Improved temporal stability in multi-effector movements.

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Final Draft: April 24, 2001

In press, Journal of Experimental Psychology: Human Perception & Performance.

Abstract

Four experiments compared the temporal stability of actions involving either one or more effectors. A reduction in within-effector temporal variability was observed during two-effector tapping compared to when either moved alone. This phenomenon was observed for various limb combinations, regardless of whether the two effectors were on the same or different sides of the body (Experiment 1) and did not require that the timed movements be produced in a repetitive manner (Experiment 3). Moreover, an additional reduction in variability was found when tapping with three effectors (Experiment 2). This multiple effector advantage is multiplicative: The magnitude of the multiple effector advantage was greater for longer target intervals (Experiment 4). A process-based account of these findings is proposed, based on the idea that independent temporal representations are generated for each effector. These representations are integrated to produce coordinated motor commands, and the multiple effector advantage is hypothesized to be a statistical consequence of the integration process.

Improved temporal stability in multi-effector movements

Bimanual coordination has proven an important avenue for understanding the dynamics of motor control. A central focus of this work has been to identify the constraints that characterize the temporal coordination of the two hands (e.g., Schöner & Kelso, 1988). When producing rhythmic movements, the two hands naturally adopt a common frequency, establishing an in-phase, symmetric relationship, or an anti-phase, opposing relationship. With training, we may learn novel phase relations (Zanone & Kelso, 1997), and skilled musicians are capable of performing complex polyrhythms (Krampe, Kliegl, Mayr, Engbert, & Vorberg, 2000). But even in these contexts, the gestures of the two hands remain strongly coupled. Drummers are likely to exploit the hierarchical relationship between the two required rhythms when tapping out patterns such as three against two or four against three. Indeed, temporal coupling would appear to be the most fundamental constraint associated with multi-limb movements.

Temporal coupling has proven to be the cornerstone for much theorizing in the motor control literature, especially in terms of the development of dynamic accounts of coordination (Kelso, 1997; Kugler & Turvey, 1987). Coupling provides an important way in which control requirements can be reduced. In bipedal locomotion, the motions of the two limbs can be described as non-linear coupled oscillators. A phase parameter can characterize different modes of locomotion; for example, a fast moving biped can be running (anti-phase) or hopping (in-phase). The lack of stability at other phase relations offers a means for understanding the attraction to certain categorical forms of behavior.

The focus of most coupled oscillator models has been on the relationship between the two limbs (for reviews, see Kelso, 1997; Schöner & Kelso, 1988). In particular, these models provide an

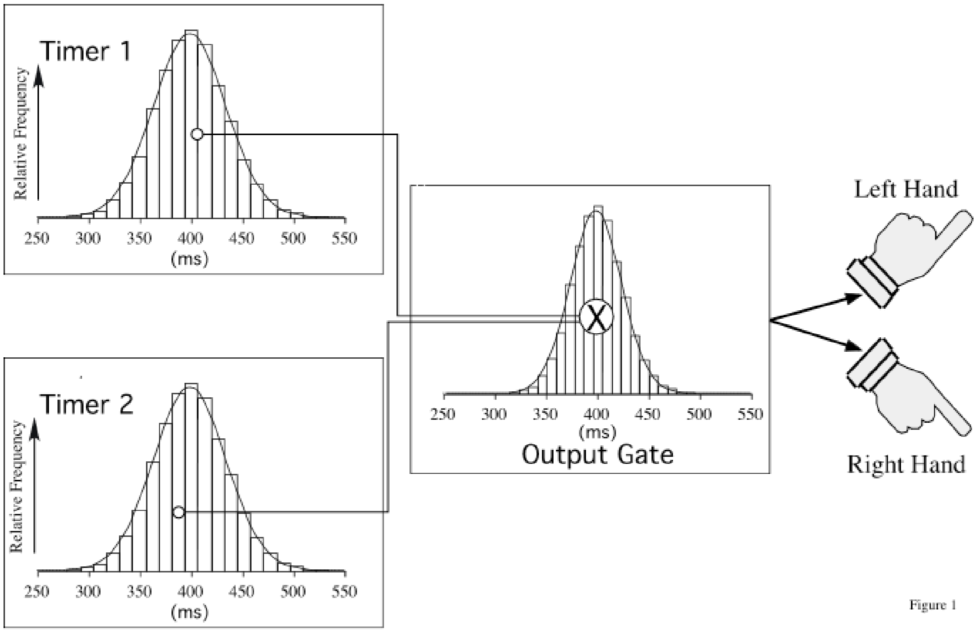


Figure 1. The multiple timer model. Left column: Separate temporal representations (Timers 1 and 2) are generated for each hand during

account of the stability of certain movement patterns, and provide an analytic tool for understanding how stability may change as a function of control parameters (i.e., frequency) or experience. Stability in this context is generally assessed in terms of the variability of the phase differences between the two limbs. The individual may be asked to maintain a particular phase relationship and the deviation from this target phase will be measured in terms of both constant and variable error as frequency is varied.

An alternative way to describe stability during repetitive movements, one that is focused on the component rather than coordinative level, is to look at the performance of each limb individually. The mean and variability of the movement periods for each limb can be measured to assess how well an individual can maintain a target frequency. Helmuth and Ivry (1996) examined this question in a series of studies using a repetitive tapping task. In their first experiment, the participants were required to tap with either the left hand alone, the right hand alone, or with both hands, trying to maintain a target inter-tap interval of 400 ms. The mean inter-tap interval was unchanged between the uni- and bimanual conditions. However, as measured by the variability of the inter-tap intervals, the performance of each hand became more stable during bimanual tapping. That is, the variability of the within-hand inter-tap intervals was lower for each hand in the bimanual context (see also Yamanishi, Kawato, & Suzuki, 1980; Semjen & Ivry, in press). A second experiment demonstrated that this multiple effector advantage did not require the movement of homologous muscles. A similar improvement was observed when finger and forearm movements were combined.

To account for the multiple effector advantage, Helmuth and Ivry (1996) proposed the Multiple Timer Model, a process account of the control processes involved in timing and temporal coupling (Figure 1). The model rests on three critical assumptions. First, it is assumed that there are independent central timing signals associated with the movements of each effector. During left hand tapping, it is assumed that an internal timing signal is generated to control when each left-hand response should occur. Likewise, during right hand tapping, an internal timing signal associated with the right hand is generated. These signals are assumed to originate in a central control process that operates as an internal timing system. The recruitment of specific elements within this timing system is dependent on the output effector, with independent representations associated with different effectors.

The second assumption is that these separate timing mechanisms continue to operate during bimanual movements. That is, the multiple timer model posits that during such movements, there are two temporal control signals being generated, one for the left hand and one for the right hand.

The third assumption centers on how these two signals are translated into motor commands. Helmuth and Ivry (1996) proposed that, although independent timing signals are generated for each effector, the internal timing system does not have direct access to the motor system. Instead, central commands to the effectors are regulated through a motor implementation process that we will refer to as an output gate. The output gate is constrained to update central commands to different effectors simultaneously. It is this constraint which underlies temporal coupling in the model. Due to this coupling constraint, the independent timing signals for the two hands become integrated.

We will contrast the dynamics of this form of coupling with more traditional coupled oscillator models in the General Discussion. At this point, we simply point out that temporal coupling in the multiple timer model does not reflect interactions between the timing mechanisms per se, but rather a process receiving input from multiple timers. The timing mechanisms are also coupled in the sense that the triggering of the gate not only initiates the responses but also serves as a signal for the next timing cycle to begin. Without coupling of this form, the two hands would quickly become out of phase.

An obvious question is how does the gate operate? How do the independent timing signals interact? We have conducted a series of simulations to explore different ways in which the two timing signals could be integrated (Helmuth and Ivry, 1996). In these simulations, two independent samples were taken from distributions representing two timing systems, one for the left hand and one for the right hand. The means and variances for these distributions were based on the observed performance during unimanual tapping in Experiment 1 of Helmuth and Ivry. Different procedures were simulated in terms of how the samples could be used by an output gate and from this, runs of inter-tap intervals were generated. The means and variances of these runs were then compared with the observed bimanual data.[F1]

The gate could perform an OR operation, firing whenever it receives an input from either timing process. Alternatively, the gate could perform an AND operation, firing only after it receives input from both timing processes. While simulations of the OR and AND gating models indicates that variability would be reduced during bimanual tapping, each model also predicts that there should be a change in mean tapping rate. For the OR model, mean tapping would be faster; for the AND model, mean tapping rate would be slower. Neither prediction is consistent with the observed data.

The best fitting model was one in which the two independent timing signals were averaged. That is, the output gate is triggered at a time that corresponds to the average of the two timing signals. With this model, the predicted reduction in variability can be analytically derived. It is the standard deviation of a new distribution formed by the average of two independent samples from the constituent distributions. If the constituent distributions are identical, then

$$\mathbf{SD_{bim} = SD_{uni} / sqrt(2)} \qquad (1)$$

Using the observed unimanual data from Helmuth and Ivry, the averaging model predicted a standard deviation of 9.4 ms during bimanual tapping. This closely approximated the observed value of 9.7 ms (averaged over left and right hands).

Averaging in the strict sense is illogical in the temporal domain. Consider a situation in which the target interval is 400 ms. Suppose that for a particular interval, the right hand timer signal is a little fast and sends its output at 380 ms, whereas the left hand timing signal is slow and sends its output at 440 ms. By averaging, the output gate would initiate the response in both hands after 410 ms even though the left hand timer is not going to provide its signal for another 30 ms.

This problem ceases to exist when the timing signals are conceptualized as continuous variables rather than discrete events. Figure 2 depicts the operation of the output gate as a threshold device: The response is triggered when the input activation reaches a threshold level. The left panel shows the operation of the gate for two successive intervals, one in which the threshold is reached earlier than the target time and one in which the threshold is reached after the target time. This variability might underlie the production of a long interval following a short interval, at least in terms of the timing signals. The right panel shows the operation of the gate when the two signals arrive simultaneously and are summed together. Assuming that activity is normalized, the summed activity from two signals will provide a continuous record of the average and the normalized threshold will be reached at the average of the two samples.

The threshold mechanism is our instantiation of the simultaneity constraint. It ensures that bimanual movements are coupled. A statistical consequence of this implementation is that the within-hand variability for each hand is lower during bimanual tapping than during unimanual tapping.

Models that assume a single timer would also, of course, predict coupling, but they do not predict the multiple effector advantage. By postulating separate mechanisms for timing and temporal coupling, we are able to account for both phenomena.

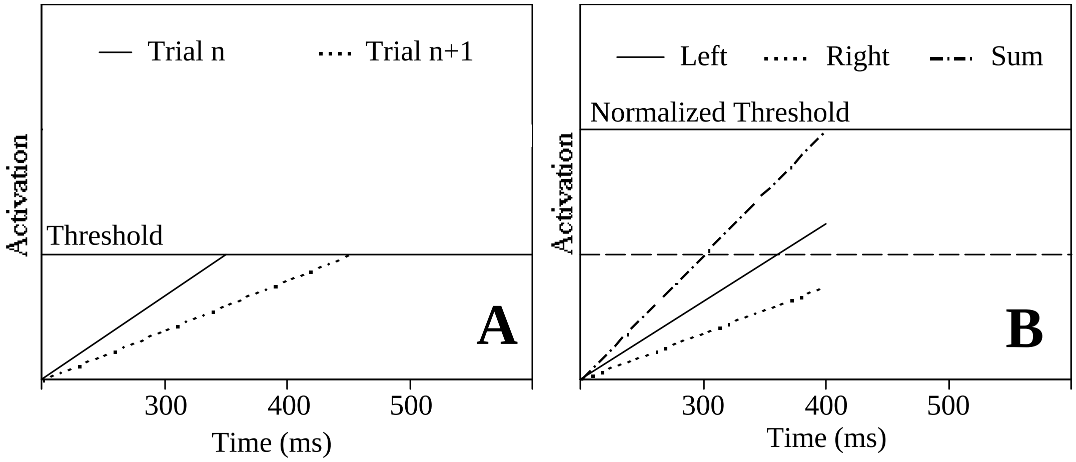


Figure 2

Figure 2 Activation process within the output gate. The gating process is depicted as a threshold mechanism. Activation arises as a consequence of timer inputs.

The multiple timer model provides a parsimonious account of the performance of normal subjects in Helmuth and Ivry (1996). It also provides a novel account of the paradoxical improvement observed in unilateral ataxia patients during bimanual movements. Franz, Ivry, and Helmuth (1996) tested four patients with unilateral cerebellar lesions on a repetitive tapping task, comparing uni- and bimanual performance in both the affected and unaffected hand. As predicted, all four patients exhibited lower temporal variability on the affected side during bimanual tapping, presumably because the effects of aberrant timing signals were mitigated by the timing signals controlling the unimpaired hand. Moreover, an analysis of the individual cases confirmed a prediction derived from the model regarding changes in the performance of the unimpaired side. If the difference in variability between the impaired and unimpaired sides was large during unimanual tapping, then the movements of the unimpaired limb during bimanual tapping became less consistent. If the impaired-unimpaired difference during unimanual tapping was small, then the movements of the unimpaired limb became more consistent during bimanual tapping. The general form of Equation 1, in which non-identical distributions are associated with the two effectors, predicts these results.

In the current paper, we examine a new set of predictions derived from the multiple timer model. We focus on the hypotheses that independent temporal representations are generated for each effector and that these representations are integrated in a manner that resembles an averaging operation. In the General Discussion, we return to a discussion of the psychological and neural implications of this process model, and examine it within the context of a more general class of dynamic systems models.

Experiment 1

The goals of Experiment 1 are two-fold. First, we examine the generality of the multiple effector advantage by using various pairs of effectors. The studies of Helmuth and Ivry (1996) were limited to upper limb movements, although they did observe that the improved temporal variability during bimanual movements was evident for movements that either involved homologous or non-homologous muscles. In the current experiment, participants will tap with two hands, two feet, or hand-foot combinations that involve effectors from either different or the same side of the body.

Second, by using effectors from the same side of the body, we sought to test an implicit assumption of the multiple timer model. A central question in the study of internal timing has been whether a common timing system is exploited across various task domains. Based on correlations in temporal acuity across time production and time perception tasks, Keele et al. (1985) argued for such a common timing system (see also, Ivry & Hazeltine, 1995). Neuropsychological evidence has also been cited in support of a common timing system hypothesis. Proponents of a cerebellar timing locus (e.g., Ivry & Keele, 1989; Ivry, 1997) have emphasized that patients with cerebellar damage perform poorly on a variety of tasks that require precise timing. Similarly, proponents of a basal ganglia locus (e.g., Harrington, Haaland, & Hermanowicz, 1998) have shown that Parkinson patients perform poorly on both tapping and time perception tasks.

Ignored in this work has been the question of what is meant by a common internal timing system. At one extreme, one might suppose there is a unitary timing mechanism whose output is gated to different processing systems that require precise temporal representations. However, our own neuropsychological studies make clear a limitation with this hypothesis. Patients with unilateral cerebellar lesions have been used as their own control to show that coordination problems on the affected side are related to a loss of temporal control during repetitive movements (Ivry, Keele, & Diener, 1988; Franz et al., 1996). This impaired performance is compared to their normal performance on the same task when using effectors on their unaffected side. At a minimum, such results would argue for at least two internal timing systems, one that is disturbed and one that is intact.

However, an alternative hypothesis would be that, while a specific psychological process may be specialized for temporal processing, the instantiation of temporal representations will involve the recruitment of computational elements that are task specific. At a neural level, this hypothesis would propose that distinct populations of neural circuits would be engaged for different tasks, even though the computational characteristics of these circuits is similar (Ivry, 1996). In this view, the idea of a common timing system is misleading: Rather than take this statement to imply a single timing mechanism, one would conceptualize a near-infinite array of timing mechanisms, each linked to particular input or output systems (and perhaps particular intervals). Thus, different elements are invoked for timing movements with the right index finger compared to tapping with the left index finger, or even the right wrist.

The comparison of various effector combinations, especially crossed and uncrossed combinations allow a first test of this hypothesis. From the work of Helmuth and Ivry (1996), one might argue that there are two timing mechanisms, one associated with the right side of the body and another associated with the left side of the body. The outputs of these two timers are integrated because of the need to coordinate the two limbs during bimanual coordination. However, the hypothesis raised in the preceding paragraph would suggest that the multiple effector advantage would hold regardless of whether the two effectors are on the same or different sides of the body.

Method

Participants. Eighty-two undergraduate students at the University of California at Berkeley participated in this experiment in partial fulfillment of psychology course requirements. All participants were right handed, as assessed by self-report.

Apparatus. Responses were produced on peripheral response devices, linked to a desktop computer. The temporal resolution of the system was 1 ms. All hand responses were made with flexion/extension movements of the right and left index fingers. For these responses, a 20 x 30 cm response board with two piano-type keys (2 x 10 cm) was used. Response boards in the shape of a wedge were designed for the extension/flexion ankle movements to produce foot responses. The surface of each board (10 x 7 cm) was fixed at a 20 degree angle from a rubber base that rested on the floor. A raised button measuring 1.2 cm per side was mounted on the board. Responses were recorded when the button was depressed 0.4 cm, bringing it level to the surface of the board.

Procedure. After reading and signing an informed consent form, participants were seated in front of a computer terminal in a quiet room. They were told that the experiment would measure how accurately and how consistently they could tap at a given speed, which would be signaled by a series of tones from the computer. They were allowed to position the response board(s) to a comfortable position. The participants were told to minimize movements during the experiment except in the effectors required for responding.

A message appearing on the computer screen before each trial indicated to the participants which effector or effector combination was to be used in the upcoming trial. Each trial consisted of a synchronization and continuation phase. The participant initiated the trial by pressing the "ENTER" key on the computer keyboard. After a 1 s delay, a series of 50 ms, 500 Hz tones were presented, separated by an inter-onset interval of 550 ms. The participants began tapping with the tones once they had internally established the beat. After producing twelve intervals during the synchronization phase, the tones were terminated. They were then required to continue tapping, attempting to maintain the target interval in as consistent a manner as possible. After 32 unpaced intervals were recorded, a low-pitch tone indicated the end of the trial. The 550 ms target interval is longer than the 400 ms pace used in our previous studies (Helmuth & Ivry, 1996; Franz et al., 1996). It was selected on the basis of pilot work designed to determine a comfortable speed for foot tapping.

Feedback was provided immediately after the trial was completed. The target interval (550 ms) appeared at the top of the screen. Listed below this were two lines, one showing the mean and standard deviation of the participants' inter-tap intervals during the synchronization phase and the second showing these measures for the continuation phase. The experimenter encouraged the participants to examine these measures after each trial in order to see how accurately they had maintained the pacing speed during the unpaced phase of the trial. Primary emphasis was given to the standard deviation measure during the unpaced phase. The experimenter explained that this number reflected the participants' consistency and that they should try to make this as small as possible.

Design. The participants were assigned to one of four groups based on the required effector combination. The four groups were finger-finger (1a), foot-foot (1b), finger-foot, crossed sides (1c), and finger-foot, uncrossed sides (1d). Within the finger-foot crossed group, half of the participants used the left index finger and right foot and half used the right index finger and left foot. Within the finger-foot uncrossed group, all of the participants used the right finger and right foot.

All of the participants were tested in three conditions. For two of the conditions, tapping was performed with a single effector; in the third condition, tapping was performed with both effectors. For example, participants in Group 1b tapped with the left foot alone, the right foot alone, and both feet together. Similarly, participants in Group 1d tapped with the right (left) index finger alone, the right (left) foot alone, and the finger and foot together. Three blocks of tapping were completed for each of the three conditions. For Groups 1a, 1c, and 1d, each block consisted of seven trials, yielding a data set of 21 trials for each condition, or a total of 63 trials per participant. For Group 1b, each block consisted of six trials and thus, 18 trials for each condition. We targeted a smaller data set for this group because pilot testing indicating that foot tapping would likely lead to more errors (see below) and we didn't want the participants to become fatigued. The first block for each condition was preceded by two practice trials for that condition. The order of presentation of the three conditions was counterbalanced across participants with the constraint that each condition was tested within a triad of blocks. The experiment lasted approximately one hour.

Data Analysis.

An initial analysis was conducted after each trial to identify any intervals that were either shorter than 200 ms or longer than 1000 ms. Almost all such trials occur when the participant failed to depress the response key fully, thus failing to activate the microswitch and leading to an interval measurement approximately twice as long as the surrounding tapping intervals. These trials were repeated within the same block up to a limit of seven repeated trials. If the participant produced seven trials containing an interval outside the minimum and maximum duration criteria, the block was terminated prematurely.

The analyses reported below are based on the data from the final 30 intervals obtained during the unpaced phase of the trials in which all of the intervals fell within the minimum and maximum duration criteria. The mean and standard deviation were computed for each trial. Our primary analysis of temporal consistency followed the procedure described in Helmuth and Ivry (1996), focusing on total variability and a decomposition of this variability based on the two-process model of Wing and Kristofferson (1973; Vorberg & Wing, 1996). This model assumes that tapping variability reflects the contribution of two independent processes: variability associated with an internal clock that determines when each response should be emitted and variability associated with motor implementation processes required to translate this central command into an action. Ivry and Hazeltine (1995) have argued that the former process is composed of various control operations only one of which is the clock, and thus will refer here to the two components as central and motor delay, respectively.

Vorberg and Wing (1996) provided a comprehensive discussion and derivation of the two-process model. Empirical confirmation of the assumptions of the model has been obtained in many studies involving healthy and neurologically impaired populations (e.g., Wing, 1980; Ivry et al., 1988; Ivry & Hazeltine, 1995). Here we provide a brief summary of the procedure used to derive the estimates of the variability associated with the central and motor delay components.

The duration of each Interval j can be expressed as

$$\mathbf{I_j = C_j + MD_j - MD_{j-1}} \qquad (2)$$

where I represents the durations of the observed interval, C the central processing time, and MD the motor implementation delays. Given the assumption that the central and motor processes are independent, the variances of the components are additive:

$$\sigma_I^2 = \sigma_C^2 + 2\,\sigma_{MD}^2 \qquad (3)$$

Successive intervals are assumed to result from independent samples of the random variables associated with the central and motor processes. In other words, unpaced tapping at rates in the hundreds of millisecond range is assumed to be an open-loop process. However, neighboring intervals share one sample of the motor delay with each other and are thus negatively correlated with each other. Given this, an estimate of motor delay variability is given by

$$\sigma_{MD}^2 = -\,\mathrm{autocovar}_{\mathrm{I}}(1) \qquad (4)$$

where autocov(1) is the covariance between Intervals j and j+1 (Lag 1). An estimate of central variability can then be obtained by subtracting the motor estimate from the total variability obtained from the raw data.

Prior to calculating the estimates of the two components, we performed a transformation on the raw data to remove the effects of global changes in tapping rate. A regression line was fit through the 30 unpaced intervals and the covariance function for lags 0 through 5 was based on this transformation. The values were averaged across the 21 trials per condition and the standard deviation scores as well as estimates of central and motor variability were based on these data. The covariance function provides a critical test of the two-process model: the lag 1 covariance should be negative and the values for lags greater than one should be zero. The linear transformation has the effect of reducing positive correlations between successive intervals, and thus the estimate of the motor variability is higher than that obtained from the raw data. It turns out that this change is minimal, usually on the order of less than 2 ms, and the results reported below would be similar if the raw data had been used instead of the transformed data.

It is important to note that this detrending procedure, and indeed, the two-process model in general, ignore potential sources of noise that might operate at different time scales during repetitive movements (e.g., 1/f noise, see Chen, Ding, & Kelso, 1997). However, given that the trials in the current experiment were limited to about 15 s, it is unlikely that any non-linear drift would contribute substantially to the observed variability (see Madison, in press)

Results and Discussion

The data for two participants were excluded from the final analysis because their mean tapping rates (less than 470 ms. in at least one condition) were much faster than the target interval. The data for eight other participants were excluded because they produced blocks that did not contain a sufficient number of trials in which all of the intervals were greater than 200 ms and less than 1000 ms. Intervals falling outside these criteria almost always occurred on trials involving foot responses and likely resulted from the failure of the participant to depress the response key with sufficient force. Of the 72 participants retained in the analysis, 17 were in groups 1a and 1d, 18 were in group 1b, and 20 were in group 1c. For these participants, 9.6% of the trials were repeated due to trials in which at least one interval failed to fall within the criterion window of 200 - 1000 ms.

The results of Experiment 1 are summarized in Table 1. The table lists the mean and standard

	Mean		$\mathrm{ITI}_{\mathrm{SD}}$		Central		MD	
	One	Two	One	Two	One	Two	One	Two
Exp 1a								
R Fing	520	517	23.4	20.1	18.3	13.8	10.3	10.3
L Fing	519	517	24.5	21.3	18.0	13.2	11.8	11.8
Exp 1b								
R Foot	523	522	32.2	26.0	21.3	16.5	17.1	14.2
L Foot	520	522	32.6	28.0	20.5	16.1	17.9	16.2
Exp 1c								
Fing, S1	534	526	25.1	26.8	20.4	17.5	10.3	14.3
Foot, S2	531	526	28.0	28.4	20.8	17.3	13.2	15.9
Exp 1d								
Fing, S1	529	529	25.3	29.5	19.9	18.0	11.1	16.6
Foot, S1	525	530	30.4	30.4	23.1	18.5	14.0	17.0

Table 1 Mean interval produced, standard deviation of the inter-tap intervals, and estimates of the central and motor delay components for Experiment 1. All values are in ms.

deviation of the inter-tap intervals, and the estimates of the central and motor delay component sources of variability. Within each group, there are two rows, one for each effector. The pairs of columns show the values for the one-effector and two-effector conditions. All of the data are within-effector measures. While the two effectors were tightly coupled in all conditions, we will not report any between-effector analyses here (see Experiment 4).

In all of the conditions, the participants tended to tap more quickly than the target interval of 550 ms. The speed-up of about 25 ms was generally continuous, with the produced intervals close to the target rate at the end of the synchronization period followed by a tendency to speed-up over the course of the unpaced phase. We have observed a similar hastening in a previous study with college students (Ivry & Keele, 1989). While we suspect the phenomenon reflects a mild degree of impatience on the part of our participants, the effect is not large and appears to be similar in the one-effector and two-effector conditions.

Turning to the standard deviation scores, an interesting difference is apparent between the two groups who performed homologous movements (Groups 1a and 1b) and the two groups who performed non-homologous movements (Groups 1c and 1c). Variability was lower during the two-effector condition for participants who tapped with two fingers (Group 1a) and the participants who tapped with the two feet (Group 1b). In contrast, the standard deviation values tend to be higher for the participants who tapped with one finger and one foot, either on opposite sides of the body (Group 1c) or the same side of the body (Group 1d). The standard deviation data for each group were analyzed in a series of 2 x 2 ANOVAs, with one factor referring to the effector (e.g., right finger or left finger for Group 1a, finger or foot for Group 1c) and the other factor referring to the condition (single-effector or two-effector). Separate ANOVAs were conducted for each group since our main interest here is on whether the multiple effector advantage is observed across a range of conditions.

The reduction during two-effector tapping was highly reliable for the two finger participants in Group 1a, $F(1,16)=33.8$, $p<.001$, and the two feet participants in Group 1b, $F(1,17)=34.8$, $p<.001$. The opposite pattern was observed for the two groups in which finger and foot tapping were combined. For these groups, tapping with two effectors tended to be more variable than tapping with a single effector. For the participants in Groups 1c performance was significantly more variable when tapping with a finger and foot on opposite sides of the body compared to when tapping with either effector alone, $F(1,19)=6.3$, $p<.05$. Similarly, the standard deviation was larger during right finger and right foot tapping for Group 1d, $F(1, 16)=7.2$, $p<.05$, although this increase was only reliable for the finger as reflected in the significant interaction, $F(1,16)=7.9$, $p<.05$. These results are similar to the pattern reported by Helmuth and Ivry (1996). In that study, the standard deviation of the inter-tap intervals was lower during bimanual tapping than in unimanual tapping, but did not change when the two-effector condition combined finger and forearm movements.

We next turn to the decomposition of the total variability into estimates of the variability associated with central and motor implementation processes. It is important to first verify that the current data are consistent with the assumptions of the two-process model. The covariance function provides three such tests (Vorberg & Wing, 1996; Wing & Kristofferson, 1973). First, the lag 1 covariance should be negative. Second, this value multiplied by negative two should be less than the lag 0 covariance (since values outside this boundary would imply a negative value for the estimate of central variability). Across the 284 covariance functions (72 participants x 2 effectors x 2 modes, single- and two-effector), the lag 1 covariance value was positive four times and greater than the boundary set by the lag 0 covariance value three times. We included these seven scores in the subsequent analyses, assuming they reflected noise in the data.

Third, the covariance function should be zero for lags greater than one. Figure 3 shows the covariance function for representative conditions. In each panel, the data are from right hand tapping, either alone or paired with the left hand (Group 1a, top panel) or the right foot (Group 1d, bottom panel). For all four covariance functions, the values for lags 2-5 are close to zero. Most important, the functions are quite similar for the single- and two-effector conditions, indicating that using two limbs does not introduce gross changes in the time series. There are a few data points that are significantly different than zero (all negative). However, when we applied variants of the two-process model that can account for such deviations (Wing, 1977), we found little change in the component estimates (see also, Helmuth & Ivry, 1996). Thus, we restrict the discussion to the estimates obtained from the basic two-process model.

Turning first to the estimates of central variability, a multiple effector advantage was observed for all four groups (see Table 1). The standard deviation associated with central processes was lower in the two-effector conditions compared to the one-effector conditions. These effects were confirmed in a series of ANOVAs identical to that described above. The number of effectors was significant for all four groups (1a: F(1,16)=52.1, p<.001; 1b: F(1, 17)=16.3, p<.001; 1c: F(1,19)=8.6, p<.01; 1d: F(1,17)=13.0, p<.01). No differences were observed between the two effectors within each group nor were any of the interactions reliable.

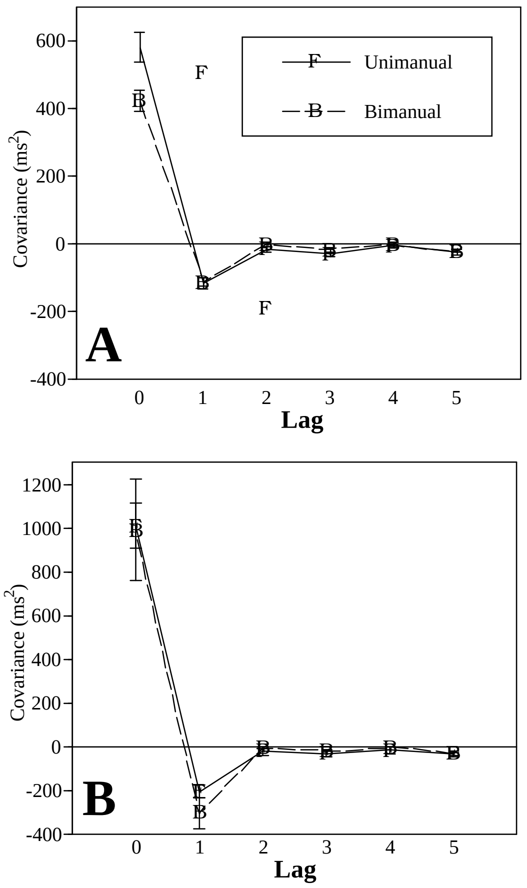


Figure 3

Figure 3. Covariance functions for Experiment 1. A: Finger-finger. Data are for right hand, unimanual and bimanual. B: Finger-foot. Data are for right foot, tapping alone and with right hand.

The results for the estimate of motor implementation variability are slightly more complicated. None of the main effects nor the interactions were significant for the two homologous movement conditions. For both of these groups, the motor delay estimate was larger for the non-dominant, left limb, although the effect only approached significance for the hand, F(1,16)=3.8, p=.07, and the foot, F(1,17)=3.3, p=.09. In the groups for which finger and foot movements were combined, there was a significant increase in the motor delay estimate during the two-effector condition (Group 1c: F(1,19)=9.0, p<.01; Group 1d: F(1,16)=28.2, p<.001). For the crossed side group (1c), there was also a main effect for the limb factor with the motor variability associated with the foot greater than that associated with the finger, F(1,19)=10.2, p<.01. Thus, the estimates of motor delay were unchanged when the two-effector movements involve homologous movements. When the two movements were non-homologous, an increase in the estimate of motor delay variability was observed.

A final analysis concerns the magnitude of the multiple effector advantage. By the multiple timer model, the improved temporal consistency during multiple effector tapping is a statistical consequence of sampling: The coupling constraint imposed by an output gate effectively acts to average the independent timing signals that have been generated for each effector. The observed improvement in the standard deviation should follow the square root of n rule, where n is the number of samples if the distributions associated with the effector-specific timing elements are identical. However, not all of the sources of variability will benefit from averaging by the process model outlined in Figure 1. For example, variability associated with motor implementation processes is imposed after the operation of the gate. Given this, we focused on the estimates of central variability, using the values observed during single-effector tapping to predict central variability during two-effector tapping. We averaged the two single-effector conditions, although simulations using the observed values yielded essentially identical results.

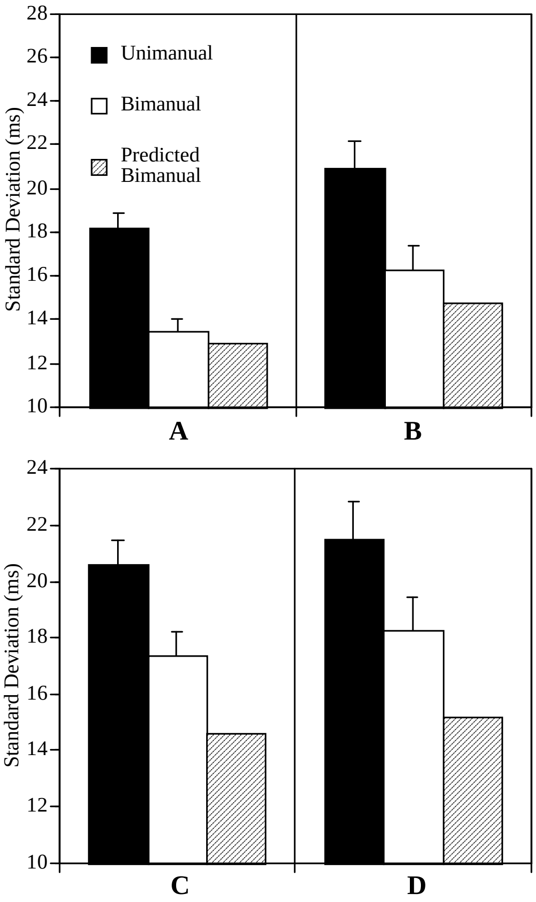
Figure 4 shows the comparison between the predicted and observed estimates of central variability. The two values are quite comparable for the bimanual group, similar to that reported by Helmuth and Ivry (1996). For the other three groups, the observed values are higher than the predicted values, and the difference is largest for the two groups in which upper and lower limbs were combined. These results raise the possibility that the processes associated with temporal coupling of the lower limbs may be different than those associated with the upper limbs. However, previous work on the dynamics of multi-limb coordination have assumed that similar principles apply for upper and lower limb coordination (Carson, Goodman, Kelso, & Elliott, 1995; Schmidt, Carello, & Turvey, 1990) and, as demonstrated in Figure 3, the covariance functions seem quite similar for the different limb combinations.

An alternative hypothesis is that, while the benefits of temporal averaging are similar in all conditions, new costs arise with multi-limb movements that involve combined movements of upper and lower limbs. Jeka and Kelso (1995) have shown that stability during repetitive movements involving the arm and leg is influenced by differences in the intrinsic frequencies of the two limbs, and that these frequencies are related to mass. From the perspective of the two-process model, the motor delay estimates point to one way in which these mass differences may influence variability. The motor delay estimates increased whenever the two-effector conditions involved limbs of unequal mass. This increase is not only found in the finger-foot conditions in the current experiment, but has also been observed for finger-forearm tapping (Helmuth & Ivry, 1996) and for bimanual studies in which external masses are added to produce an asymmetry between the two arms (Turvey, Rosenblum, Schmidt, & Kugler, 1986). It may be that additional central sources of variability are also introduced in such conditions and these attenuate the magnitude of the multiple effector advantage. The added peripheral noise may result from the fact that different forces are required for the two movements, and this requirement could also affect central processes. An evaluation of this hypothesis would require unconfounding the effects of homology and mass, as well as measurements of kinetic variables.

In summary, the results of Experiment 1 demonstrate the robustness of the multiple effector advantage. The temporal consistency with which a single limb produces repetitive movements improves when another limb is moved in a synchronous fashion. Thus, the stability of multi-effector movement patterns is not only manifest in terms of the coordination between the limbs, but is also apparent within the series of movements produced by each limb. The current study shows that the multiple effector advantage can be replicated at a new interval (550 ms compared to 400 ms in previous studies) and generalizes to leg movements. The phenomenon does not require movements with homologous effectors, although under these conditions, the temporal improvement is only observed in the estimates of central variability.

Experiment 1 provides new support for the multiple timer model outlined in the Introduction. At the heart of this model is the idea that the reduced variability during multi-limb tapping reflects an interaction between independent timing signals associated with the two limbs. The improved temporal performance was found for movements restricted to either upper or lower limbs, as well as for upper- and lower-limb combinations. Moreover, the pattern of results was quite similar for those participants using a finger and foot on the same side of the body as for those using a finger and foot from opposite sides of the body. These findings are

Figure 4. Estimates of central variability in Experiment 1 and predicted estimate based on the multiple timer model. Unimanual and bimanual values are averaged over left and righ hands. A: finger-finger. B: foot-foot. C: finger-foot crossed. C: finger-foot uncrossed.



consistent with the central hypothesis of the multiple timer model that effector-specific elements are recruited for controlling movement timing. At a more general level, an internal timing system would be conceptualized as an array of dedicated timing elements that are linked to specific input and output systems.

Experiment 2

To this point, the generality of the multiple effector advantage has been established in experiments comparing single- and two-effector tapping. In Experiment 2, we added a condition in which the participants tapped with three effectors at the same time. Assuming independent timing signals are generated for each effector, we expected to observe an additional reduction in temporal variability in the three-effector condition compared to the two-effector condition. This prediction would seem to be at odds with expectations based on attentional considerations. Although all of the effectors are required to produce simultaneous movements, the addition of extra effectors would be expected to entail a cost, rather than a benefit.

In designing the study, two considerations were taken into account. First, if as is assumed in the multiple timer model, the improvement is the result of averaging independent samples, the effect of adding a third effector will be relatively small. If the standard deviation of each timing element was 20 ms, averaging two samples would result in almost a 6 ms benefit (14.1 ms) whereas averaging three samples would only confer an additional 2.6 ms advantage (11.5 ms). Since the expected effect size is small, we doubled the targeted number of participants.

Second, and more important, it was difficult to determine the appropriate combination of effectors. Using all possible combinations of three effectors would require seven conditions (3 single conditions, 3 pairs, and 1 triad). Moreover, as shown in Experiment 1, there are differences between combining homologous effectors and non-homologous effectors. Motor implementation estimates consistently increase when limbs of unequal mass are combined, and this might make it difficult to interpret a comparison between bimanual tapping and a three-effector condition consisting of two hands and one foot. Given these considerations, we elected to combine the index finger and foot in the two-effector condition and focus on what happens when the other index finger is added in the three-effector condition. We expected that the added motor noise would be present in both the two and three-effector conditions, thus allowing a cleaner assay of changes in total variability and estimates of central variability.

Method

Participants. Thirty-nine right-handed undergraduates at UC, Berkeley participated in the experiment in partial fulfillment of psychology course requirements.

Procedure and Design. Each participant was tested in three conditions: single effector (right finger alone), two effector (right finger and right foot), and three effector (right finger, right foot, and left finger). At the beginning of each block, a message was displayed on the computer screen indicating the effector(s) for the forthcoming set of trials. The participants were instructed to restrict movements to the designated effectors. All other aspects of the design and procedure were identical to Experiment 1 with the exception that only six trials were included in each block. The last 30 intervals during the unpaced phase of each trial were included in the analyses. Trials in which an interval was shorter than 200 ms or longer than 1000 ms were repeated. An error in the data acquisition program led to some inconsistency in terms of the number of trials collected per condition. For some participants, the trials with aberrant intervals were not repeated; for others, seven trials were collected per condition. Thus, the actual number of trials per condition varied from 15 to 21.

Results and Discussion

All 39 participants were included in the analysis. Overall, approximately 9% of the trials were repeated because they contained at least one aberrant interval. As in Experiment 1, the long intervals appeared to result from instances in which insufficient force was used to depress the foot response key.

There was little variation in the mean produced interval across the three conditions. When tapping with only the right finger, the mean interval during the unpaced phase was 536 ms. In both the two- and three-effector conditions, the means for all of the effectors was 531 ms. Observation of the participants' performance as well as an informal examination of the time series at the level of individual trials indicated that the movements were always tightly coupled (see Experiment 4 for a more formal analysis). The data in all conditions conformed with the basic predictions of the two-process model. The lag 1 covariances were within the boundary conditions for all conditions except for one participant in one condition (right foot during two-effector tapping). Moreover, the covariance functions were similar in all three conditions.

The within-effector variability scores (calculated as deviations from the regression line), as well as the component estimates of central and motor variability are shown in Table 2. For the statistical analysis, we focused on the data for the right index finger and the right foot during the two- and three-effector conditions. In terms of the standard deviation scores, variability was lower during three-effector tapping compared to two-effector tapping, F(1,38)=38.9, p<.001. However, the effect of the number of effectors differed for the right finger and right foot as reflected in the significant interaction, F(1,38)=38.3, p<.001. When tapping these two effectors together, only the intervals produced by the right index finger became more consistent when the left index finger was engaged. Thus, at least for the finger, the data are consistent with the prediction that temporal variability will be inversely related to the number of activated effectors. Note that the central estimate for the finger was lower for the two- and three-effector conditions compared to when the finger tapped alone.

	ITI_{SD}			Central			Motor Delay		
	One	Two	Three	One	Two	Three	One	Two	Three
R Finger	23.9	27.6	24.1	17.8	16.0	15.1	11.3	15.9	13.3
R Foot		29.4	29.4		17.1	15.0		16.9	17.9
L Finger			25.7			14.7			14.9

Table 2 Standard Deviation of the inter-tap intervals and component estimates for Experiment 2.

Clearer support for the prediction of the multiple timer model comes from the analysis of the central variability component. Here, only the number of effectors variable proved reliable, F(1,38)=4.4, p<.05. Averaging over the right finger and right foot, the estimate is 16.6 ms during two-effector tapping and 15.0 ms during three-effector tapping. While the magnitude of the effect is greater for the foot, the interaction term did not approach significance, F(1,38)=1.3, p>.25.

Unexpectedly, there was also a reduction in motor variability during three-effector tapping, F(1,38)=4.5, p<.05, although this main effect was qualified by the significant interaction, F(1,38)=25.3, p<.001. For the right foot, motor variability increased when the left index finger was added in the three-effector condition; for the right index finger, motor variability decreased when the left finger was added. It is possible that adding an effector stabilizes peripheral noise factors associated with similar effectors (e.g., left finger and right finger), an idea that could be tested by making the third effector the left foot. As in Experiment 1, it is also not possible to determine if the effects here are related to the homology of the two index fingers or their similarity in mass (see Jeka & Kelso, 1995).

The above analyses of the overall standard deviation scores and the estimates of central variability provide a qualitative confirmation of the predictions of the multiple timer model. From the independent sampling assumption of the model, we can also examine this issue quantitatively. The most straightforward test would be to use the estimate of central variability for the right index finger in the single-effector condition, and use that to predict the estimates in the two- and three-effector conditions. The observed value during unimanual tapping was 17.8 ms. The predicted values for the two- and three-effector conditions would then be 12.6 ms and 10.3 ms. Both are considerably lower than the observed values (see Table 2). This is similar to what was found for the finger-foot conditions in Experiment 1, and there we suggested that there may be new contributions to central variability when combining effectors of unequal mass.

An alternative way to derive quantitative predictions based on the independent sampling hypothesis is to use the central estimates from the two-effector condition. For this, the average of the observed estimates is multiplied by the square root of 2 to estimate the variability of the underlying sampling distribution. This value is then divided by the square root of three, reflecting the number of samples presumed to occur in the three-effector condition. From this procedure, the predicted value of the central estimate during three effector tapping is 13.5 ms. Although closer to the observed value of 15.1 ms, the results again show that the improvement in temporal performance is less than would be expected by the strict version of the multiple timer model. To date, we have only obtained the square root of n reduction during bimanual tapping.

Nonetheless, the results of Experiment 2 show that temporal variability is reduced when three effectors are used compared to two effectors. By the logic of the multiple timer model, we would expect that further reductions would be found if more effectors were added to the mix. Of course, it would become quite difficult to observe such improvements if we are correct in attributing these effects to the exploitation of independent samples of temporal representations. The multiple effector advantage we have elicited in these experiments may well be a laboratory demonstration of a phenomenon long appreciated by musical performers. Most musicians tap their feet or let their body sway when performing. Even a drummer who is using a snare to maintain the beat for a group will tap his or her feet, even when not using a foot pedal. These actions are intended to stabilize temporal performance. The multiple timer model provides a mechanistic account of how this is achieved.

Experiment 3

Studies on temporal variability in motor control have generally involved repetitive movements. Performance is observed over cycles of continuous behavior to ask questions about the stability of different phase relations (Schöner & Kelso, 1988) or to examine whether people are capable of producing complex polyrhythms (e.g., Jagacinski, Marshburn, Klapp, & Jones, 1988; Krampe et al., 2000). Similarly, in our work to date on the multiple effector advantage (Franz et al., 1996; Helmuth & Ivry, 1996; Ivry & Hazeltine, 1999), as well as the first two experiments of this paper, we have always required the participants to produce a series of paced and unpaced intervals. This has allowed us to apply the two-process model in order to partition the total variability into central and motor implementation components.

However, a strong prediction of the multiple timer model is that temporal variability during bimanual movements should be reduced even when participants are producing single intervals in isolation. We tested this prediction in Experiment 3. The participants were trained to produce single intervals by pressing the response key twice, once to mark the beginning of the interval and once to mark the end of the interval. After an initial phase in which computer-generated tones were presented to provide a reference for the target interval, a set of single intervals was produced with a variable delay between each production. In this way, we obtained data sets comparable to that obtained in the earlier studies, but now each interval was produced in isolation rather than as a series of rhythmic movements.

We assume that the control processes, at least for timing the intervals, are comparable for the single interval task as in the standard repetitive tapping task. Independent signals must be generated for each hand, indicating the target delay between the two taps. Assuming that the implementation of these signals is again constrained by the output gate, we expected the observed variability during bimanual movements to be lower than that found during unimanual movements. With this method, we did not expect to observe the square root of two reduction since it is not possible to isolate central sources of variability from those associated with motor implementation. Nonetheless, we tested the weaker prediction that the multiple effector advantage is not dependent on the production of repetitive movements.

This experiment also allows us to explore an alternative hypothesis for the multiple effector advantage. We have attributed this effect to the generation of multiple timing signals, one for each effector. As such, our model emphasizes an open-loop aspect of the task, the central signals that represent the target intervals. An alternative idea is that when people use more than one limb, there are new sources of feedback that could confer stability on the movements of each limb. The movements of each limb could serve as a reference for the other limb. For example, the time at which one limb activates the response key might be used to modify the movement of the other limb. A model of this form emphasizes a closed-loop aspect of the task. While it is possible that feedback can be useful during the production of single intervals, we might expect that this sort of process would be most viable during a repetitive movement task. Observing the multiple effector advantage during single-interval tapping would be problematic for a feedback-based account.

Method

Participants. Twelve right-handed undergraduates at UC, Berkeley participated in Experiment 3.

Procedure and Design. The participants were only tested in finger tapping conditions, either using their right hand alone, their left hand alone, or both hands together. As in the previous experiments, a trial was composed of 8 paced and 21 unpaced intervals. However, each interval was produced as a separate entity. During the paced phase, two computer tones were presented with a tone-onset asynchrony of 400 ms. The 400 ms rate was chosen since only finger movements were used in this study and we expected the potential to use feedback would be further reduced as the interval becomes shorter. After a delay of 550 ms, 700 ms, or 850 ms., the word "TAP" was displayed in the center of the screen. The participants were then required to make two keypresses, attempting to separate the two taps by the target interval. The variable delays were chosen so that the participants could not adopt a rhythmic mode of responding. The presentation of the tone pair was repeated 1 s after the second tap, and this procedure was repeated until 8 paced intervals had been produced. Following this phase, the word "TAP was presented another 21 times without the tones. The participants produced 21 pairs of responses each time to produce the set of unpaced intervals.[F2] At the end of the trial, feedback was provided as in the preceding experiments. The means and standard deviations for the paced and unpaced phases were presented on the screen. The instructions emphasized that the primary task was to achieve the lowest possible scores on the standard deviation score during the unpaced phase. The final 20 intervals during the unpaced phase were used in the analyses reported below.

Each block consisted of 6 trials. Each participant completed two blocks of tapping with the right index finger alone, the left index finger alone, and with both hands. The order of blocks was counterbalanced with the constraint that each effector condition was presented once every three blocks.

Results and Discussion

Only intervals that were greater than 200 ms and less than 600 ms in duration were included in the analysis. Overall, about 2% of all of the intervals failed to fall within this boundary. Most of these occurred when the participant made his or her first tap prior to the onset of the imperative signal. Since the single interval method is not amenable to the two-component analysis, we did not repeat the entire trial when violations occurred, but rather simply excluded the violations from the analysis.

The mean produced interval during the unpaced phase was 403.9 ms in the left-hand condition and 404.4 ms in the right-hand condition. For the bimanual condition, the means were 410.5 and 408.4 ms for the left and right hands, respectively. No significant differences were observed between these values.

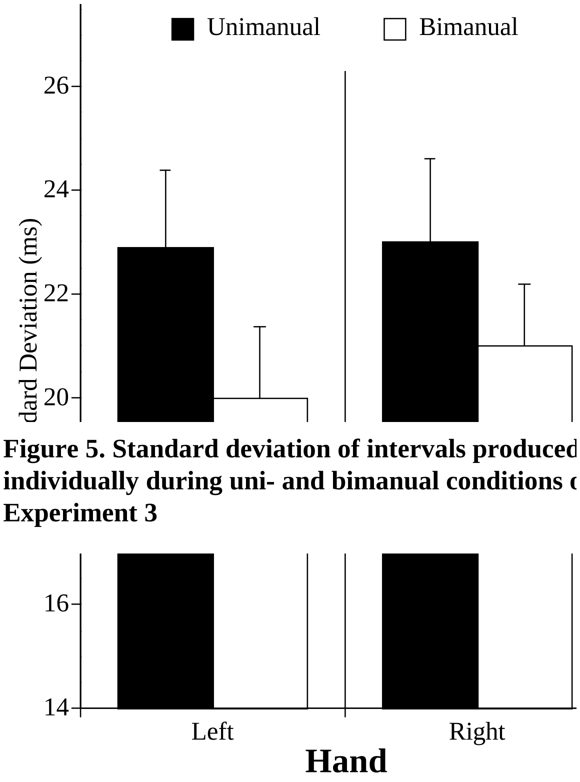


Figure 5. Standard deviation of intervals produced individually during uni- and bimanual conditions Experiment 3

Figure 5

We used the same detrending process as in Experiments 1 and 2 prior to analyzing the variability data. A regression line was calculated with the series of 20 unpaced intervals and calculated the variability from this regression line. This procedure minimized the effects of any linear trend across the unpaced phase that would result from the participants either speeding up or slowing down. However, the detrending procedure had only a slight change on the variability measures and the results for the raw data essentially mirror that observed with the transformed data.

The mean standard deviation scores are presented in Figure 5. As can be seen in the figure, the multiple effector advantage was observed for both the right and left hands. Averaging over the left and right hands, the standard deviation was 23.0 ms during unimanual tapping. During bimanual tapping, this value fell to 20.5 ms, F(1,11)=6.64, p<.03. Neither the effect of hand, F(1,11)=1.341, p>.271, nor the hand by number of effectors interaction, F(1,11)=0.602, p>.454 were significant.

The multiple effector reduction is considerably less than would be expected if two independent signals were being averaged. However, it is not reasonable to expect this prediction to hold in the current experiment. Because the intervals are being produced in isolation rather than as a continuous series, we are not able to apply the two-process model to decompose the total variability into central and implementation components. As indicated previously, the multiple timer model postulates that only the former would benefit from the averaging operation. Nonetheless, the absolute size of the reduction is less than was found for the central estimates in the two-hand condition of Experiment 1 (see also, Helmuth & Ivry, Experiment 1).

In summary, the results of Experiment 3 demonstrate that the multiple effector advantage does not require that the temporal intervals be produced as a continuous series. The reduction in within-effector was observed even when each interval was produced as a separate entity. This finding accords with the predictions of the multiple timer model. As in repetitive tapping, we assume that central temporal control signals are generated for each hand, but that the implementation of these commands is subject to the operation of an output gate. The gate is assumed to instantiate a form of averaging as it integrates the two timing signals.

We do not claim that a feedback-based hypothesis is ruled out by the current results. Two successive taps produced the intervals in the current experiment. It is possible that afferent information from the two effectors during these taps may still provide reference signals that improve the temporal stability of the single interval. However, the current results constrain how such an account could account for the multiple effector advantage. First, the utility of salient sources of feedback such as the asynchrony between when the two hands tap would be of minimal help in the single interval condition since this information could not be used to adjust subsequent responses. Second, the current design eliminates any benefit that might come about from rhythmic entrainment between the two hands over the course of a series of continuous movements. The benefit of feedback, if relevant, would have to be restricted to that obtained during the course of a single interval.

Experiment 4

Numerous studies have shown that temporal variability on motor and perceptual tasks is a function of the target interval. As the interval to be tapped or judged becomes longer, variability increases. The nature of this relationship appears to follow a form of Weber's law in the temporal domain such that the standard deviation divided by the mean equals a constant value over a range of intervals (e.g., Getty, 1975; Ivry & Hazeltine, 1995). This phenomenon has been the focus of much theoretical interest, with the scalar property indicating that at least one major source of variability on such tasks is multiplicative, growing in a proportional manner with the interval being represented (see Gibbon, Malapani, Dale, & Gallistel, 1997; Killeen & Weiss, 1987)

In Experiment 4, we exploited this property to test a strong prediction of the multiple timer model. Specifically, the hypothesis that independent timing signals are averaged during bimanual tapping predicts that the magnitude of the multiple effector advantage should become larger as variability increases. At a qualitative level, the prediction is that, in terms of standard deviation scores, there should be an interaction between the number of effectors and the target duration. The reduction during bimanual tapping should become greater as the target interval is lengthened. At a quantitative level, the prediction is that the slope relating the increase in variability as a function of the target interval during bimanual tapping should be lower by the square root of two than that observed during unimanual tapping.

Participants in Experiment 4 were tested on the repetitive tapping task at four different rates, 325 ms, 400 ms, 475 ms, and 550 ms. This procedure allowed us to test two key predictions with the two-process model of Wing and Kristofferson (1973). First, the logic of the model suggests that only the estimate of central variability should increase as the target interval (see Wing, 1980). Second and more important for the present purposes, we expected that the improvement during bimanual tapping would be restricted to the estimate of central variability and that the multiple effector advantage would become greater as the target interval increased. These predictions follow from the assumption that implementation variability arises from processes downstream of the internal timing system and the gating process. That is, implementation variability is assumed to be duration independent.

The idea that temporal variability during tapping is composed of duration-independent and duration-dependent sources of variability also affords a second, independent method for partitioning total variability into component sources. In a series of experiments, Ivry and Hazeltine (1995) applied a procedure called slope analysis to show that a common internal timing system was invoked in both motor and perceptual tasks that require precise timing. The essence of this procedure is that the slope of the function relating the standard deviation as a function of the produced or perceived interval provides a direct estimate of the variability associated with the internal timing system. One advantage of this procedure over the Wing-Kristofferson model is that the slope analysis provides a more direct estimate of timing variability. The Wing-Kristofferson model estimates implementation variability from the lag one covariance values and, via subtraction, generates an estimate of central variability. The latter, as a residual, actually contains all sources of non-motor variability, only one component of which is associated with an internal timer. In contrast, the slope analysis method isolates duration-dependent variability and uses the intercept to estimate all sources of duration-independent variability, be they central or peripheral. In the current study, we predicted that the slope values would be lower during bimanual tapping than during unimanual tapping. Changes in the intercept values would indicate that the bimanual conditions alter the contribution of other sources of variability.

We also used the richer data sets of Experiment 4 to explore between-hand measures of temporal performance. At all four durations, the movements in the bimanual condition should exhibit strong temporal coupling given the task instructions to move the hands in a synchronous fashion. A point estimate of the phase relationship between the two hands can be made from the time difference at which the two microswitches are activated. From Figure 1, it can be seen that the multiple timer model would attribute these asynchronies to variability in motor implementation: While the commands to initiate the two responses are issued simultaneously, peripheral variability will influence the two hands independently. From this perspective, two predictions can be tested. First, it is expected that the mean asynchrony will be invariant across the four durations. Second, the standard deviation of the distributions of the asynchronies should also remain unchanged as tapping rate varies.

Finally, the phase differences can also be used to obtain a third estimate of central variability. Vorberg and Hambuch (1984) have proposed a model for analyzing bimanual tapping data that is similar to the general structure of the multiple timer model in terms of the division of central and peripheral sources of variability. In their model, a single timer is used to generate the target intervals for each hand, and thus operates similar to the gating operation we propose in Figure 1. Central variability can thus be estimated by the between-hand covariance. While this model cannot be applied to single hand data, it does offer another method for evaluating the change in temporal variability as a function of tapping speed. We expect that the slope obtained with this method will be comparable to that derived from the slope analysis.

Method

Participants. Ten subjects from the University of California, Berkeley participated in the experiment and were reimbursed for their participation. Each subject was tested on four different days and was paid $7/day for their participation.

Procedure. Each experimental session was devoted to repetitive finger tapping at one target duration. A Latin Square design was used to determine the order for the four test durations across sessions. Within an experimental session, the participant completed three blocks of tapping with the right index finger alone, the left index finger alone, or with both fingers together. A trial was composed of 12 paced and 21 unpaced intervals, and the participants produced six trials for each block, or 18 trials per condition. Trials in which any interval was less than or greater than 50% of the target interval were repeated.

Data Analysis.

Three methods were used to estimate component sources of variability from the time series data. First, similar to Experiments 1 and 2, we used the Wing-Kristofferson model, a method that focuses on the within-hand covariance function. Second, we applied the slope analysis, a method that estimates variability directly from the observed variance measures (Ivry & Hazeltine, 1995). Third, we used the between-hand covariance function to estimate central variability (Vorberg & Hambuch, 1984). This latter method can only be used in the bimanual conditions.

Slope Analysis: The starting premise for the slope analysis is that total variability can be partitioned into duration dependent (DD) and duration independent (DI) components (Ivry & Hazeltine, 1995):

$$\mathbf{Variance_{Total} = Variance_{DD} + Variance_{DI}} \qquad (5)$$

Duration dependent variability is assumed to reflect the operation of an internal mechanism that provides the timing signals needed to accurately initiate each movement. Duration independent variability is associated with the implementation of the responses. By definition, duration dependent variability will increase as a function of the interval being timed while the estimate of duration independent variability will remain constant.

The relationship between temporal variability and duration has been the subject of considerable study (see Killeen & Weiss, 1987). In general, the literature indicates that a generalized form of Weber's law holds in the temporal domain where the standard deviation is a linear function of the base duration (Getty, 1975; Ivry & Hazeltine, 1995). This can be formally expressed as

$$\mathbf{Variance_{DD} = \mathit{k}^2D^2} \qquad (6)$$

where *k* is the Weber constant and D is the mean inter-tap interval produced. Substituting Equation 6 into Equation 5 and replacing the duration independent component with a constant, c, we obtain:

$$\mathbf{Variance_{Total} = \mathit{k}^2D^2 + c} \qquad (7)$$

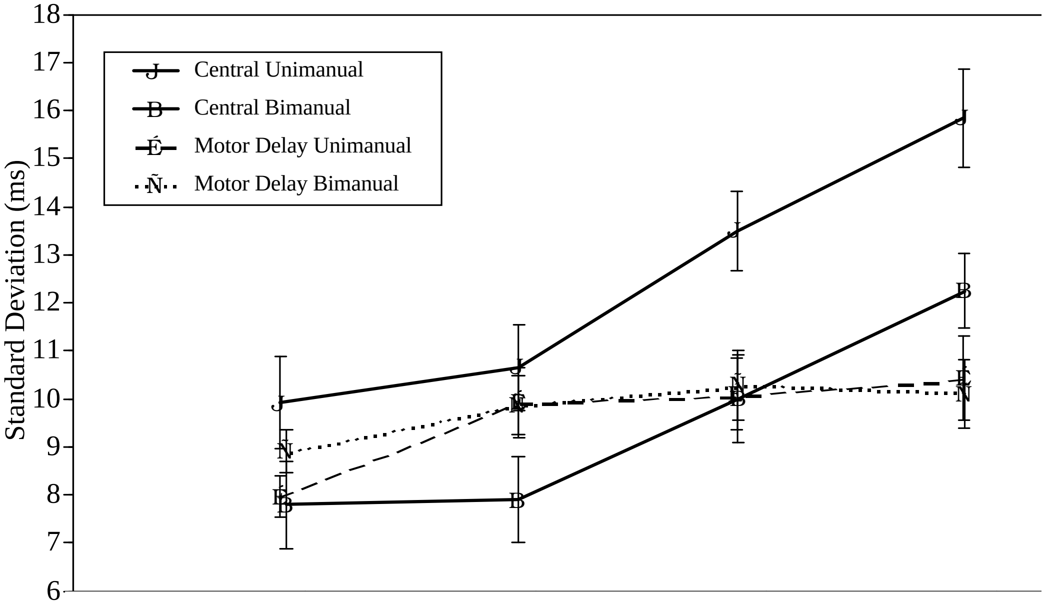


Figure 6. Component estimates for four target durations in Experiment 4. The data are plotted as a function of the mean produced interval rather than the target values

Figure 6

A complete discussion as well empirical validation of the slope analysis can be found in Ivry and Hazeltine (1995). This equation provides an excellent account of the data in both time production and time perception studies. Moreover, alternative formulations (e.g., where the linearity is assumed between duration and the variance rather than duration and the standard deviation) provide a poorer fit with consistent negative intercepts.

For each participant, a regression analysis based on Equation 7 was performed for the four functions, left and right hands during unimanual and bimanual tapping. The primary analysis focused on the slope and intercept values obtained from these analyses. The square root of the slope term yields *k*, the Weber constant.

Vorberg-Hambuch model: As described above, the between-hand covariance function provides an estimate of shared variability between the two hands during bimanual tapping. The key assumption here is that the shared component reflects variability in the operation of a common central signal, a signal that Vorberg and Hambuch associate with an internal clock. The between-hand covariance at lag 0 (i.e., for simultaneous intervals) will be less than the within-hand variance because of noise in motor implementation processes. That is, the two hands will produce non-identical intervals because of variability in implementing the right and left responses. Thus, by the Vorberg-Hambuch model, an estimate of the variability of the central component is obtained by:

$$\mathbf{SD_{Central} = sqrt(Covar(Lag\ 0))} \qquad (8)$$

Note that because this calculation is based on a between-hand measure, a single estimate of temporal variability is derived. The method does not provide separate estimates for the two hands.

Results and Discussion

Less than 2% of the trials contained an interval that was outside the 50% criterion window. The low number here compared to Experiments 1 and 2 likely reflects the fact that the participants were tested over multiple sessions.

Wing-Kristofferson analysis: We begin with the two-process model of Wing and Kristofferson (1973). As before, the effects of global drift in the mean produced interval were minimized by a transformation on the time series that removed any linear components. The resulting within-hand covariance functions were similar to those obtained in the earlier experiments. The lag 1 covariance was negative for all 160 conditions (10 participants x 2 hands x 2 tapping modes x 4 durations), and the values for lags 2-5 were close to zero. There were, however, four conditions in which the lag 1 correlation was less than the theoretical limit of -.50. For these conditions, central variability is estimated to be zero. We assume these violations reflect noise in the estimation process.

Figure 6 presents the estimates of central and implementation variability at each of the four durations. The data have been averaged over the left and right hands to simplify the figure. As can be seen, the estimates of implementation variability remain essentially constant, although the mean value in both the uni- and bimanual conditions for the 325 ms condition are slightly lower than for the other three target durations. In contrast, the estimates of central variability increase across the range of durations. While there are no systematic differences between the uni- and bimanual conditions on the implementation scores, a consistent bimanual advantage is observed with the estimates of central variability. The magnitude of this advantage appears to increase for the longer target durations.

These data were analyzed in a four-way ANOVA with the variables hand (left or right), tapping mode (unimanual or bimanual), duration (325, 400, 475, and 550ms), and component (central or motor delay). Our initial focus is on the basic question of whether temporal variability increases as a function of duration. As expected, a main effect of duration was observed, F(3,27=20.2, p<.001). The two-process model makes a more specific prediction: The estimate of the central component should increase with duration whereas the estimate of the motor delay component should remain invariant. Thus, there should be a Component x Duration interaction. Indeed, this interaction was reliable, F(3,27)=3.3, p<.05. While the central and motor delay estimates both increase over the four durations, the interaction reflects the fact that the increase is significantly greater for the estimate of the clock component. We did not find a reliable difference between the two hands, F(1,9)<1, nor was there an interaction between the hand and component variables. Thus, unlike in Experiment 1 and Helmuth and Ivry (1996), we did not find a right-hand advantage on the estimate of motor variability with these more experienced participants.

Turning to the comparison of uni- and bimanual tapping, a highly significant effect was observed for tapping mode, F(1,9)=42.4, p<.001, indicating that overall, performance was consistently less variable during bimanual tapping. This effect is qualified by the interaction between tapping mode and the component variable, F(1,9)=17.9, p<.01. There was no difference between the motor delay

Table 3

Regression analysis results for experiment 4

	Tapping Mode	Slope	Intercept	R^2	Weber Fraction
Left					
	Unimanual	0.001305	150.62	0.61	0.0337
	Bimanual	0.000723	155.38	0.60	0.0272
Right					
	Unimanual	0.001447	97.64	0.83	0.0388
	Bimanual	0.000823	181.10	0.52	0.0271
V-H Analysis					
	Bimanual	0.000904	-0.55	0.77	0.0295

estimates in the unimanual (9.6 ms) and bimanual conditions (9.8 ms). In contrast, the estimates of the central component for the uni- and bimanual conditions were 12.5 ms and 9.5 ms, respectively. Thus, the multiple effector advantage was restricted to the estimate of central variability. The Tapping Mode x Duration interaction was marginally significant, F(3,27)=2.6, p<.08. As can be seen in Figure 6, the increase in variability tended to be greater in the unimanual condition compared to the bimanual condition.

Based on the multiple timer model, we had predicted a three-way interaction of Tapping Mode x Component Estimate x Duration. Specifically, we expected that the increase in variability as a function of duration would be greater in the unimanual condition, but only for the estimate of the central component. This interaction, however, did not approach significance, F(3,27)<1. One reason for the failure of this interaction to hold is the drop in the motor estimate for the shortest target interval.

Slope analysis: The slope analysis provides an alternative to the two-process model that is not dependent on indirect estimates of component sources of variability. The slope analysis is performed on the observed data, thus avoiding problems that may arise from error in the estimation process. Using Equation 7, regression analyses were performed on the four functions produced by each participant (left and right hands during uni- and bimanual tapping). The results of these analyses are presented in Table 3. While the percentage of variability accounted for by a linear component was reasonably high, there were a number of individual cases in which the values were quite low. It is likely that the low values reflect the fact that the data sets are not extensive (18 trials/condition) and the order with which individuals were tested on the four durations varied. Note that the R^2 values in Table 3 are the average of the individual values. If a regression was performed on the averaged data, the R^2 values would be greater than .96 for three of the conditions and .87 for one condition (bimanual right hand).

The slope and intercept data were analyzed in separate 2 (hand) x 2 (tapping mode) ANOVAs.[F3] For the slope values, there was a significant effect of tapping mode, F(1,9)=5.7, p<.05. As predicted by the multiple timer model, the slope was reliably lower in the bimanual condition, indicating that the advantage became greater as the target duration increased. Thus, the multiple effector advantage is manifest as a multiplicative reduction in temporal variability rather than as a constant (additive) improvement. The effect of hand, F(1,9)=1.1, p>.3 and the Mode x Hand interaction, F(1,9)<1.0, were not significant. None of the effects were significant for the intercept terms.

The Weber fractions are calculated as the square root of the slope values. These fractions indicate the magnitude of temporal variability as a function of the target interval. In the unimanual conditions, the Weber fractions were between 3-4%, values that are similar to those reported in the literature (e.g., Ivry & Hazeltine, 1995). In the bimanual conditions, the Weber fractions dropped to under 3%. Theoretically, the multiple timer model predicts that the Weber fraction during bimanual tapping should be equal to the Weber fraction during unimanual tapping divided by the square root of two. The predicted and observed values for the left hand during bimanual tapping are .024 and .027, respectively. Thus, the improvement during bimanual tapping is slightly less than predicted. The predicted and observed values for the right hand are identical, .027.

Vorberg-Hambuch analysis: Estimates of central variability based on the between-hand covariance were calculated according to Equation 7. As would be expected of a measure of timing variability, these estimates increase with duration, and the increase is generally linear. The mean regression values for these data are included in the bottom row of Table 3. Note that the mean R^2 value over individuals here is quite high. While this method can not be used to compare uni- and bimanual tapping performance, it does provide an independent method for calculating the change in variability across durations during bimanual tapping. The Weber fraction calculated with the between-hand covariances is .029 (square root of the slope, calculated on an individual basis). Thus, we find excellent agreement between the Weber fractions when measured using the within-hand variance data in the slope analysis and the between-hand covariance data in the Vorberg-Hambuch analysis. This results lends strong support for the assumption that these analytic tools are estimating a common construct.

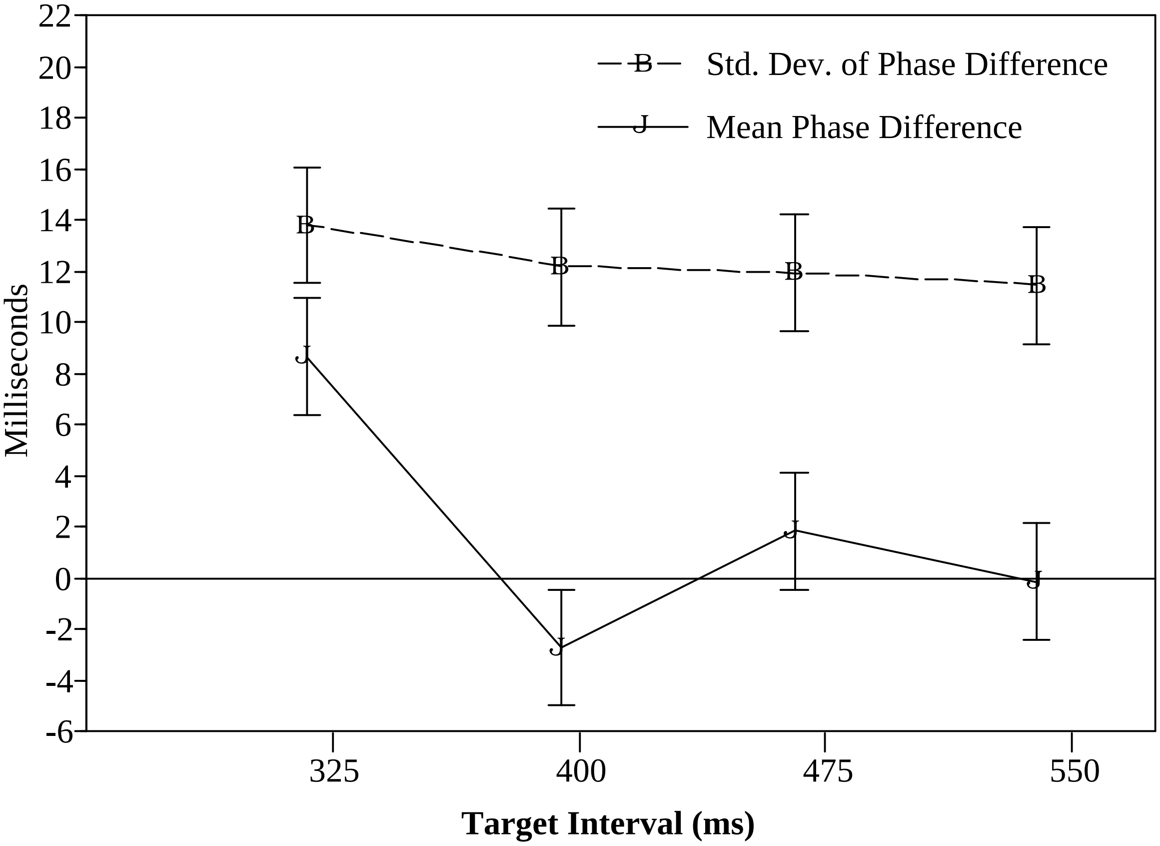


Figure 7

Figure 7. Asynchrony data for experiment 4. Negative values for the mean phase difference data indicate left hand leading. Positive values are for right hand leading. The data are plotted as a function of the mean produced interval rather than the target values.

<u>Tapping asynchrony analysis</u>: The asynchrony between the left hand and right hand responses was calculated for each interval during bimanual tapping. From these data sets (18 trials x 30 intervals per trial), the distribution of the asynchronies was tabulated. These distrubutions were approximately normal and their means and standard deviations are shown in Figure 7.

Based on the multiple timer model, we would expect the mean and standard deviation values to remain invariant over the four durations. This prediction is based on the assumption that the asynchronies result from motor implementation processes. There may be a consistent lead in one hand over the other; for example, lower implementation noise in the dominant hand might result in right hand responses being initiated prior to left hand responses. However, we would expect this asymmetry to remain constant over the range of target intervals. Similarly, the variability of the asynchronies should be independent of duration. Contrary to these predictions, an effect of duration was observed for both the mean phase difference, F(3,27)=5.6, p<.01, and the standard deviation of the phase differences, F(3,27)=6.6, p<.01. There is no consistent effect of one hand leading the other for the target durations of 400 ms, 475 ms, and 550 ms. However, for the fastest duration of 325 ms, the right hand led the left by over 8 ms on average. Note that variability is largest for the fastest interval, a result opposite that found in the variability of the tapping intervals themselves. As with the mean asynchronies, the standard deviation of the asynchrony distributions remains relatively constant across the three longer intervals.

Taken together, these data provide mixed support for the predictions derived from the multiple timer model. For the three slower target durations, the mean and standard deviation of the asynchrony distributions were constant. However, differences were observed at the fastest rate of 325 ms. It remains to be seen why the asynchrony measures changed at this fastest rate. One possibility is that the participants increased the stiffness of their finger in the 325 ms condition. Such an increase might make it easier to tap at this relatively fast rate, perhaps because the finger movement can be triggered by a smaller descending volley. Assuming such a change had a more pronounced effect on the dominant hand could account for both the lead in right hand tapping and an increase in the asynchrony variability. This hypothesis is, admittedly, speculative. Another possibility is that some of the participants adopted a different tapping strategy for the fastest condition. The mean phase lead for the right hand was over 10 ms for four of the participants; for the other seven, it was less than 5 ms.

An alternative way to examine the asynchrony data is in terms of relative phase differences, that is, by dividing the asynchrony value, the point estimate of relative phase, by the produced interval. Expressed this way, the standard deviations of the phase differences for the target durations of 325 ms, 400 ms, 475 ms, and 550 ms are 15.3°, 11.0°, 9.0°, and 7.5°. This change would be consistent with the hypothesis that the coupling strength between the two limbs becomes stronger as the tapping rate slows down. It is not clear why one would find a concomitant change in the mean phase difference at the fastest frequency. Moreover, this decrease is also what one would expect given that the standard deviation of the asynchronies remains relatively constant across the four target durations.

<u>Summary</u>: Experiment 4 was designed to provide a strong test of the multiple timer model. We have proposed that the output gate performs a form of temporal averaging when provided with independent temporal control signals during bimanual movements. Based on this prediction, we would expect the multiple effector advantage to be multiplicative rather than additive. We tested this prediction by having the participants perform the repetitive tapping task under uni- and bimanual conditions over a range of target intervals. In accord with our predictions, an interaction was observed between tapping mode and duration. The multiple effector advantage became larger as the target interval increased. This interaction was observed with two analytic techniques designed to isolate central variability, the Wing-Kristofferson model and the slope analysis of Ivry and Hazeltine (1995). Moreover, the magnitude of the improvement as measured by the change in slope from the unimanual to bimanual conditions was close to what would be expected based on an averaging hypothesis. Finally, the results of Experiment 4 are in accord with previous studies showing that variability associated with motor implementation processes remains constant over a range of tapping rates.

General Discussion

As described by Helmuth and Ivry (1996), people become more consistent in producing a series of isochronous intervals when the movements are produced by more than one effector. In their initial studies, the multiple effector advantage was observed for bimanual movements requiring homologous movements (i.e., bimanual finger tapping) and non-homologous movements (i.e., tapping with one finger and one forearm). The current experiments examined the generality of this phenomenon. Moreover, the experiments were designed to test the multiple timer model proposed by Helmuth and Ivry to account for the multiple effector advantage.

<u>Evaluating the assumptions of the multiple timer model</u>

In Experiment 1, we observed that the multiple effector advantage was quite robust, holding over various movement combinations involving the finger and foot. There was no apparent difference between movements that involved effectors on different sides of the body (e.g., right finger and left foot) compared to movement that involved effectors on the same side of the body (e.g., right finger and right foot). Using the two-process model of Wing and Kristofferson (1973), the improved temporal variability was attributed to a reduction in the estimate of central variability. Indeed, overall variability tended to become larger when the participants were asked to tap with limbs of unequal mass (see also, Helmuth and Ivry, 1996). This increase is assumed to result from instabilities in generating differential forces to activate the asymmetric limbs (Jeka & Kelso, 1995). Nonetheless, the variability associated with the operation of an internal timing system was always reduced for all effector combinations.

The multiple timer model proposes that the improved temporal performance is the statistical consequence of the control operations required in the production of multiple effector rhythmic movements. We assume that these operations include timing mechanisms that regulate the timing of each cycle. At this point, we do not make specific claims about how this regulation is achieved. It may be that a central command initiates each cycle, triggering the onset of the downstroke of the movement during finger or foot tapping. Or it may be that the central command is in terms of a representation of the desired temporal pattern to be formed by the contact of the effector with the response board (Billon, Semjen, & Stelmach, 1996). What is essential to our model is that a representation of the target interval is generated for each cycle and it is this representation that provides the primary control of the timing of the movements. Most critical, we assume that these representations are effector-specific. For each effector that is engaged in the task, an independent representation of the target interval is generated to control the movements of that effector.

However, as outlined in Figure 1, we assume these central representations do not have direct access to their associated effectors. Rather, the implementation of the commands is constrained by a gating operation, allowing the movements to be produced in a synchronized fashion. We propose that the manner in which the gating operation integrates the effector-specific signals effectively acts as an averaging device, and it is this averaging process that underlies the multiple effector advantage (Helmuth and Ivry, 1996). In essence, the advantage is hypothesized to be a manifestation of the central limit theorem. Variability is reduced as the sample size becomes larger. The constraint imposed by the gating operation may result from the task demands. In our studies, we require that the movements be produced in a synchronized fashion. However, across a range of bimanual tasks, people have great difficulty in achieving temporal independence, even in situations designed to promote such independence (Franz, Eliassen, Ivry, & Gazzaniga, 1996; Kelso, Southard, & Goodman, 1979; Krampe et al., 2000; Zanone & Kelso, 1997). These observations suggest that the gating constraint may reflect a fundamental limitation in the motor system, perhaps providing a means for reducing control requirements by ensuring that selected actions are implemented in a coordinated fashion (Ivry & Hazeltine, 1999; Ivry & Richardson, in press).

Experiments 2, 3, and 4 tested specific predictions of the multiple timer model. In Experiment 2 we observed a further reduction in within-effector temporal variability when a third limb was added to the mix. We attribute this reduction to the activation of a third representation of the target interval and the added benefits obtained when the gating operation is now provided with three inputs. We assume that temporal stability would continue to improve as more effectors were engaged, although our ability to empirically observe this benefit would become difficult given that the magnitude of the improvement decreases with each additional effector.

Experiment 3 demonstrated that the multiple effector advantage was not dependent on the production of repetitive movements. A significant reduction in within-effector variability was found even when the participants produced each interval in isolation. Thus, the effect does not depend on some sort of entrainment process.

Experiment 4 used a different approach to test a quantitative prediction of the multiple timer model. In this study, the target duration was varied. The multiple effector advantage was expected to hold across all tapping rates. More critical, given that the standard deviation is proportional to the interval being timed, we would expect the magnitude of the reduction to increase as the inter-tap interval is lengthened. This prediction was confirmed. Not only was the tapping mode by duration interaction significant, but the observed slope during bimanual tapping was close to that predicted by the model. This study provided a novel demonstration of the advantage of the slope method (Ivry & Hazeltine, 1995). This procedure offers an alternative tool for identifying component sources of variability, one that attempts to directly measure central variability rather than use the indirect, subtractive approach of the two-process Wing-Kristofferson model.

While the hypothesis of multiple timers may not seem parsimonious, there are a number of appealing features of this sort of model. First, the model does not require that a single clock be accessed by different tasks. Although outside the scope of this paper, we assume that distinct neural elements are not only linked to specific effectors, but are also tuned to represent specific intervals, an idea promoted in a number of recent papers (e.g., Ivry, 1996; Meegan, Aslin, & Jacobs, 2000; Rosenbaum, 1998; Wright, Buonomano, Mahncke, & Merzenich, 1997). Thus, we assume that there exist a set of timing elements to regulate tapping at different rates with one effector, and that this organization is repeated for other effectors (Ivry, 1996). By assuming that the exact circuits required for representing temporal information will vary from task to task, the anatomical prerequisites would seem to be simplified. The circuitry for an amodal, single mechanism would have to be quite complex, having the capability to broadcast a signal to all output systems. Note that in the multiple timer model, correlations across different temporal tasks (e.g., Keele et al., 1985) do not reflect the operation of a single clock, but rather the fact that the timing system as a whole is associated with common noise properties. Thus, the model is consistent with the hypothesis that temporal representations may depend on the operation of a common timing system (e.g., the cerebellum), but within this system, elements will be recruited in a task-specific manner.

Second, the gating constraint may help ensure that all movements generated at any one point in time are coordinated or, at least, not mutually exclusive of one another. For example, if competing actions, one calling for moving the right hand forward and the other for moving the right hand backward were simultaneously active, inhibitory connections between these gestures would make it unlikely that either gesture would achieve sufficient activation to cross threshold. In this sense, the gate captures the idea of a winner-take-all process (Berns & Sejnowski, 1996).

At present, we have focused exclusively on tasks in which the instructions emphasize that the two limbs should move in a synchronized fashion. Our motivation for this approach comes from the fact that predictions derived from the multiple timer model are straightforward when the gating process is assumed to occur simultaneously for both limbs. However, movements can be coupled, even when they are not synchronized. For example, during paced, anti-phase tapping, only one limb is synchronized with the pacing signal if we define synchronization by events such as the time of contact with the response key and the pacing signal. Nevertheless, the stability of anti-phase tapping suggests the persistence of strong temporal coupling. It remains to be seen how the multiple timer model can be extended to such tasks. One possibility is that under such conditions, the timing signals for each limb are not integrated. Indeed, Ivry and Richardson (in press) suggest that the instability that emerges when frequency is increased during anti-phase tapping may reflect unwanted interactions between the separate timing signals. A second hypothesis is that hierarchical temporal representations are generated to ensure that successive actions continue to exploit the simultaneous operation of the gating process. For example, during 2:1 tapping the gate might operate at the fastest beat, but only initiate movement for the slower hand on every other cycle (Krampe et al., 2000; Semjen & Ivry, in press; Vorberg & Wing, 1986). These are obviously important questions for future study.

Can the multiple effector advantage result from feedback between the two limbs?

While we have focused on the multiple timer model in our account of the multiple effector advantage, it is important to consider alternative models. One alternative is based on the idea that feedback signals generated during multi-effector movements can lead to reduced temporal variability. During unimanual tapping, feedback is, of course, available from multiple sources including the clicks generated when the response keys reach their maximal excursion as well as from the somatosensory input from the moving effector. When tapping with two hands, these sources of feedback are now available from both hands, perhaps resulting in more salient feedback signals. Moreover, an additional source of feedback can be obtained by comparing the movements of the two hands. For example, a discrete feedback process could monitor the asynchrony between the two hands at the start and finish of each tap, or a continuous feedback process could monitor the phase relationship between the two hands throughout the movement cycle. Such feedback signals during bimanual tapping would seem to offer an opportunity to make adjustments for deviations in performance that were not possible during unimanual tapping.

At present, our preference for the multiple timer model is based on a set of indirect arguments against the feedback hypothesis. First, the multiple timer model is a relatively straightforward extension of the Wing and Kristofferson (1973) model. In their two-process model, the estimation of central and motor estimates of variability assumes that the clock and motor implementation processes operate independently of one another and that successive outputs from each process are independent. Studies with neurologically healthy (e.g., Wing, 1980; Ivry & Hazeltine, 1995; see Pressing, 1999) and impaired populations (e.g., Ivry & Keele, 1989; Ivry et al., 1988) have, in general, provided strong support for these basic tenets, at least when the inter-tap interval is less than 1 s. In the multiple timer model, the same processes operate during multiple effector movements; by a feedback model, we would have to assume that new processes come into play during such movements. Of course, as noted in the preceding paragraph, the multiple effector condition affords new sources of information.

We have conducted simulations of feedback models to evaluate the viability of such an approach. These simulations have taken various forms. For example, in one simulation, we assumed that a single, central timing command was projected to all effectors. Any asynchrony between the two hands is attributed to independent variability in motor implementation processes (e.g., Vorberg & Hambuch, 1984). This asynchrony could then be used to make adjustments in the timing of the responses. In another simulation, we retained the idea of multiple clocks and independent implementation processes, but again used the resultant asynchrony to adjust the timing of the responses. For the adjustment, we opted for the simple method. If the left hand led the right by X ms, we delayed the next tap of the left hand by X/2 ms and increased the tap of the right hand by X/2 ms (after obtaining the next clock and motor implementation samples for each hand). It turns out that models in which the asynchrony on Response N is used to adjust the timing of Response N+1 end up leading to an increase in overall variability.

At first glance, it might seem counter-intuitive that feedback would impair performance. However, this phenomenon has been observed in other conditions. For example, variability during both unimanual and bimanual tapping is significantly larger if the pacing signals are preserved over the entire trial (unpublished observations). This cost is observed even though the multiple effector advantage continues to be manifest. Similarly, the visual feedback available when two individuals tap with a single finger leads to an increase in the within-subject temporal variability (Helmuth & Ivry, 1996). Pressing (1999; see also Vorberg & Wing, 1996) has formally analyzed the feedback situation, arguing in addition to the clock and motor implementation sources of variability, paced tapping introduces a novel source of variability associated with the utilization of the error signal generated by the mismatch between the pacing signals and the taps. Similarly, we have all experienced the problem of over-correction when calibrating a motor skill such as dart throwing. We tend to assume that all of the error is central in origin; we fail to recognize that a proportion of the error is more peripheral in nature (e.g., Schmidt, 1975).

Our simulations have all been based on the idea that feedback signals are used in a relatively discrete manner. Asynchronies between the two hands on one response are used to adjust the timing of the next response. An alternative procedure would be to use feedback in a continuous manner. For example, a proprioceptive-based feedback process could continuously monitor the phase relationship between the two hands and make adjustments to keep this difference near zero. Such a process would surely reduce the variability of each hand (see below for a qualitative description of this idea). Whether such processes are viable during tasks such as repetitive tapping remain unclear. Studies involving multi-joint movements such as throwing, however, have shown that the timing of the finger release is unaffected by perturbations during elbow extension or wrist flexion (Hore, Ritchie, & Watts, 1999).

In addition to our theoretical explorations, we have also tried to empirically evaluate the feedback idea. In the present paper, we found that the multiple effector advantage was evident even when the intervals were produced in isolation. These results argue against the idea that the improved temporal performance results from some sort of extended entrainment between the two limbs during cyclic movements. However, the interpretation of these data provides, at best, a weak test of a feedback hypothesis. First, the participants did produce taps to mark both ends of the interval in this study and thus could have used feedback from the first tap to adjust the timing of the second tap. Second, the magnitude of the effect appeared to be considerably less than what would be predicted by the averaging model.

A second line of evidence against a feedback model rests on the finding that the multiple effector advantage was obtained in a split-brain patient, even when this patient tapped with her fingers (Ivry & Hazeltine, 1999). While there is ample opportunity for cross-talk of afferents from proximal muscles, including bilateral projections to somatosensory cortex, the ascending pathways from their fingers are thought to project exclusively to the contralateral hemisphere (e.g., Guillemot, Richer, Prevost, Ptito, & Lepore, 1987; Iwamura, 2000; Shanks, Pearson, & Powell, 1985). Nonetheless, the bimanual finger movements of the patient remained tightly coupled (see also, Tuller, & Kelso, 1989) and the within-effector variability was significantly reduced for each hand during bimanual tapping. In this study care was taken to eliminate auditory and visual sources of feedback. Thus, it is unclear how afferent information from each hand would be able to influence the movements of the other hand.

Despite these arguments, definitive evaluation of the feedback hypothesis remains a goal of future research. One approach would be to introduce perturbations during the movement cycle for one hand and evaluate the effects on the other hand. However, we do not doubt that people can (and will) use feedback. The question is whether this information can lead to reduced temporal variability. A more dramatic approach would be to test patients who suffer peripheral neuopathies that render them functionally deafferented. Such patients, especially those with intact output pathways, are rare.

The multiple timer model considered within the dynamic systems framework

A second alternative is to consider the multiple effector advantage from the perspective of the dynamic systems framework. This approach has been extremely prominent in the field of motor control. Indeed, the influential work of Kelso, Turvey, and their colleagues was initially developed from the experimental analysis of bimanual movements (Kelso, 1997; Kugler & Turvey, 1987), although the approach has now been applied to a wide variety of task domains. The focus of this work has been on inter-limb coordination. For example, the coupled oscillator model provides an elegant description of the stability of certain phase relationships and the transitions observed as various control parameters are varied (Schöner & Kelso, 1988).

With the exception of only a couple of studies (e.g., Yamanishi et al., 1980; see Semjen & Ivry, in press), the temporal stability within each limb has been of secondary concern within the dynamic systems approach. However, at a descriptive level, an account of the multiple effector advantage can be conceptualized within the framework of a coupled oscillator model. Consider the limit cycle, the dynamic state that describes stable conditions during repetitive movements under conditions to produce in-phase movements (Figure 8). Noise can have two effects on the position of a single oscillator moving along the limit cycle. First, it can perturb the oscillator to a position off of the limit cycle. Such perturbations would be corrected due to the attractive forces of the limit cycle. Second, it could perturb the oscillator along the limit cycle. During unimanual movements, such perturbations would go uncompensated: all positions along the limit cycle are stable (Figure 8a). However, during bimanual movements, each oscillator also can be conceptualized as point attractors and thus provide a means for adjustment (Figure 8b).[F4] This description can be seen as one instantiation of a continuous feedback model. We would assume that the control parameters (or output signals corresponding to the current phase) are equivalent for the two oscillators, reflecting the effects of coupling and the task requirements to tap in phase. Perturbations that impose phase deviations are assumed to reflect noise and the adjustment to such noise would in essence constitute a feedback process. Alternatively, a comparison could be made of the state of the output signals and an adjustment made if these signals were out of phase with one another.

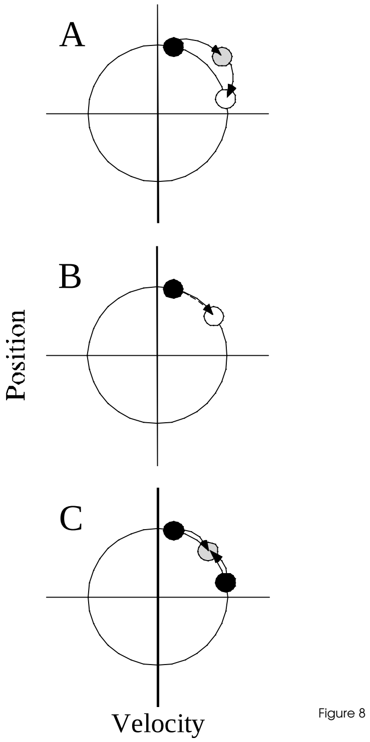


Figure 8. Reduced timing variability from coupled oscillators. Repetitive movement is depicted as a limit cycle in which velocity varies in a continuous manner with position. Panel A: Perturbations of a single oscillator off of the limit cycle will be corrected due to the stable nature of the limit cycle. Panel B: Perturbations along the limit cycle are not corrected since performance is stable at all points on the limit cycle. Panel C: In bimanual tapping, perturbations along the limit cycle are corrected due to the coupling between the oscillators.

There are points of similarity and difference between the multiple timer and coupled oscillator models. Both models posit separable timing mechanisms for each limb, as well as a form of coupling between the outputs of these mechanisms. In a sense, the multiple timer model entails a specific type of coupled oscillators. The model is, of course, dynamic, in that it attempts to account for the time-varying interactions that occur between the processes associated with the movements of each effector (Schöner, 2000). However, the coupling is of a very different form than that articulated in current forms of the coupled oscillator model. Rather than conceptualizing coupling as a continuous process, the gating operation operates as a threshold mechanism, introducing a level of discreteness in the interactions between central control processes and movement implementation processes. This threshold process provides coupling in two ways. First, there are the interactions between the activation functions of the timing mechanisms, an interaction that culminates in the common gating of the output signals and ensures that the movements are generated in a synchronous fashion. Second, there is the mutual resetting of each timer for the next cycle following the triggering of the gate. These properties of the hypothesized gating operation impose a discontinuity on the dynamics. A consequence of this discontinuity is that the formal approaches developed for coupled oscillator models are difficult to adapt to the multiple timer model (Schöner, 2000).

Empirically, we have sought to identify places where the models diverge. Schmidt et al.

(1990) looked at the dynamics during repetitive movements when the movements were produced by different individuals. In this experiment, two individuals faced each other and each moved one leg in time with a metronome. Similar to what had been observed in traditional within-individual experiments, the movements of the two individuals were tightly coupled, and when the frequency increased under anti-phase conditions, a phase transition was observed. This led the authors to argue that the coupled oscillators operate at an abstract level; a common framework can be used to account for dynamical interactions that arise within an individual and between individuals.

Helmuth and Ivry (1996) examined this same issue in a finger tapping study, but with the focus on within-effector variability. Contrary to the results of Schmidt et al. (1990), this dependent variable showed a striking difference between the within- and between-individual conditions. The multiple effector advantage was only found in the within-individual condition; for the between-individual condition, total variability and the estimate of central variability increased. This increase is likely similar to that observed when tapping with a pacing signal with the pacing signal now being the other person's finger movements. The lack of reduced temporal variability in the between-individual condition is in accord with the multiple timer model. As sketched in Figure 1, the gating process would not be expected to receive input from the timing mechanism of another individual!

We have also sought to identify predictions that are specific to the multiple timer model. The prediction that central variability will be reduced by the square root of two and the reduced slope describing temporal variability as a function of duration are two such examples. The results of Experiments 1 and 4 in the current study as well as the findings of Helmuth and Ivry (1996) provide reasonable support for these predictions, at least when the movements are produced by effectors of similar mass. Thus, the data are consistent with the quantitative predictions of the multiple timer model. Of course, tests that confirm a hypothesis offer a weaker form of argument than tests that disconfirm an alternative hypothesis. At present, however, quantitative predictions based on the coupled oscillator model are not as constrained as those based on the multiple timer model.

The relationship between the multiple timer and coupled oscillator models remains an issue for debate. At one level, the two seem quite disparate. Certainly the issue of discrete versus continuous coupling should be ripe for investigation (see Schöner, 1990 for a theoretical analysis of the relationship between discrete and continuous movements from a dynamic systems perspective). On the other hand, the two approaches may be compatible, offering different levels of description. The coupled oscillator model offers a rich, abstract description of the dynamics across a wide range of movement conditions. The multiple timer model is narrower, specifying component processes involved in the control and coordination of timed movements. In its favor, the multiple timer model embodies specific hypotheses concerning the control processes involved in the temporal representations for such movements and the dynamics that allow these movements to be coupled. Whether the basic ideas can be extended to provide more general principles of coordination, for example those observed with different coordination modes as well as the transitions observed between coordination modes, remains to be seen.

References

Berns, G.S. & Sejnowski, T.J. (1996). How the basal ganglia make decisions. In A. Damasio, H. Damasio, & Y. Christen (Eds.), The neurobiology of decision making, (pp. 101-113). Berlin: Springer-Verlag.

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.

Carson, R.G., Goodman, D., Kelso, J.A.S., & Elliott, D. (1995). Phase transitions and critical fluctuations in rhythmic coordination of ipsilateral hand and foot. Journal of Motor Behavior, 27, 211-224.

Chen, Y., Ding, M., & Kelso, J.A.S. (1997). Long memory processes ($1/f$ type) in human coordination. Physical Review Letters, 79, 4501-4504.

Franz, E., Eliassen, J., Ivry, R.B., & Gazzaniga, M. (1996). Dissociation of spatial and temporal coupling in the bimanual movements of callosotomy patients. Psychological Science, 7, 306-310.

Franz, E., Ivry, R.B., & Helmuth, L. (1996). Reduced timing variability in patients with unilateral cerebellar lesions during bimanual movements. Journal of Cognitive Neuroscience, 8, 107-118.

Getty D. (1975). Discrimination of short temporal intervals: a comparison of two models. Perception & Psychophysics, 18, 1-8.

Gibbon, J., Malapani, C., Dale, C.L., & Gallistel, C.R. (1997). Toward a neurobiology of temporal cognition: Advances and challenges. Current Opinion in Neurobiology, 7, 170-184.

Guillemot, J.P., Richer, L., Prevost, L., Ptito, M., & Lepore, F. (1987). Receptive field properties of somatosensory callosal fibres in the monkey. Brain Research, 402, 293-302.

Harrington, D.L., Haaland, K.Y., &Hermanowicz, N. (1998). Temporal processing in the basal ganglia. Neuropsychology, 12, 3-12.

Helmuth, L. & Ivry, R.B. (1996). When two hands are better than one: Reduced timing variability during bimanual movements. Journal of Experimental Psychology: Human Perception & Performance, 22, 278-293.

Hore, J., Ritchie, R., & Watts S. (1999). Finger opening in an overarm throw is not triggered by proprioceptive feedback from elbow extension or wrist flexion. Experimental Brain Research, 125, 302-312.

Ivry, R.B. (1996). The representation of temporal information in perception and motor control. Current Opinion in Neurobiology, 6, 851-857.

Ivry, R.B. (1997). Cerebellar timing systems. International Review of Neurobiology, 41, 555-573.

Ivry, R.B. & Hazeltine, R.E. (1995). The 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, 1-12.

Ivry, R.B. & Hazeltine, R.E. (1999). Subcortical locus of temporal coupling in the bimanual movements of a callosotomy patient. Human Movement Science, 18, 345-375.

Ivry, R.B. & Keele, S. (1989). Timing functions of the cerebellum. Journal of Cognitive Neuroscience, 1, 136-152.

Ivry, R.B., Keele, S., & Diener, H. (l988). Dissociation of the lateral and medial cerebellum in movement timing and movement execution. Experimental Brain Research, 73, l67-l80.

Ivry, R.B. & Richardson, T.C. (in press). Temporal control and coordination: The multiple timer model. Brain and Cognition.

Iwamura , Y. (2000). Bilateral receptive field neurons and callosal connections in the somatosensory cortex. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 355, 267-73.

Jagacinski, R.J., Marshburn, E., Klapp, S.T., & Jones, M.R. (1988). Tests of parallel versus integrated structure in polyrhythmic tapping. Journal of Motor Behavior, 20, 416-442.

Jeka, J.J. & Kelso, J.A.S. (1995). Manipulating symmetry in the coordination dynamics of human movement. Journal of Experimental Psychology: Human Perception & Performance, 21, 360-374.

Keele, S., Pokorny, R., Corcos, D., & Ivry, R.B. (l985). Do perception and motor production share common timing mechanisms? Acta Psychologia, 60, l73-l93.

Kelso, J.A.S. (1997). Dynamic patterns: The self-organization of brain and behavior. The Mit Press, Cambridge, MA.

Kelso, J.S., Southard, D.L., & Goodman, D. (1979). On the coordination of two-handed movements. Journal of Experimental Psychology: Human Perception & Performance, 5, 229-238.

Killeen, P.R., & Weiss, N.A. (1987). Optimal timing and the Weber function. Psychological Review, 94, 455-468.

Krampe, R.T., Kliegl, R., Mayr, U., Engbert, R., and others. (2000). The fast and the slow of skilled bimanual rhythm production: Parallel versus integrated timing. Journal of Experimental Psychology: Human Perception & Performance, 26, 206-233.

Kugler, P.N., & Turvey, M.T. (1987). Information, natural law, and the self-assembly of rhythmic movement. Hillsdale, NJ: Lawrence Erlbaum Associates, Inc,.

Madison, G. (in press). Variability in isochronous tapping. Journal of Experimental Psychology: Human Perception and Performance.

Meegan, D.V., Aslin, R.N., & Jacobs, R.A. (2000). Motor timing learned without motor training. Nature Neuroscience, 3, 860-862.

Pressing, J. (1999). The referential dynamics of cognition and action. Psychological Review, 106, 714-747.

Rosenbaum, D.A. (1998). Broadcast theory of timing. In David A. Rosenbaum, Ed; Charles E. Collyer, Ed; et al. Timing of behavior: Neural, psychological, and computational perspectives, (pp. 215-235 of xii, 384 pp.). Cambridge, MA: The Mit Press.

Schmidt, R.C., Carello, C., & Turvey, M.T. (1990). Phase transitions and critical fluctuations in the visual coordination of rhythmic movements between people. Journal of Experimental Psychology: Human Perception and Performance, 16, 227-247.

Schmidt, R.A. (1975). A Schema Theory of Discrete Motor Skill Learning. Psychological Review, 82, 225-260.

Schöner, G. (in press). Timing, clocks, and dynamical systems. Brain and Cognition.

Schöner, G. (1990). A dynamic theory of coordination of discrete movement. Biological Cybernetics, 63: 257-270.

Schöner, G; & Kelso, J.A. (1988). Dynamic pattern generation in behavioral and neural systems. Science, 239, 1513-1520.

Semjen, A. & Ivry, R.B. (in press). The coupled oscillator model of between-hand coordination in alternate-hand tapping: A reappraisal. Journal of Experimental Psychology: Human Perception and Performance.

Shanks, M.F., Pearson, R.C., & Powell, T.P. (1985). The callosal connexions of the primary somatic sensory cortex in the monkey. Brain Research, 356, 43-65.

Tuller, B., & Kelso, J.A. (1989). Environmentally-specified patterns of movement coordination in normal and split-brain subjects. Experimental Brain Research, 75, 306-316.

Turvey, M.T., Rosenblum, L.D., Schmidt, R.C., & Kugler, P.N. (1986). Fluctuations and phase symmetry in coordinated rhythmic movements. Journal of Experimental Psychology: Human Perception & Performance, 12, 564-583.

Vorberg, D., & Hambuch, R. (1984). Timing of two-handed rhythmic performance. Annals of the New York Academy of Sciences, 423, 390-406.

Vorberg, D., & Wing, A. (1996). Modeling variability and dependence in timing. In HerbertHeuer, Ed; Steven W. Keele, Ed; et al. Handbook of perception and action, Vol. 2: Motor skills, (pp. 181-262). Academic Press, Inc, London, England.

Wing, A. (1980). The long and short of timing in response sequences. In G. Stelmach and J. Requin (Eds.), Tutorials in Motor Behavior, (pp. 469-484). New York: North-Holland.

Wing, A. & Kristofferson, A. (1973). Response delays and the timing of discrete motor responses. Perception & Psychophysics, 14, 5-12.

Wing, A.M. (1977). Effects of type of movement on the temporal precision of response sequences. British Journal of Mathematical & Statistical Psychology, 30, 60-72.

Wright, B.A., Buonomano, D.V., Mahncke, H.W., and Merzenich, M.M. (1997). Learning and generalization of auditory temporal-interval discrimination in humans. Journal of Neuroscience, 17, 3956-3963.

Yamanishi, J., Kawato, M., & Suzuki, R. (1980). Two coupled oscillators as a model for the coordinated finger tapping by both hands. Biological Cybernetics, 37, 219-25.

Zanone, P.G., & Kelso, J.A.S. (1997). Coordination dynamics of learning and transfer: Collective and component levels. Journal of Experimental Psychology: Human Perception & Performance, 23, 1454-1480

Notes

F1. In the simulations, the means and variances for the interval distributions were based on estimates of the central variance in Helmuth and Ivry (1996), derived according to the two-process model of Wing and Kristofferson (1973). We also added an additional delay to represent the time required to implement a motor command. The delay distributions were independently sampled for the left and right hands, using a fixed mean for the two hands and distribution variances based on the observed unimanual data.

F2. To minimize feedback even further, we would have preferred to have the participants produce a single response for each interval. We piloted a study in which the onset of the interval was indicated by a tone and the participants were instructed to produce one tap, marking the end of the interval. However, the participants were considerably more variable, both in terms of the mean interval produced and variability of the produced intervals with this method. Another alternative would have been to ask the participants to make one response by pressing and holding the key for the requisite interval. However, this type of movement would also likely involve two sub-movements, one related to the hold phase and the other related to the lift.

F3. One participant produced a negative slope in two of the conditions, indicating that she was more variable when tapping at the faster rates. The statistics were run twice, once with her data included, and once with her data excluded. No differences were seen in the two analyses so we only report the statistics involving the complete data set.

F4. We thank Gregor Schöner for his helpful discussions in developing these ideas.

Author Notes

We are grateful to Andras Semjen, Jörn Diedrichsen, Eliot Hazeltine, and Brent Stansfield for their comments on the ideas expressed in this paper. This work was supported by grants from the National Institute of Health (NS30256, NS2778) and the National Science Foundation (ECS-987