig. 4. Subject means of cycle measures for amplitude and period of SC4 (upper panel) and SC5 (lower panel) in Experiment 1.

paring each cycle measure (period, amplitude) separately across cycle number (c1–c4 and c1–c5, for SC4 and SC5, respectively). While there were no significant effects for period in either SC4 or SC5, there were significant effects for amplitude in both SC4, $F(3,15) = 18.71$; $p < 0.0001$, and SC5, $F(4,20) = 17.88$, $p < 0.0001$. Post-hoc Tukey tests revealed that the only significant amplitude effects were that the coupled cycles (c4 in SC4, and c5 in SC5) were larger than all other cycles. It thus appears that the continuous hand was

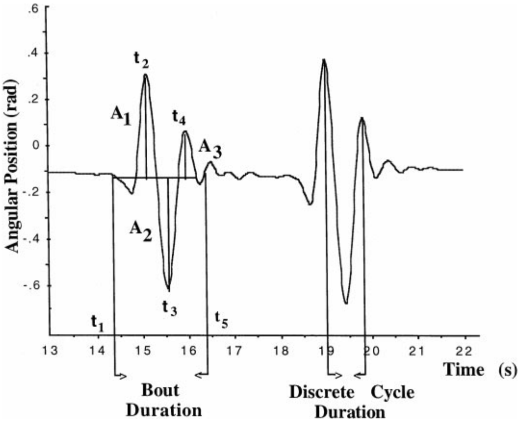

Fig. 5. Specifications of amplitude and period values in the discrete hand: A_1, A_2, A_3: amplitudes of the first three large excursions; t_1–t_5 denote the respective time values. $t_5 - t_1$ is the duration of the global period or bout, $t_4 - t_2$ is used to indicate the duration of one cycle.

affected by the discrete hand's bout of activity solely in a spatial sense as reflected in perturbations of cycle amplitude, but not temporally in terms of perturbations of cycle period.

2.2.2. Serial coordination: Discrete left unit

It is evident from inspection of Fig. 2(B) and (C) that the discrete hand's activity bout extended beyond one cycle of oscillation, contrary to the instructed form of the task, and never became completely motionless in the inter-bout intervals. The structure of each discrete bout was quantified according to the segmentation shown in Fig. 5. It can be seen that the major features of a typical discrete bout were an initial small backward motion from baseline (perhaps due to a tightening of the grip or a preparatory extension of the ulnar flexor), followed by the main sequence (forward, backward, forward, backward) of larger amplitude movements, and ending with a variable number of ringing oscillations of decreasing amplitude. The duration of a discrete bout was defined operationally from the onset of the initial small backward motion until the return to baseline after the fourth large amplitude motion (*bout duration* is defined between times t_1 and t_5 in Fig. 5). Corresponding to the peak-to-peak period measure defined for the continuous hand, a second duration measure was defined for the discrete hand as the interval between the first and second positive peaks of the discrete bout (*discrete cycle duration* defined between t_2 and t_4 in Fig. 5). Three consecutive movement amplitudes were also defined for the discrete bout, as the deviations from baseline of the three major displacement peaks (*discrete amplitudes* A_1, A_2, and A_3 in Fig. 5; movement baseline for each bout is defined at time t_1).

The mean bout duration was 2.54 s for SC4 and 2.64 s for SC5, and the mean discrete cycle duration was 1.0 s for SC4 and 0.99 s for SC5. A two-way ANOVA on condition (SC4, SC5) × measure (bout and discrete cycle durations) showed significance only for the main effect of measure, $F(1,5) = 217.06$, $p < 0.0001$. This indicated that the instructed global period for the task (spanning four or five cycles of the right continuous hand) had no effect on the discrete hand's duration measures.

The relation among the three movement amplitudes was also examined. Specifically, the absolute values of the amplitudes were used in a two-way amplitude (A_1, A_2, A_3) × condition (SC4, SC5) ANOVA, revealing only a significant main effect of amplitude, $F(2,10) = 13.88$, $p < 0.01$. Confirming visual inspection of the data (Fig. 2), post-hoc pairwise Tukey tests showed that: (a) within each condition all three amplitudes differed significantly from one another in the pattern $A_1 > A_2 > A_3$ (A_1: 0.63 rad; A_2: 0.45 rad; A_3: 0.31 rad), and (b) the corresponding A_is did not differ from each other across global period conditions.

In an additional analysis the corresponding amplitudes A_1, A_2 and A_3 in the right continuous hand were included. A three-way amplitude (A_1, A_2, A_3) × condition (SC4, SC5) × hand (discrete, continuous) ANOVA detected a small but significant main effect for amplitude ($F(1,60) = 4.43$, $p < 0.05$) showing that, similar to the discrete hand alone, A_1 was larger than A_2 and A_3 (A_1: 0.79 rad; A_2: 0.71 rad; A_3: 0.69 rad). That this decrease in amplitude was more pronounced in the left than in the right hand was underscored by a two-way interaction showing that the amplitudes of the continuous right hand were larger than the discrete hand ($F(2,60) = 5.21$, $p < 0.01$). The serial condition had no measurable effect. Taken together, these analyses are consistent with the characterization of the discrete unit as an "almost oscillator" (Kopell, 1988) that is switched on close to each targeted cycle (the fourth or the fifth) of the continuous unit and then slowly damped out.

2.2.3. Serial coordination: Mutual spatiotemporal influences of the continuous and discrete units

How do the cycle durations and amplitudes of the continuous and discrete units relate on the critical coupled cycles (c4 in SC4; c5 in SC5)? To examine the relation between the temporal behavior of the discrete and continuous hands during the discrete hand's activity bout in both SC4 and SC5, the mean period was computed for each trial's set of *coupled cycles* for the continuous hand, and *discrete cycles* for the discrete hand. Subject means for each hand were then computed across the five trials per condition, and used in a two-way hand (discrete, continuous) × condition (SC4, SC5) ANOVA. The only significant effect was that of hand, $F(1,5) = 6.86$, $p < 0.05$, indicating that: (a) there was no reliable difference in period between SC4 and SC5 within both the rhythmic and the discrete units, and (b) regardless of condition, the discrete cycle period (0.995 s) was significantly shorter than the continuous cycle period (1.05 s).

A similar analysis was performed on the amplitude measures for the discrete and the continuous units during the coupled cycles in SC4 and SC5. The continuous unit's amplitude was defined as the angular excursion from the positive peak at the beginning of the coupled cycle (c4/c5) to the immediately following trough. The corresponding amplitude for the discrete unit was defined as the sum of A_1 and A_2. A two-way ANOVA on hand (discrete, continuous) × condition (SC4, SC5) was conducted. Similar to the temporal comparison, only the hand effect was significant, $F(1,5) = 21.80$, $p < 0.01$. The discrete cycle's amplitude (0.938 rad) was smaller than the continuous cycle's amplitude (1.193 rad).

Taken together, these spatial and temporal comparisons indicate that: (a) the spatio-temporal patterning in the coupled cycles of the continuous and discrete units was not affected by the number of continuous cycles between each discrete bout of activity; and (b) the temporal differences between the discrete and continuous units might be related to the corresponding amplitude differences, i.e., the discrete durations might be shorter than those of the continuous unit because the discrete unit moves through a shorter distance overall.

2.2.4. Serial and parallel coordination: Relative phasing between right and left units

The determination of discrete relative phase, ρ, between the left and right units began by computing the following sets of temporal difference measures for each trial: In the SC conditions, these differences were the times of the first positive peak in each discrete bout of the left hand (i.e., the event labeled t_2 in Fig. 5) minus the times of the corresponding closest positive peaks in the right hand (i.e., the peak that defined the beginning of the continuous hand's coupled cycle; see Fig. 2(C)). In PC, these differences were the times of the positive peaks in the left hand minus the times of the corresponding closest positive peaks in the right hand. For both the SC and PC measures, negative/positive values indicate that the left hand leads/lags the right hand. For purposes of comparison it is important to note that the physical situation of left hand lagging right hand is characterized by a positive relative phase value using the method adopted in the present study. A negative relative phase value results for this same physical situation when using the so-called "continuous relative phase" measure, defined by $\Phi(t) = \theta_L(t) - \theta_R(t)$.

Within-trial means were computed for these difference measures, and converted to normalized relative phase values by dividing by the average cycle period of the continuous right hand in the corresponding trial. Finally, mean within-subject phase values were computed for each condition, and analyzed in a one-way ANOVA. Results were not significant, indicating that the patterns of relative phasing were identical for PC ($\rho = 0.005$ rad), SC4 ($\rho = -0.018$ rad) and SC5 ($\rho = -0.018$ rad).

2.2.5. Serial, parallel and isolated condition: Comparison of the right, continuous units

In this section we focus on the spatio-temporal behavior of the continuous right rhythmic unit, and ask how its behavior varied across PC, SC and IC conditions. In other words, we analyze how the continuous right unit's uncoupled kinematics, measured under the IC condition, were changed during coordination with the left unit in SC and PC.

Comparing the mean periods of the continuous right unit's performance in the IC, PC and SC conditions in a one-way ANOVA showed no significant differences between the periods. The means were: IC: 1.027 s, PC: 1.030 s, SC4: 1.054 s, SC5: 1.046 s. While for PC and IC, the mean period was computed from all cycles of each trial, for SC, the mean period was determined from each trial's set of *coupled* cycles (i.e., every fourth or fifth). Subsequently, the subject means for each condition across the five trials per condition were computed and used in a one-way ANOVA which compared these periods across the four conditions.

A similar analysis was conducted using a one-way ANOVA to compare amplitudes across conditions. Contrary to the nonsignificant period effects, the amplitude analysis showed significant differences, $F(3,15) = 28.44$, $p < 0.0001$. The values were: IC: 1.00 rad; PC: 0.96 rad; SC4: 1.18 rad; SC5: 1.21 rad. Post-hoc Tukey tests revealed that: (a) IC and PC did not differ, (b) SC4 and SC5 did not differ, and (c) both IC and PC differed from SC4 and SC5. These results agree with the findings from Section 2.2.1 which analyzed the cycles within the SC conditions and reported only amplitude but no period effects during the coupled cycle.

3. Discussion

Experiment 1 was directed at a very simple form of serial coordination in which a single oscillation of the left hand occurred every *n*th oscillation of the continuously oscillating right hand. That is, the participants were required to time the onset of a discrete cyclic motion relative to an ongoing, continuous cyclic process in the contralateral limb segment. Of primary concern were the questions: How do the two cyclic behaviors, discrete and continuous, influence or perturb each other? What are the implications of these influences for modeling this simple sequencing behavior as a dynamic process? There were five main experimental results: (1) The discrete oscillation of the left hand affected the amplitude but not the period of the *n*th oscillation of the continuously oscillating right hand; (2) the amplitude and period of the discrete oscillation of the left hand were characteristic of a damped oscillator; (3) the amplitude and period of the discrete oscillation of the left hand were smaller than the amplitude and period of the *n*th oscillation of the continuously oscillating right hand; (4) the onset of the discrete oscillation of the left hand was perfectly synchronized with the onset of the *n*th oscillation of the right hand; (5) the *n*th oscillation of the continuous right hand was of larger amplitude when it occurred simultaneously with a discrete oscillation of the left hand than when it occurred simultaneously with the *n*th oscillation of a continuously oscillating left hand and when it occurred without any left hand oscillations, either discrete or continuous. Results 1–5 above provide the basis for capturing the simple serial coordination in a task dynamic framework with sequential change addressed as a parameter-dynamic process.

4. Qualitative modeling of serial coordination

4.1. A task-dynamic modeling strategy

In modeling parallel coordination the equations of motion used to simulate the coupled rhythmic movements have been defined as two sets of coupled second-order equations with constant parameters, with each set describing the motion of the state variables of a given oscillator's position and velocity. A distinction between different *levels* of a coordinate system has been shown to be useful in understanding skilled activities performed with effector systems involving many biomechanical degrees of freedom. For example, the actions performed by speech articulators have been modeled as *task-dynamic* systems in the so-called task-space and body-space, with model articulator (or task network), and real articulator (or articulator network) coordinates (e.g., Saltzman, 1986; Saltzman and Kelso, 1987; Saltzman and Munhall, 1989; see also Schöner, 1994; Taga, 1995a, b; Taga et al., 1991). Such a multi-level definition of an action system's dynamics is required in order to model, for example, the spatially adaptive compensatory responses observed when mechanical perturbations are introduced during the performance of variety of limb and speech tasks. It is also necessary to account for gradual transitions and carry-over effects between task segments that arise due to inertial forces.

For the present task, a one-to-one relationship is assumed between task-space coordinates and model articulator coordinates such that, for example, limit cycle equations of motion defined in task-space coordinates are mapped into identical motion equations in model articulator coordinates. Fig. 6 shows how the model articulator level contains a limit cycle dynamic and a point attractor dynamic specified as a damped oscillation. The configuration of the model articulator system is used as the ongoing input to the equations of motion defined at the effector level. Importantly, the motion equations at the effector level capture the particular biomechanical properties of the moving limb. For the present task, two nonlinear equations for pendular motions are used with real mass and length dimensions. Finally, the ongoing state of these two articulators is fed back to the equations for the model articulators. Thus, the two levels are coupled bidirectionally. Eq. (1) gives the complete system of equations that was used for the following simulations:

$$\ddot{x}_R + kx_R + b\dot{x}_R + cx_R^2\dot{x}_R + d\dot{x}_R^3 = \alpha(x_L - x_R)^2(\dot{x}_L - \dot{x}_R) + \beta(\dot{x}_L - \dot{x}_R) + \gamma(\dot{x}_R - \dot{u}_R), \tag{1a}$$

$$\ddot{x}_L + k(x_L - P) + D\dot{x}_L + cx_L^2\dot{x}_L + d\dot{x}_L^3 = \alpha(x_R - x_L)^2(\dot{x}_R - \dot{x}_L) + \beta(\dot{x}_R - \dot{x}_L) + \gamma(\dot{x}_L - \dot{u}_L), \tag{1b}$$

$$\ddot{u}_R + gL_R^{-1}\sin u_R + Bm_R^{-1}L_R^{-2}\dot{u}_R = \lambda m_R^{-1}L_R^{-2}\sin(x_R - u_R), \tag{1c}$$

$$\ddot{u}_L + gL_L^{-1}\sin u_L + Bm_L^{-1}L_L^{-2}\dot{u}_L = \lambda m_L^{-1}L_L^{-2}\sin(x_L - u_L). \tag{1d}$$

x_R and its derivatives in Eq. (1a) denote the continuous autonomous oscillator's motion consisting of the nonlinear Duffing and Rayleigh terms as specified by Kay et al. (1987) and as derived from the kinematics by Beek et al. (1995). $x_L, \dot{x}_L$ and $\ddot{x}_L$ designate position, velocity and acceleration of the damped oscillation. The two model articulators are symmetrically coupled by a

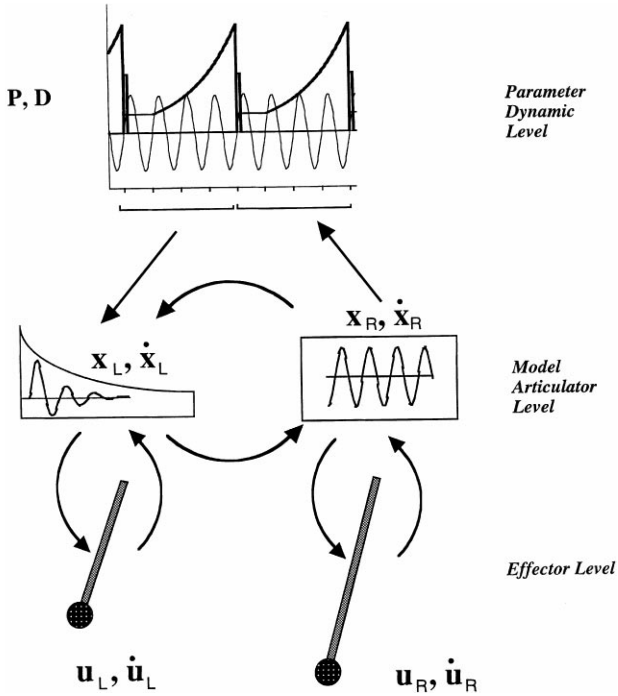

Fig. 6. Schematic of three-leveled model. The parameter dynamic level consists of a step-like pulse which activates the damped oscillation in the discrete hand every fourth cycle. An exponentially growing damping is activated at the end of the one discrete cycle that is required in the task. The model articulator level consists of one damped and one continuous oscillation which are coupled together. The model articulators drive the effectors which are modeled as pendular limbs. These pendula are parameterized with the real values of the wrist-pendula used in the experiment.

van der Pol-like coupling term as suggested by Haken et al. (1985). While this coupling term was motivated by the empirical observations of transitions from anti- to in-phase behavior, it was subsequently shown that it is likewise suited to predict systematic properties of relative phase during steady state behavior in in-phase and antiphase behavior (Sternad et al., 1996). Both oscillators are identical in their parameterization with the exception of the linear damping parameter *D* and an additional parameter *P* for the rest position of the left unit. A linear coupling term based on relative velocity of model and real articulators connects the pendular units with the model level. In the converse direction, from pendulum to model articulators, a sine-coupling over relative position of the two articulators provides for influences from the pendular limbs to the model articulators. This sine-coupling is like a soft spring. It should be pointed out that the effectors are only coupled via the model level.

To address the additional complexity introduced by the sequential nature of the given task the parameters D and P of the task level themselves were subject to change contingent upon the phase of the global cycle. The following set of equations were used to achieve the sequential onset and offset of cycles:

$$P(\theta) = \begin{cases} p, & \text{if } 0 < \theta \leqslant \Delta, \\ 0, & \text{if } \Delta < \theta \leqslant 8\pi, \end{cases} \tag{2a}$$

$$D = \varepsilon, \quad \text{if } \theta = 0, \tag{2b}$$

$$D = \begin{cases} 0, & \text{if } 0 < \theta \leqslant 2\pi, \\ aD, & \text{if } \theta > 2\pi \end{cases} \tag{2c}$$

where θ is the running cycle phase of oscillator x_R, mod 8π (for 4-cycle counting) or mod 10π (for 5-cycle counting), beginning when $x_R = 0$ and $\dot{x}_R > 0$ for the first time in each trial. Δ is the duration of the pulse defined in percent of cycle period. In order to generate activity in the damped oscillator each nth cycle, the simplest solution to achieve a discontinuous onset as specified by the task is to reset briefly the damped oscillator's rest position P. As shown in Eq. (2a), this is introduced in form of a step function of duration which marks the beginning of every global cycle. Any other gradual ramp-like onset does not produce the observed immediate bimanual synchronization. With only this pulse, the discrete cycle would dampen out, but a small amplitude oscillation of the left hand would persist beyond one cycle due to the coupling between the two units and the influence from the pendular effector dynamic. A flexible solution that limits these oscillations is to include an additional dynamic of the linear damping parameter D, expressed in Eqs. (2b) and (2c). This dynamic process can be interpreted as the voluntary "silencing" of the left unit after one cycle according to the task specifications. Importantly, due to the damping D, the synchronization of oscillations between the two units remains present but with negligible amplitude. The constant a determines the strength of the damping. The timing of the damping is tied directly to the timing of the pulse such that at the onset of the pulse P, D starts to grow exponentially, and is terminated and restarted with the onset of the next pulse. During the first cycle D is set to a constant value ε.

This kind of parameter dynamics also allows for other related tasks. For example, if the task is to produce two bimanual cycles followed by two unimanual cycles, the onset of the exponential damping must be changed to cycle 3. To obtain two "discrete" cycles, the damping could be reduced and the onset of the damping dynamic delayed. Alternatively, two pulses trigger the two cycles, respectively.

This parameter dynamic process is the simplest instantiation of the counting task. An alternative way to achieve a discontinuous onset of the discrete cycle at a designated phase of the continuous oscillation is to adopt an "integrate-and-fire" approach (Glass and Mackey, 1988). A system integrates landmark values such as the maximal excursions of the continuous oscillation. At a given threshold value, an energy squirt is injected into the silent unit in a manner similar to above. While "integrate-and-fire" is typically applied in neural models, its effect in the equation above would be essentially the same as the parameter dynamic interpretation of counting. The disadvantage of "integrate-and-fire" is that if the threshold value is not carefully adapted to the chosen landmark, miscounts could easily occur.

4.2. Comparison with experimental data

Fig. 7 shows a time series that was simulated by using Eqs. (1) and (2). The parameter values are listed in the figure caption. Inspection of the simulated time profile of the two pendulum effectors shows the major quantitative and qualitative features observed in the data. (As the model is completely deterministic, the global period's behavior after the start-up transient repeats itself exactly and for a quantitative evaluation one global cycle is sufficient.) As in the time profile of one exemplary subject in Fig. 2(C) the average amplitudes of the continuous hand are approximately 0.60 rad and the frequency is close to 1 Hz (note, however, that average amplitudes are higher, Section 2.2.5). More specifically with respect to Result 1, the continuous unit shows an increased amplitude at the coupled cycle. This increase is approximately 1% of maximum amplitude A_1 which is comparable to the data. The amplitude increase is most marked at the first maximum of the coupled cycle A_1 but the effect is still present at A_2 (compare Figs. 2 and 5). As parameter manipulation showed this effect is a direct function of the coupling parameters α and β that link the two oscillations at the model level.

With respect to Result 2, the discrete unit's amplitudes in SC decrease with a pattern $A_1 > A_2 > A_3$, which is qualitatively consistent with the pattern of the data. Compared with the data the simulation's amplitudes were generally lower: $A_1 = 0.45$; $A_2 = 0.16$; $A_3 = 0.09$. This decrease was obtained from the linear damping D and the nonlinear damping d.

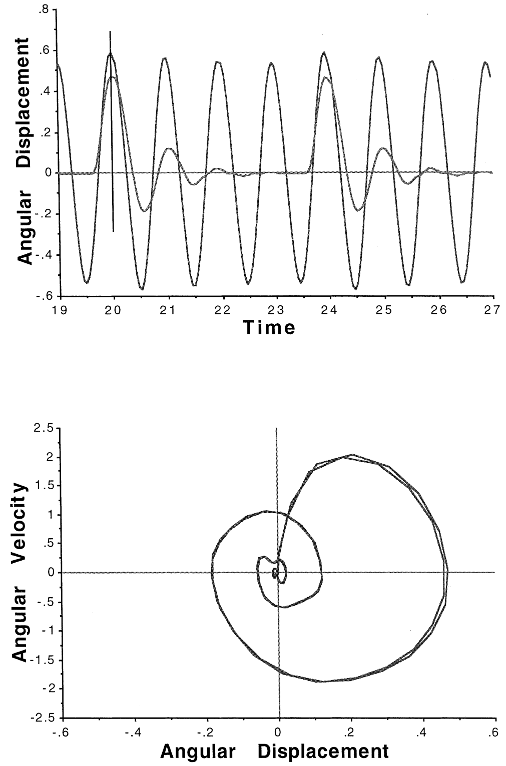

Fig. 7. Simulated time series (upper panel) and discrete unit's phase portrait (lower panel) for the SC conditions of Experiment 1 using Eqs. (1) and (2). The parameters for the model articulators dynamics were: $k = 39.0$; $b = -6.28$; $c = 6.28$; $d = 0.16$. The coupling parameters for the two model articulators were: $\alpha = 7.0$; $\beta = -1.3$. The coupling between effector and model level is symmetric with: $\lambda = 0.20$. The pulse duration Δ was set to 12% of one cycle's period. The growth factor for the damping $a = 1.2$ and $\varepsilon = 1.0$. The pulse amplitude $p = 1.6$. The parameters for the two identical pendular equations were: $L = 0.37$; $m = 0.817$; $B = 17.88$. The coupling between the model articulator and effector was: $\lambda = 80.0$.

With respect to Result 3 no coincidence between data and simulation could be obtained. Whereas the amplitude of the discrete hand during the coupled cycle is less than the amplitude of the continuous hand, the period of the discrete hand during the coupled cycle is longer than the continuous hand. This can be read directly from Fig. 7. As the parameters L, m and g are given, only the coupling parameter γ is available to simulate this result. The direct relation in the data between amplitude and period of the discrete oscillation, such that a smaller amplitude goes together with a shorter period, is not obtained in the simulation. The synchronization between the continuous hand and the discrete hand overrides this effect. The consequence of this synchronization though is that Result 4 can be reproduced. As can be seen in Fig. 7, the discrete estimate of relative phase at the peak of the coupled cycle is close to zero, which is the expected value for two continuously coupled identical oscillators (e.g., Sternad et al., 1996; see Experiment 2).

To address Result 5, the same task network was also used to simulate PC and IC. For this purpose the task network was adapted such that the specific functions for P and D in SC were removed. Both model articulators were parameterized in identical fashion and the parameter values were the same as the continuous model articulator in the simulation for SC. The coupling was symmetrical and of identical strength compared to the SC simulation. The effectors remained the same as before. Results of the simulated PC and IC condition showed that both periods and amplitudes were the same as in the simulated SC condition (amplitudes in PC and IC: 0.58 rad; average SC: 0.57 rad; periods in PC and IC: 1.03 s; SC: 1.01 s. However, while identical periods in PC, IC and SC conform with Result 5, identical amplitudes do not. This contrast between the simulation and the data suggests that oscillator properties must change when an oscillator is engaged in SC versus PC and IC. In order to explore this alternative, the damping parameter b of the model articulators in PC and IC was decreased by a factor of two (from 0.15 to 0.30) while keeping all other parameters identical to SC. This parameterization produced the observed decrease in amplitude in PC and IC of the data, without changing the periods. Simulation of IC produced identical amplitudes and periods as PC suggesting that the coupling of continuously moving oscillators has no significant effect on the kinematic features of the oscillations.

In summary, the stratified task network shown in Fig. 6, with dynamic primitives at the model articulator level, equations of motions for pendular limbs and a parameter dynamics governing the sequencing aspect, reproduces most of the kinematic features of the effector in the present experiment. Experiment 2 provides a further evaluation of the proposed modeling strategy for the present simple example of serial behavior.

5. Experiment 2

An important manipulation in the investigation of parallel coordination has been the asymmetry in the component units. The systematic influence of this asymmetry on the steady state behavior has been experimentally and theoretically addressed in a series of studies. A motion equation in relative phase for interlimb coupling, advanced by Haken et al. (1985) and extended by Kelso et al. (1990), was shown to successfully predict the equilibria and bifurcations of parallel interlimb rhythmic coordination (for summaries see Amazeen et al., 1997; Kelso, 1994; Schmidt and Turvey, 1995 and recent demonstrations by Amazeen et al., 1996; Sternad et al., 1995). The asymmetry, largely due to different inertial properties of the component limbs, has been captured in an "imperfection parameter", or also referred to as detuning δ (Collins et al., 1996; Sternad et al., 1996; Strogatz, 1994). In Experiment 2, this detuning was manipulated in the SC4 and PC conditions by having participants move different size pendula in their left and right hands. This provided a means of re-assessing major aspects of Experiment 1 and of testing to what degree they are consequences of the inertial loading of the left hand. Particular focus will be on: (a) the increase in amplitude of the right continuous oscillator on cycle *n*, the cycle at which the left discrete oscillator kicked in, and (b) the persistence of the discrete oscillation beyond the period of cycle *n* of the continuous oscillator, that is, the "ringing" of the discrete oscillator. The greater the resistance to rotational acceleration of the left hand, the greater the effort to produce the discrete cycle on cue with a carry-over effect to the continuously oscillating right hand. Further, the larger the rotational inertia of the left hand, the more difficult is the task of stopping the left oscillator once it has been set into motion. Alternatively, the aspects (a) and (b) could be independent of rotational inertia (and, therefore, eigenfrequency) and due strictly to the nature of the coupling function required to produce the simple form of serial coordination studied in Experiment 1. Manipulation of δ will permit an evaluation of these alternatives.

5.1. Method

5.1.1. Participants

Four graduate students from the University of Connecticut volunteered to participate in the experiment.

5.1.2. Apparatus and pendula

All pendula had attached weights of 200 g each. As in Experiment 1 the right hand producing the continuous oscillation always held a pendulum of length 46 cm, with $\omega_R = 5.15$ rad/s. The pendula held in the left hand performing the discrete oscillation, referred to as P1–P5, were of five different lengths and, therefore, of five different eigenfrequencies. For a pair of left and right hand-held pendula, detuning was calculated as: $\delta = \omega_L - \omega_R$.

Table 1
Physical characteristics of left pendula in Experiment 2 together with their eigenfrequencies ω and the δ values when coupled to the right (constant) pendulum with an equivalent length of 0.37 and an eigenfrequency ω of 5.15 rad/s.

Pendulum	Actual length [m]	Equivalent mass [kg]	Equivalent length [m]	ω [rad/s]	δ [rad/s]
P1	0.32	0.77	0.25	6.19	1.04
P2	0.40	0.80	0.31	5.56	0.41
P3	0.46	0.82	0.37	5.15	0
P4	0.52	0.84	0.42	4.83	−0.32
P5	0.60	0.87	0.49	4.60	−0.55

The physical characteristics of the five pendulum pairings are summarized in Table 1. Data collection was performed with the same Sonic Digitizer and customized software as used in Experiment 1.

5.1.3. Procedure

In contrast with Experiment 1, the serial task was only performed in the SC4 condition. Instructions to the subjects were the same. The three coordination patterns, SC, PC and IC, were performed in two blocks. Each block began with two trials of IC with SC and PC examined in the remaining trials. Within these latter trials, the five pendulum pairings were presented in randomized order. In order to reduce the number of changes in the left pendulum during the course of the experiment, subjects performed one trial PC and one trial SC with the same left pendulum. The same procedure was repeated in the second block with a different randomized presentation of pendula and with the reverse sequencing of PC and SC within one pendulum combination. Each of the 24 trials lasted 60 s and the total experiment lasted approximately 1 h.

5.2. Results

5.2.1. Continuous right rhythmic unit in SC

The mean cycle duration and mean cycle amplitude are presented in Fig. 8 as a function of cycle number (c1–c4, with the left unit oscillating every fourth cycle) and δ. Focusing on the period as the dependent measure first, a 4 × 5 ANOVA revealed significance for both main effects and their interaction: δ, $F(4,12) = 5.20$, $p < 0.05$; cycle number, $F(3,12) = 6.18$, $p < 0.05$; $\delta \times$ cycle number, $F(12,36) = 4.27$, $p < 0.001$. The significant interaction

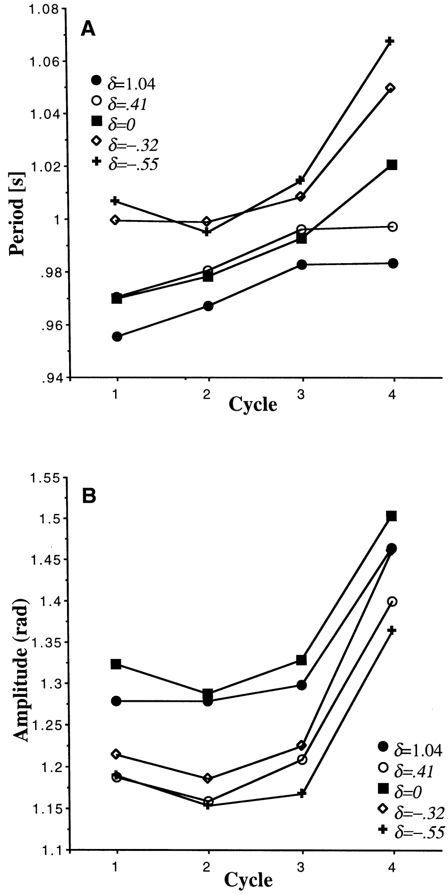

Fig. 8. (A) Mean cycle periods and (B) mean amplitudes of four cycles in SC for the five detuning conditions of Experiment 2.

points to a nonuniformity in the influence of the left, discrete pendulum on the right, continuous pendulum. A closer examination of the interaction through simple effects revealed that for all δ, with the exception of $\delta = 1.04$ rad/s, the periods showed significant differences across cycle number, $p < 0.05$. Inspection of Fig. 8(A) reveals a significant tendency for the period to increase, particularly at the coupled cycle c4. Additionally, simple effects analysis of the interaction revealed reliable differences among δ only at c4, $F(4,12) = 16.76$, $p < 0.0001$, and c1, the cycle immediately following the coupled cycle (see Fig. 3(C)), $F(4,12) = 3.79$, $p < 0.05$. From these data it can be concluded that the discrete cycle perturbed the periodicity of the continuous cycle. In Experiment 1, limited to $\delta = 0$, the period of the right continuous oscillator was unaffected by the left discrete oscillator.

A corresponding ANOVA with cycle amplitude as the dependent measure revealed only a significant effect of cycle, $F(3,9) = 23.07$, $p < 0.0001$. Neither the interaction between δ and cycle, nor the main effect of δ proved to be significant. Post-hoc Tukey comparisons within the cycle effect indicated a significant difference between the coupled cycle c4 (the largest) and each of c1, c2 and c3 (Fig. 9(B)). The absence of interactions involving the left unit's

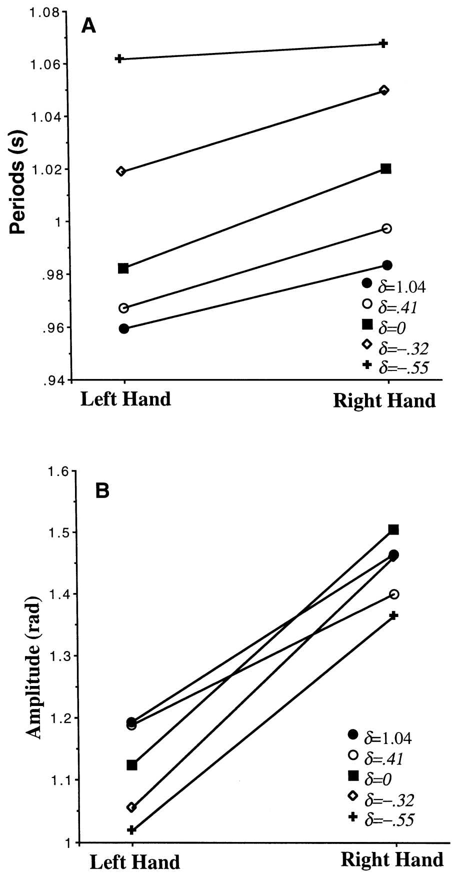

Fig. 9. Comparison of right and left hand's duration measures in Experiment 2. The value for the left hand is $t_4 - t_2$, the value for the right hand is the period of the coupled cycle. (A) Periods of the left and right hand. The value for the left hand is the sum of A_1 and A_2, the value for the right hand is the amplitude of the coupled cycle c4. (B) Mean amplitudes of the four cycles in the right continuous hand, as a function of pendulum in Experiment 2.

eigenfrequency means that the changes in the right unit's amplitude were indifferent to δ. In order to facilitate comparison with Experiment 1, a separate ANOVA was performed on amplitudes for $\delta = 0$. It revealed a significant effect, $F(3,9) = 30.05$; $p < 0.001$. Replicating the results of Experiment 1, pairwise comparisons showed only that c4, the coupled cycle, was significantly larger than all other cycles.

In summary, the findings identified in the preceding generalize those of Experiment 1 in that the discrete hand's activity significantly affected the kinematics of the continuous hand. These findings reinforce the impression that there are strong coupling effects during the cycles of bimanual activity. Additionally, while δ systematically affected the durations of the coupled and "post-coupled" cycles, the size of the amplitude increase at c4 was indifferent to δ.

5.2.2. Discrete left unit in SC

The cycle durations and amplitudes of the left unit were calculated as in Experiment 1. A two-way $\delta \times$ measure (bout and discrete cycle durations) ANOVA was used to compare the bout duration ($t_5 - t_1$) and the discrete cycle period ($t_4 - t_2$) at each δ. There was only a main effect of measure, $F(1,3) = 21.50$, $p < 0.05$ (mean discrete cycle period = 0.998 s, mean bout duration = 2.218 s). This measure effect was also significant in Experiment 1. Since P3 was the only pendulum used in Experiment 1, a separate analysis was performed for the P3 data alone, that is, for $\delta = 0$. The results from Experiment 1 were replicated in that bout duration was greater than discrete cycle duration. There was no effect of δ, meaning that there was no effect of the left hand's loading or eigenfrequency, and there was no $\delta \times$ measure interaction.

The relation among the three movement amplitudes of the discrete cycle was examined as in Experiment 1, using the absolute values of the amplitudes in a two-way ANOVA of amplitude (A_1, A_2, A_3) $\times$ δ. While neither δ, nor the interaction were significant, the main effect for amplitude was significant ($F(2,12) = 19.35$; $p < 0.05$). The amplitudes averaged across all δ values decreased ($A_1 > A_2 > A_3$) in the manner of Experiment 1 ($A_1 = 0.609$, $A_2 = 0.481$, $A_3 = 0.317$ rad). In order to compare Experiment 2 and Experiment 1 directly, a separate one-way ANOVA was performed on $\delta = 0$. Amplitude was significant with pairwise comparisons revealing A_1 different from A_3 ($A_1 = 0.661$, $A_2 = 0.462$, $A_3 = 0.353$ rad). This pattern was consistent with, although not identical to, the pattern of significant amplitude differences found in Experiment 1.

5.2.3. Mutual spatiotemporal influences of the right and left units in SC

How did the durations and amplitudes of the continuous and discrete hands relate on the critical coupled cycles during the SC condition? With respect to cycle duration, a two-way hand (discrete versus continuous) × δ ANOVA revealed significant main effects for both hand and δ (Fig. 9(A)). The hand effect indicated that, averaged across δ, the duration of the left discrete cycle was significantly shorter than the duration of the coupled cycle of the right continuous hand, $F(4,12) = 21.23$, $p < 0.05$. The δ effect indicated that, averaged across hands, the cycle periods were shorter when the discrete pendulum's eigenfrequency was higher, that is, $\delta > 0$, $F(4,12) = 21.83$, $p < 0.0001$. Contrary to Experiment 1, however, a separate analysis for $\delta = 0$ found no significant hand difference (discrete duration = 0.982 s, continuous duration = 1.020 s), although the trend was in the same direction. The lack of a significant interaction indicates that δ affected the cycle durations of both hands similarly.

With respect to amplitude, a comparable 2 × 5 ANOVA revealed only a significant effect of hand, $F(1,3) = 328.59$, $p < 0.001$, indicating that, averaged across δ, the amplitude was smaller for the discrete hand than for the continuous hand (Fig. 9(B)). This effect remained significant when $\delta = 0$ was analyzed separately, in accordance with Experiment 1 (discrete amplitude = 1.12 rad, continuous amplitude = 1.50 rad).

Taken together, the spatial and temporal data of Experiment 2 were consistent with those from Experiment 1 in that the period difference between the hands could be derived from corresponding amplitude differences. In addition, these findings generalized those of Experiment 1 showing that δ systematically affected the durations, but not amplitudes, of the coupled cycles in the continuous and discrete hands.

5.2.4. Relative phasing between right and left units in SC and PC

Relative phase, ρ, between the left and right units was computed as described in Experiment 1, and a two-way ANOVA was performed for conditions SC and PC, and δ. No significant difference was found between the two conditions, indicating that the patterns of relative phasing were identical for PC ($\rho = 0.001$) and SC ($\rho = -0.006$) replicating the results from Experiment 1. A main effect for δ, however, revealed a significant increase from negative values for the shorter left hand pendula (left hand leads the right hand) to positive values for the longer left hand pendula (left hand lags the right hand), consistent with previous analyses of continuously parallel bimanual rhythms (Fig. 10) (e.g., Amazeen et al., 1996; Sternad et al., 1992, 1996;

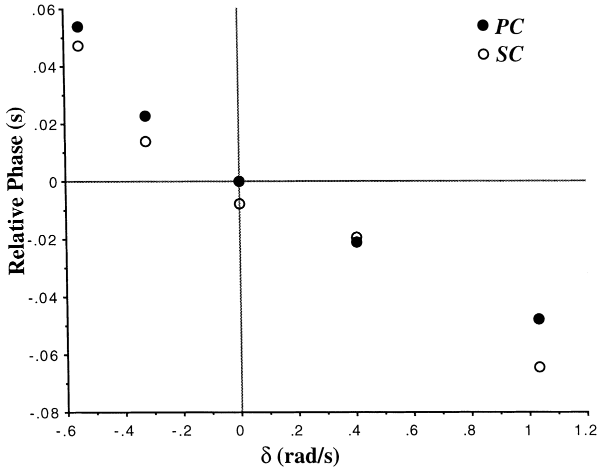

Fig. 10. Relative phase as a function of detuning for PC and SC in Experiment 2.

Schmidt et al., 1993; see Section 2.2.4 for translating between different conventions for defining relative phase in the present and previous studies). Linear regressions performed on the SC and PC conditions separately were both significant, $r^2 = 0.95$.

5.2.5. Comparison of the right, continuous units in SC, PC, and IC

In this section we focus on how the continuous right unit's uncoupled periods and amplitudes, measured under the isolated (IC) condition, were changed during coordination with the left unit under SC and PC conditions. For PC and IC, the mean period and amplitude for all cycles of each trial were computed; for SC, the mean period and amplitude for each trial's set of *coupled* cycles (i.e., c4) were calculated. Subject means for each condition across the five trials per condition were determined, and used to compare these measures across conditions.

Focusing on the period measure first, a 2 (SC vs. PC) × 5 (δ) ANOVA revealed only an effect of δ, $F(4,12) = 39.18$, $p < 0.0001$. Thus, similar to Experiment 1, the periods of PC and SC were identical. Additionally, regardless of coupling condition, the larger the left pendulum the longer was the right unit's period on the coupled cycles.

To compare the SC and PC conditions with the IC condition, difference scores were computed by subtracting the mean IC period from the periods of each of the five δ conditions within PC and SC. Two sets of t-tests

Table 2
Freely chosen mean period (s) of the right unit in SC, PC, and IC as a function of the left pendulum in Experiment 2

Left pendulum	SC	PC	IC
P1	0.983	0.959	–
P2	0.997	0.981	–
P3	1.020	0.981	1.026
P4	1.050	1.032	–
P5	1.067	1.085	–

Table 3
Freely chosen mean amplitude (rad) of the right unit in SC, PC, and IC as a function of the left pendulum in Experiment 2

Left pendulum	SC	PC	IC
P1	1.463	1.09	–
P2	1.400	1.06	–
P3	1.050	1.01	1.21
P4	1.460	1.06	–
P5	1.364	1.03	–

compared the difference scores for SC − IC and PC − IC against zero. They yielded no significant differences. Thus, replicating the results of Experiment 1, the right continuous units showed no period differences between PC and SC, between PC and IC, or SC and IC (see Table 2).

Identical analyses were conducted for the amplitudes of the continuous hand in the SC, PC, and IC conditions (Table 3). The 2 (SC vs. PC) × 5 (δ) ANOVA showed only a significant main effect for condition, $F(1,4) = 22.18$, $p < 0.05$, with SC having a greater amplitude (1.38 rad) than PC (1.05 rad), in agreement with the results of Experiment 1. Additionally, separate t-tests on the PC − IC and SC − IC difference scores were performed in order to test for differences from zero. Results showed significant differences for both PC − IC, $p < 0.02$, and SC − IC, $p < 0.03$, (PC − IC = −0.200 rad; SC − IC = 0.294 rad). These differences were in the same direction as those in Experiment 1, in that the amplitudes for the right hand's oscillation were larger in SC, and smaller in PC, than in IC. However, while the SC vs. IC tests reached significance in both Experiment 1 and 2, the contrast of PC and IC was significant only in Experiment 2.

6. Discussion

Experiment 2 involved participants swinging five different pendula in the left hand while paired with a constant pendulum in the right hand. This manipulation produced contrasting discrete and continuous oscillators and, thereby, systematic variations in the detuning δ defined as the difference between the eigenfrequencies of the two units. Experiment 2 had two primary objectives. First, to generalize the results of Experiment 1 to coordinations involving oscillators with contrasting preferred frequencies and to link the results in the present simple serial coordination task to the body of data collected on parallel coordination. Second, the experimental manipulations supplied results that provided a further test case for the stratified model. In the following we will summarize the three major results and compare them with the model simulations that included manipulations of the parameters that specified the pendular characteristics.

6.1. Spatial and temporal influences in the continuous hand

Result 1 established amplitude magnifications in the continuous right oscillator by the discrete oscillation of the left hand. This is a noteworthy extension of the strong spatial influence of the discrete movement on the continuous movement observed in Experiment 1. In Experiment 2 this increase showed to be unaffected by δ and, therefore, indifferent to the inertial loading or eigenfrequency of left hand plus pendulum. This constancy of the amplitude magnification suggests that perturbations of the continuous right unit's limit cycle by the discrete left unit are due to a coupling term (see Eq. (1)) whose magnitude does not depend on the oscillator characteristics of the two units. Two simulations using Eqs. (1) and (2) are shown in Fig. 11. For the simulation depicted in Fig. 11(A), the left pendulum dimensions were those of P5 and the right pendulum dimensions were those of P3 (see Table 1). For the simulation shown in Fig. 11(B), the pendulum in the left hand was 3.0 kg and 1.0 m, which corresponded to a considerably slower pendulum than P5 in order to emphasize the effects. Analyzing the simulated kinematics of the continuous hand reveals that the amplitude at c4 was magnified for the two δ conditions, in accordance with the experimental data. The periods of two the simulations were indifferent to δ, however, contrary to the experimental data.

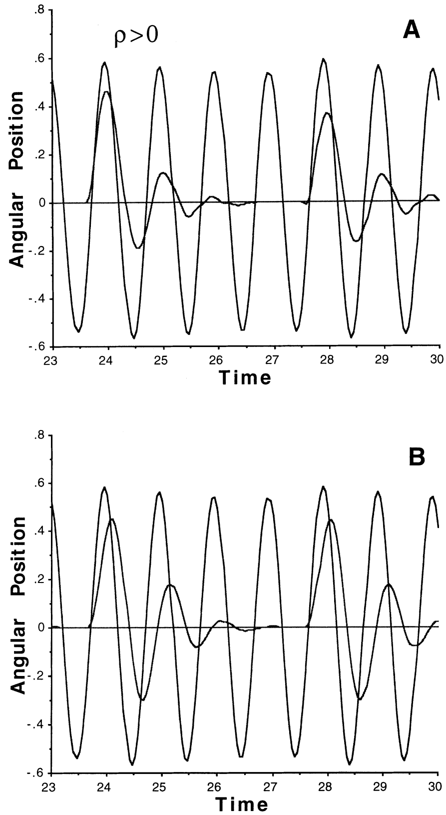

Fig. 11. (A) Simulated time series using Eqs. (1) and (2). Equivalent mass and length corresponded to the pendulum pairing PS3 with PS5 of Experiment 2. (B) Equivalent mass and length of the continuous unit was identical to PS3, equivalent mass of the discrete unit was 3.0 kg and equivalent length was 1.0 m.

6.2. Bout duration and damped ringing in the discrete hand

The analysis of bout duration and discrete period of the left hand replicated the findings of Experiment 1 in that it showed that the single discrete oscillation was longer than specified by the task. What is of particular importance in Experiment 2 is the fact that δ did not affect the duration of the discrete left-hand cycle (Result 2), suggesting that the inertial properties of the pendulum were not the source of protracted oscillation in either Experiment 1 or Experiment 2. Rather, the "ringing" must have been due primarily to the coupling. Additionally, the ordering of the component amplitudes of the discrete oscillation paralleled that observed experimentally ($A_1 > A_2 > A_3$) (Result 2) but, contrary to observation, the magnitudes of these amplitudes and the cycle period varied with δ. Comparing the simulations in Fig. 11(A) with (B) reveals that while the periods and amplitudes of the continuous hand remain virtually the same, the manipulation of δ increased A_2 (and possibly A_1) and the cycle period of the discrete hand.

6.3. Relative phase as a function of detuning

Fig. 10 summarizes the effect of δ on relative phase (Result 4). First, it is notable that the dependency of ρ on δ in SC mirrors the systematic dependency observed in interlimb PC dynamics. Second, it is noteworthy that values of ρ were relatively small and, therefore, the transients leading to the instructed synchronization of the two cycles are extremely short. If the left discrete oscillator were truly not in motion until the point of required bimanual activity, then it would be difficult to envisage how a relative phase tailored to δ would come about within the first quarter of the discrete cycle. This observation seems to suggest that the left oscillator maintained its periodic motion throughout, albeit at very low amplitude outside the duration of the coupled cycle. In the simulations, this latter effect is achieved by the following relations: The discrete oscillator is damped, and therefore provides a first approach to simulate the single cycle according to task instructions. However, the coupling between the two model articulators induces a transfer of the oscillatory pattern which, essentially maintains the periodicity in the "discrete" hand, even during the silent phase. This effect is so noticeable that additional damping has to be superposed to effect the task-required rest in the three uncoupled cycles.

With respect to the first finding, the phase leads and lags of SC resurrect an alternative reading of the effect of δ originally introduced by Rosenblum and Turvey (1988), namely, that a movement relative phase does not directly reflect the neural relative phase but, rather, it reflects a phase relation of 0 rad (or π rad) in neural processes as well as response latencies of differently loaded muscles. That is, although the neural activations of the right and left muscle systems are in phase at the start of the critical cycle in SC, the lead or lag arises from the fact that the greater the inertia to be overcome by the muscle, the greater the lag between neural activation and muscular response (Partridge, 1966, 1967, 1981). Research by Anson

(1982, 1989) has shown that when the moment of inertia of a body segment is varied, both the simple reaction time to a signal and the resulting movement time are systematically affected but not the onset of electromyographic activity.

Turning to the simulations shown in Fig. 11, they indicate that as the left discrete oscillator becomes physically more distinct from the right continuous oscillator (Panel A versus Panel B), the dynamics of Eqs. (1) and (2) qualitatively produce the relative phase differences seen in the data. That is, the effects of δ can be obtained without manipulating the parameters of the coupling function at the model articulator by (a) simply allowing the biomechanical properties at the effector level to vary as they would with different pendulum pairings, and (b) exerting an influence on the task level through the sine coupling.

In sum, Eqs. (1) and (2) are able to address a number of the results of Experiment 2 but not all of them. There are a number of shortcomings, e.g., the predicted but unobserved amplitude and period changes in the discrete oscillation with changes in pendulum length. One obvious direction for improving the simulations would be to use an asymmetric coupling. The need for such a coupling is evident in research on 1:2 frequency locking (Sternad et al., submitted a, submitted b, in press) and that may be a major lesson of the present research. We abstained from breaking the symmetry of the left–right coupling in the present modeling effort given that our focus was on the extent to which an invariant model level coupled to a variant effector level could account for the kinematics of our simple serial coordination task.

7. General discussion

In the present research we have examined a very simple form of serial behavior in which our subjects, explicitly or implicitly, followed the rule: ‘‘On the *n*th beat of one hand moving rhythmically by itself, move both hands together for just one beat and then repeat the sequence.’’ This task aims to extend the kind of behaviors that most of the research on the dynamics of coordination has been directed at the continuous rhythmic movement that typifies locomotion – 1:1 frequency locking - and, to a lesser degree, the continuous multifrequency behavior that tends to typify the musical skills of humans. Our expectation was that the requirement of sequencing simple rhythmic movements would introduce important variations to the dynamical models that currently address the continuous frequency and phase locked coordinations. The present theorizing and experimentation has focused not on the production of the sequence as such but on the spatiotemporal details of co-producing a single movement in concert with a continuous movement. Abbs and Connor (1992) stressed that the aspects of the correct sequential order and the co-dependencies of overlapping units are inseparable and issues of temporal onsets and offsets and carry-over effects arise along with issues of mutual influence. Such issues figure prominently in investigations of speech production (e.g., Browman and Goldstein, 1992; Fowler, 1980, 1996; Fowler et al., 1980; Hardcastle, 1981; MacNeilage, 1970). Our focus has been on the kinematics of the two hands, the right hand that moves continuously and the left hand that joins the right for one cycle every *n*th cycle. It was assumed at the outset that the close examination of the kinematic differences and similarities between the continuous and discrete oscillating hands, under various conditions that affected the uncoupled frequency relation between them, would be revealing of the dynamics assembled for performing the task.

One particular departure from purely parallel coordination in bimanual rhythmic coordination has been investigated by Kelso and colleagues who extended the dynamic framework for behaviors that involve an intentional switching from one coordination pattern to another (Kelso et al., 1988; Schöner and Kelso, 1988a–c). Similar to the present study, the objective was to find a way to cast an intentional changing of movement patterns into the formal language of dynamic systems. In this pursuit, the authors suggested that an intended or extrinsically required action pattern changes the shape of the potential of the so-called intrinsic dynamic in that it creates a new globally attractive behavioral pattern. The shape of the potential then becomes a result of the interaction between the intrinsic and extrinsic dynamics. The actual switching of the action pattern can then be understood in terms of a phase transition or bifurcation. The time required to switch between two stable patterns can be predicted from the shape of the bistable potential and experiments have provided evidence that switching times are consistent with these predictions (Scholz and Kelso, 1990). Typical for this line of theorizing, which is couched in the language of synergetics (Haken, 1977, 1983), is a focus on the change in the order parameter while the intentional parameter(s) are assumed to be constant.

In contrast, the present approach proposes a three-level model where a parameter dynamic process specifies the sequential aspect of the task, and a state dynamic process, divided into effector and task layers, captures the kinematic realization of the task (Saltzman, 1986, 1995; Saltzman and Kelso, 1987; Saltzman and Munhall, 1989, 1992; see also Browman and Goldstein, 1992). Fig. 6 schematically depicts the relational structure of the modeling approach: while the dynamics of the parameters unidirectionally specifies the sequencing, the model articulators are bidirectionally coupled to give expression to the mutual influences during intermittent activity. Each model articulator is bidirectionally coupled with the effector whose biomechanical properties give rise to the specific characteristics in the kinematic realization.

This theoretical approach is not identical to the often-voiced claim that serial behavior must be hierarchical, composed of several tiers of control, with a rule-like capability characterizing the higher tiers (e.g., Lashley, 1951; Rosenbaum, 1991). The emphasis in theorizing and experimentation conducted from the hierarchical perspective has tended to be on the sequencing of temporally non-overlapping movements where the correct order of usually abstract tokens is at issue (e.g., Keele et al., 1995; Jordan, 1995; Sternberg et al., 1978). In contrast, the task dynamic model illustrated in Fig. 6, is an example of a functional heterarchy due to the symmetric couplings within and between layers. These relations are motivated to capture the co-dependencies assumed to occur on task and effector level. With a similar focus on both sequencing and coproduction effects, Spijkers and Heuer (1995) examined a two-level model where movement sequences are directed at the programming level and an execution level accounts for cross-talk due to mechanical and neural coupling effects. In a rhythmic bimanual task where left and right hand performed movements of different and alternating amplitudes the authors parsed up the cross-talk observed at the kinematic features of the two hands' amplitudes and ascribed them to the execution level and cross-talk ascribed to the programming level (see also Heuer, 1997). In comparison to the present study, there is no explicit formulation of the generating program.

A promising attempt has been the connectionist model advanced by Jordan (1986). With respect to the functional level in his sequential network, the network's output is best thought of as "influencing articulator trajectories indirectly, by setting parameters or providing boundary conditions for lower level processes which have their own inherent dynamics" (Jordan, 1986, p. 23). The parameter setting or boundary conditions to which Jordan refers are most closely paralleled by the time-varying damping D that captures the task-specified stopping of the left hand after having performed one discrete cycle and the pulse P which is a non-specific energy input that functions to displace the discrete oscillator from its point attractor thereby reinitiating its motion. The potential significance of D and P is that they provide explicit examples of the indirect influences of higher functional levels – influences that interfere minimally with the dynamics of the lower functional levels, serving only to modulate and initiate.

Turning to the specifics of the task-level/model articulator dynamics, the most important features are (a) the limit cycle and point attractor dynamics of the right and left hands, respectively, and (b) the coupling function that links them. With respect to feature (a), the reasonableness of the fit between model and data reinforces the impression that the language of limit cycle and point attractors is a potentially useful language through which to express the subtasks of a sequential behavior (e.g., Browman and Goldstein, 1992; Saltzman and Munhall, 1989). With respect to feature (b), we adopted the explicit function used by Haken et al. (1985) to express the link between two limit cycles in PC. To a tolerable degree, it seems that this van der Pol coupling function was sufficient for purposes of accommodating major features of the present data (such as spatial without temporal influences across the two hands in Experiment 1 together with an amplitude difference favoring the continuous hand) providing, thereby, further support for the strategy of approaching SC dynamics through PC dynamics.

The methodological strategy in the present investigation of serial behavior was that the experimental task should deviate minimally from the parallel interlimb coordinations investigated successfully from a dynamical systems perspective so that the demands of sequencing should still be approachable in dynamical terms. The manner in which we have chosen to proceed would seem to be in line with Abraham's view (Abraham, 1983, 1987; Abraham and Shaw, 1987) of the future development of dynamics in a direction more suited to the characteristic sequential functions of biological systems. He writes (Abraham, 1987, p. 610) "Probably the first step will be experimental work primarily to discover the basic properties of serially coupled hierarchical systems. The simplest case, two dynamical systems with controls, with a linkage map from the output projection of one to the controls of the other... involves a 'generic coupling' hypothesis for the linkage map, problems of observations on both levels, and new questions of entrainment between levels." The magnitude of these new challenges is conveyed by his concluding remark (Abraham, 1987, p. 610): "There are miles to go before we sleep... "

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