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Timing and Trajectory in Rhythm Production

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The Wing–Kristofferson movement timing model (A. M. Wing & A. B. Kristofferson, 1973a, 1973b) distinguishes central timer and motor implementation processes. Previous studies have shown that increases in interresponse interval (IRI) variability with mean IRI are due to central timer processes, not motor implementation. The authors examine whether this is true with IRI duration changes in binary rhythm production. Ten participants provided IRI and movement data in bimanual synchronous tapping under equal (isochronous) and alternating (rhythm) interval conditions. Movement trajectory changes were observed with IRI duration (300, 500, or 833 ms) and for 500-ms IRIs produced in rhythm contexts (300/500 ms, 500/833 ms). However, application of the Wing–Kristofferson model showed that duration and context effects on IRI variability were attributable largely to timer processes with relatively little effect on motor processes.

Keywords: timing, trajectory, movement, rhythm

Explicit timing skills, such as those in musical performance, involve sensory, cognitive, and motor factors. An example of a cognitive factor in timing is the generation of a rhythm, a pattern of two or more different time intervals in which the serial order of the intervals is critical. A given rhythm may be performed with different effectors, for instance, the hand or foot. It is therefore plausible to assume a modular timing system that is general across different effectors. Consistency of individual differences in variability in perception and production of temporal patterns (Ivry & Hazeltine, 1995; Keele, Pokorný, Corcos, & Ivry, 1985) suggests that a common timing module serves afferent and efferent timing.

If there is a cognitive timing module that may be applied to a variety of sensory input or motor output modalities, changes in input or output modality might be expected to have consequences for timing. These differences would reflect constraints of the modalities concerned even though there is no change in the cognitive timing component. This leads us to consider the mapping between external sensory or motor events and the internal timer. Thus, on the sensory side, synchronization of tapping with a visual stimulus is less precise than with an auditory stimulus (Kolers & Brewster, 1985; Repp & Penel, 2002). On the motor side, finger tapping using finger flexion and extension has been found to be more variable than when wrist flexion and extension is used to tap the finger (Wing, 1977), and tapping with the foot is more variable than with the hand (Ivry, Richardson, & Helmuth, 2002). Such variance differences may be taken to reflect changes in sensory or motor properties with constant central timing.

It has often been assumed that central and motor factors in timing are independent. Wing and Kristofferson (1973a, 1973b) proposed a two-level model identifying two sources of variance in repetitive finger-tapping performance. According to the Wing–Kristofferson (W-K) model, movement is triggered by a central timer but is subject to a motor implementation delay before the occurrence of the response. Even though the system operates in an open-loop manner without feedback correction, the model predicts negative lag 1 autocorrelation between adjacent interresponse intervals (IRIs) with a value between 0 and $-.50$. Under the W-K model, the lag 1 autocovariance of the IRIs estimates the motor implementation variance, and the IRI variance corresponds to the variance of the timer plus twice the motor variance. Thus, both central timing and motor variance components of the model may be estimated, and a number of studies have shown they are dissociated (for a review, see Wing, 2002). For example, as the target interval increases, timer variance increases without an increase in motor variance (Wing & Kristofferson, 1973a), and neurological disorder affecting the basal ganglia causes an increase in timer variance rather than motor variance (Harrington, Haaland, & Hermanowicz, 1998).

Estimates of the W-K model variance components based on lag 1 autocovariance are biased (Vorberg & Wing, 1996; Wing, 1979). The bias reduces with the length of the sequence of IRIs being analyzed, but longer sequences are more prone to drift in the mean. Drift is a form of nonstationarity that violates the assumptions of the W-K model and affects estimation of the component variances. Various approaches have been suggested to solve the problem of drift, including linear detrending (Vorberg & Wing, 1996), high-pass filtering (Madison, 2001), and differencing (Collier & Ogden, 2001) the IRI time series. It is worth noting that the drift may be seen as representing an important aspect of timer function deserving study in its own right (Collier & Ogden, 2004). A possible experimental model for studying drift proposed by Yu, Russell, and Sternad (2003) involves introducing a discrepancy between the period due to the intrinsic dynamics of the moving limb and the target interval during paced responding. This discrepancy results in

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a drift from the target interval toward the natural period during subsequent unpaced responding.

An alternative approach to estimating the timer and motor components of the W-K model that can use short sequences yet avoids the bias of the autocovariance approach is based on regression (Ivry & Corcos, 1993; Ivry & Hazeltine, 1995). If one assumes a linear relation between the standard deviation (*SD*) and the mean of the IRIs, the slope of the regression line provides an estimate of the duration-dependent timer *SD*, and the intercept, an estimate of the duration-independent motor *SD*. Yet another approach to estimating component variances in the W-K model, which also avoids the bias of the autocovariance estimator, uses simultaneous two-handed tapping. Here, the lag 0 cross-covariance between the IRIs produced by each hand can be used as an estimate of central timer variability, while the variability of the asynchrony between hands estimates motor variability (Ulrich & Stapf, 1984; Vorberg & Hambuch, 1978, 1984).

The models described so far are mostly used to assess isochronous timing; however, it would be interesting to contrast central and motor aspects of timing in the production of rhythms comprising a number of different intervals, possibly in a repeating cycle. It is reasonable to suppose that producing a rhythm involves more complex cognitive processes than the production of a sequence of isochronous intervals. Previous studies have shown that intervals produced in a rhythm context are more variable than those produced in an isochronous context (Krampe, Mayr, & Kliegl, 2005; Vorberg & Hambuch, 1978, 1984). Vorberg and Hambuch (1978, 1984) suggested that the generation of rhythms may involve multiple, hierarchically organized timers. In that case the variance of the cycle duration (the interval defined by the sum of the elemental intervals composing the rhythm) depends on the level in the hierarchy from which the response is controlled. Thus, responses driven from lower in the hierarchy are more variable than those driven from higher levels, even though the mean cycle duration is the same. In support of this view, Vorberg and Hambuch (1978, 1984) observed systematic differences in cycle variance across responses terminating different intervals in the cycle. However, they noted positive correlations between some component intervals in the rhythms, whereas their model with hierarchically organized timers predicts only negative or zero correlations.

As an account of the positive correlations in rhythm production, Vorberg and Wing (1996) proposed that the hierarchical representation of a rhythm is transformed into a linear representation and then executed with a single timer operating in a serial manner. If there are rate fluctuations in the output timer, this will result in positive correlations superimposed on the negative or zero correlations expected under a hierarchy. Execution of such a linearized representation of the rhythm would entail switching the timer between the different intervals in the rhythm. Such switching may therefore be expected to introduce additional variance in timekeeping, which could underlie greater variability of intervals produced in a rhythmic context.

Switching between intervals in a rhythm cycle may also affect the accuracy of the mean interval produced, especially in tasks with complex temporal structure. Interval production in a rhythm may involve a simple integer ratio (e.g., 2:1 between the long and short intervals in a two-element rhythm) or a more complex noninteger ratio (e.g., 1.5:1), with the ratio produced in the former case being closer to the target than in the latter (Collier & Wright,

1995). Essens and Povel (1985) showed that in rhythms with a noninteger ratio such as 1.5:1, adjustments in the duration of the intervals occur, the short interval being shortened and the long interval being lengthened so that the ratio approaches 2:1. Even in production of the integer 2:1 ratio, adjustments follow a similar trend, with the short interval being shortened and the long interval being lengthened; however, these adjustments are smaller than in the noninteger ratio. These changes in the ratio of the component intervals over the course of a sequence can take the form of a linear drift (Povel, 1981). Given the previously noted effects of drift on autocovariance estimation, the presence of drift in rhythm production would also be expected to affect estimates of the timer and motor components in the W-K model, but this has not been examined previously. In this study we apply a linear detrending procedure separately to the time series of each component interval in rhythms, so that we can determine whether there is an effect of interval switching on estimates of timer variance even after drift effects are taken out.

The above account of rhythm emphasizes the cognitive demands of serial timing changes demanded by rhythm production. However, the motor system might also be expected to be challenged by serial changes in time interval. Each tap produced by finger flexion must be preceded by finger extension. If the target interval changes, so will the time available for restoration of the finger position for the next tap. Previous studies have sought links between timing and aspects of trajectory; however, they examined only equal-interval responding. For example, Wing (1980) investigated whether the lift movement at the end of each tap might be driven by, and so be dependent on, the occurrence of the preceding finger contact defining the onset of the tap. In that case a hierarchical relation between the timing of the two response events would be expected, and this was not observed to be the case. In a similar vein, Billon, Semjen, and Stelmach (1996) had expected that timing of flexion onset prior to a tap would be less variable than timing of the tap itself, because less motor delay up to flexion onset compared with the tap would imply less accumulated motor variance. In fact, they found the opposite to be the case, and timing of the tap was less variable. Although this might appear to represent timing driven by the end event, under the W-K model it could be explained by assuming a negative correlation between the duration of the final flexion movement and earlier components of the motor delay leading up to flexion onset. However, another class of explanation is that timing is adjusted in relation to the movement trajectory. Thus, it is interesting to note that in a tapping task requiring increase in force (an aspect of trajectory) of one in a series of equal interval responses, Billon and Semjen (1995) reported that timing and force are related, with a harder response occurring later, especially in musically trained participants.

In this study we investigate changes in timing behavior when intervals are produced in the context of a rhythm with alternating short-long intervals, compared with when the same intervals occur in equal interval sequences. Specifically, first we aim to show that intervals produced in the context of a rhythm are more variable than the same intervals produced in an isochronous context, and we predict that this increase in variability is due to timer rather than motor processes. Variability arising from the two processes is identified using slope analysis and two-hand cross-covariance and asynchronies. Second, we aim to determine whether the structure of the central timing mechanism governing rhythm production is

organized in a serial or hierarchical manner. Following previous suggestions (Vorberg & Wing, 1996) we propose that rhythms are produced in a serial manner by a single output timer, which switches its value between a short and a long interval, and that this switching introduces additional variance compared with isochronous timing. This account predicts equal variability of rhythm cycles defined as the sum of the component intervals, short plus long versus long plus short. This lack of differences in cycle variability would suggest that rhythm is triggered by a single output timer, rather than multiple hierarchically organized timers. Finally, we examine for the first time whether interval switching in rhythm performance alters the kinematic characteristics of movements produced between successive responses.

We address these issues in an experiment that includes producing one interval (500 ms) in three contexts: either isochronously or as one of two intervals in binary rhythms in which the 500-ms interval is paired, with either a shorter (300-ms) or a longer (833-ms) interval. These pairs of intervals result in a noninteger (1.67:1) ratio, which may be expected to be more difficult to produce than an integer ratio, such as 2:1. The study also includes isochronous series with 300-ms and 833-ms target intervals.

Method

Participants

Five female and 5 male right-handed volunteers (age range of 19 to 33 years) participated in the study. Participants had no formal musical training, and none reported any auditory or neurological impairment.

Apparatus

Participants sat at a table and placed their pronated forearms on two armrests in order to position the hands comfortably at the level of two response plates spaced 10 cm on either side of the midline. The plates were secured to two force transducers (Novatech F241), which were attached to the table. Force recordings made at 1 kHz provided information about the times of finger contact when tapping on the plates. A 5-mm-diameter spherical reflective marker attached with double-sided sticky tape to the nail of each index finger allowed finger position to be recorded at 100 Hz with a three-camera motion capture system (Qualisys ProReflex). Reflective markers were also placed on the second metacarpophalangeal (MCP) joint of the index fingers and on both wrists, allowing checks to be made that participants' finger tap movements were restricted to the MCP joint. Pacing tones (duration 100 ms, frequency 750 Hz) were delivered through a speaker placed centrally 1 m behind the participant.

Procedure

Participants were asked to tap bimanually using flexion and extension movements of the index fingers to make brief contact with the two response plates. A paced-free tapping paradigm was used in which participants first synchronized with the auditory pacing tones and, after 10 tones, continued tapping with the tones silenced for the rest of the 40-s trial. Tapping was performed in two contexts: isochronous, with interstimulus intervals (ISIs) of 300, 500, and 833 ms; and two different rhythms, with ISI alter-

nating (a) between 300 ms and 500 ms and (b) between 500 ms and 833 ms. The two rhythms had the same 1.67:1 ratio. Testing was carried out in 10 blocks of five trials, with the three isochronous and two rhythmic conditions occurring once in random order in each block. Prior to the experimental blocks, participants performed 2 practice blocks to ensure that they were familiar with the task and understood the conditions of the experiment.

Data Analysis

IRI means. Tapping responses were identified as the onset of each finger contact determined from the force-time functions for both hands. The IRI time series for each hand was first analyzed in terms of average difference from the target interval and the ratio of the IRIs produced in the two rhythms.

IRI variability. The following analyses were performed in each time series obtained from the isochronous conditions, and separately for long and short elements, which were parsed into two series in the rhythm conditions. First, a linear regression was fitted to the IRIs in each time series to remove linear trends in the data (Spencer & Zelaznik, 2003; Vorberg & Wing, 1996). Then, *SDs* of the IRIs were estimated, in the time series of the IRIs both before (raw intervals) and after detrending (detrended intervals), using the residuals of the linear regression. Slope analysis (Ivry & Corcos, 1993) was carried out separately for both raw and detrended intervals using the linear regression of *SD* on mean IRI for each sequence. The approach of Vorberg and Hambuch (1978, 1984) was also used to identify timer and motor *SD*. Thus, timer variability was estimated as the square root of the between-hand cross-covariance at lag zero, and motor variability as the *SD* of the between-hand asynchronies. Asynchrony was calculated as the time difference between right and left hand-tap onsets.

Cycle variability. In the rhythm condition, cycles were defined by adding the short interval with the following long interval and vice versa over the whole trial. Cycle variability was defined as the square root of the variance of these two time series.

Trajectories. The vertical position-time function acquired from the fingertip marker was used to evaluate the form of the movement trajectories between successive responses. For each trial, the individual response trajectories were pooled (separately for long and short intervals in the rhythmic conditions) using the following procedure. The position-time trajectory was first low-pass filtered at 20 Hz (second-order Butterworth dual-pass filter) and interpolated up to 500 Hz using spline interpolation. The movement trajectories were then segmented using a threshold set above the collision point, in order to exclude the dwell time when the finger was in contact with the surface. Following this, a fourth-order polynomial function was used to fit each curve above the threshold, and the five coefficients of the fit (intercept, linear, quadratic, cubic, and quartic constants) were taken and averaged to obtain a single overall function for each condition for each participant. A fourth-order function was chosen in order to satisfy a goodness-of-fit criterion for r^2 of above .85. Lower order polynomial functions failed to satisfy this criterion in longer interval conditions.

Velocities. In a further analysis, maximum (extension phase) and minimum (flexion phase) velocity values of each movement cycle were estimated from the differentiated measures of finger vertical position. To identify velocity minima and maxima in

rhythm, velocity waveforms were segmented at the point of extension onset, using a fixed threshold procedure. Each segmented velocity waveform consisted of a positive followed by a negative velocity phase (extension followed by flexion). After segmentation, waveforms of short intervals were pooled and analyzed separately from waveforms for long intervals. In a further analysis the maximum (extension) and minimum (flexion) velocity in each segmented waveform was identified, and average and *SD* for flexion and extension velocities were calculated. Finally, cross-correlations between extension and flexion velocity, extension velocity and IRI, and flexion velocity and IRI were determined for lags -1, 0, and 1. Lag 0 cross-correlations were defined between extension velocity, the subsequent flexion velocity, and the IRI ending with the finger contact after flexion.

Results

Several movement cycles from an illustrative rhythm trial are shown in Figure 1. The upper traces show the position of the index fingers of the left and right hand, with each downward movement resulting in a response registered by the force transducers' recordings, shown in the bottom trace. The middle trace shows the velocity profile of the finger.

In the following we present response timing and kinematic results from the continuation phase to assess three issues. The first issue we address is whether the elevated timing variability in

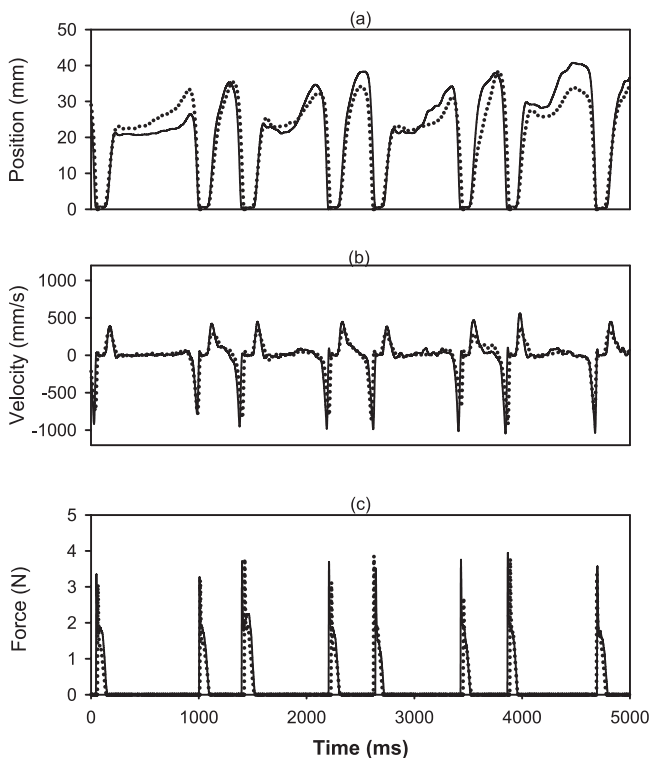


Figure 1. Illustrative data from (a) a long (500/833-ms) rhythm trial showing position traces for left and right hand, (b) velocity traces, and (c) force traces used to identify responses. Continuous lines represent data obtained from the right finger; dotted lines represent data from the left finger.

rhythm performance is due to timer or motor processes. Timing was assessed in terms of the mean and variability (*SD*) of the IRIs, as well as the variability components, timer and motor implementation, identified using two methods: slope analysis and two-hand cross-covariance and asynchronies. The second issue we address is whether central timing is organized in hierarchical or serial fashion using the cycle variability and variability of a given interval (500 ms) produced as the short or the long in a rhythm. The third issue we take up is whether rhythm production affects the trajectory characteristics of extension-flexion movements between tapping responses. To address this point, we used a curve-fitting procedure to obtain grand averages of the trajectories in each condition, and then we performed a detailed analysis on peak velocities in extension and flexion.

In general, we first describe interval (300-, 500-, or 833-ms) and task (isochronous, rhythm) effects. Then we focus specifically on the 500-ms interval in isochronous, short (300/500-ms) and long (500/833-ms) rhythms to pull out context effects. In the case of the mean and *SD* of the IRIs as well as trajectories and velocities, only results from the right hand are reported, because no differences were observed between the two hands.

IRI Means

To check whether tapping responses were accurate in the mean, differences of the IRI from the target interval were assessed. In isochronous tapping, the IRIs were generally slightly shorter than the target interval. However, in rhythm performance, sizable deviations from the target interval were observed (see Figure 2a). In the 300/500-ms rhythm, the short interval was slightly shorter than the target, and the long interval was longer. A similar effect, but with greater deviations from the target, was observed for the 500/833-ms rhythm.

Separate repeated measures analyses of variance (ANOVAs) on the IRIs produced in the isochronous 300-, 500-, and 833-ms and the short and long rhythm conditions were performed with the factors interval (short, long) and task (isochronous, rhythm). In the short rhythm condition, there were reliable main effects of interval, $F(1, 9) = 7.58, p < .05$, and task $F(1, 9) = 10.27, p < .05$. A significant interaction showed that the 300-ms interval in the rhythm condition was shorter than this interval in the isochronous condition and that the 500-ms interval was correspondingly longer, $F(1, 9) = 34.80, p < .01$. In the long rhythm condition there was a main effect of interval, $F(1, 9) = 31.47, p < .01$. An interaction was also observed, $F(1, 9) = 31.42, p < .01$, with the 500-ms interval shorter and the 833-ms interval longer than the corresponding intervals in the isochronous conditions (see Figure 2a). One-way repeated measures ANOVA was performed on the IRIs targeted at the 500-ms interval in the three conditions. There was a reliable main effect of task, $F(1, 9) = 40.38, p < .01$. Multiple contrasts showed that when the 500-ms interval was paired with the 300-ms interval it was longer, $F(1, 9) = 26.45, p < .01$, than during isochronous performance. When it was paired with the 833-ms interval it was shorter, $F(1, 9) = 88.05, p < .01$, than in the isochronous condition.

To further characterize the accuracy of rhythm production, an analysis of the ratio of the two intervals was performed separately in three sections of the trial: the last six intervals of synchronization and two sets of intervals produced in the first and second

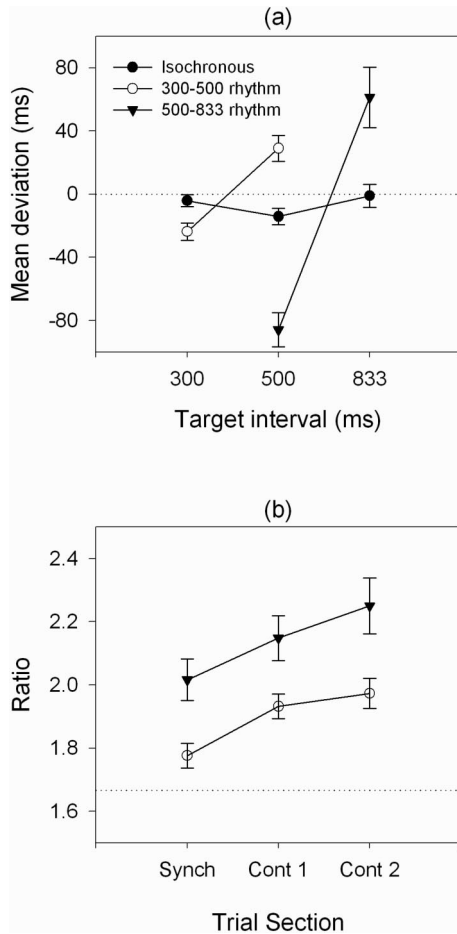


Figure 2. Accuracy of mean interresponse interval. (a) Mean difference from the target interval for all experimental conditions. The dotted line represents the target interval. (b) Mean ratio of intervals produced in the two rhythm conditions, separately for each of the three sections of the trial: the last six intervals in synchronization (synch) and the first and second halves of the continuation (cont) phase. The dotted line represents the target ratio, and error bars represent plus or minus 1 standard error of the mean.

halves of the continuation phase. The ratio was estimated by dividing the long by the short interval in each rhythm cycle. The target ratio for both rhythms in the synchronization phase was 1.67; however, the average ratios produced in all three phases were higher than this figure, even in synchronization (see Figure 2b). A repeated measures ANOVA with the factors section (synchronization, continuation first half, continuation second half) and rhythm (300/500 ms, 500/833 ms) revealed a main effect of section, $F(1, 9) = 15.98$, $p < .01$, reflecting a progressive increase in ratio across the three sections of the trial. There was also a main effect of rhythm, $F(1, 9) = 25.84$, $p < .01$, due to the ratio being larger for the long rhythm.

The increase in rhythm ratio over the three sections of the trial suggests the duration of either the short or the long interval of a rhythm, or both, drifted over time. Representative data from one trial in the long rhythm shown in Figure 3a reveal a pronounced increase in the long intervals with a small decrease in the short

intervals. Covariance is sensitive to such trends, and consistent with this, persisting positive values were noted in the cross-covariance at higher lags (see Figure 3c). To correct for this bias in the covariance estimates, the linear trend was removed separately for each of the two elements in the rhythm (see Figure 3b). Estimates of the cross-covariance between the intervals produced by the two hands were lower after detrending, not only at lag zero (timer variance) but at higher lags as well, although the overall shape of the cross-covariance function was preserved (see Figure 3c). The cross-covariance function converged toward zero at higher lags, suggesting the trend had largely been removed. In the next set of analyses, isochronous and rhythm variability (SD) as well as the timer and motor components were analyzed for the IRI time series before (raw intervals) and after detrending (detrended intervals).

IRI Variability

To examine our first prediction, suggesting that variability is greater in rhythm compared with isochronous responding and that this increase arises at the central rather than the motor level, IRI variability (SD) was analyzed with the raw interval and timer SD s and the detrended interval, timer, and motor SD s as dependent variables (see Figures 4a–4e). For each of these variables, separate 2×2 repeated measures ANOVAs were performed for SD in each pair of intervals (300/500 ms and 500/833 ms) with the factors interval (short, long) and task (isochronous, rhythm). F values for these analyses are presented in Table 1. For both raw and detrended intervals (see Figures 4a and 4b), a main effect of task indicated that performance in the rhythm conditions was more variable than in the isochronous conditions. This main effect of task was also observed for timer variability (see Figures 4c and 4d) but was absent for motor variability. This finding is in agreement with our first prediction, that intervals are more variable in a rhythm than in an isochronous context and that this increase is attributable to timer rather than motor processes. Furthermore, a main effect of interval was observed in raw interval and timer SD s and in the detrended interval and timer SD s, showing that in these measures, variability increased with the mean interval. Interval–task interactions showed that the increase in SD with interval was greater in rhythm compared with isochronous conditions. Estimates of motor SD were low compared with the timer SD , with relatively minor, albeit significant, differences between conditions. Motor SD decreased with interval and was lower for the intervals in the short rhythm compared with the isochronous condition. An important observation in this analysis is that although variability was lower for detrended time series (see Figures 4b and 4d), both raw and detrended time series showed the same pattern of results, with rhythm associated largely with greater timer variability.

To assess the contribution of drift to the overall variability in isochronous and rhythm conditions, we analyzed the difference in SD between detrended and raw intervals (i.e., SD due to drift) for interval SD and timer SD . Repeated measures ANOVAs for each pair of intervals with the factors interval (short, long) and task (isochronous, rhythm) were performed. For the 300/500 ms pair of intervals, a main effect of interval showed that SD due to drift was higher in the 500-ms interval in both interval SD , $F(1, 9) = 10.03$, $p < .05$, and timer SD , $F(1, 9) = 10.25$, $p < .05$; however, it was not higher for rhythm. For the 500/833 ms pair, SD due to drift was

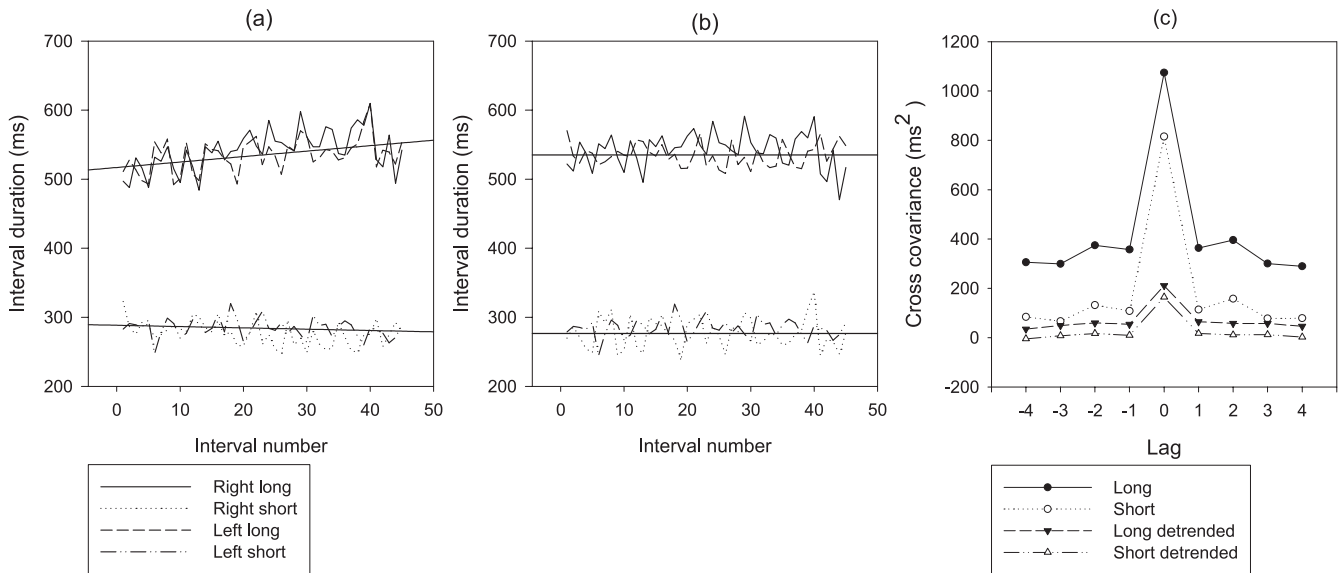


Figure 3. (a) Illustrative time series of left and right intervals from one participant performing the short (300/500-ms) rhythm. The straight lines represent linear regression functions fitted to the time series of the right hand. (b) The same time series after detrending. (c) Grand averages across all participants of the cross-covariance functions separately for each of the component intervals for the 300/500-ms rhythm condition before and after detrending.

higher in rhythm compared with isochronous conditions in both interval SD , $F(1, 9) = 6.06$, $p < .05$, and timer SD , $F(1, 9) = 8.61$, $p < .05$, and it was higher for the longer interval (833 ms) only in interval SD , $F(1, 9) = 9.77$, $p < .05$, not in timer SD .

Another way to assess our prediction of increased variability in rhythm due to timer processes is slope analysis. Linear regression functions were fitted to the raw and detrended interval SD data points of the isochronous and rhythm tasks for each participant. The overall average slopes, intercepts, and r^2 for the raw intervals (see Figure 4a) were 0.05, 7.95, and .92 (isochronous) and 0.07, 2.25, and .95 (rhythm); for the detrended intervals (see Figure 4b), values were 0.04, 8.82, and .94 (isochronous) and 0.05, 5.84, and .91 (rhythm). The slope for the rhythm conditions was reliably steeper than in the isochronous conditions in both raw, $t(9) = 2.49$, $p < .05$, and detrended intervals, $t(9) = 2.81$, $p < .05$. No differences were observed in the intercepts. In this method, the slope reflects duration-dependent (timer) processes; thus, the observed increase in slope for rhythm provides further support for our prediction that the increased variability in rhythm is due to timer processes. Also, the equal intercepts suggest that duration-independent (motor) processes are the same in the two tasks.

After showing that rhythm performance is more variable due to additional variability arising from timer processes, our second aim was to examine the specific timer processes involved in rhythm production—namely, whether rhythm is produced by multiple timers organized hierarchically or by a single timer producing short and long intervals in alternation. If rhythm is hierarchically structured, one of the component intervals, say, the short, will be triggered by a different level at the hierarchy than the long. Thus, if we compare variability for the same interval (500 ms) produced as the long (300/500 ms) or the short (500/833 ms) component of a rhythm, differences in variability for this interval would suggest

that the short and the long intervals are triggered by different levels in the hierarchy. Alternatively, if there is no difference in variability in the two cases, it would suggest that both the short and the long intervals are represented at the same level in the timing system, and thus that rhythm performance is likely to be triggered by a single output timer rather than hierarchically.

To assess this issue, we performed two one-way ANOVAs for SD in the 500-ms interval, one for raw and one for detrended intervals, with three levels: isochronous, long (300/500 ms), and short (500/833 ms). Rhythm performance was more variable than isochronous for both raw, $F(1, 9) = 6.79$, $p < .05$, and detrended intervals, $F(1, 9) = 9.66$, $p < .05$. Pairwise comparisons showed a difference between isochronous and both rhythm conditions for raw, $F(1, 9) = 14.14$, $p < .05$, and detrended intervals, $F(1, 9) = 21.17$, $p < .05$, but no difference was observed between the two rhythm conditions, suggesting that in rhythm, the 500-ms interval is represented at the same level of the timing system, whether it is produced as the long (300/500-ms) or the short (500/833-ms) interval of a binary rhythm. This result was confirmed by ANOVAs with the same factors, for timer variability. Again, rhythm was more variable than isochronous in raw, $F(1, 9) = 10.63$, $p < .05$, and detrended intervals, $F(1, 9) = 18.19$, $p < .05$. Pairwise comparisons revealed a difference between isochronous and both rhythm tasks for raw, $F(1, 9) = 23.46$, $p < .05$, and detrended intervals, $F(1, 9) = 39.43$, $p < .05$, and no difference between the two rhythm conditions. No differences in motor SD were found between the three conditions.

Cycle Variability

Cycle variability was analyzed to further assess whether rhythm performance operates in a serial or hierarchical manner. In our

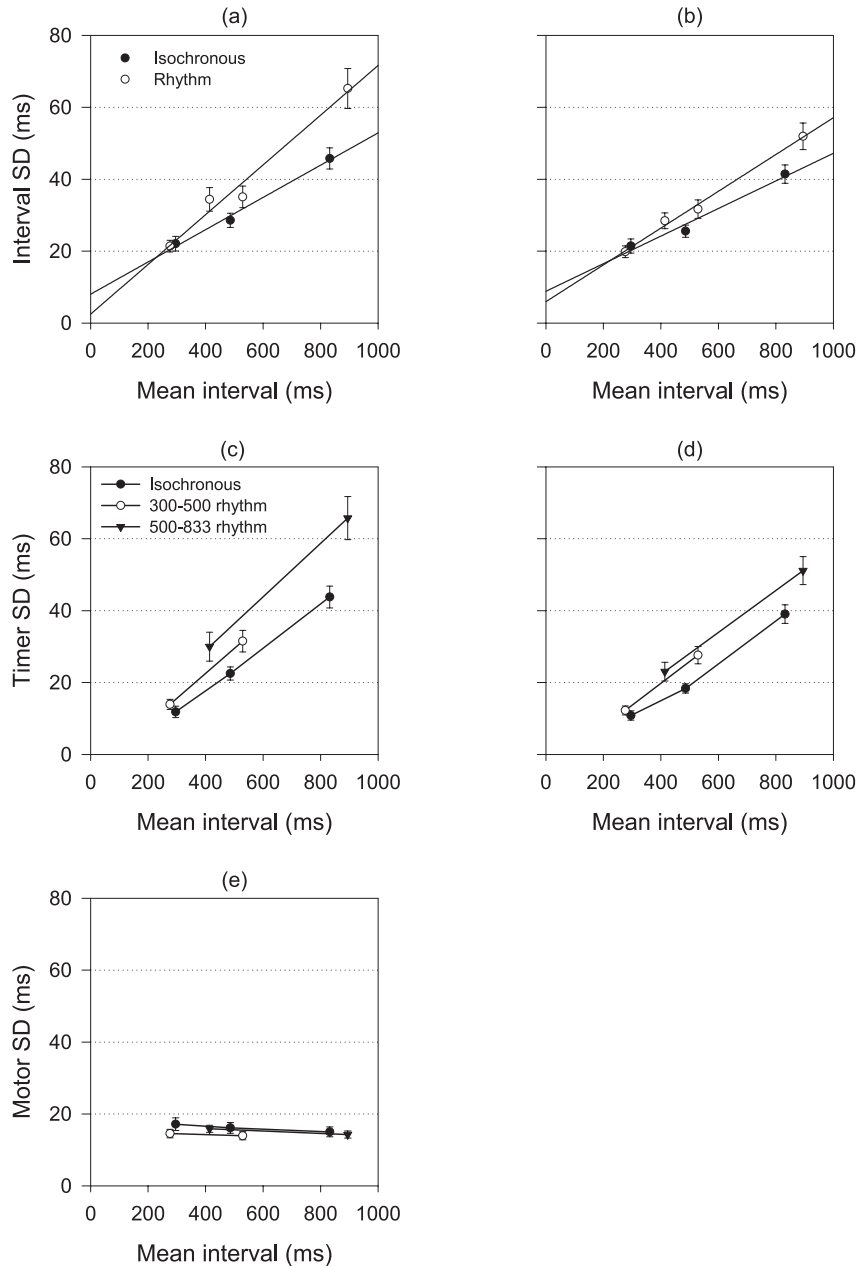


Figure 4. Interresponse interval variability (*SD*) for (a) raw and (b) detrended intervals. *SD* of isochronous and rhythm performance is plotted against the mean interval produced. Two linear regression functions were fitted to the average data of each participant, one for isochronous and one for rhythm performance (solid lines). Plots c, d, and e represent *SD* of the variability components as a function of the mean interval: (c) the timer *SD* of the raw intervals, (d) the timer *SD* of the detrended intervals, and (e) the motor *SD*. Decomposition of the variability components was performed using the method of Vorberg and Hambuch (1978, 1984). Error bars represent plus or minus 1 standard error of the mean.

study, a higher level timer might have been responsible for the cycle defined by the combination of the short and long intervals, and a lower level timer might have been assigned to the short (or long) component of the rhythm (see Figure 5a). Such an organization predicts that there will be differences in the variability of a rhythm cycle (i.e., short plus long interval [SL] or long plus short

interval [LS]). Differences in variability between SL and LS would support the notion of a hierarchical structure for rhythm. Figure 5b shows the cycle *SD* for both raw and detrended intervals for SL and LS, plotted as a function of the cycle times. A repeated measures ANOVA was performed for cycle *SD* with the factors duration (800 ms, 1,333 ms), type (SL, LS), and drift (raw,

Table 1
Results From the Statistical Analyses of Interval SD

Variable	300/500 ms			500/833 ms		
	Interval <i>F</i> (1, 9)	Task <i>F</i> (1, 9)	Interval × Task <i>F</i> (1, 9)	Interval <i>F</i> (1, 9)	Task <i>F</i> (1, 9)	Interval × Task <i>F</i> (1, 9)
Interval <i>SD</i>	42.83	7.17	9.25	121.07	16.32	5.09 ^a
Detrended <i>SD</i>	50.51	8.89	13.01	142.59	18.82	6.80
Timer <i>SD</i>	86.32	10.18	7.82	95.72	18.07	4.69 ^b
Detrended timer <i>SD</i>	125.77	11.96	13.89	93.79	22.61	5.69
Motor <i>SD</i>	6.09	23.54	<i>ns</i>	15.64	<i>ns</i>	<i>ns</i>

Note. *SD* = standard deviation.

^a *p* = .051. ^b *p* = .059.

detrended). Cycle *SD* increased with the mean cycle time, as was shown by a main effect of duration, $F(1, 9) = 43.06$, $p < .05$, and was lower for detrended time series, shown by a main effect of drift, $F(1, 9) = 23.13$, $p < .05$. A duration–drift interaction, $F(1, 9) = 13.92$, $p < .05$, showed that cycle *SD* increased with the mean in both SL and LS types, only for the raw time series, not the detrended. However, no difference was observed between SL and LS in cycle *SD*. This lack of difference is evidence against the possibility of a hierarchical timer structure in the production of

rhythm and, together with the increase in variability in rhythm production, supports the idea of a single output timer operating in rhythm production, generating intervals of different durations. Changes in the value of the timer (short–long) are likely the source of the additional variance observed in rhythm.

Movement Trajectories

Having assessed response timing and characterized the effects of rhythm in terms of mean and variability of intervals produced between responses, we now turn to a description and analysis of the kinematic characteristics of the trajectories between these responses. The issue here is whether trajectories are different in rhythm compared with isochronous performance and whether these differences are related to the ones observed above in response timing.

Movement trajectories produced by one participant in a single trial at each of the three intervals in the isochronous condition are shown in Figure 6. The trajectories, which are aligned with the response, consist of an extension phase (the finger is lifted from the response key) and a flexion phase (the finger is brought down onto the response key) separated by an intervening hold phase whose shape varies markedly across conditions.

Trajectories in each condition were averaged using a curve-fitting procedure, based on a fourth-order polynomial function. This procedure included fitting a curve with four coefficients for each trajectory between every pair of taps. Coefficients were averaged for each participant and then across participants to generate a curve representative of the overall movement shape in each condition: three isochronous (300, 500, and 833 ms; see Figure 7a) and two rhythm (300/500 ms and 500/833 ms; see Figure 7b). Also, to contrast movement shape for the 500-ms interval performed in different contexts (isochronous, 300/500-ms rhythm, and 500/833-ms rhythm), Figure 7c depicts the functions generated from the overall average coefficients for this interval only.

Mean Velocities

Examination of the trajectories in Figure 7 indicates that they are asymmetric in the sense that flexion and extension phases differ, and there is a steeper slope in flexion before the response than in extension after the response. This is confirmed by the maximum flexion and extension velocities, which are shown in

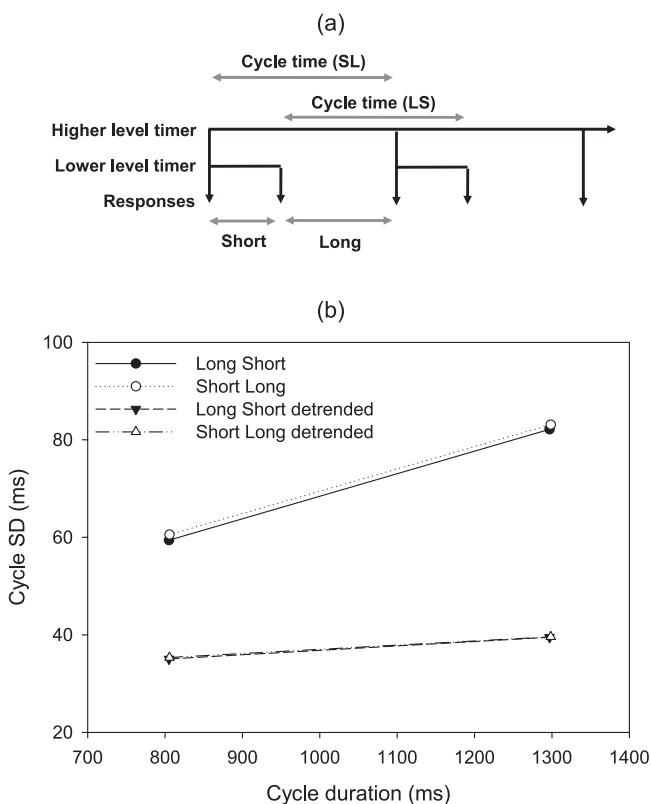


Figure 5. (a) Hierarchical model for rhythm production. (b) Cycle variability plotted as a function of the mean cycle times for raw and detrended time series. The rhythm cycle was calculated as the sum of the short interval and the next long (SL), or the sum of the long interval and the next short (LS).

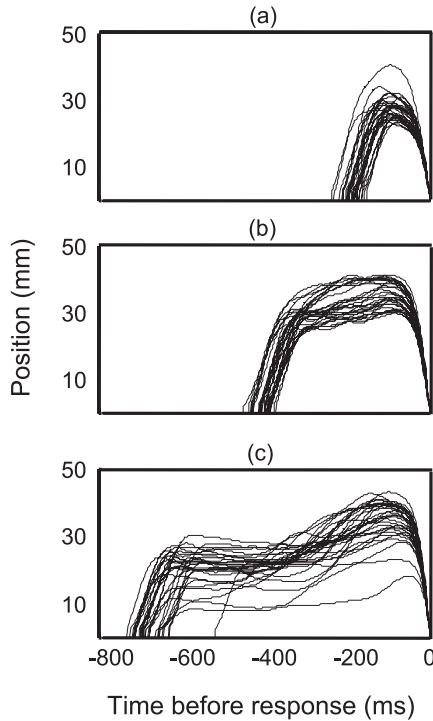


Figure 6. Representative movement trajectories of one isochronous trial in the three isochronous conditions from a single participant: (a) 300 ms, (b) 500 ms, and (c) 833 ms.

Figure 8. Two-way repeated measures ANOVA with the factors interval (300, 500, or 833 ms) and phase (flexion, extension) showed a main effect of phase, with higher velocity in flexion than in extension, $F(1, 9) = 117.35, p < .001$. An interval–phase interaction, $F(2, 18) = 77.65, p < .001$, was observed. Separate one-way ANOVAs for each movement phase revealed that velocity decreased with interval—the finger moved more slowly at longer target intervals—only in the extension phase, $F(2, 18) = 61.81, p < .001$. The trend toward an increase in velocity in the flexion phase was not significant.

To test for context effects on velocities associated with the 500-ms interval in isochronous and rhythm contexts, we performed two-way within-subject ANOVA with the factors context (isochronous, short rhythm, long rhythm) and phase (flexion, extension). Again, velocity in flexion was higher than in extension, $F(1, 9) = 99.36, p < .001$. An effect of context in the two phases of the movement cycle was revealed by a reliable context–phase interaction, $F(2, 18) = 21.71, p < .01$. Separate one-way ANOVAs for the two phases showed a main effect of context only in extension, showing that in rhythm, extension velocity is lower than isochronous for the short interval, whereas it is higher than isochronous for the long interval, $F(1, 9) = 31.95, p < .001$. To examine the differences in extension velocity (see Figure 9) in more detail, we performed separate two-way ANOVAs with the factors context (isochronous, rhythm) and interval (short, long) for the two pairs of intervals (300/500 ms; 500/833 ms). Significant interactions confirmed that in isochronous performance, velocity in extension was higher for the short interval, but in rhythm performance, velocity of the short interval was lower and velocity of the long

interval was higher than in isochronous performance, in both the 300/500-ms, $F(1, 9) = 22.82, p < .001$, and 500/833-ms, $F(1, 9) = 46.55, p < .001$, pairs of intervals (see Figure 9).

In summary, in all conditions velocities were higher in flexion than in extension. In isochronous tapping, only extension velocities showed a decrease with interval, indicating that just the upward movement of a tapping cycle is slowed in longer intervals (see Figure 6). However, in rhythm, extension velocities were higher for the long interval of both rhythms, showing context-dependent adjustments.

Velocity Variability

The variability (*SD*) of flexion and extension velocities is depicted in Figure 10. Repeated measures ANOVAs were performed on the two pairs of intervals (300/500 ms; 500/833 ms), with the factors interval (short, long), task (isochronous, rhythm), and phase (extension, flexion). In the case of the 300/500-ms intervals, velocity in the rhythm condition was more variable than in the isochronous condition, $F(1, 9) = 8.78, p < .001$; velocity in the short interval was more variable than in the long interval, $F(1, 9) = 12.11, p < .01$; and velocity in flexion was more variable than in extension, $F(1, 9) = 10.38, p < .001$. An interval–task interaction showed that there was no difference between the velocity variability for short and long intervals in the isochronous condition, but in the rhythm condition, the velocity in the short interval was more variable in both flexion and extension, $F(1, 9) = 15.95, p < .001$. In the case of the 500/833-ms intervals, velocity variability in the rhythm condition was larger than in the isochronous condition, $F(1, 9) = 4.75, p = .057$, and flexion showed

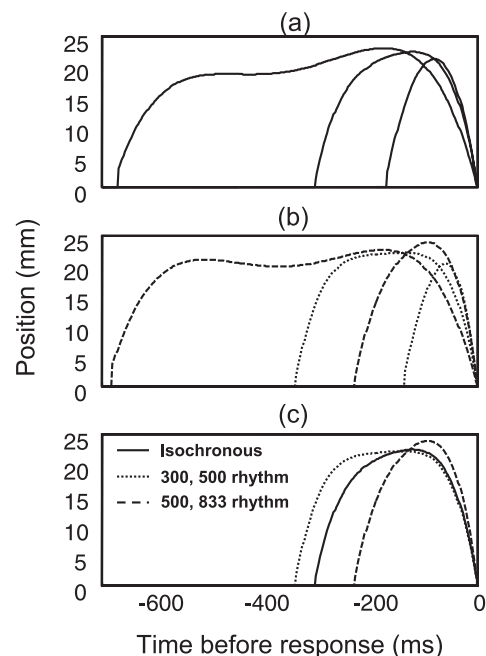


Figure 7. Movement trajectories generated from the average fourth-order polynomial coefficients for (a) isochronous, (b) rhythm, and (c) 500-ms interval in three contexts: isochronous and in a rhythm paired with a shorter or a longer interval.

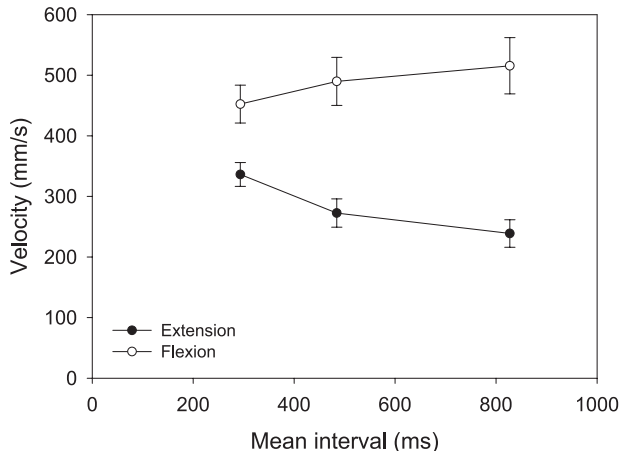


Figure 8. Average flexion and extension velocity for the three isochronous tapping conditions plotted as a function of the mean interval produced (300, 500, or 833 ms). Error bars represent plus or minus 1 standard error of the mean.

higher velocity variability than extension, $F(1, 9) = 17.64$, $p < .01$. A task-phase interaction, $F(1, 9) = 6.22$, $p < .05$, showed that flexion velocity was more variable in the rhythm condition, whereas extension velocity showed no difference in variability in the two tasks.

A final analysis revealed low correlations between flexion and extension velocity and the produced interval (absolute correlation value $< .20$) as well as with the preceding and following interval. No differences were found between these correlations in isochronous and rhythm conditions.

Discussion

The main aim of the present study was to investigate timing context effects on cognitive and motor aspects of performance in a repetitive tapping task. We predicted that timing variability in alternate-interval rhythm production would be greater than variability in isochronous interval production. We also predicted that central timer structure in rhythm would be serial rather than hierarchical. Finally, we asked whether rhythm production affects the movement characteristics. In the following we first consider implications of the results from the analysis of time intervals between discrete responses, then we address the interpretation of our trajectory findings.

Timing variability increased linearly with the mean, and as predicted, variability was greater in rhythm compared with isochronous responding. We used slope analysis (Ivry & Corcos, 1993) to estimate timer and motor contributions (Wing & Kristofferson, 1973a) to IRI variability in isochronous and rhythm tasks directly from the relationship between the *SD* and the mean interval. The slopes for the rhythm conditions were steeper, indicating an effect of rhythm on the central timer component. The absence of changes in the intercept showed that the motor aspects of timing did not change in the different tasks. Because participants tapped with two hands, we were also able to use the bimanual extension of the W-K model of timing (Vorberg & Hambuch, 1978, 1984) to decompose IRI variability into timer and motor implementation

components. Again, we observed that the main source of increased variability in producing rhythms was in the central timer, whereas the motor variability was relatively constant. Increased timing variability in rhythm production was also observed in a study comparing the performance of young and older adults (Krampe et al., 2005). Isochronous performance was found to be the same in the two groups, but when the individuals were asked to perform rhythm sequences, variability increased with sequence complexity to a greater degree in the older group. These results suggest that two different processes are involved in rhythm production: a low-level timer process, generating the basic timing pulses, and a high-level sequencing process, controlling the arrangement of intervals in a rhythm cycle.

To extend these findings, we focused on the timer process and examined whether in rhythm this process operates in a serial or hierarchical manner. It might be assumed that separate timers are involved in each level of a hierarchy, in order to separate the cycle in unequal intervals, in which case the presence of separate timers in each level results in higher variability (Vorberg & Wing, 1996). However, one prediction of such a hierarchical model is unequal variance for cycle durations defined by responses terminating short and long components of the rhythm (Vorberg & Hambuch, 1978, 1984), whereas we observed equality of cycle variances. Another prediction of a hierarchical model is that variability of a given interval (e.g., 500 ms) would be different when it is produced in two rhythm contexts, as the longer (300/500 ms) or as the shorter (500/833 ms) of two alternating intervals, because in each case it is triggered by a different level in the hierarchy. Variability for the 500-ms interval was the same in the two contexts, providing further evidence for a serial rather than hierarchical triggering of responses in rhythm timing. Our results do not exclude the possibility that rhythm is represented hierarchically at some stage, but if so, the hierarchical structure of a rhythm is changed into a serial representation at output, with a single timer switching between long and short intervals (Vorberg & Wing, 1996). We suppose it is this switching between intervals that introduces the additional variability we observed.

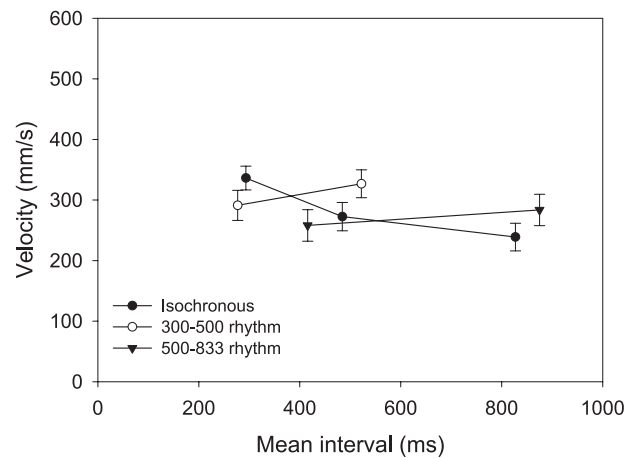


Figure 9. Average velocity in extension for rhythm compared with isochronous performance in the two pairs of intervals, plotted as a function of the mean interval produced. Error bars represent plus or minus 1 standard error of the mean.

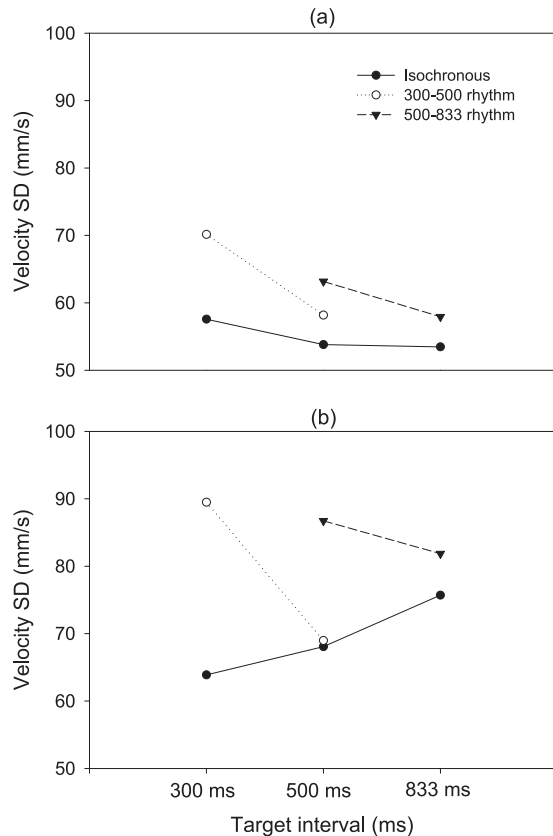


Figure 10. Variability (*SD*) of (a) extension and (b) flexion velocity in isochronous and the two rhythm conditions as a function of target interval.

Using current models of timing we showed that the main source of elevated variability in rhythm is interval switching in the central timer. However, we also observed changes in the component intervals in rhythm over time, with the short interval being shortened and the long lengthened, revealing the presence of drift in the time series. Drift is a form of nonstationarity and may be a potential source of the increased variability observed in rhythm, together with the central timer. To assess this issue, we removed drift by linear detrending of the intervals. After detrending, the reduction in timer variance estimates was greater for rhythmic than for isochronous sequences, especially in the long rhythm. However, a reliable difference in variability between rhythm and isochronous conditions remained, indicating that switching the duration of the timer is the main factor contributing to variability in rhythm production, in addition to the greater tendency to drift in this condition. These results suggest that drift and timer variability reflect separable processes and that drift is an important aspect of timing, sensitive to experimental manipulations not only in isochronous (Collier & Ogden, 2004) but also in rhythm performance. In summary, our finding that the main factor affected by rhythm production is the central timer supports the idea that additional cognitive processes are involved in rhythm compared with isochronous interval production, and they result in increased variability.

Given that our results suggest that rhythm engages additional cognitive processes, a number of questions arise. For instance,

would other cognitive factors interact with the rhythm effect? Sergent, Hellige, and Cherry (1993) used a dual-task paradigm to show that solving anagrams increased timer, not motor, variance, and it is interesting to ask whether this effect might be more pronounced for rhythm. Another issue is what the underlying neural circuitry might tell us. Subcortical structures such as the cerebellum and basal ganglia are usually implicated in equal-interval timing (Harrington et al., 1998; Ivry, Spencer, Zelaznik, & Diedrichsen, 2002; Rao et al., 1997). However, cortical contributions increase in significance in rhythm acquisition (Lewis, Wing, Pope, Praamstra, & Miall, 2004; Penhune & Doyon, 2002; Sakai, Hikosaka, & Nakamura, 2004), and these may be the substrate for the variability effects seen in the present study.

Variability of motor implementation was relatively constant in both rhythm and isochronous contexts and across interval durations. The question arising from this finding is whether this constancy in motor variability is reflected in the movement trajectory. Estimates of the movement shape, obtained using the grand averaged coefficients of a polynomial fitting procedure, indicated changes in the form of the movement trajectories with changes in interval. At longer intervals, a pronounced hold phase developed between the extension (lift) and flexion (drop) phases. In contrast, the form of the movement for the 500-ms interval, as evaluated by the curve-fitting procedure, changed relatively little when it was performed as the shorter or the longer interval of a binary rhythm. One factor contributing to the finding of changes in the 500-ms-interval trajectory might be the departures from the 500-ms target interval under the rhythm conditions; the 500-ms interval was produced longer than the target in the short rhythm and shorter than the target in the long rhythm. However, the analysis of peak velocity also revealed differences in the extension velocity for the 500-ms interval across conditions. These differences cannot be attributed to the departures from the 500-ms target, as the direction of effect in the rhythm conditions was opposite that observed in the isochronous conditions. In the isochronous conditions, extension velocity decreased with interval, whereas in the rhythm conditions, the extension velocity of the longer interval was the same as or greater than the extension velocity of the shorter interval.

We found an asymmetry in the movement trajectory between responses, with flexion velocity being greater than extension velocity. In the isochronous task, trajectories for short intervals exhibited less asymmetry than those for long intervals, although even here, flexion velocity was over 30% greater than extension velocity. Asymmetry between the two phases of reciprocal movements has been noted previously. Wachholder and Altenburger (1926; see Sternad, 2001) reported that in repetitive movements of the wrist, participants tended to accentuate one of the movement phases, either flexion or extension. In finger movements, the authors found an accentuation only in the flexion phase. An asymmetry in timed finger movement trajectories was also reported by Balasubramaniam, Wing, and Daffertshofer (2004). They used three tasks with different timing goals: synchronization with a beat at the end of extension, synchronization with a beat at the end of flexion, and flexing between the beats (syncopation). In synchronization at the end of flexion and in syncopation, flexion time was shorter than extension time. However, in synchronization at the end of extension the complementary pattern was observed, with extension time shorter than flexion time. Balasubramaniam et al. (2004) suggested that the asymmetry, with higher velocity in

one phase than in the other, contributed a useful cue in achieving the synchronization target, although task demands determined whether flexion or extension was emphasized. In the present study, it might seem that a different account of the asymmetry is required, as our analysis focused on continuation. Moreover, Balasubramanian et al. (2004) used a paradigm of free responding, with no touch contact with a response key, whereas in our study, flexion terminated on the response key without the need for active control over the movement endpoint. Introduction of a touch contact in a tapping task provides a salient timing cue, making timing more stable than without touch contact (Kelso, Fink, DeLaplain, & Carson, 2001). Yet even with finger contact, we still observed marked asymmetry in flexion and extension. We consider that flexion velocity is being held relatively high and constant to assist synchronization, and this asymmetry was maintained in unpaced tapping. Whether such asymmetry benefits unpaced tapping is not clear from our results. However, if further research were to show this to be the case, it would then be interesting to determine whether the effect relates to motor output (consistent with the W-K model) or whether it is a sensory effect (implying the use of feedback, which would be inconsistent with the W-K model).

In performance of the short (300/500-ms) and long (500/833-ms) rhythms, the two intervals had to be alternated in each cycle, and the same interval (500 ms) was produced as either the shorter or the longer interval. A comparison between isochronous and rhythm performance in each pair of intervals revealed that when the 500-ms interval was produced in alternation with a shorter interval, the trajectory was more nearly symmetrical with increased extension velocity. Moreover, extension velocity of the shorter interval decreased. A complementary adjustment occurred when the 500-ms interval was paired with a longer interval; compared with the isochronous conditions, the extension velocity of the shorter 500-ms interval decreased while that of the longer interval increased. This finding suggests that in a repetitive movement sequence in which two movements with different durations are alternated, extension velocities are approximately matched. One possible reason for this matching is that participants seek to make successive tapping actions (i.e., flexion followed by extension) equivalent, even though the time intervals between successive extension–flexion pairs are different for the short and long intervals. Thus, we suppose that implementation of tapping movements follows a different grouping principle (organized around the tap) from that governing timing (organized around the interval between taps).

Velocity adjustments in rhythm appear to have parallels with coarticulation in speech, where production of a phoneme is changed due to influence from the previous, or in preparation for the next, phoneme (Fowler & Saltzman, 1993). In human motor performance, it has also been observed that anticipation of a subsequent movement can affect the characteristics of the preceding movement. This effect has been observed in sign language (Jerde, Soechting, & Flanders, 2003), in drawing line segments of triangles (Klein, Hondzinski, & Flanders, 2003), and after learning a pattern of movements taking the hand through a series of targets (Sosnik, Hauptman, Karni, & Flash, 2004). These studies may each be considered as demonstrating coarticulation driven by spatial demands, as there were no explicit temporal requirements. Our results extend these findings to a task with temporal targets. Production of the 500-ms interval in rhythm involved changes in

the trajectory characteristics of the extension movement in relation to the extension movement of the adjacent shorter or longer interval. These changes in extension velocity in rhythm provide evidence for a form of coarticulation in rhythm production. Following this finding we examined whether this form of coarticulation is evident in isochronous responding as well. If movements are adjusted in anticipation of the next interval or as a consequence of the previous, then in isochronous tapping, when a given response produces an interval longer than the mean, the next extension might be faster, to produce an interval shorter than the mean. However, the lack of correlations between interval and extension and flexion velocity suggests that the kinematic characteristics bear little or no relation with the produced intervals. Thus, interactions between kinematic characteristics of adjacent movements in tapping are limited to rhythm tasks, comprising a series of unequal intervals.

Our approach to movement control in timing emphasizes flexion and extension as distinct components that are subject to different constraints in isochronous and rhythm tasks. The first point distinguishing flexion and extension is that flexion velocity is greater. The second distinction is that flexion velocity is relatively unaffected by the various conditions we investigated. In the isochronous task, as interval increases, extension velocity shows a marked decrease. In the rhythm task, extension velocities of the short and long response become nearly equal. We suggested that, in this case, the movement control problem is to produce two taps in which flexion and extension as a unit are approximately the same, although flexion velocity remains higher than extension velocity. In this respect it is interesting to note that both extension and flexion velocity variability for the 500-ms interval were greater in the rhythm conditions than in the isochronous condition. This might be interpreted as reflecting a cost in maintaining similar flexion–extension movement patterns for both intervals. However, it could also be argued that the elevated variability may be due to the greater tendency in the rhythm condition for interval timing to drift, which requires continual adjustment to trajectory. Thus, the elevated variability might represent a factor driving the flexion–extension movements to be more similar in an attempt to keep the variability down to manageable levels.

It is instructive to contrast our approach to trajectory in timing with that of Vaughan and colleagues (Vaughan, Mattson, & Rosenbaum, 1998; Vaughan, Rosenbaum, Diedrich, & Moore, 1996). These authors drew on harmonic oscillator theory (Feynman, Leighton, & Sands, 1963) to suggest that tapping trajectories are performed as continuous oscillatory movements interrupted once in each cycle by contact with the response key. Thus, they considered extension and flexion to be produced as a unit, a segment of a sinusoid, which implies that this segment should be symmetric with, for instance, equal slope in extension and flexion. They assumed that changes in tapping frequency are achieved by changes in stiffness, in accord with Kay, Kelso, Saltzman, and Schöner's (1987) observations of amplitude reduction with frequency in unstopped wrist flexion–extension movements. Vaughan et al. (1996) reported that their model provided a reasonable account of varying segmental (finger, wrist, arm) contributions in repetitive tapping. However, the symmetry of the extension–flexion cycle remained an untested assumption of the model.

The issue of symmetry was raised by Vaughan et al. (1998), who presented illustrative trajectory data from an experiment in which participants were asked to tap at different frequencies with different degrees of force. Inspection of their data suggests that although amplitude decreased with frequency as expected under the model, the functions were symmetric only at the highest frequencies when tapping with low force. In the other cases, flexion was clearly more rapid than extension. What implications do our findings have for the approach advocated by Vaughan and colleagues? If tapping is an interrupted sinusoidal movement, then we would expect symmetry between flexion and extension velocity. However, in the isochronous conditions we find highly asymmetrical movements, even for the fastest tapping rates. Moreover, in the rhythms we show flexion is faster than extension, in both short and long intervals. Thus, our results undermine a fundamental assumption of Vaughan and colleagues' account. Instead we advocate an approach in which the separate flexion and extension components are evaluated explicitly and the tendency in rhythm for flexion and extension to group as a unit is recognized.

Our findings, although different from the predictions of the model by Vaughan and colleagues (1998), do not rule out the possibility of a modeling approach using another form of oscillator, or a model including two or more coupled oscillators. Past oscillator models have mainly examined interlimb coordination (e.g., Haken, Kelso, & Bunz, 1985); however, more recent modeling attempts have suggested that single limb movements can be studied from an oscillator perspective by using interacting dynamical levels (Beek, Peper, & Daffertshofer, 2002; Jirsa & Haken, 1997; Sternad, Saltzman, & Turvey, 1998). For instance, the model by Beek et al. (2002) includes a nonlinear (limit cycle) neural oscillator situated at the neural level, which forces a linear oscillator at the effector level. This approach has some formal similarity to the two-level W-K model used in the present study. Such a two-level dynamical model may in the future prove useful in describing interactions between timing, which is generated (or controlled) centrally, and trajectory formation, which is organized semiautonomously as a motor output process. However, these models are not yet amenable to parameter estimation (for a review, see Peper, Ridderikhoff, Daffertshofer, & Beek, 2004). Further development of these models is needed before their applicability to interactions between timing and movement production, such as those described in the present study, can be determined.

In conclusion, we have shown that variability of the central timer increases when two intervals are alternated in rhythm compared with isochronous conditions. We also showed that this effect is present even when drift in the component intervals of a rhythm is removed, emphasizing that increase in variability in rhythm arises from switching the target interval by a single output timer. Furthermore, we showed for the first time that changes in the task demands challenge not only interval production but also movement characteristics between successive responses, by showing context-dependent changes in the shape of the movement trajectory and the velocities of extension and flexion. These results might seem to suggest that timing and movement characteristics are interdependent. Nevertheless, cross-correlation analyses of flexion and extension velocity with interval showed that there was little dependence between interval timing and movement characteristics. Moreover, there were negligible changes in motor variability with interval or rhythm context. Taken together, our results

suggest that timing variability in rhythm arises primarily at the cognitive (timer) level and not at the level of movement production. Thus, we conclude that interval timing is centrally specified and that movements are produced in order to fit in with the timing requirements of the task.

References

- Balasubramaniam, R., Wing, A. M., & Daffertshofer, A. (2004). Keeping with the beat: Movement trajectories contribute to movement timing. *Experimental Brain Research*, *159*, 129–134.
- Beek, P. J., Peper, C. E., & Daffertshofer, A. (2002). Modeling rhythmic interlimb coordination: Beyond the Haken–Kelso–Bunz model. *Brain Cognition*, *48*, 149–165.
- Billon, M., & Semjen, A. (1995). The timing of accent production in synchronization and continuation tasks performed by musicians and nonmusicians. *Psychological Research*, *58*, 206–217.
- Billon, M., Semjen, A., & Stelmach, G. E. (1996). The timing effects of accent production in periodic finger-tapping sequences. *Journal of Motor Behavior*, *28*, 198–210.
- Collier, G. L., & Ogden, R. T. (2001). Variance decomposition of tempo drift in isochronous rhythmic tapping. In R. J. Zatorre & I. Peretz (Eds.), *The biological foundations of music* (Vol. 930, pp. 405–408). New York: New York Academy of Sciences.
- Collier, G. L., & Ogden, R. T. (2004). Adding drift to the decomposition of simple isochronous rhythmic tapping: An extension of the Wing–Kristofferson model. *Journal of Experimental Psychology: Human Perception and Performance*, *30*, 853–872.
- Collier, G. L., & Wright, C. E. (1995). Temporal rescaling of simple and complex ratios in rhythmic tapping. *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 602–627.
- Essens, P. J., & Povel, D. J. (1985). Metrical and nonmetrical representations of temporal patterns. *Perception & Psychophysics*, *37*, 1–7.
- Feynman, R. P., Leighton, R. B., & Sands, M. (1963). *The Feynman lectures on physics* (Vol. 1). Reading, MA: Addison-Wesley.
- Fowler, C. A., & Saltzman, E. (1993). Coordination and coarticulation in speech production. *Language and Speech*, *36*(Pts. 2–3), 171–195.
- Haken, H., Kelso, J. A., & Bunz, H. (1985). A theoretical model of phase transitions in human hand movements. *Biological Cybernetics*, *51*, 347–356.
- Harrington, D. L., Haaland, K. Y., & Hermanowicz, N. (1998). Temporal processing in the basal ganglia. *Neuropsychology*, *12*, 3–12.
- Ivry, R., & Corcos, D. (1993). Slicing the variability pie: Component analysis of coordination and motor dysfunction. In K. Newell & D. Corcos (Eds.), *Variability and motor control* (pp. 415–447). Champaign, IL: Human Kinetics.
- Ivry, R. B., & Hazeltine, R. E. (1995). Perception and production of temporal intervals across a range of durations: Evidence for a common timing mechanism. *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 3–18.
- Ivry, R. B., Richardson, T. C., & Helmuth, L. L. (2002). Improved temporal stability in multieffector movements. *Journal of Experimental Psychology: Human Perception and Performance*, *28*, 78–92.
- Ivry, R. B., Spencer, R. M., Zelaznik, H. N., & Diedrichsen, J. (2002). The cerebellum and event timing. In S. M. Highstein & W. T. Thach (Eds.), *The cerebellum: Recent developments in cerebellar research* (Annals of the New York Academy of Sciences, Vol. 978, pp. 302–317). New York: New York Academy of Sciences.
- Jerde, T. E., Soechting, J. F., & Flanders, M. (2003). Coarticulation in fluent finger spelling. *Journal of Neuroscience*, *23*, 2383–2393.
- Jirsa, V. K., & Haken, H. (1997). A derivation of a macroscopic field theory of the brain from the quasi-microscopic neural dynamics. *Physica D*, *99*, 503–526.
- Kay, B. A., Kelso, J. A., 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*, 178–192.
- Keele, S. W., Pokorny, R. A., Corcos, D. M., & Ivry, R. (1985). Do perception and motor production share common timing mechanisms? A correctional analysis. *Acta Psychologica (Amsterdam)*, *60*, 173–191.
- Kelso, J. A., Fink, P. W., DeLaplain, C. R., & Carson, R. G. (2001). Haptic information stabilizes and destabilizes coordination dynamics. *Proceedings of the Royal Society of London, Series B*, *7*, 1207–1213.
- Klein, B., Hondzinski, J. M., & Flanders, M. (2003). Drawing sequences of segments in 3D: Kinetic influences on arm configuration. *Journal of Neurophysiology*, *89*, 3253–3263.
- Kolers, P. A., & Brewster, J. M. (1985). Rhythms and responses. *Journal of Experimental Psychology: Human Perception and Performance*, *11*, 150–167.
- Krampe, R. T., Mayr, U., & Kliegl, R. (2005). Timing, sequencing, and executive control in repetitive movement production. *Journal of Experimental Psychology: Human Perception and Performance*, *31*, 379–397.
- Lewis, P. A., Wing, A. M., Pope, P. A., Praamstra, P., & Miall, R. C. (2004). Brain activity correlates differentially with increasing temporal complexity of rhythms during initialisation, synchronisation, and continuation phases of paced finger tapping. *Neuropsychologia*, *42*, 1301–1312.
- Madison, G. (2001). Variability in isochronous tapping: Higher order dependencies as a function of intertap interval. *Journal of Experimental Psychology: Human Perception and Performance*, *27*, 411–422.
- Penhune, V. B., & Doyon, J. (2002). Dynamic cortical and subcortical networks in learning and delayed recall of timed motor sequences. *Journal of Neuroscience*, *15*, 1397–1406.
- Peper, C. L., Ridderikhoff, A., Daffertshofer, A., & Beek, P. J. (2004). Explanatory limitations of the HKB model: Incentives for a two-tiered model of rhythmic interlimb coordination. *Human Movement Science*, *23*, 673–697.
- Povel, D. J. (1981). Internal representation of simple temporal patterns. *Journal of Experimental Psychology: Human Perception Performance*, *7*, 3–18.
- Rao, S. M., Harrington, D. L., Haaland, K. Y., Bobholz, J. A., Cox, R. W., & Binder, J. R. (1997). Distributed neural systems underlying the timing of movements. *Journal of Neuroscience*, *17*, 5528–5535.
- Repp, B. H., & Penel, A. (2002). Auditory dominance in temporal processing: New evidence from synchronization with simultaneous visual and auditory sequences. *Journal of Experimental Psychology: Human Perception and Performance*, *28*, 1085–1099.
- Sakai, K., Hikosaka, O., & Nakamura, K. (2004). Emergence of rhythm during motor learning. *Trends in Cognitive Sciences*, *8*, 547–553.
- Sergent, V., Hellige, J. B., & Cherry, B. (1993). Effects of responding hand and concurrent verbal processing on time-keeping and motor-implementation processes. *Brain and Cognition*, *23*, 243–262.
- Sosnik, R., Hauptman, B., Karni, A., & Flash, T. (2004). When practice leads to co-articulation: The evolution of geometrically defined movement primitives. *Experimental Brain Research*, *156*, 422–438.
- Spencer, R. M., & Zelaznik, H. N. (2003). Weber (slope) analyses of timing variability in tapping and drawing tasks. *Journal of Motor Behavior*, *35*, 371–381.
- Sternad, D. (2001). Kurt Wachholder: Pioneering electrophysiological investigations on voluntary movements. In M. L. Latash & V. M. Zatsiorsky (Eds.), *Classics in movement science* (pp. 375–408). Champaign, IL: Human Kinetics.
- Sternad, D., Saltzman, E. L., & Turvey, M. T. (1998). Interlimb coupling in a simple serial behavior: A task dynamic approach. *Human Movement Science*, *17*, 393–433.
- Ulrich, R., & Stapf, K. H. (1984). A double-response paradigm to study stimulus intensity effects upon the motor system in simple reaction time experiments. *Perception & Psychophysics*, *36*, 545–558.
- Vaughan, J., Mattson, T. R., & Rosenbaum, D. A. (1998). The regulation of contact in rhythmic tapping. In D. A. Rosenbaum & C. E. Collyer (Eds.), *Timing of behavior: Neural, psychological, and computational perspectives* (pp. 195–211). Cambridge, MA: MIT Press.
- Vaughan, J., Rosenbaum, D. A., Diedrich, F. J., & Moore, C. M. (1996). Cooperative selection of movements: The optimal selection model. *Psychological Research*, *58*, 254–273.
- Vorberg, D., & Hambuch, R. (1978). On the temporal control of rhythmic performance. In J. Requin (Ed.), *Attention and performance VII* (pp. 535–555). Hillsdale, NJ: Erlbaum.
- Vorberg, D., & Hambuch, R. (1984). Timing of two-handed rhythmic performance. In J. Gibbon & L. Allan (Eds.), *Timing and time perception* (Vol. 423, pp. 390–406). New York: New York Academy of Sciences.
- Vorberg, D., & Wing, A. M. (1996). Modeling variability and dependence in timing. In H. Heuer & S. Keele (Eds.), *Handbook of perception and action* (Vol. 2, pp. 181–262). New York: Academic Press.
- Wachholder, K., & Altenburger, H. (1926). Beiträge zur Physiologie der willkürlichen Bewegung: IX. Mitteilung. Fortlaufende Hin- und Herbewegungen [Contributions to the physiology of voluntary movement: IX. Article. Continuous forth and back movements]. *Pflügers Archive*, *214*, 625–641.
- Wing, A. M. (1977). Effects of type of movement on the temporal precision of response sequences. *British Journal of Mathematical and Statistical Psychology*, *32*, 60–72.
- Wing, A. M. (1979). A note on estimation of the autocovariance function in the analysis of timing of repetitive responses. *British Journal of Mathematical and Statistical Psychology*, *32*, 143–145.
- Wing, A. M. (1980). Timing of movement phases of a repeated response. *Journal of Motor Behavior*, *12*, 113–124.
- Wing, A. M. (2002). Voluntary timing and brain function: An information processing approach. *Brain and Cognition*, *48*, 7–30.
- Wing, A. M., & Kristofferson, A. B. (1973a). Response delays and the timing of discrete motor responses. *Perception & Psychophysics*, *14*, 5–12.
- Wing, A. M., & Kristofferson, A. B. (1973b). The timing of interresponse intervals. *Perception & Psychophysics*, *13*, 455–460.
- Yu, H., Russell, D. M., & Sternad, D. (2003). Task-effector asymmetries in a rhythmic continuation task. *Journal of Experimental Psychology: Human Perception and Performance*, *29*, 616–630.

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