

Interactions Between Rhythmic and Discrete Components in a Bimanual Task

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An asymmetric bimanual task was investigated in which participants performed a rhythmic movement with their dominant arm and initiated a second movement with their nondominant arm at a random phase of the continued oscillations. The objective was to examine whether different constraints existed between rhythmic and discrete movements and, more generally, whether rhythmic and discrete movements can be regarded as two different movement primitives. Participants performed rhythmic forearm rotations at 1 of 4 prescribed metronome periods. After a random interval, a trigger signaled to initiate either a discrete or rhythmic movement with the left forearm as fast as possible while continuing the oscillations. Analyses extracted the mutual influences that the two movements exerted on each other and contrasted discrete-rhythmic and rhythmic-rhythmic coupling. (a) The initiation of the rhythmic movement was constrained to occur in-phase with the ongoing rhythmic movement, while the discrete movement could be initiated at any arbitrary phase. (b) Reaction time of the initiated rhythmic movement scaled with the oscillation period, while the discrete movement's reaction time was invariant across periods. (c) Peak velocity of the initiated movement scaled with the oscillatory period in both tasks but more strongly in the discrete movement. (d) Synchronization of EMG bursts of both arm flexors was evident in both tasks but more strongly in the rhythmic-rhythmic combination. The results are interpreted as support for the hypothesis that discrete and rhythmic actions are two different control regimes, and coupling occurs at a higher level in the central nervous system.

Key Words: bimanual coordination, discrete and rhythmic movements, coupling

The coordination between two hands presents one of the most essential components of our daily behaviors. Humans pick up and manipulate objects, they open jars, they use hammers and pliers, they tie shoelaces, and they play piano or the violin, using either one or both hands. When these actions require two hands, they can be divided into those tasks that involve symmetrical coordination of the two hands and others in which the two hands perform different, often complementary

roles. The class of actions that involves symmetrical movements, specifically in rhythmic coordination, has received a lot of inquiry (for overviews, see Amazeen, Amazeen, & Turvey, 1998; Heuer, 1996; Katsumata & Sternad, 2002; Kelso, 1995). Another much smaller body of research has examined bimanual coordination in tasks where the two hands perform asymmetrical actions, such as in the manipulation of an object or playing the violin. While this is probably the prevalent type of behavior in prehensile activities, far fewer studies have been dedicated to it. Exceptions are studies by Swinnen and Heuer and colleagues who examined bimanual movements with different directional and timing constraints (Heuer, Kleinsorge, Spijkers, & Steglich, 2001; Swinnen, Jardin, Meulenbroek, Dounskaia, & Hofken-van den Brandt, 1997; Swinnen, Walter, & Shapiro, 1988; Swinnen, Young, Walter, & Serrien, 1991). The present study will address bimanual coordination where the two arms perform different types of movements. Specifically, one arm will perform a continuously rhythmic movement, while the other hand simultaneously initiates a discrete movement.

The interlacing of rhythmic and discrete elements is indeed an essential aspect of many everyday behaviors and skills. A football player initiates a kick of the ball with his leg while he is still running. The actions of a drummer not only involve the polyrhythmic patterns between the hands but also reaching to different instruments at different places. Similar observations hold for playing the piano: While rhythmically striking the keys, the hands also translate across the keyboard. The focus of the present experiments is on such more complex combinations of rhythmic and discrete movements in a bimanual task. Previous studies have explored such combinations of rhythmic and discrete actions but focused on single-joint tasks (Adamovich, Levin, & Feldman, 1994; de Rugy & Sternad, submitted; Staude, Dengler, & Wolf, 2002; Sternad, de Rugy, Pataky, & Dean, 2002; Sternad, Dean, & Schaal, 2000). These studies specifically examined the constraints between voluntary rhythmic and discrete elements in a single-joint task. The combination of the two movement components was limited by a tight phase locking of the discrete movement into a window of the rhythmic cycle. The discrete movement's maximum velocity was limited by the oscillatory period (i.e., oscillatory velocity). The rhythmic movement was perturbed as indicated by phase resetting (the oscillation was shifted in phase due to the secondary movement) and the periods shortened slightly after the secondary movement. The phase shift was a function of the oscillatory period. Two experiments by Wei et al. (submitted) showed that inertial loading did not significantly change these interaction effects. But to what degree are these interaction effects determined by the very fact that both movement elements shared the same effector?

In previous work, we proposed the hypothesis that rhythmic and discrete actions are two different classes of behaviors and form units or primitives of more complex actions (Sternad et al., 2000). On the shoulders of two prominent lines of research and adopting a dynamical systems interpretation of human behavior, we have stated that discrete actions are governed by fixed-point attractors, and rhythmic actions are governed by limit cycle behavior. (For an introduction into nonlinear dynamics and these basic concepts, see for instance Strogatz, 1994.) While studies from the equilibrium-point hypothesis provided evidence that discrete pointing movements display point attractor behavior, studies on rhythmic movements demonstrated features of limit cycle attractors in rhythmic single-joint and two-limb movements (Feldman, 1966; Kay, Kelso, Saltzman, & Schöner, 1987; Kay,

Saltzman, & Kelso, 1991; Latash, 1993). Recent brain imaging studies revealed that different cortical areas are involved in the two types of behavior (Schaal, Sternad, Osu, & Kawato, 2001; submitted). While rhythmic wrist movements were primarily accompanied by primary motor and somatosensory areas, discrete wrist movements showed additional cortical activity in parietal and cingulate areas. On the basis of these theoretical and empirical results, the present question is whether the coupling of rhythmic and discrete movements is constrained to high-level cortical areas. In this case, the simultaneous performance of rhythmic and discrete movements should show similar constraints, regardless of the limbs involved. The same effects that were identified in single-joint movements should also be seen in two-joint bimanual movements.

Alternatively, if the interaction effects were specific to the single-joint nature of the task, then bimanual performance should show different effects. Adamovich and colleagues (1994) suggested that the discrete and rhythmic movement commands have to be issued sequentially, and kinematic coupling features were relegated to the peripheral merging of the two movements. This explanation has little to say about a similar task combination in a two-limb case.

Two studies have considered a two-handed task involving rhythmic and discrete movements. Michaels and Bongers (1994) examined the time to initiate a discrete finger movement upon triggering by a stimulus, while a rhythmic tracking movement was performed with the same or the contralateral arm. Reaction time (RT) was shown to be dependent on the phase of the ongoing oscillation. Interesting in the present context is that even when the discrete movement was performed by the other hand, the phase dependence of RT on the oscillation still existed, even though less consistent. The authors consequently argued that the interaction between the discrete and rhythmic components happened at some higher level of the central nervous system. In a similar study, Latash (2000) measured simple reaction time of elbow or ankle movements performed against the background of rhythmic wrist movements. However, he arrived at slightly different results. Only when both movements were performed by the same limb was RT modulated by the phase of the rhythmic movement. If participants performed a sinusoidal isometric force to the bottom of a cup that they held in the other hand and released the grip force in response to a visual stimulus, RT of the releasing hand still showed similar but very variable modulations by the phase of oscillatory movement. If the sinusoidal force was exerted onto some unrelated surface, this modulation disappeared. The author proposed that anatomical or contextual coupling was necessary for RT modulation in a discrete-rhythmic dual task.

Based on these preceding studies, several issues need to be further addressed in the present experiments. First, while the studies on reaction time in interlimb coordination are close in spirit to the present experiments, the only measured variable was reaction time. Their focus was on the time constraints for initiating a new movement, leaving aside the interaction effects throughout the concurrent performance, which are also of interest in the present experiments. As we identified in the single arm movement, the interactions between these two movement components were genuinely bidirectional. How do these mutual influences fare, if the two movement components are performed by separate limbs? Second, if the interactions are specific to the combination of the discrete and rhythmic movements, then the coupling between an ongoing rhythmic movement and a newly initiated rhythmic movement should lead to different interaction effects. Two experiments will address these issues. In Experiment 1, participants will oscillate their domi-

nant arm with a horizontal elbow rotation and initiate a discrete movement with their nondominant arm while continuing the oscillation. In Experiment 2, the second movement will also be a rhythmic movement that is similarly triggered by an auditory stimulus and should be continued in synchrony with the first rhythmic movement. Comparative analyses will reveal the features of initiation and combination of rhythmic and discrete movements and whether they have different perturbing effects.

Method

Participants

For Experiment 1 (DI-R), there were 7 volunteers from The Pennsylvania State University (5 male, 2 female). Their ages ranged from 19 to 41 years. Seven reported to be right-hand dominant, while 1 reported himself to be left-hand dominant. For Experiment 2 (RI-R), there were 9 volunteers from The Pennsylvania State University (6 male, 3 female). Their ages ranged from 20 to 41 years. All subjects reported to be right-hand dominant. None of the participants had suffered any serious injury to either arm. Prior to data collection, the participants were informed about the experimental procedure and signed the consent form in agreement with the University's Regulatory Committee.

Experimental Apparatus and Data Collection

The participant was seated in front of a table with each forearm placed horizontally on a foam-padded metal support arm affixed to a vertical axle. The height of the chair was adjusted so that the upper arms were horizontal and at the same height as the forearms. The center of rotation of each elbow joint was aligned with the axle of the respective apparatus. As the chest also rested against the table, trunk and thereby shoulder movements were minimized. Elbow flexion and extension occurred in the horizontal plane (see Figure 1). The participants grasped a wooden handle affixed to the end of each arm support. To ensure a fixed forearm position, a Velcro band strapped the forearms moderately tightly to the support arms. Two vertical wooden rods of 15 cm in height (T1 and T2) served as amplitude targets (minimum and maximum) for the rhythmic dominant arm and were placed on the

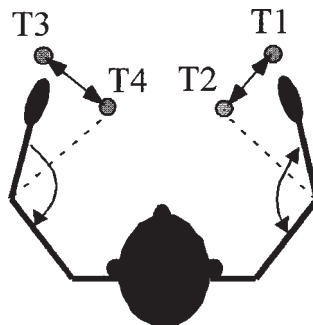


Figure 1 — Top-down view of the experimental setup. The circles indicate the four targets for the two arms (see text for details).

table on an arc whose origin was at the elbow joint of the arm and whose radius extended approximately 5 cm beyond the fingertips. For Experiment 1, target T1 was positioned where the elbow is flexed to 110° (where 180° was defined as full arm extension); T2 was placed at 90° . Two identical targets (T3 and T4) were placed symmetrically for the nondominant arm. Experiment 2 increased all periods by 50 ms, as the shortest period in Experiment 1 proved to be very short. Consequently, also the target amplitude was increased to a range of 30° between 115° and 85° .

Data Acquisition and Data Processing

Data of joint angular positions were collected by two potentiometers, one affixed to the axle of each arm apparatus. The rotational resolution of the potentiometer was 0.04° . Electromyographic data was collected from the biceps brachii and the lateral head of the triceps of both dominant and nondominant arm. The sampling frequency for both kinematic and electromyographic data was 500 Hz. The analog EMG signals were band-pass filtered with cutoffs at 10 Hz and 1000 Hz and subsequently amplified with a gain of 5K. (The low-pass cutoff could not be set lower due to a hardware constraint; however, the unfiltered data did not contain frequencies higher than 250 Hz. Hence, a sampling frequency of 500 Hz proved to be sufficient.) A computer-generated auditory signal (tone duration: 50 ms, frequency: 770 Hz) set the oscillation periods for the initial 5 s of the movement task. After its termination, a silent interval of randomized duration between 3 and 5 s followed before another auditory signal (duration: 400 ms, frequency: 1000 Hz) marked the onset of the initiation of the movement. The output of the computer speaker was recorded to provide information about the temporal onset of the rhythmic and the imperative signal at the same time basis as the other data. The collection of all signals was controlled by a customized program written in LabView Software (National Instruments, TX, USA) on a Macintosh Computer (PowerCenter Pro 210, Power Computing). The digitized EMG signals were rectified and filtered using a 4th-order low-pass Butterworth filter with a cutoff frequency of 25 Hz. The joint angle data were filtered by a low-pass 4th-order Butterworth filter with a 25-Hz cutoff frequency.

Procedure and Experimental Conditions

In both experiments, the participant began each trial with his/her elbows positioned so that the forearm of the dominant arm was aligned with T1 and the forearm of the nondominant was aligned with T3. He/she was instructed to begin oscillating the dominant rhythmic arm between T1 and T2, completing one full cycle per metronome signal. After 5 s, the metronome signal ceased, but the participant continued to oscillate at the same prescribed period and amplitude until he/she heard the imperative signal. This signal occurred at a random interval and hence occurred at a random phase of the oscillation.

In Experiment 1, hereafter referred to as DI-R (*Discrete Initiation against Rhythmic movements*), the participant performed a discrete movement with the nondominant arm while the dominant arm continued to perform rhythmic elbow rotations. In Experiment 2, hereafter referred to as RI-R (*Rhythmic Initiation against Rhythmic movements*), the nondominant arm performed a rhythmic movement. In DI-R, he/she was instructed, upon hearing the imperative signal, to “shift your

nondominant arm from T3 to T4 as fast as possible, without stopping the ongoing rhythmic movements between T1 and T2.” After stopping the discrete movement at T4, the participant continued to oscillate the dominant limb between T1 and T2 until the experimenter signaled the end of the trial. As the instruction contained two important task elements, Experiment DI-R was performed in two blocks, where the instruction explicitly set two different foci of attention: In the “rhythmic attention” condition the participant was instructed to fix his/her gaze on the dominant rhythmic limb and to primarily “focus on not allowing the rhythmic movement to be disturbed”. In the “discrete attention” condition, the participant’s gaze was fixed on the nondominant discrete limb and he/she was instructed to primarily “focus on reacting and moving as fast as possible”. The amplitude for the continuously rhythmic and the discrete movements was 20°. This amplitude was chosen to be the same as in previous single-joint experiments (Sternad et al., 2000) for better comparison with previous results.

The two attention conditions were presented in two blocks, with the order counterbalanced across participants. Within each block, four metronome periods were used: 250 ms, 350 ms, 450 ms, and 550 ms, each presented 15 times for each attention condition and their order fully randomized. In each trial, the trigger signal occurred at a random phase of the oscillation, leading to an approximately uniform distribution of the trigger signal across trials. To keep the number of trials manageable, the discrete movement was only performed in the flexion direction, as previous experiments had not found any differences between flexion and extension movements for the dependent measures determined in the present study (see below and Sternad et al., 2000). Each trial lasted 15 s. Each block lasted approximately 30 min.

For Experiment RI-R, the participant was seated in the same way with the targets T1 to T4 placed as described above. The auditory signals were also identical. The difference in the task was that upon hearing the imperative signal, the participant was instructed to “initiate a rhythmic movement in the nondominant arm starting as fast as possible, from T3 and moving to T4, and then continue to oscillate at the same rhythm as the dominant arm”. During the experiment the participant was repeatedly reminded to initiate the movement as fast as possible. No instruction was given whether the bimanual oscillation should be in-phase or anti-phase. After initiation of the nondominant arm movement from T3 to T4, the participant continued to oscillate both arms until the experimenter signaled the end of the trial. The amplitudes for both the continuously rhythmic and initiated rhythmic movements were 30°.

Four period conditions of 300 ms, 400 ms, 500 ms, and 600 ms were presented. (The fastest period, 250 ms in Experiment DI-R, had proved to be very fast. Hence, we increased all four periods by 50 ms.) Each of them was presented 15 times, with their order fully randomized. Because the results from Experiment DI-R indicated no significant difference between the two attention conditions in the variables of interest, the experiment was conducted with one instruction only, where participants were told to focus straight ahead. Each trial lasted approximately 15 s. The total experiment lasted about 30 min.

Calculation of Dependent Measures

Figure 2 shows a representative trial with the time series of position and EMG activity of both arms to provide a visual guide to the calculation of the dependent

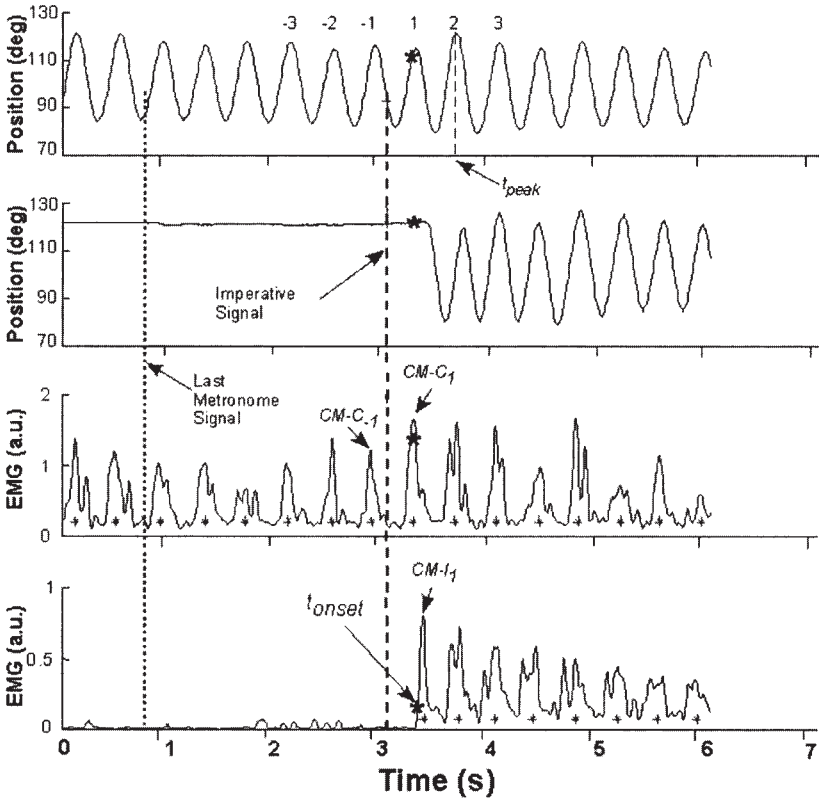


Figure 2 — Time series of a single trial showing the position signals and the two EMG signals of biceps brachii of both arms in a rhythmic initiation trial. The dependent measures are described in the methods. The EMG signals are in arbitrary units.

measures. To begin, the times of the peaks of the rhythmic position signal were determined and numbered with negative integers i before the onset of the initiated movement, and with positive integers after the onset. The EMG bursts were numbered in analogous fashion. The individual cycle periods were calculated between the times of successive peaks at $i - 1$ and i . The individual cycle amplitudes of the rhythmic signal were calculated as the difference between successive peaks and valleys. The mean period and the mean amplitude for the trial segment prior to the movement initiation were calculated as the average over of the cycles between the last metronome beep and the imperative signal (see dashed lines) and labeled T_{pre} and A_{pre} . To calculate the means for the trial segment after the discrete movement, three cycles from $i = 3$ to $i = 5$ were entered into the means T_{post} , A_{post} . The first two cycles were excluded to reduce transient effects, which was captured in the phase shift.

To determine the timing of the bursts of the EMG activity of the biceps brachii, the center of mass of each burst CM_i was found. The time of this CM proved to be a more robust estimate of the time of maximum EMG activity than the maxima of the bursts. To calculate the CM , the EMG signal for the rhythmi-

cally moving hand was first divided into cycle windows defined between two successive minima of the corresponding displacement signal. The rhythmic burst was always near the center of the window. The window of the first $CM-I_i$ of the initiating arm spanned from the onset of the imperative signal to the first kinematic minimum. Although this window was of varying duration as imperative signal occurred at different time intervals before the movement onset, this windowing did not introduce any bias, because the EMG signal of the nondominant hand was at a relatively low level prior to onset. The rectified EMG bursts in each window were then numerically integrated using the trapezoid method. The CM_i was found as the time at which the integral reached half its total value for the i^{th} window. The time of these CM s are shown as stars in Figure 2. The cycle periods were calculated as the difference between two successive CM 's. The CM 's for the initiating arm were labeled as $CM-I$ and, for the continuous arm, $CM-C$. The average period T was calculated across the five cycles directly preceding the imperative signal. This average period was compared to a period estimate that was determined on the basis of the kinematic landmarks. The difference within a trial between these two estimates was of the order of a few milliseconds. Comparing the two period estimates across different trials, this discrepancy showed no bias.

The time of the onset of the movement of the discrete or rhythmic initiation arm t_{onset} was determined on the basis of the biceps brachii signal. We determined the time of the onset of the first EMG burst in the initiating arm using a graphic method picking the time of supra-threshold activity. In Figure 2, t_{onset} is shown by a star in the EMG signal of the initiating arm. This time is projected into the other three times series and similarly indicated by a star. To confirm the reliability of the "hand-picking," two experimenters repeated the procedure. The results were compared, and no significant differences were found. Premotor reaction time RT was calculated as the temporal difference between the beginning of the recorded imperative signal t_{imp} and the onset of the rhythmic initiation arm's movement t_{onset} .

Calculation of Phase Variables

In order to compare the relative timing of events between trials of different movement periods, the above measures were converted into phases. The phase shift of the continuing rhythmic arm D_f , which captures the perturbation of the rhythmic movement by the second movement, was calculated as follows:

$$\Delta\phi = 2\pi \left(\frac{t_{peak,1} - (t_{peak,-2} + 2T_{pre})}{T_{pre}} \right)$$

where $t_{peak,-2}$ refers to the time of the peak two cycles before t_{onset} , and $t_{peak,1}$ to the first peak after the transition (see Figure 2). By adding two cycle periods T_{pre} to $t_{peak,-2}$, the oscillation was projected forward as if unperturbed. The resulting time was subtracted from the actual $t_{peak,1}$, and the time difference was then transformed into a phase. If there was no perturbation, this metric should be zero. If the cycle of the oscillation was lengthened, this metric was positive. Conversely, it is negative if a cycle of the rhythmic arm movement was shortened.

The phase of the imperative signal f_{imp} was calculated as follows:

$$\phi_{imp} = 2\pi [(t_{imp} - CM-C_{-1}) / T].$$

The phase onset of the initiated movement f_{onset} was calculated using the time difference between $CM-C_{-l}$ and $CM-I_l$, converted into phase:

$$\phi_{onset} = 2\pi [(CM-C_{-l} - CM-I_l) / T].$$

In order to assess the degree to which activity in the continuous and initiating EMG bursts synchronize, the phase of alignment between the two EMG signals f_{AL} was computed as follows:

$$\phi_{AL} = 2\pi (CM-I_l - CM-C_l) / T.$$

Note that for f_{AL} , the initiating burst was compared to different burst than for f_{onset} . Hence, f_{AL} can be positive and negative.

Statistical Analyses

The dependent measures of each experiment were evaluated with repeated-measures ANOVAs. For DI-R, a 2 (attention) 3 4 (period) repeated-measures ANOVA was applied in most cases, with a $p > .05$ to define statistical significance. When the within-trial parameters were compared, an extra factor trial segment was added to make a 2 3 4 3 2 repeated-measures ANOVA. For RI-R, a one-way ANOVA with four period conditions was applied for most dependent measures. When within-trial changes were tested, a 4 3 2 ANOVA was conducted. The comparison between the two experiments, RI-R and DI-R, was only done qualitatively by comparing distributions with χ^2 tests, as there were too many design differences between the two experiments to warrant a direct comparison.

Results

Perturbation of the Oscillation By the Initiation of the Second Movement

Mean Periods and Amplitudes Before and After the Discrete Movement.

Before analyzing the perturbing effect of the discrete movement onto the continuing rhythmic movement of the dominant arm directly, it needs to be established whether the oscillations in the steady state segments of the continuing oscillations after the second movement were maintained after the transient interval as instructed. Hence, mean periods and mean amplitudes were submitted to ANOVAs comparing the behavior before and after the imperative signal separately for the four different period conditions.

In Experiment DI-R, the average periods were calculated for each trial and condition per participant and were submitted to a 2 (attention) 3 4 (period) 3 2 (trial segment) repeated-measures ANOVA. The interaction between period and trial segment was significant ($F_{3,18} = 57.20, p < .0001$), indicating that the longer periods shortened in the post-transition segment and shorter periods tended to lengthen in the post-transition segment. A significant main effect for trial segment signaled that a shortening of the period after the discrete event was dominant ($F_{1,6} = 120.78, p < .0001$). While systematic, these changes were only 8 ms on average, as can be seen from Table 1. A highly significant main effect for period verified that the subjects followed the metronome pacing ($F_{3,18} > 1000, p < .0001$). Attention also produced a main effect ($F_{1,18} = 6.51, p < .05$).

Table 1 Mean Cycle Periods (ms) and Amplitudes (deg) for Before (Pre) and After (Post) the Discrete Transition Listed for Experiments DI-R and RI-R

	DI-R					
	Discrete Attention		Rhythmic Attention		RI-R	
	Pre	Post	Pre	Post	Pre	Post
Period						
250/300	253	259	257	260	306	318
350/400	340	337	342	340	394	393
450/500	436	422	437	424	485	464
550/600	527	501	527	505	586	545
Amplitude						
250/300	17.1	17.5	16.3	16.6	30.5	31.7
350/400	20.8	21.1	18.8	18.8	33.1	33.4
450/500	23.3	23.3	20.4	20.5	34.6	34.9
550/600	22.7	23.0	21.4	21.5	34.5	35.0

As the instruction did not emphasize accuracy in the amplitudes, there was room for modulation of amplitude in conjunction with different periods. The same 2 3 4 3 2 ANOVA detected a significant interaction between the two Attention modes and Period ($F_{3,18} = 4.84, p < .05$). This indicated that when attention was directed at the discrete arm, there tended to be an increase in amplitude in the rhythmic arm. This increase was not as pronounced when attention was directed at the rhythmic arm. As Table 1 shows, though, these differences were only by maximally .4°. The analysis also showed a significant main effect in which the amplitude increased as the period increased ($F_{3,18} = 142.14, p < .0001$). A significant main effect showed that amplitudes were larger in the discrete attention mode ($F_{1,6} = 77.25, p < .0001$). It should be noted that there was no overall change in the mean amplitude for the time before and after the imperative signal. The means across participants are also included in Table 1.

In Experiment RI-R, analyses on the same average periods with a 2 (trial segment) 3 4 (period) ANOVA rendered very similar effects as in Experiment DI-R. A significant interaction between trial segment and period showed that the longer periods shortened in the post-transition segment and shorter periods tended to lengthen in the post-transition segment ($F_{3,24} = 50.88, p < .0001$). Also consistent with Experiment DI-R, there was a significant main effect observed between the mean period before and after the imperative signal, indicating an overall speeding up ($F_{1,8} = 65.85, p < .001$). A significant difference between periods verified once again that the participants followed the metronome pacing ($F_{3,24} > 1000, p < .0001$).

The same 2 3 4 ANOVA was conducted on the mean amplitudes for the time before (A_{pre}) and after (A_{post}) the imperative signal at different period conditions. A significant main effect showed that again the amplitudes increased across periods ($F_{3,24} = 23.90, p < .0001$). There was no significant effect found between the amplitudes before and after the initiation of the second rhythmic movement.

Phase Shift of the Continuous Rhythmic Arm. To determine if the continuously rhythmic arm was perturbed by the initiation of the second movement, the phase shift $D\phi$ was calculated for each trial. For both experiments ANOVAs tested whether $D\phi$ depended on the task conditions, specifically the period of oscillation. For each participant the mean values of $D\phi$ were determined across the 15 trials for each Period and Attention condition and entered into the ANOVA. For Experiment DI-R, a 2 (attention) \times 4 (period) ANOVA identified significant differences in $D\phi$ for the different periods but not for the instruction conditions ($F_{3,18} = 30.07, p < .001$). Similarly for Experiment RI-R, a one-way ANOVA identified different $D\phi$ for the four different periods ($F_{3,24} = 12.73, p < .0001$). The bar charts in Figure 3 illustrate these results. As can be seen, all $D\phi$ were negative, indicating a shortening of the oscillatory cycle due to the secondary movement. In DI-R there was a trend that the perturbation was greater—that is, larger shifts—when the attention was directed at the initiating arm. Also, $D\phi$ had a tendency to be smaller in RI-R compared to DI-R, but a direct statistical comparison was difficult due to the differences in design.

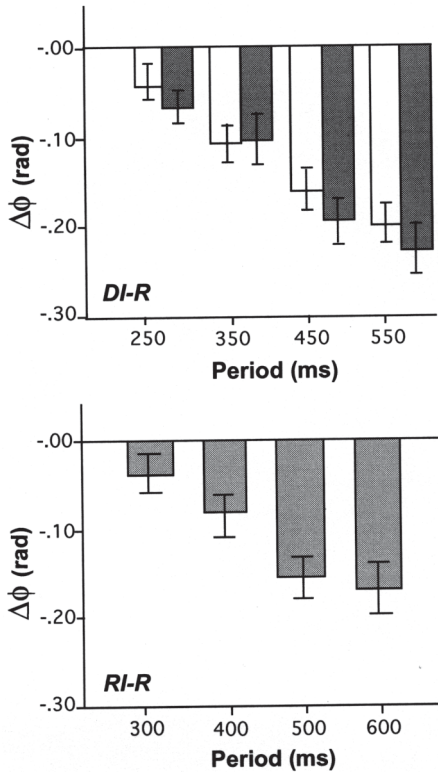


Figure 3 — Average phase shifts $\Delta\phi$ and their standard error in different period conditions shown separately for Experiments DI-R and RI-R. In the top panel, the darker bars depict the discrete attention condition, and lighter bars depict the rhythmic attention condition.

Effect of the Rhythmic Movement Onto the Secondary Movement

Reaction Time of the Initiated Movement. The premotor reaction time *RT* was determined for each trial, and the values were averaged for each participant and condition. For Experiment DI-R, the 2 (attention) 3 4 (period) ANOVA produced significance for the main effect between the two attention conditions. As to be expected, *RT* was shorter when attention was directed to the initiation of the discrete movement ($F_{1,6} = 13.89, p < .01$). It should be noted that *RT* did not change significantly between the different periods (Figure 4).

For Experiment RI-R, *RT* was also compared across the four periods. The one-way ANOVA revealed a significant main effect in which *RT* increased with increasing period as seen in Figure 4 ($F_{3,24} = 4.56, p < .05$). The mean *RT*s for each period were as follows: 204 ms for the 300-ms period, 202 ms for the 400-ms period, 219 ms for the 500-ms period, and 245 ms for the 600-ms period. Post hoc Tukey tests identified pairwise differences between the 600-ms period and the

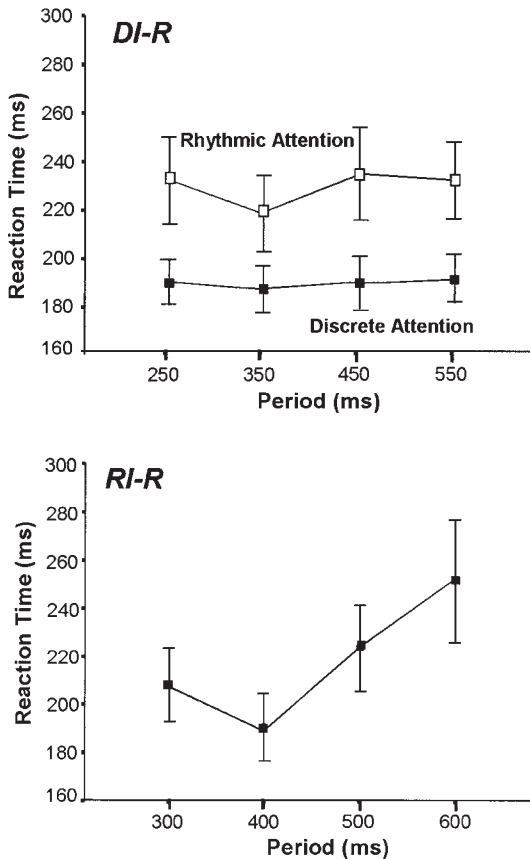


Figure 4 — Mean reaction times with standard errors as a function of the oscillation periods. In Experiments DI-R, average values are plotted separately for the two attention conditions.

300-ms period, and between the 600-ms and 400-ms periods ($p < .05$; see Figure 4). In addition, from the perspective of a perturbed oscillation, it can be expected that RT is a function of the phase of the perturbation—that is, the phase of the imperative signal f_{imp} or the phase of the initiation f_{onset} . However, regressions of RT on f_{imp} or f_{onset} did not identify a significant relationship in either of the two experiments.

Phase of the Discrete Movement Onset. A primary interest of the bimanual experiments was whether the initiation of the secondary movement was constrained to a subset of phases of the ongoing oscillatory movement, similar to the results of the single-joint actions. The phases of onset of the discrete movement f_{onset} in Experiment DI-R were pooled for all participants and both attention and all four period conditions and inspected in a histogram. As Figure 5 shows, there is a relative uniform distribution, showing no preference for any particular phase of the oscillation. The bold line indicates the distribution of the phases of the imperative signal. A χ^2 test comparing the distributions of f_{onset} and f_{imp} with a uniform distribution found no significant difference. The χ^2 values were 22.35 ($p = .50$) and 19.75 ($p = .50$), respectively. Comparing the histograms in the same way for the individual attention and period conditions did not detect any differences.

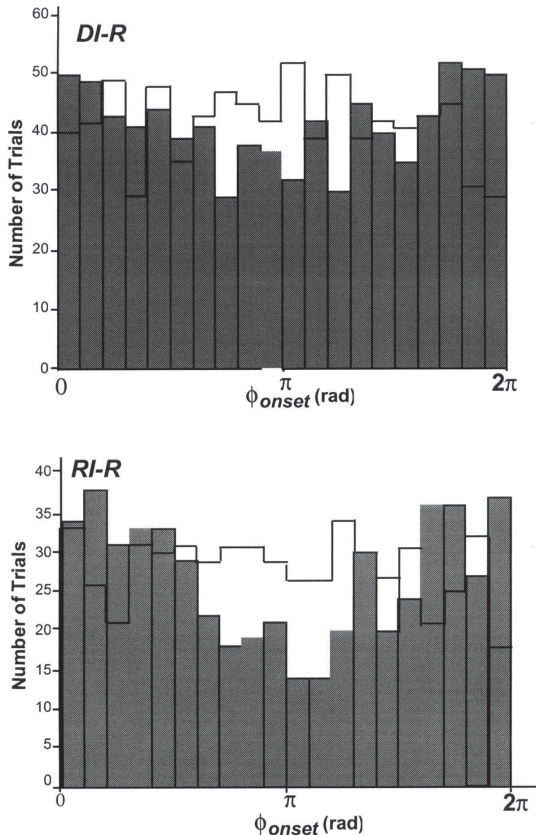


Figure 5 — Histograms of phases of the initiation ϕ_{onset} of the secondary movement for Experiments DI-R and RI-R. All conditions are pooled together.

In Experiment RI-R the same histogram showed that f_{onset} clustered around 0 or 2π rad, or conversely, the initiation occurred least often at a phase of π rad of the ongoing oscillation (Figure 5). The bold line shows the distribution of f_{imp} . A χ^2 test verified that the distribution of f_{onset} was non-uniform, with a significant value of 44.15 ($df = 19, p < .001$). The distribution of f_{imp} was not different from a uniform distribution ($\chi^2 = 21.78, p = .50$). This non-uniform distribution was observed for all period conditions.

Alignment of the Ongoing Rhythmic and the Initiation Arm. The degree of synchronization between the ongoing rhythmic and the secondary movements was evaluated by measuring how the two arms aligned in time following the initiation. To this end, the timing of the EMG bursts directly following t_{onset} were compared, and the time difference was converted into phase f_{AL} as described in the Methods section. Figure 6 shows a histogram from Experiment DI-R, depicting f_{AL} from all trials and all participants. The histogram reveals that there is an inclination for the arms to synchronize with a single mode close to zero ($-.02$ rad). The χ^2 test verified this non-uniform distribution with a significant value of 30.23 ($df = 19, p < .001$). Experiment RI-R's results show this feature even more prominently. In Figure 7 three histograms are shown for three f_{AL} , determined at the first, second, and third burst following the initiation. Comparison of the first f_{AL} in DI-R and RI-R revealed a similar distribution. However, with the continued oscillation in both arms in RI-R, it can be seen that this distribution became increasingly sharper at the second and third bursts.

Peak Velocity of the Continuous Rhythmic and the Discrete Initiation Arm. Another feature for the influence of the primary rhythmic onto the secondary movement is the peak velocity achieved in the secondary movement directly after the initiation. Note that the instruction always emphasized to move as fast as possible. To determine these temporal constraints between the two arms in Experiment DI-R, a 2 (arm) 3 2 (attention) 3 4 (period) ANOVA was performed. The results revealed a significant interaction between the two arms and four periods ($F_{3, 18} = 20.46, p < .0001$). As illustrated in Figure 8, peak velocity decreased as period increased. A significant main effect for periods confirmed this period

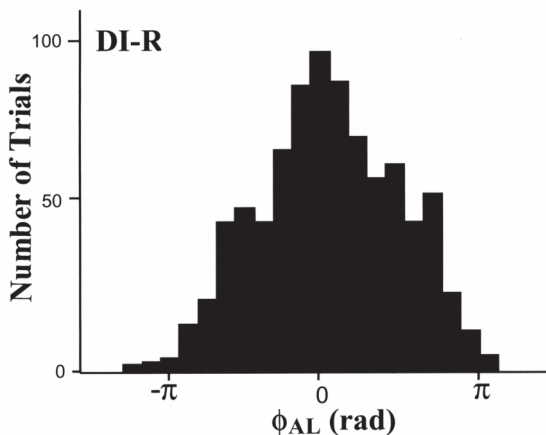


Figure 6 — Phase of alignment ϕ_{AL} of the first EMG burst with the closest rhythmic burst directly following the initiation of the discrete movement in Experiment DI-R.

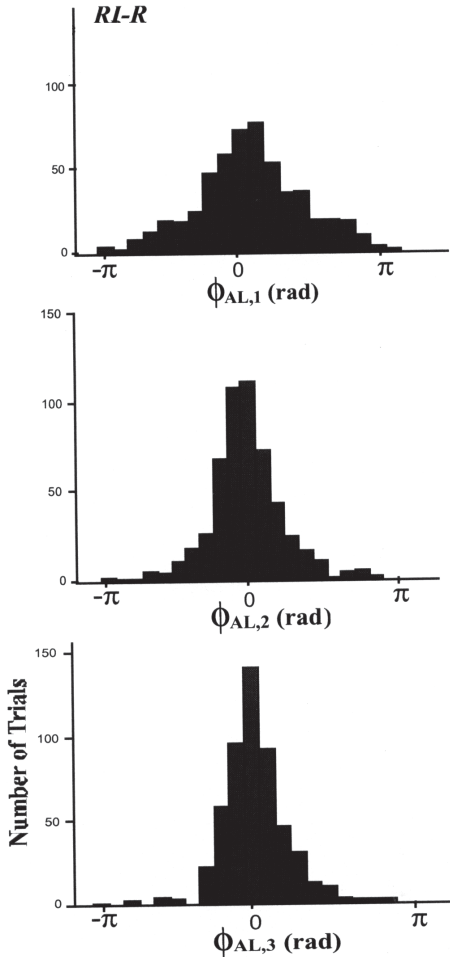


Figure 7 — Alignment of the EMG bursts of both arms following the initiation of the secondary rhythmic movement. The three panels show the alignment in the first, second, and third cycles of the bimanual rhythmic movements of Experiment RI-R.

dependency ($F_{3,18} = 16.02, p < .0001$). Another main effect signaled that peak velocity in the discrete initiation arm was higher than in the continuously rhythmic arm ($F_{1,6} = 6.52, p < .05$). The two different attention instructions did not produce differences in peak velocity. While the decrease in the continuous rhythmic arm is to be expected, a simple effect analysis tested whether the decrease in peak velocity seen in the initiating arm was also significant. The simple effect was close to significance but did not reach it ($p < .061$).

For Experiment RI-R, a 2 (arm) 3 4 (period) ANOVA was performed on the mean values of peak velocity, and results are presented in Figure 8. A significant interaction between the different arms and periods indicated that again peak velocity scaled with the oscillation period, but the initiating arm was slower and was modulated less than the continuous arm ($F_{3,24} = 27.47, p < .0001$). The differences between values for the four period conditions were scrutinized by post hoc Tukey

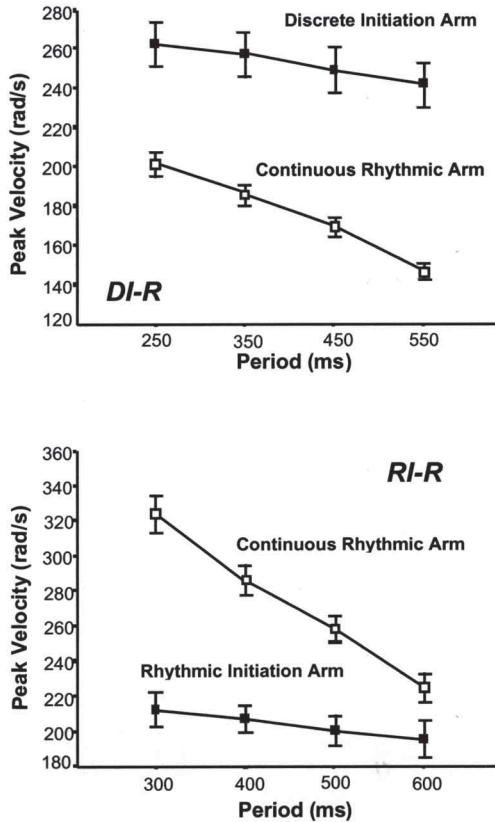


Figure 8 — Peak velocity of both arms directly following the initiation in different period conditions shown for both Experiments RI-R and DI-R. The graphs show averages and their standard errors across all trials and participants. For Experiment DI-R, the two attention conditions are pooled together.

tests. Only the values for the slowest and fastest showed to be significantly different ($p < .05$). This overall decrease was confirmed in a significant main effect for period ($F_{3,24} = 46.66, p < .0001$). The simple effect for period at the initiating arm was close to significance but did not reach it ($p = .057$). When comparing the peak velocity between the ongoing rhythmic and rhythmic initiation arms, a significant main effect was found indicating a greater peak velocity in the ongoing rhythmic arm ($F_{1,8} = 13.31, p < .01$). Note that in Experiment DI-R, the discrete arm showed a faster velocity, while the rhythmic initiation arm showed a slower velocity than the continuous arm. In absolute terms, the velocity averaged across the four periods in DI-R was 250 deg/s, while it was 210 deg/s in RI-R.

Discussion

Asymmetrical bimanual tasks are ubiquitous in our daily behaviors, with examples ranging from tying shoelaces to cutting bread. One specific case is when one hand is engaged in a rhythmic movement and the other hand begins another action, either a single reach or another rhythmic movement. Are we unlimited in such

combinations or are there certain limitations, specifically when discrete movements are coupled to rhythmic movements? In previous work, we pursued the hypothesis that rhythmic and discrete actions are fundamental units of behavior such that complex behavioral actions can be broken down into these two primitives. Single- and two-joint tasks were examined that required relatively complex trajectories but could be broken down into discrete and rhythmic elements. Experimental and modeling results showed that these trajectories could be simulated by discrete and rhythmic pattern generators that interacted by a mutually inhibitive coupling (de Rugy & Sternad, *in press*; Sternad et al., 2000; Sternad et al., 2002; Sternad & Dean, *submitted*). The present experiment presents a related line of pursuit where rhythmic and discrete elements are performed by two arms. The overarching question is: Are rhythmic and discrete actions fundamentally different control regimes? A subordinate question is: Are there invariant constraints between the two units regardless of the specific joints involved that speak to their locus of control and their interactions at some higher level?

The first focus of attention was directed at the rhythmic movement and to what degree a second discrete or rhythmic movement perturbed the oscillation. Analysis of the oscillation parameters period and amplitude before and after the initiation gave a consistent picture, regardless of which movement was initiated. Shortly following the initiation of the secondary movement, the oscillatory period changed slightly but systematically in both tasks. When the task component—reacting as soon as possible—was prominent in the discrete initiation, the oscillation showed a trend to an intermediate, probably preferred movement rate. In addition, a trend to speed up for the slower periods was observed, but an overall acceleration prevailed. This small but systematic speeding up is in accordance with the previous results, which were interpreted as an increased level of co-contraction after a reaction time movement, leading to higher stiffness and, hence, faster oscillations (Sternad et al., 2000, 2002). These temporal changes were accompanied by an overall but very small increase in the amplitudes. This was probably due to the fact that the amplitude targets were in general small for the given periods. The focus of attention, whether directed at the discrete or the rhythmic arm, did not show any influence on these changes. In sum, small systematic changes occurred in the oscillation parameters due to the time-stressed action of the second arm that persisted for some cycles. The same pattern was observed when a rhythmic or discrete movement was initiated.

The perturbation of the oscillation was also quantified by its resetting of phase. Again, the results for both movement combinations rendered similar patterns. The time-stressed initiation of the secondary movement caused a shortening of the cycle in the continuous movement that concurred with the secondary movement. This shortening of the cycle depended on the period of the oscillatory movement. The overall result of period-dependent phase shifts was in accordance with results reported in the previous experiments with single-joint tasks performed over a range of different periods (Sternad et al., 2002). Such transient compression of the rhythmic cycle can be better understood when one considers the duration of the discrete movement when performed in isolation. For instance, Gottlieb and colleagues reported for about 50° elbow joint movements durations of less than 220 ms (Gottlieb, 1998; Gottlieb, Corcos, & Agarwal, 1989). Despite the larger extent compared to our discrete actions, this duration is clearly shorter than even the fastest oscillatory period performed in the present experiments. It appears that there is a strong tendency for achieving immediate temporal symmetry between

the two flexion movements, such that the discrete movement is lengthened and the simultaneous rhythmic cycle is shortened. When attention was directed to the rhythmic movement in DI-R, there was a slightly smaller phase shift. This shows that the volition to maintain the oscillation can slightly reduce the perturbing effect from the discrete movement but only to a small degree.

This strong tendency for synchronization between the two arm movements is further supported by the temporal aligning of the two flexor bursts of the two arms that are closest in time. Note that for this measure, the center of mass of the initiation burst was aligned with the center of mass of the nearest burst of the continuous arm. This means that for the initiation phases between 0 and p rad, the EMG burst in the continuous arm prior to initiation was used—that is, the same burst served as comparison for the calculation of phase of onset. However, for initiation phases between p and $2p$ rad, it was the subsequent burst that was used for the calculation. Further, the alignment also captures that the EMG burst of the continuous arm was advanced in order to make the two EMG activities synchronized. This advance was indicated by the phase resetting above. In both tasks alike, the phase differences between the maxima of the two flexor bursts of the two arms immediately following the initiation were predominantly close to zero. While this strong tendency for the synchronization of the two homologous muscle activations is a robust phenomenon reported in many studies (Heuer, 1993; Swinnen et al., 1997), it is remarkable in the present case that this became prominent even if there were still asynchronies at the moment of initiation. In sum, measures that captured the perturbations of the rhythmic movement did not distinguish differences between the discrete and rhythmic initiation.

Turning to the initiation of the secondary movement, however, a clear difference between the two movement tasks emerged. In DI-R, there was no constraint evident that limited the onset of the discrete movement. The discrete flexion could be initiated at any phase of the ongoing rhythmic cycle in the other hand, as evidenced by a uniform distribution of the onset phases and reaction times under both attention conditions. This result is clearly different from what has been observed in the single-hand version of the task (Sternad et al., 2000). However, it replicates the findings by Latash (2000), who reported that, for a task involving the initiation of an elbow flexion while oscillating the wrist of the same or other arm, the phase of initiation of the elbow movement was only modulated if the two movements were performed by the same arm. Latash argued that the two movements had to be part of an anatomical or functional unit in order to exert coupling constraints onto each other. Such anatomical or functional coupling was apparently not present in our task. Commencing a rhythmic movement is constrained to be close to in-phase with the ongoing rhythmic movement. This confirms the findings of a large body of literature, which has documented that in-phase coordination is preferred and is more stable than anti-phase in bimanual rhythmic movements (e.g., Kelso, 1995; Sternad, Amazeen, & Turvey, 1996). The present results, however, document that this even holds for the initiation of a second rhythmic movement. The tendency for in-phase synchronization was further traced in the increasing alignment towards in-phase activity of the two flexor bursts in the three cycles following the initiation.

Premotor reaction time was another marker that revealed the difference between rhythmic and discrete movements. First, in both RI-R and DI-R experiments, the average values of reaction time tended to be longer than those reported for single responses to an auditory trigger. For a unimanual elbow rotation performed

to an auditory trigger signal, we showed in a small additional experiment with the same apparatus that 5 subjects had average premotor reaction times between 114 and 163 ms. These were means of 15 trials each (their overall average was 139 ms, unpublished study). This indicated that some interaction between the control signals of the two hands must have occurred before the overt movement that delayed the initiation. This result also resonates findings by Spijkers and colleagues (1997), who reported a lengthening of reaction time when the two hands initiated movements with two different amplitudes compared to same amplitudes. The authors interpreted these results as indicative of interactions at a parametric level prior to movement initiation.

Second, and of specific interest for the present question, is that while reaction time for a discrete movement was invariant with respect to the simultaneous oscillation period, reaction time for the oscillatory movement was modulated by the oscillatory period of the other arm. For slower oscillations, it took longer to initiate a rhythmic movement. The fact that reaction time was modulated by the rhythmic period in RI-R and not in DI-R indicates that the preparation of a rhythmic movement is different than that of a discrete movement. Sensitivity or synchronization to the activity cycle of the continuous rhythmic movement is already present prior to initiation, such that the initiating hand's movement immediately synchronizes with the ongoing rhythmic movement. As for longer periods, the time difference between the random signal and the rhythmic burst can be longer; the reaction times are also longer on average.

In sum, the variables quantifying the initiation clearly highlight that it matters what kinds of movements are coupled and show that rhythmic and discrete movements pose different challenges to the motor system. This gives support to the hypothesis that specific couplings take place for the rhythmic-rhythmic compared to the discrete-rhythmic case. These data are also consistent with the hypothesis that discrete movements may be governed by a different control structure compared to the rhythmic movement. This difference was recently highlighted in an imaging study that identified significantly different cortical areas involved in the production of discrete movements compared to rhythmic movements (Schaal, Sternad, Osu, & Kawato, 2001; Schaal et al., submitted). Over and above the expected activation in the contralateral primary motor areas and the ipsilateral cerebellum, discrete movements were associated with significant activity in the ipsi- and contralateral parietal cortex and cingulate areas. These additional areas are typically involved in cognitive and intentional aspects of tasks and hence reflect that a target-oriented discrete movement may have other, more "wide-spread" demands on the sensorimotor system.

One last comparison highlights such differences in the coupling between the two movement tasks. Inspection of the peak velocities shows that in DI-R, the discrete velocity was higher than the one of the parallel rhythmic movement. While this is not surprising, it is noteworthy that the peak velocity was still slower than when the discrete movement was performed in isolation, as for instance reported by Gottlieb and colleagues. Typically, peak velocities of isolated fast point-to-point movements have been reported to be in the order of 500 to 600 deg/s (Gottlieb, 1998; Gottlieb et al., 1989), while the maximum velocities of individual trials only reached 400 deg/s in our experiments. Furthermore, peak velocity scaled with the period of the continuous rhythmic hand such that there were slower movements coupled to slower oscillations. This is in accordance with earlier findings in single-joint movements and corroborates the interpretation that this effect is due to the

coupling between the two control signals and not merely caused by mechanical coupling in the single joint (Sternad et al., 2000, 2002). In RI-R, the peak velocity of the second rhythmic movement was slower than the ongoing rhythmic movement. Further, in RI-R peak velocities were less strongly affected by the different oscillatory periods. Given that at initiation an in-phase alignment between the two rhythmic arm movements was already prepared, apparently the modulation was not as prominent in the main part of the flexion movement. Note, though, that when the peak velocities are compared between the two experiments, peak velocities of the continuous rhythmic hand are faster in RI-R than in DI-R. This is due to the fact that the amplitudes were generally larger, and some subjects performed amplitudes up to 35° compared to 20° in DI-R.

In sum, the comparison between the two bimanual tasks revealed similarities and differences in the bi-directional coupling between the two hands when a discrete or a rhythmic movement was coupled to an ongoing rhythmic movement. While the perturbation of the ongoing rhythmic movement was independent of the kind of movement that was initiated, differences were revealed for the initiation. This indicates that at an early stage of control there are specific interactions for rhythmic-rhythmic and discrete-rhythmic coupling. After movement initiation, though, the strong tendency for in-phase synchronization between the two hands shapes discrete and rhythmic movements alike.

With respect to the overall goal to reveal the differences between rhythmic and discrete movements, the experiments provided partial further support to the hypothesis that different control mechanisms are responsible for discrete and rhythmic movements. Discrete movements are not aborted rhythmic movements as has been suggested (e.g., Schöner, 1990), and rhythmic movements are not the concatenation of back and forth flexions and extensions (e.g., Latash, 1992). If this were the case, both the timing of the initiation and the kinematic features of the first flexion part of the two initiated movements should have displayed the same features.

References

- Adamovich, S.V., Levin, M.F., & Feldman, A.G. (1994). Merging different motor patterns: coordination between rhythmical and discrete single-joint movements. *Experimental Brain Research*, **99**, 325-337.
- Amazeen, P.G., Amazeen, E.L., & Turvey, M.T. (1998). Dynamics of human intersegmental coordination: Theory and research. In D.A. Rosenbaum & C.E. Collyer (Eds.), *Timing of behavior: Neural, computational, and psychological perspectives* (pp. 237-259). Cambridge, MA: MIT Press.
- de Rugy, A., & Sternad, D.. *Interaction between discrete and rhythmic movements: Reaction time and phase of discrete movement initiation against oscillatory movements*. Manuscript submitted for publication.
- Feldman, A.G. (1966). Functional tuning of the nervous system with control of movement or maintenance of a steady posture: ii) Controllable parameters of the muscle. *Biophysics*, **11**, 565-578.
- Gottlieb, G.L. (1998). Muscle activation patterns during two types of voluntary single-joint movements. *Journal of Neurophysiology*, **80**, 1860-1867.
- Gottlieb, G.L., Corcos, D.M., & Agarwal, G.C. (1989). Strategies for the control of voluntary movements with one mechanical degree of freedom. *Behavioral and Brain Sciences*, **12**, 189-250.
- Heuer, H. (1993). Structural constraints on bimanual movements. *Psychological Research/Psychologische Forschung*, **55**, 83-98.
- Heuer, H. (1996). Coordination. In H. Heuer & S.W. Keele (Eds.), *Handbook of perception and action. Vol 2. Motor skills* (pp. 121-180). London: Academic Press.

- Heuer, H., Kleinsorge, T., Spijkers, W., & Steglich, C. (2001). Static and phasic cross-talk effects in discrete bimanual reversal movements. *Journal of Motor Behavior*, **33**, 67-85.
- Katsumata, H., & Sternad, D. (2002). Movement coordination from a dynamical systems perspective. *Japanese Journal of Biomechanics in Sports and Exercise*, **6**(2), 76-95.
- Kay, B.A., Kelso, J.A.S., Saltzman, E.L., & Schöner, G. (1987). Space-time behavior of single and bimanual rhythmical movements: Data and limit cycle model. *Journal of Experimental Psychology: Human Perception and Performance*, **13**(2), 178-192.
- Kay, B.A., Saltzman, E.L., & Kelso, J.A.S. (1991). Steady-state and perturbed rhythmical movements: A dynamic analysis. *Journal of Experimental Psychology: Human Perception and Performance*, **17**(1), 183-197.
- Kelso, J.A.S. (1995). *Dynamic patterns: The self-organization of brain and behavior*. Cambridge, MA: MIT Press.
- Latash, M.L. (1993). *Control of human movement*. Champaign, IL: Human Kinetics.
- Latash, M.L. (2000). Modulation of simple reaction time on the background of an oscillatory action: Implications for synergy organization. *Experimental Brain Research*, **131**, 85-100.
- Michaels, C.F., & Bongers, R.M. (1994). The dependence of discrete movements on rhythmic movements: Simple RT during oscillatory tracking. *Human Movement Science*, **13**, 473-493.
- Schaal, S., Sternad, D., Osu, R., & Kawato, M. (2001). Rhythmic movement is not discrete. *Neuroscience Abstracts*.
- Schaal, S., Sternad, D., Osu, R., & Kawato, M.. *Rhythmic arm movement is not discrete*. Manuscript submitted for publication.
- Schöner, G. (1990). A dynamic theory of coordination of discrete movement. *Biological Cybernetics*, **63**, 257-270.
- Spijkers, W., Heuer, H., Kleinsorge, T., & van der Loo, H. (1997). Preparation of bimanual movements with same and different amplitudes: Specification interference as revealed by reaction time. *Acta Psychologica*, **96**, 207-227.
- Staudte, G., Dengler, R., & Wolf, W. (2002). The discontinuous nature of motor execution II. Merging discrete and rhythmic movements in a single-joint system - the phase entrainment effect. *Biological Cybernetics*, **86**, 427-443.
- Sternad, D., de Rugy, A., Pataky, T., & Dean, W.J. (2002). Interactions of discrete and rhythmic movements over a wide range of periods. *Experimental Brain Research*, **147**, 162-174.
- Sternad, D., & Dean, W.J.. *Rhythmic and discrete elements in multi-joint coordination*. Manuscript submitted for publication.
- Sternad, D., Dean, W.J., & Schaal, S. (2000). Interaction of rhythmic and discrete pattern generators in single-joint movements. *Human Movement Science*, **19**, 627-665.
- Sternad, D., Amazeen, E.L., & Turvey, M.T. (1996). Diffusive, synaptic, and synergetic coupling: An evaluation through inphase and antiphase rhythmic movements. *Journal of Motor Behavior*, **28**, 255-269.
- Strogatz, S.H. (1994). *Nonlinear dynamics and chaos: with applications to physics, biology, chemistry, and engineering*. Reading, MA: Addison-Wesley.
- Swinnen, S.P., Jardin, K., Meulenbroek, R., Dounskaia, N.V., & Hofken-Van den Brandt, M. (1997). Egocentric and allocentric constraints in the expression of interlimb coordination. *Journal of Cognitive Neuroscience*, **9**, 348-377.
- Swinnen, S.P., Walter, C.B., & Shapiro, D.C. (1988). The coordination of limb movements with different kinematic patterns. *Brain and Cognition*, **8**, 326-347.
- Swinnen, S.P., Young, D.E., Walter, C.B., & Serrien, D.J. (1991). Control of asymmetrical bimanual movements. *Experimental Brain Research*, **85**, 163-173.
- Wei, K., Dean, W.J., Wertman, G., & Sternad, D. (submitted). *Effect of load on the interaction of rhythmic and discrete movements in single-joint movements*.

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