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When Two Hands Are Better Than One: Reduced Timing Variability During Bimanual Movements

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Within-hand variability was reduced on a repetitive tapping task when individuals tapped with 2 hands in comparison to single-handed tapping. When the total variability was decomposed into central timing and peripheral implementation components (A.M. Wing & A.B. Kristofferson, 1973), the bimanual advantage was attributed to decreased central variability. The improved consistency does not require that the movements involve homologous muscles. However, unlike phase coupling, the bimanual advantage is not found when the 2 movements are produced by different individuals, but rather requires that the 2 movements be produced by 1 individual. It is proposed that separate timing mechanisms are associated with each effector. During bimanual movements, the outputs from these timing mechanisms are integrated prior to movement execution, and it is this integration that results in the bimanual advantage.

Many actions are performed in a cyclic fashion. The hammering of a carpenter, the hand gestures of the traffic officer, and the casts of the fly fisher all involve the repetition of a simple sequence of muscular actions. In these actions, the cyclic movements are all performed with a single limb. In other skills, such as walking or rowing, the repetitive gestures require temporal coupling between different effectors. In the experiments reported in this article, we examined the temporal consistency of repetitive actions, comparing the timing of movements made with one effector with the timing of movements performed with two effectors.

The motivation for this research came from findings obtained in the study of neurological patients on simple timing tasks. Ivry and Keele (1989) examined three groups of patients, each with lesions associated with a distinct neural system of the central motor pathways. They found that patients with lesions of the cerebellum were consistently impaired on motor and perceptual tasks that required precise timing. These results suggested that one function of this neural system is to operate as an internal timing mechanism.

In a second study (Ivry, Keele, & Diener, 1988), a subset of the cerebellar patients was tested extensively on a repetitive tapping task (Wing & Kristofferson, 1973), a task that is the focus of this article. A tapping trial began with the presentation of a tone every 550 ms. The participants were instructed to tap a response key in time with the tones. After 12 synchronizing taps (paced phase), the tones stopped and the participants attempted to continue tapping at the target rate (unpaced phase). Of particular interest with this task has been the variability of the unpaced intervals. Wing and Kristofferson presented a model that decomposes the total variability into two independent components. One component reflects variability in the motor implementation system; the second component is assumed to reflect variability in central processes, including an internal timing mechanism (see also Ivry & Corcos, 1993).

Ivry et al. (1988) tested seven patients with unilateral cerebellar lesions, four in which the focus was in the lateral cerebellum and three in which the focus was more medial. Output from the cerebellum is doubly crossed, such that the left half of the cerebellum influences the left half of the body. This neuroanatomical arrangement allowed each patient to serve as his or her own control: The patients could perform the tapping task with either the ipsilesional, impaired hand or the contralesional, unimpaired hand. As expected, the patients' performance was more variable when tapping with the ipsilesional finger in comparison to when tapping with the contralesional finger.

A double dissociation was observed between patients with medial cerebellar lesions and those with lateral lesions. Although the Wing–Kristofferson model (1973) attributed the increased variability for the medial group to the implementation component, the deficit for the lateral cerebellar group was associated with the central component. Taken together with the findings of problems on time perception tasks (Ivry & Diener, 1991; Ivry & Keele, 1989), we hypothesized that the cerebellum functions as a central timing mechanism.

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Upon consideration, these results suggest a paradox. On the basis of these neuropsychological results as well as previous correlational findings with normal individuals (Keele, Ivry, & Pokorny, 1987; Keele, Pokorny, Corcos, & Ivry, 1985), we postulated the existence of a cerebellar timing mechanism that is accessed in a range of motor and perceptual tasks (Ivry, 1993; Keele & Ivry, 1991). However, the results from the patients with unilateral lesions suggest that separate mechanisms regulate the timing of different limbs. Thus, at a minimum, it would be necessary to propose the existence of at least two timing mechanisms, one for each side of the body. One resolution to this paradox is to assume that representing temporal information is a generic property of the cerebellum (e.g., Braitenberg, 1967; Desmond & Moore, 1988; Grossberg & Schmajuk, 1989). However, the exact region of the cerebellum utilized for this computation might vary, reflecting task-specific and effector-specific properties.

The notion of separate timing regulation of different limbs is of interest in the investigation of bimanual movements. Indeed, the focus of most bimanual research has been on describing the strong temporal coupling that occurs between limbs. Kelso, Southard, and Goodman (1979) had participants simultaneously reach for two targets, one located to the left of the midline and one located to the right of the midline. Different sizes and distances were combined such that some conditions required symmetric movements and others required asymmetric movements. Regardless of the condition, participants always showed strong temporal coupling, beginning the movements of each limb and ending them at approximately the same points in time. This constraint implied that, in asymmetric conditions, the left and right arms moved at vastly different velocities and forces. Nonetheless, temporal coupling was also evident in the kinematic analyses with each effector achieving peak velocity and peak acceleration at approximately the same point in time (but see Marteniuk, MacKenzie, & Baba, 1984).

Temporal coupling can reduce control requirements (e.g., Kelso & Scholz, 1985). For example, different muscles may be grouped into a single coordinative structure whose action can be described with a small set of parameters. Thus, in repetitive bimanual movements, both limbs move at a common frequency, and their relative motions can be described by a single phase parameter (Haken, Kelso, & Bunz, 1985; Kelso, 1984; Turvey, Rosenblum, Kugler, & Schmidt, 1986; Zanone & Kelso, 1992). Kelso and his colleagues have demonstrated that there are basically two stable phase relations for repetitive bimanual movements: inphase movements, in which each effector simultaneously follows a common trajectory, and antiphase movements, in which the trajectories of the effectors are offset by 180°. Although other phase relations can be learned (Zanone & Kelso, 1992), a large body of evidence shows performance to be vastly more stable for inphase and antiphase movements.

Stability in these studies is typically assessed in terms of the ability of the individuals to produce different phase relations or in the variability of the phase differences between the two limbs for a given phase relation. The individuals are given a target phase difference (e.g., 0° for inphase), and the deviation from this target is measured in terms of constant and variable error. This dependent variable is quite different from that measured in the cerebellar studies (Ivry & Keele, 1989; Ivry et al., 1988). In the neuropsychological studies the focus was on the variability of the intertap intervals produced by a single hand.

There have been studies exploring how within-hand variability on repetitive timing tasks is influenced during bimanual movements. Yamanishi, Kawato, and Suzuki (1980) focused on phase coupling, and they also briefly noted that within-hand variability was reduced during inphase bimanual movements. In a case study, Wing, Keele, and Margolin (1984) tested a Parkinsonian patient, in which the symptoms were more evident on her dominant, right side. Although this patient was much more variable when tapping with the right hand in unimanual tapping, the difference between the two hands was greatly reduced during bimanual tapping, primarily because performance with the left hand became worse. Vorberg and Hambuch (1984) as well as Wing, Church, and Gentner (1989) have provided assessments of different sources of variability by using an assortment of bimanual tapping conditions. In all of these studies, the analyses focused on models that postulated the operation of a single timing mechanism during bimanual movements (see also Turvey, Schmidt, & Rosenblum, 1989).

Given the ubiquity of temporal coupling and theoretical emphasis on single timer models of bimanual movements, we were motivated to study the performance of cerebellar patients on a bimanual version of the repetitive tapping task (Franz, Ivry, & Helmuth, in press). As discussed previously, patients with unilateral lesions show large differences in timing accuracy between their impaired effectors and unimpaired effectors (Ivry et al., 1988), a result we interpreted as showing selective disruption of an internal timing mechanism on the lesioned side. What would the performance of these patients be during bimanual tapping? Three outcomes can be considered. First, the patients' movements may not be coupled in a normal manner, and thus the between-hand differences observed in unimanual tapping would be maintained in bimanual tapping. Second, the patients' performance might be limited by the accuracy of the impaired hand. If this were so, then in the bimanual condition, the variability for the unimpaired hand would increase, a result similar to that reported by Wing et al. (1984). Third, because of some sort of coupling, tapping with the unimpaired hand might lead to improved performance in the impaired hand. For example, the output from the timing mechanism for the unimpaired hand might provide a stronger signal.

The results were quite intriguing. Timing variability of the impaired hand was consistently improved in the bimanual condition in comparison to the unimanual condition. For example, one patient with a unilateral right cerebellar lesion completed 30 trials each with the left hand alone, the right hand alone, and bimanually. In a replication of Ivry et al. (1988), a large difference was found between the hands in the unimanual condition. Based on the Wing-Kristofferson model (1973), the central timing variability estimates were 29 and 13 ms for the impaired and unimpaired hands, respectively. Performance with the unimpaired hand was unchanged in the bimanual condition. Most interesting, however, the patient's performance with the impaired hand was significantly better in the bimanual condition. In this condition, her timing variability estimate dropped to 21 ms. The improvement in bimanual tapping is also evident in the overall variability scores.

Taken together, the patient results suggest a number of properties concerning the timing of repetitive movements. The unimanual results pointed to separate timing mechanisms for different effectors (Ivry et al., 1988). Our recent bimanual results, however, indicate that the processes involved in timing bimanual movements interact. The source of this interaction remains unclear. It may be that under bimanual conditions, the timing mechanisms themselves interact. Alternatively, the output from these mechanisms may be constrained (i.e., coupled).

To explore these issues, we assessed performance on unimanual and bimanual tapping tasks in normal individuals. There have been previous studies comparing left-hand and right-hand performance, but this research has been directed toward questions of hemispheric specialization (Sergent, Hellige, & Cherry, 1993; Truman & Hammond, 1990; Wolff, Hurwitz, & Moss, 1977). In the current experiments, we were interested in comparing within-hand variability under unimanual and bimanual conditions. Specifically, is within-hand variability reduced in normal individuals when they are simultaneously tapping with the other hand? If so, understanding this phenomenon should provide useful information regarding the nature and interactions of internal timing mechanisms.

Experiment 1

Experiment 1 is a variation of the standard repetitive tapping task designed by Wing and Kristofferson (1973). Participants in this task are asked to repetitively tap at a fixed interval, first in time to a synchronizing signal and then in a self-paced continuation phase. In the current study, participants performed this task under three conditions: left hand only, right hand only, and both hands. In the bimanual condition, the two hands tapped inphase.

Method

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

Apparatus. A desktop computer was used to control stimuli and collect responses. A response board (20 cm × 30 cm) with two piano-type keys (2 cm × 10 cm), one on the right and one on the left, was used to collect the data. Minimal force was required to depress the response board keys (e.g., passive weight of 25 g would activate the microswitch). Responses were recorded as digital interrupts with temporal resolution of 1 ms.

Procedure. Participants were seated in front of a computer terminal in a quiet room. They were told to place their hands on the board in a comfortable position and to move only the index finger of the appropriate hand(s). In the single-hand condition, the participants rested the inactive hand at the side of the response board.

Participants initiated each trial by typing the "ENTER" key on a standard keyboard. Following a 1-s pause, the computer generated a series of 50-ms tones, separated by 400 ms. Participants began tapping once they were ready to synchronize their responses with the tones. After 12 paced intervals, the tones were discontinued. The participants continued tapping in an unpaced phase, attempting to maintain the target interval. After 32 unpaced responses, the end of the trial was signaled by a loud, long tone.

After each trial, the computer screen presented the participant with feedback. The mean interval duration, in ms, was presented as well as the standard deviation. The target rate of 400 ms was also printed on the screen so that participants could compare their mean interval duration with the target duration. In the both hands condition, data for the left and right hands were presented. Participants were encouraged to use the feedback to help them improve their performance. The experimenter emphasized that consistency, as measured by the standard deviation, was an important measure of their performance.

Design. Trials were grouped into blocks of eight. There were three blocks of each of three conditions: right hand only, left hand only, and both hands at once. Each time the participant encountered a condition for the first time, two practice trials preceded the block of eight test trials. Practice trials were not analyzed.

To counterbalance the order of presentation of the three conditions, there were six possible sequences of blocks. For example, Participant 1 completed a block of right hand only (r), then left (l), then both (b); l, b, r, b, l, r. Participants were randomly assigned to one of the six sequences. The experiment lasted approximately 50 min.

Data analysis. The primary data for analysis were the final 30 intervals produced during the unpaced phase of each trial. The mean and standard deviation for each trial was computed. In addition, a transformed measure of variability was obtained by calculating the standard deviation from a trend line fitted through the 30 data points for each trial. The transformation has been used in previous studies of repetitive tapping (Ivry et al., 1988; Keele et al., 1985) and removes any global changes in tapping rate that may have occurred during the trial.[1] The mean and transformed standard deviation scores were averaged over each block of eight trials. Trials in which a participant tapped an interval of less than 200 ms or more than 600 ms were excluded from analysis and repeated at the end of a block. Such trials generally were the result of participants failing to activate the microswitch.

We further analyzed the standard deviation scores using the Wing-Kristofferson model (1973). As stated previously, this model decomposes the total variability into two components: variability associated with response implementation (motor delay) and variability associated with central processes. Wing and Kristofferson proposed that a central timing mechanism determines when the target interval has elapsed. At this point, a command to tap is issued. However, the actual tap occurs only after delays introduced by peripheral implementation processes. A central assumption of their model is that the central command processes and implementation processes are independent. Moreover, the activation of each process occurs in an open-loop mode (feedback free). Specifically, the timing on Interval j + 1 begins as soon as the timing mechanism issues the command signaling the end of Interval j, indepen-

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[1] The transformation facilitates the covariance analysis required for the Wing-Kristofferson (1973) decomposition of total variability. However, calculations based on the raw data are very similar to those obtained from the transformed data.

dent of any variability in the implementation of preceding movement commands.

Formally, the duration Interval j can be expressed as

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

in which I, C, and MD represent the durations of the interval, clock, and motor delays, respectively. Given the assumption of independence, the variances associated with each component are additive:

$$\sigma_I^2 = \sigma_c^2 + 2\sigma_{MD}^2. \qquad (2)$$

The open-loop assumption allows an estimate of the peripheral variability to be given by

$$\sigma_{MD}^2 = -\text{autocovar}_I(1), \qquad (3)$$

where autocovar(1) is the covariance between Intervals j and j + 1 (Lag 1). Because the total variability is obtained from the raw data, an estimate of the clock variance can be obtained from Equation 1 by using subtraction.

Wing and Kristofferson (1973) referred to all of the variance not associated with response implementation as *clock* variance. In this article, we refer to this source as *central variance.* This more inclusive term acknowledges that there are other processes involved in motor planning in addition to a timing mechanism and that these may be expected to affect performance on this task (see Ivry & Corcos, 1993, for further discussion of this issue and justification of the model's assumptions).

Results and Discussion

Performance was quite stable on this task and there was no difference on any of the measures across blocks. Therefore, in the following analyses, the data were combined across the three blocks. A subset of trials was repeated (14%) because there was an excessively short interval (<200 ms) or long interval (>600 ms) within the run. For almost all of these trials, the problem was that on one response the participant failed to produce sufficient force to activate the microswitch. This problem was especially evident for three of the participants who failed to produce at least 20 trials without an aberrant interval.

Participants generally were accurate in maintaining the target pace. In the unimanual conditions, the mean intertap interval was 392 ms for the right hand. For the left hand, the comparable figure was 389 ms. During bimanual tapping, the movements of the two hands were tightly coupled, and the mean interval for each hand was 391 ms. The mean phase difference, averaged for all participants, was −0.7 ms (SD = 4.95 ms), with the negative value indicating a minuscule lead time for the left hand. Because there is not a priori reason to expect one hand to consistently lead the other, individual phase differences are more meaningful. The largest mean phase difference for an individual was 12.1 ms. Ignoring the sign of the mean phase differences, the median value for the 27 participants was 3.9 ms. This corresponds to a phase difference of 3.5° when converted to polar coordinates.

Our focus in this experiment is on the variability of the intertap intervals. Participants were more consistent when tapping with their dominant, right hand, $F(1, 26) = 8.20$, $p < .01$. The mean variability for the right hand was 20.1 ms, and for the left hand it was 21.3 ms. Although Wolff et al. (1977) found no asymmetry on a similar task, the current results are in accord with more recent reports of lower variability when individuals tap with their dominant hand (Sergent et al., 1993; Truman & Hammond, 1990). We return to this point when we discuss the Wing–Kristofferson (1973) decomposition of the total standard deviation.

The critical finding of Experiment 1 is that total variability was significantly lower in bimanual tapping in comparison to unimanual tapping. That is, within-hand performance was more consistent when the participants were simultaneously tapping with their other hand. This bimanual advantage was present for both the right and left hands. Variability dropped from 21.6 ms unimanually to 18.7 ms bimanually for the right hand, and from 22.3 ms unimanually to 20.3 ms bimanually for the left hand. The interaction was not significant.

We used the Wing–Kristofferson (1973) model to determine whether the reduction in total variability could be attributed to a change in either the central or peripheral components, or both. Before presenting these data, it is necessary to verify that the predictions of the model hold in both the unimanual and bimanual conditions. Figure 1 presents the covariance functions for Lags 0–5. Note that the square root of the autocovariance at Lag 0, $\text{autocovar}_I(0)$ gives the total variability score for each condition. The most basic prediction of the Wing–Kristofferson model was supported in that the autocovariance between successive intervals was negative. Indeed, the Lag 1 covariance was negative in 107 of the 108 conditions (27 participants × 4 Conditions each).

However, although there was no consistent correlation at Lag 2, the covariance function at Lags 1–5 tended to alternate between negative and positive values for all four conditions. For example, the Lag 3 covariance was smaller than the Lag 2 covariance for 81 of the 108 conditions. Significant nonzero correlations at lags greater than 1 indicate violations of the basic Wing–Kristofferson model (1973). Wing (1977) discussed possible mechanisms that might yield such covariance functions. In particular, the covariance function is expected to have a sawtooth pattern if either successive timing signals are negatively correlated, or successive implementation delays are negatively correlated. Wing (1977; see also Wing, 1979) has shown how estimates of variability in the timing and implementation components can be obtained given these possible dependencies. Thus, we chose to calculate the two components using both the basic Wing-Kristofferson model and the two models assuming negative dependencies.[2] It should be noted that, unlike the sawtooth pattern observed in the present experiment, Wing (1977) reported a covariance function suggesting a

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[2] We used the method described by Wing (1977) to test the two alternative models in which either successive timing or implementation signals are assumed to be negatively correlated. For each model, we minimized a least-squares goodness-of-fit measure by iteratively adjusting one free parameter corresponding to the magnitude of the correlation between successive samples.

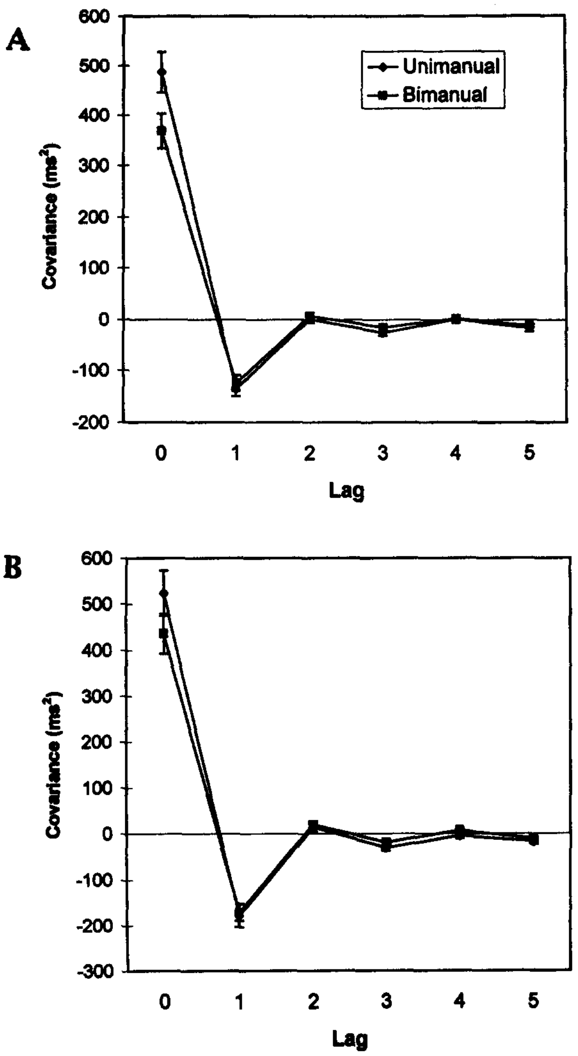

Figure 1. Covariance functions for Experiment 1. A: Covariance functions for the right hand, tapping alone and bimanually. B: The values for left-handed tapping.

positive correlation between successive motor delays (but see Wing et al., 1989). Although the reasons underlying this difference are unclear, it may reflect the fact that Wing (1977) provided individuals with a feedback signal during the unpaced portion of each trial.

The mean estimates of the central and implementation components are shown in Figure 2. Analysis with the basic Wing–Kristofferson model (1973) reveals a striking dissociation. The estimate of central variability is lower during bimanual tapping in comparison to unimanual tapping, $F(1, 26) = 49.87$, $p < .0001$. There was no difference in the motor delay estimates between the unimanual and bimanual conditions, $F(1, 26) < 1.0$. Thus, the component analysis indicates that the bimanual advantage reflects a reduction in central variability for each hand when the two hands tap simultaneously.

The analysis of the hand effect was more problematic. The estimate of implementation variability was lower for the right hand in comparison to the left hand, $F(1, 26) = 10.94$, $p < .01$. This result suggests that the advantage in tapping with the dominant hand is because of reduced noise in the peripheral implementation system. This finding was reported by Sergent et al. (1993) in a study investigating interactions of verbal processing and tapping. However, in the current study, the basic model showed that the estimate of central variability was significantly lower for the left hand in comparison to the right hand, $F(1, 26) = 6.10$, $p < .05$. Although this result was not found in the Sergent et al. study, the trend is in the same direction—clock variability—was lower for the left hand in comparison to the right hand (see Figure 1 of Sergent et al., 1993).

A less ambiguous pattern of results emerged when we made the central and peripheral estimates using the alternative models that account for the observed sawtooth covariance functions. First, we estimated the components under the assumption that successive clock signals were negatively correlated. This phenomenon might be expected to emerge if the timing mechanism operated as an oscillator or

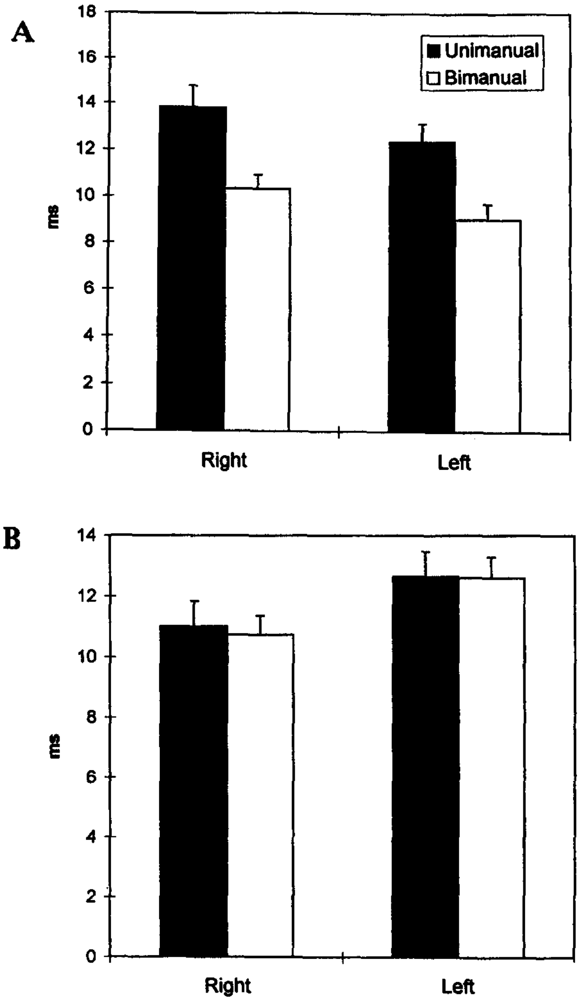

Figure 2. Components of total variability for Experiment 1. A: central variability, B: implementation variability.

limit cycle (Schoener, 1994). A double dissociation was observed with this model. The bimanual advantage was again attributed to a reduction in central variability, $F(1, 26) = 25.74, p < .0001$, with estimates of 15.4 ms and 12.1 ms for the unimanual and bimanual conditions, respectively. The less consistent performance with the left hand was solely attributed to the implementation component, $F(1, 26) = 5.06, p < .05$. The central variability estimate did not differ between the two hands, $F(1, 26) < 1.0$. This same pattern of results was obtained when the data were fit using the alternative model that assumed a negative correlation between successive motor delays. Again, the lower variability during bimanual tapping was associated with the central variability estimate, $F(1, 26) = 45.71, p < .0001$ (unimanual = 13.5 ms; bimanual = 10.7 ms), and the hand effect was linked to the peripheral variability estimate, $F(1, 26) = 6.94, p < .05$. For both alternative models, the interaction terms were not significant.[3]

The current experiment provides a direct comparison of within-hand timing variability during unimanual and bimanual tapping. In previous studies, covariance analyses have been applied to bimanual data to examine whether the two effectors share common sources of variability. Vorberg and Hambuch (1984) assumed that a single timing mechanism was involved during bimanual tapping. Given this assumption, an estimate of the implementation variance can be obtained by calculating the asynchronies in the left and right key presses. In brief, these asynchronies are assumed to reflect effector-specific variability because the commands to each effector are issued at a common point in time. Thus, the variability of the timer is estimated by the covariance of the intervals produced by each hand. By this procedure, the estimate of central variability averaged for all 27 participants was 12.15 ms (SD = 3.83 ms). By definition, this value is identical for both hands. Although this method cannot be used to provide a comparison with unimanual tapping, the bimanual estimate is close to that obtained with the models provided by Wing (1977; Wing & Kristofferson, 1973).

Starting with a similar assumption of a single timer, Wing (1982) provided a further method for decomposing implementation variability into two hypothetical sources. One source is effector specific; the other is assumed to reflect an implementation process that is shared by both effectors. Wing (1982) found the shared source of variability to be negligible. In contrast, the estimate of this component was consistently greater than zero in the present study. For all participants, the estimate of the effector-independent implementation variability was 3.45 ms (SD = 6.17 ms). The large standard deviation is primarily due to a single participant with a large negative estimate. Of the 27 participants, 23 had a positive value (sign test, $p < .05$). There are substantial methodological differences between the current study and that of Wing (1982). For example, in Wing (1982), successive key presses by each hand were made on different keys.

In summary, the results of Experiment 1 show that for participants performing a task of motor timing ability, two hands are better than one. Timing variability within each hand is reduced during bimanual repetitive tapping in comparison to unimanual tapping. Moreover, based on the Wing–Kristofferson model (1973; also Wing, 1977), the source of the improvement in the bimanual condition is entirely attributed to a reduction in variability associated with central processes. This result is similar to that obtained in our research with cerebellar patients (Franz et al., in press). These patients show an asymmetry in performance under unimanual conditions because of the unilateral pathology. However, this asymmetry is reduced during bimanual tapping, and this reduction was also attributed to the central component.

Contrary to models which assume the operation of a single timing mechanism during bimanual movements (Vorberg & Hambuch, 1984; Wing, 1982), we hypothesized *that the reduced central variability may reflect an interaction* between separate timers associated with each hand. An elaboration of this model is presented in the General Discussion. However, there are other processes that contribute to the estimate of central variability (Ivry & Corcos, 1993; Ivry & Hazeltine, 1995). In the following two experiments, we test hypotheses that attribute the bimanual improvement to factors other than interactions between central timing mechanisms.

Experiment 2

The first experiment demonstrated that within-hand variability was reduced when participants were asked to produce simultaneous movements with both hands. The bimanual movements involved homologous muscles: The movements were all produced by flexion and extension of the index fingers of each hand. An important question is whether the bimanual advantage requires that the movements be homologous. To answer this, the two movements in Experiment 2 were produced by nonhomologous actions. For one limb, the movement was again flexion and extension of the index finger; for the other limb, the movement now involved forearm flexion and extension. If the bimanual advantage were obtained with nonhomologous movements, then it would suggest that the underlying mechanism

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[3] It could be argued that one model might be appropriate for certain participants and a different model for other participants. To allow for individual differences, we also used a procedure in which the variability estimates from the best fitting model for each participant was used. For this analysis, the correlation parameter could be either negative or positive. Because these alternative models contain an extra parameter, they are guaranteed to provide at least as good a fit as the basic two-parameter model, and in most cases, a better fit. To offset this, we replaced the variability estimates from the basic model only if the least-squares measure was reduced by 70% with an alternative model. For the 108 fits (27 participants × 4 Conditions), 23 of the scores were revised according to this arbitrary criterion. For the most part, the revised scores were similar to the original scores. When an analysis of variance was run with the new estimates substituted in those places where a substantial change was found, the lowering of the central variability estimate under bimanual tapping was still obtained, $F(1, 26) = 33.72, p < .0001$.

may arise at a level that is independent of particular combinations of response implementation systems.

The use of nonhomologous movements can also provide a test of an attentional account of the bimanual advantage. Suppose that in the planning of a movement, people represent an abstract goal they hope to achieve, for example, to drink from a mug or type a word. At some level of processing, this goal must be translated into a specific movement plan. One hand must be selected to pick up the mug; a finger must be specified to strike the keyboard. It is possible that initially, multiple actions are generated, each of which could achieve this goal. However, over time, one of these potential actions is selected. People rarely find themselves simultaneously reaching for a mug with both hands or pecking a key with more than one finger.

This scenario suggests that in producing unimanual movements, there may be a need to inhibit alternative actions. With bimanual movements, this requirement would be reduced. Applied to our tapping task, it may be that the bimanual advantage is the result of reduced selection demands in comparison to unimanual tapping. In the latter condition, the selection of one finger may require an inhibition of activation of the homologous finger on the other hand. In bimanual tapping, this selection process would be eliminated.

Although the selection hypothesis may appear counterintuitive, it merits exploration for a number of reasons. First, consider some neurological evidence. Patients who have suffered a unilateral stroke resulting in hemiparesis frequently show mirror, or associated movements. When these patients attempt to perform a task with their affected limb, homologous muscles are sometimes activated on the unimpaired side. Curiously, the patients report that they are not consciously attempting to move the ipsilesional limb and are generally surprised to observe this phenomenon (e.g., Zulch & Muller, 1969). Second, neuroimaging studies with healthy adults suggest bilateral activation during unilateral movements. Using positron emission tomography Roland, Meyer, Shibusaki, Yamamoto, and Thompson (1982) found bilateral activation of many cortical and subcortical areas when individuals performed a series of ballistic movements unilaterally. In particular, supplementary and premotor areas showed bilateral metabolic increases compared with resting rate, whereas the primary motor hand area showed contralateral activation. They suggest that a motor program is initially elaborated bilaterally, and only at final cortical processing stages does the activation become asymmetric. Similarly, Kim et al. (1993) observed bilateral activation during the production of unilateral finger movement sequences. The activation was not symmetric, with only the left hemisphere showing comparable activation for both left-hand and right-hand sequences.

Bilateral activation rarely has obvious behavioral consequences. However, homologous errors have been observed in typing (Lessenberry, 1928, cited in Rumelhart & Norman, 1982). These errors occur when the person intends to type a key with a particular finger and movement but instead executes the mirror symmetric action with the other hand.

These examples demonstrate not only that there is bilateral activation in preparing movements, but also that there is a special status for the activation of homologous muscles. According to the selection hypothesis, the bimanual advantage may thus result from the fact that processing demands are reduced during bimanual tapping because there is no need to inhibit homologous muscles of the inactive hand. If this were so, then the bimanual advantage should be lost when the movements involve nonhomologous movements. This follows because with nonhomologous movements, the selection process would have to operate twice. For example, consider an individual who is using the right index finger and the left forearm. In this case, the selection process would have to inhibit activation of the left index finger and inhibit activation of the right forearm. Thus, in comparison to unimanual movements, the demands on this process would be increased. Not only should the bimanual advantage disappear, but we might expect to see an increase in variability during bimanual tapping.

Method

Participants. Twenty-eight participants from the University of California, Berkeley psychology subject pool participated in this experiment.

Procedure and design. The standard repetitive tapping task was modified slightly for Experiment 2. For one limb, participants tapped as in the preceding experiments by simple flexion–extension of the extended index finger. For the other limb, participants tapped by moving their forearm at the elbow. The hand in this condition was clenched into a fist, and the wrist was kept in line with the forearm. The elbow rested on the table in front of the response board, and a response was made by lowering the entire forearm, bringing the ulnar side of the fist into contact with the key. The experimenter demonstrated the technique to the participants and observed their practice blocks to ensure correct performance. Participants were randomly assigned to perform the task with either the right finger and left forearm or the left finger and right forearm.

Participants completed three conditions: two involving unimanual tapping (finger only or forearm only) and one involving bimanual tapping (finger and forearm). All trials consisted of 12 paced responses and 32 unpaced responses. Trials were grouped into blocks of seven, and three blocks of each condition were presented. The order in which the blocks occurred was counterbalanced across participants.

Results and Discussion

The data from 1 participant were excluded from the final analysis because of high variability. For the remaining 27 participants, 285 trials (13%) were repeated because of an extremely short or long response. The estimates of central and implementation variability were obtained by averaging over the 21 trials per condition to obtain the most stable measure of performance.

The interresponse intervals did not differ among conditions, averaging 396 ms for unimanual conditions and 393 ms for bimanual conditions. For both finger and forearm tapping, the mean interval was 395 ms.

Unlike in the previous experiment, there was no significant reduction in total variability during bimanual tapping, $F(1, 26) = 1.59, p > .05$. However, there was a significant interaction of this factor and the effector used, $F(1, 26) = 7.03, p < .05$. When tapping with the finger, total variability was 21.3 ms under unimanual conditions in comparison to 19.1 ms under bimanual conditions. In contrast, when participants tapped with the fist, total variability was slightly higher under bimanual conditions (unimanual: 19.2 ms; bimanual: 20.3 ms).

We used the Wing–Kristofferson model (1973) to examine the sources of the changes in total variance. The covariance functions for the four conditions (unimanual fist tapping, unimanual finger, bimanual fist, and bimanual finger tapping) are shown in Figure 3. Of 108 Lag 1 estimates (27 participants for each of 4 conditions), 107 were found to be negative. As in Experiment 1, there was a consistent sawtooth pattern across Lags 1–5. Thus, the data were again evaluated with both the basic Wing–Kristofferson model (1973) and the two alternative models that predict this pattern of responses. However, the alternative models led to no changes in the basic conclusions and are not considered further.

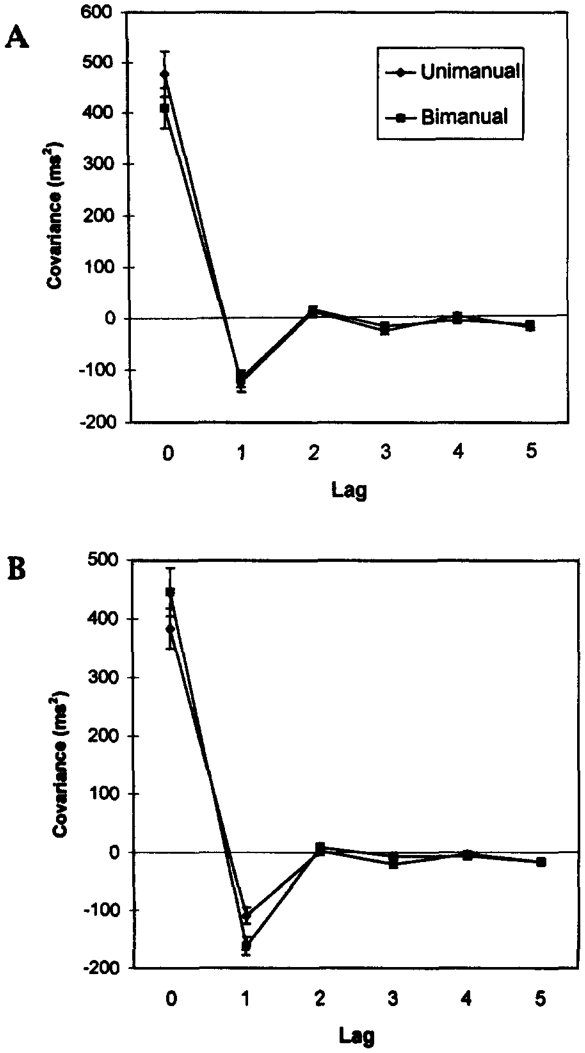

Figure 3. Covariance functions for Experiment 2. A: Covariance functions for finger tapping alone and bimanually. B: Covariance functions for the forearm tapping.

The estimates of central timing and implementation variability derived from the Wing–Kristofferson model (1973) are presented in Figure 4. As in Experiments 1 and 2, the estimate of central timing variance drops significantly when participants tap during bimanual conditions, $F(1, 26) = 20.28, p < .0001$. This effect is apparent for both limbs: The reduction is 4.4 ms and 3.2 ms for the finger and forearm, respectively, when comparing unimanual and bimanual tapping.

There was a main effect of limb, $F(1, 26) = 7.2, p < .05$, for the estimate of central variability. This estimate was lower when participants tapped with their forearm in comparison to the finger. This result was unexpected, and is, to some extent, at odds with previous results reported by Wing (1977). Using only unimanual conditions, Wing found that total variability was greater for finger movements in comparison to forearm movements. This trend is also evident in the current experiment (SDs of 21.3 ms vs. 19.2 ms for the finger and forearm, respectively). However, Wing (1977) attributed this difference to lower implementation variability for the forearm, whereas we fund the difference to be in the estimate of central variability. In addition to this discrepancy in the component estimates, the covariance functions were quite different. Whereas Wing (1977) found a significant negative covariance at Lag 2, the covariance functions in Experiments 1 and 2 in the current study were sawtooth in shape with a positive Lag 2 covariance. As previously noted, an important methodological difference is that Wing (1977) provided a feedback tone after each response.

The estimate of implementation variability was found to increase during bimanual tapping, $F(1, 26) = 4.92, p < .05$. Whereas Figure 4 indicates that this increase is predominant for the forearm, the Limb × Mode interaction was only marginally significant, $F(1, 26) = 3.74, p < .07$. The increase in implementation estimate may be related to a phenomenon reported by Turvey et al. (1989). In that study, participants rotated their arms while holding pendula of different masses. As the difference between the masses held by the two arms became greater, the Lag 1 covariance became more negative (e.g., larger estimate of implementation variability). Combining two effectors of different masses, the finger and the forearm, might produce an analogous effect. It may be that when the two limbs require very different forces, peripheral variability increases because of cross talk between the effector systems.

In summary, two important conclusions can be drawn from the results of Experiment 2. First, the bimanual advantage is not dependent on homologous movements. The effect generalizes to situations in which the movements involve nonhomologous effector combinations. Second, the results do not support the attention hypothesis. This hypothesis predicted that the bimanual advantage would be re-

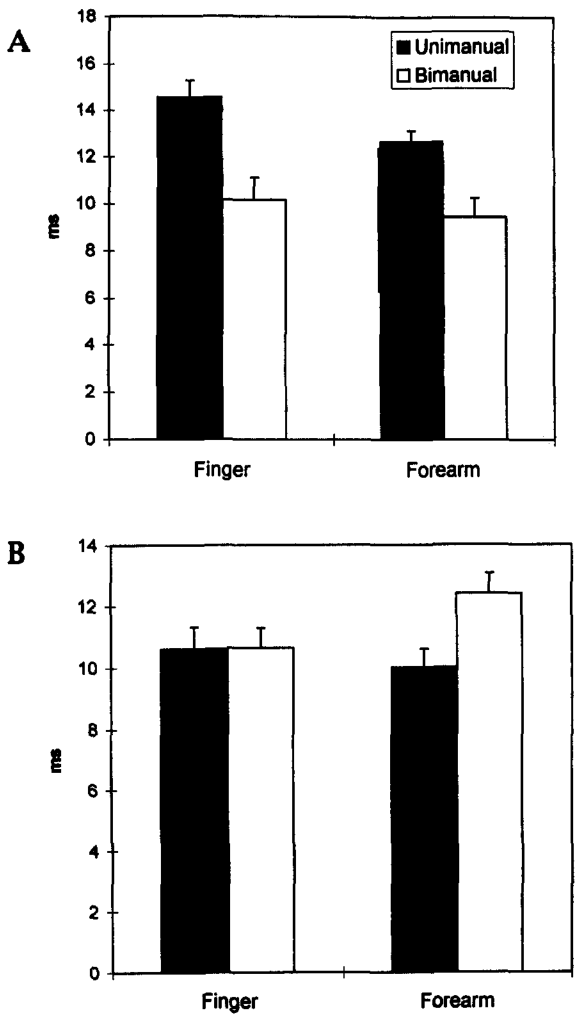

Figure 4. Components of total variability for finger and forearm tapping. A: central variability, B: implementation variability.

versed, or at least eliminated, if participants tapped with nonhomologous muscles. This prediction was based on the assumption that this form of bimanual tapping would increase attentional demands because a selection process would have to operate twice (i.e., for each limb). However, the data show that the bimanual advantage persists even when the movements are made with different groups of muscles. A comparison of Figures 2 and 4 suggests that the reduction in the central variability estimate appears to be as large in this experiment as in the Experiment 1. No formal statistical comparisons, however, were made because of various methodological differences.

Experiment 3

As noted in the introduction, previous research on bimanual movements has emphasized constraints on phase relations that can be adopted by the two effectors. New insights into the level at which these constraints are imposed are provided by the findings of Schmidt, Carello, and Turvey (1990). These researchers examined whether similar constraints would emerge in multieffector movements produced by two people. Specifically, 2 participants were seated next to each other and asked to swing one leg in synchrony with a metronome signal. On some trials, the participants were required to produce inphase movements by coordinating flexion and extension cycles with their partner's movements. On other trials, the participants attempted to produce their movements in an antiphase mode: When 1 participant was extending his or her leg, the other was to flex his or her leg. These two modes were tested at different frequencies ranging from 0.6 Hz to 2 Hz.

The striking result from this study was that many of the dynamical phenomena found in multieffector movements produced by a single participant also were evident when the two limbs were moved by two different participants. For example, the relative phase of the two limbs was maintained more accurately and consistently in the inphase mode in comparison to the antiphase mode. Moreover, this difference became amplified at higher frequencies with participants showing a tendency for phase shifts from antiphase to inphase mode at the highest frequencies tested. Schmidt et al. (1990) argued that the dynamical system producing the coupling phenomena need not require any sort of material linkage, but rather could be the result of an informational linkage. In particular, they emphasized that the linkage must result from the visual information afforded each individual concerning his or her own movements and those of the partner. No interindividual coupling was observed when the individuals were prevented from viewing the moving limbs.

The provocative results of Schmidt et al. (1990) led us to ask whether the bimanual advantage described in the current Experiments 1 and 2 would also be found when the movements were produced by two individuals. Specifically, would the within-hand variability (associated with the movements of a single individual) be reduced when those movements were coordinated with those produced by another individual? If this were so, it would suggest that the within-hand bimanual advantage reflects processes similar to those that constrain between-hand phase relations.

Another motivation for the current Experiment 3 is that it provides a test of one source of feedback that might contribute to the bimanual advantage. In particular, during bimanual tapping, visual and auditory feedback may help participants maintain the consistency of the movements of each limb. For example, if one limb were to produce an aberrant cycle, feedback from the other limb might help the participant reinstate the proper frequency. In unimanual tapping, no such information would be available (other than a participant's internal model of the interval). Note that the open-loop assumption of the Wing–Kristofferson model (1973) is based on how a single limb might be affected by feedback from its own action. It remains possible that feedback from a different limb might be important. Experiment

3 provides an assessment of whether visual or auditory feedback from a different limb (individual) contributes to the bimanual advantage.[4]

Method

Participants. Forty-four participants from the University of California, Berkeley psychology subject pool participated in this experiment.

Procedure and design. Participants were tested in pairs in Experiment 3. At the beginning of the session, the participants were seated side by side in front of the computer. A keyboard was placed in front of each participant, and the two keyboards were adjacent to one another. Each participant tapped with only the right index finger. There were three conditions. Two conditions involved unimanual tapping. For one condition, the participant on the right tapped alone. For the second unimanual condition, the participant on the left tapped alone. The participant who was not tapping simply rested.

The third type of trial was the bimanual condition. Here, the two participants were asked to tap in synchrony. Each participant tapped with the right index finger as in the unimanual condition. The participants were instructed to watch the movements of their own and their partner's fingers. In addition, the sounds from both keyboards were clearly audible to both participants.

All other aspects of the design were as in Experiments 1 and 2. Each trial consisted of 12 paced responses and 32 unpaced responses. The initiation of the paced responses began with the first key press detected from either participant. On almost all trials, the other participant began tapping within one response. A block of trials was composed of seven error-free trials, and each condition was repeated for three blocks. The order in which the blocks occurred was counterbalanced across participants. Thus, within a pair, there were instances in which both participants performed a block of unimanual tapping prior to the bimanual blocks. In other instances, one or both participants performed in the bimanual condition prior to the first unimanual block.

Results and Discussion

Eleven percent of the 1,539 trials were repeated because intervals were either shorter than 200 ms or longer than 600 ms. Most of these trials occurred during the bimanual condition, perhaps resulting from interference that arose between the 2 participants as they attempted to coordinate their responses. As before, the central and implementation estimates were made after combining the analyses over the 21 trials per condition.

The mean interresponse intervals for the unimanual conditions were 391 ms and 384 ms for the participants on the right and participants on the left, respectively. The comparable values for bimanual tapping were 389 ms and 385 ms. Note that unlike in the single-person Experiments 1 and 2, the mean intervals were not identical for the two-person experiment during bimanual tapping. Nonetheless, the movements in the bimanual condition were coupled. The phase differences between the two fingers were not uniformly distributed but rather tended to cluster around a small range. For some pairs of participants, this range was near 0 ms (e.g., tapping in synchrony); for others there was a consistent phase difference between the participants. This consistent phase difference might reflect the use of different forces by the participants to depress the response key.

The critical comparison in this experiment is whether each participant's within-hand variability is reduced when participants tapped with a partner in comparison to when they tapped alone. The results show that this is not the case. Neither the total variability nor the central estimate, as calculated by the Wing-Kristofferson model (1973), decreased when 2 participants tapped together. In fact, for both of these measures, variability increased during the bimanual condition. During unimanual tapping, the mean standard deviation of the interresponse intervals was 21.6 ms. In the bimanual condition, this value rose to 24.4 ms, $F(1, 21) = 38.15$, $p < .001$. Unexpectedly, there was a marginally significant effect of person, with the participants seated on the right being more consistent, $F(1, 21) = 4.02$, $p < .10$.

The covariance functions were in accord with the predictions of the Wing-Kristofferson model (1973). The Lag 1 covariance was negative for all but 4 of the 88 data points (44 Participants × 2 Conditions each). Moreover, the covariance functions for all lags greater than 1 were not significantly different from 0.

The estimates of central and peripheral variability are shown in Figure 5. As with the total variability, the estimate of central variability during bimanual tapping increased to 16.5 ms from 14.6 ms, $F(1, 21) = 6.48$, $p < .05$. For this component, the values were comparable for the groups seated on the right and left. For the implementation estimate, there was no significant difference between the unimanual and bimanual conditions. However, the interaction was significant, $F(1, 21) = 7.43$, $p < .05$. As shown in Figure 5, the implementation estimate rose for the person on the left during bimanual tapping. No change was found for the person on the right. It is possible that the higher implementation estimates for the person on the left occurred because these participants had to adopt a less natural posture to watch the two hands.

The results from this experiment clearly indicate that the bimanual advantage does not emerge when the two effectors are controlled by different individuals. In other words, the

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[4] We have also explored whether the bimanual advantage might result from enhanced auditory feedback available during bimanual tapping. In brief, we hypothesized that each hand might provide a pacing signal for the other hand. If this source of information is important, we reasoned that participants should benefit from having a perfect auditory pacing signal. To test this idea, we compared unimanual and bimanual tapping when the pacing signal was maintained for the entire trial. Because this manipulation provides a perfect auditory model in both conditions, the bimanual advantage would disappear if auditory feedback was important. Contrary to this prediction, the bimanual advantage was as large during paced tapping as unpaced tapping (2.3 ms and 1.7 ms, respectively). In addition, participants were actually more variable during paced tapping (21.0 ms) in comparison to unpaced tapping (19.6 ms). These results provide further evidence that timing on this task is not improved by external feedback.

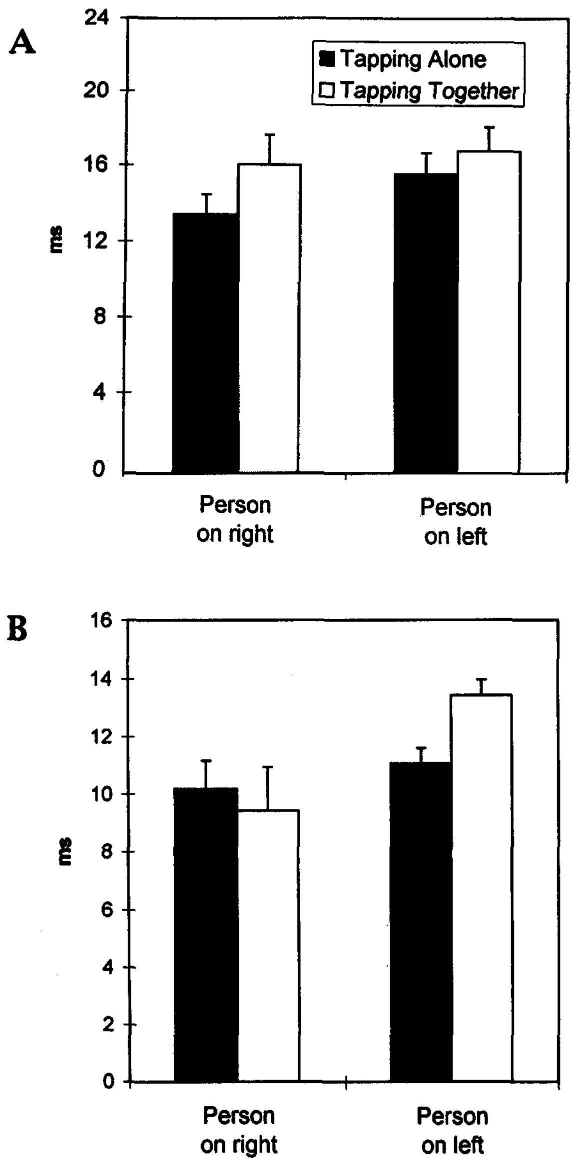

Figure 5. Components of total variability for Experiment 3. A: central variability, B: implementation variability. Participants seated on the left and right performed the tapping task either alone or with their partner.

improvement during bimanual tapping requires that a single individual produce both movements. This finding suggests that different mechanisms may underlie the dynamics of phase relations in rhythmic movements and those related to the within-effector consistency in bimanual movements. For example, as shown by Schmidt et al. (1990), visual feedback may be sufficient to produce certain stable phase relations in repetitive movements produced by different individuals. In contrast, visual feedback does not appear to be a relevant source of the bimanual advantage. In fact, the results suggest that the consistency of an individual's movements is disrupted when observing synchronized movements produced by another person.

General Discussion

In Experiments 1–3 we examined the timing of repetitive movements under unimanual and bimanual conditions. Unlike previous studies of bimanual movements (e.g., Kelso, 1984; Zanone & Kelso, 1992), our primary interest was to compare within-hand variability under the two conditions. Temporal variability was consistently reduced during bimanual movements.

Experiment 2 showed that the bimanual advantage does not require that the two movements be produced by homologous effectors. The bimanual reduction was also found with nonhomologous movements involving the finger and forearm. This result provides an important generalization of the phenomenon.

In addition, Experiment 2 provides an evaluation of an attentional account of the bimanual advantage. The bimanual advantage is counterintuitive from the perspective of resource theories of cognitive capacity (e.g., Kahneman, 1973). Such theories predict that when task demands increase, performance on a given task should deteriorate, or at best remain unchanged. In the current experiments, we observed a situation in which performance (e.g., right-hand tapping) improved when the task became more complex (e.g., performed simultaneously with left-hand tapping). Moreover, the results of Experiment 2 rule out a specific attentional hypothesis of the bimanual advantage. Neurological, neurophysiological, and behavioral evidence suggests that, at some stage of processing, unimanual movements are represented bilaterally. On the basis of this, we hypothesized that unimanual movements may be more variable because of increased demands required to inhibit homologous actions with the contralateral effector. This hypothesis led to the prediction that the bimanual advantage would be lost, or perhaps reversed, if the movements were produced by nonhomologous effectors. This prediction was not confirmed.

Experiment 3 demonstrated that there is no reduction in within-hand variability when the two movements are produced by different individuals. This result provides two insights. First, there appear to be differences between the mechanisms that underlie within-effector variability and those that influence between-effector coupling. This hypothesis is based on the finding that between-effector coupling appears to be similarly constrained whether the two movements are produced by one or two individuals (Schmidt et al., 1990). In the current study, the bimanual advantage was found only when the two movements were produced by a single individual. Second, Experiment 3 demonstrates that visual and auditory feedback are not sufficient to produce the bimanual advantage. A feedback-based hypothesis might be that, during bimanual tapping, each effector provides a "model" of the target interval for the other effector. In unimanual tapping, such a model is not available. This hypothesis, however, leads to the prediction that the bimanual advantage should emerge in the two-person experiment.

Note that it remains possible that somatosensory feedback could be contributing to the bimanual improvement. However, previous studies with both normal and neurological individuals (see Ivry & Keele, 1989) indicate that feedback processes play a minimal role in the repetitive tapping task.

Given that feedback and attentional hypotheses cannot account for the bimanual advantage, we now turn to a discussion of how internal timing mechanisms might produce this effect. We used the Wing–Kristofferson model (1973) to evaluate whether the reduced variability was attributed to changes in central processes or motor implementation processes. In both experiments, the results were clear: Lower estimates of central variability for each effector were obtained during bimanual tapping.

The use of covariance functions to estimate component sources of variability during bimanual movements has been used by a number of investigators (Turvey, et al., 1989; Vorberg & Hambuch, 1984; Wing, 1982; Wing et al., 1989). These investigators have consistently concluded or assumed that a single timing system regulated the movements of the different limbs. That is, the time at which the movements should occur was attributed to a shared process, although the times at which responses were made were influenced by additional processes that might be effector specific. It is not clear how this form of analysis could account for the bimanual advantage. Why would a single timing mechanism become more consistent when its output is directed to multiple effector systems? An alternative approach is to postulate different timing signals associated with each limb. Perhaps the bimanual advantage (and temporal coupling) reflect an interaction between these two signals.

Different hypotheses can be generated regarding the type of central interactions that could produce this effect. It has been hypothesized that rhythmic movements reflect the operation of internal oscillators (see Schoener & Kelso, 1988). In bimanual movements, two oscillators are postulated, one associated with each effector. However, these oscillators are coupled, and the dynamics of bimanual movements will reflect the strength of this coupling. This form of analysis has previously been used to account for the stability of certain phase relations during bimanual movements (Kelso, 1984; Yamanishi et al., 1980; Zanone & Kelso, 1992).

Little attention has been given to how coupling may affect within-effector variability. However, it seems reasonable to expect that within-effector variability might be reduced as coupling strength increases. An analogy might be to consider the stability of two pendula of different mass. The smaller pendulum can represent the unimanual condition. The larger pendulum can represent the bimanual condition where two small pendula have been strictly coupled (and thus form the larger mass). A perturbation of a given size will have unequal effects on these two dynamical systems. The larger pendulum will show less displacement from its limit cycle than the smaller pendulum. The coupled system will have reduced variability. It is important to note that, although the preceding metaphor draws on a physical example, similar interlimb coordination dynamics are found in intraindividual and interindividual movements (Schmidt, et al., 1990). Thus, the "larger" pendulum must emerge at an abstract, nonbiomechanical level.

A different version of a coupling hypothesis may also account for the bimanual advantage. As shown in previous research, patients with unilateral cerebellar lesions show increased central variability when tapping with their ipsilesional hand (Ivry et al., 1988). This within-subject dissociation suggests that different effectors engage the operation of different timing mechanisms. However, these patients also show a strong frequency and phase coupling when performing bimanual movements (Franz et al., in press). One way to account for this is to assume that the outputs from separate timing mechanisms are integrated. Perhaps this integration reflects a response bottleneck: Output to peripheral motor pathways cannot occur at arbitrary points in time, but is constrained. For example, when two hands are moving in phase, motor commands for each hand are issued simultaneously. By this model, the coupling does not reflect any interactions between the timing mechanisms per se, but rather a process receiving the output from the timers.[5]

There are many possible forms that an output constraint could take. We explored a set of models in a series of simulations. The models share the following properties: First, in each, separate timing mechanisms are associated with each effector (hand–hand or hand–forearm). For the current discussion, random samples from each timing mechanism are assumed to form a normal distribution. One normal distribution is used to represent samples from the "left" timer, and a different normal distribution is used to represent the "right" timer. The means of these distributions were set to the means of the interresponse intervals produced during the unpaced tapping phase. The standard deviations were set to the estimated central variability components as derived from the Wing-Kristofferson model (1973). Thus, the means and standard deviations are not equal for the two distributions. Our decision to use only the central estimates is motivated by the assumption that the bimanual advantage reflects central interactions. This is further justified by the experimental results showing that the motor delay estimates did not decrease during bimanual tapping.[6]

To simulate the central variability in a unimanual tapping trial, we took 30 samples from one of the distributions of intertap intervals and calculated the mean and standard deviation of the samples. This procedure was repeated separately for the left and right timers. For bimanual trials, separate sets of 30 samples were obtained, one from the distribution of the left timer and one from the distribution of the right timer. These samples were then combined (see

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[5] The current model does not require the two timing mechanisms to be associated with the different sides of the body. Indeed, we would expect within-effector variability to be reduced during finger–foot movements that involved effectors on the same or different sides of the body.

[6] The qualitative pattern of results would be the same if total variability scores were used in the simulations. However, the use of these values would distort any quantitative comparisons. This is because the motor component is unaffected by the coupling constraint.

below) to simulate the hypothesized output constraint. The mean and standard deviation of the new, integrated distribution were then calculated to obtain an estimate of central variability during bimanual tapping for that trial. These procedures were repeated for 24 unimanual and 24 bimanual trials for each of the 27 participants.

Six different models were tested. To repeat, the models share two primary assumptions. First, each model is based on the assumption that there are separate timing mechanisms associated with each effector. Second, in each model a coupling mechanism constrains bimanual movements so that a single central output is sent to both effectors simultaneously. The models differ in how the samples from the two timing distributions are combined. Table 1 presents the simulated mean interresponse interval and estimate of central variability for each model calculated for the 27 participants. The unimanual estimates are an average of right- and left-hand performance. We also ran large-scale simulations by taking 3,000 samples from each of two distributions: one matched to the estimate of central variability for the right hand averaged across participants and the other matched to the left-hand estimate. These simulations yielded essentially the same results as those shown in Table 1.

The null models are essentially identical to the unimanual conditions. *Null right* would mean that during bimanual tapping, performance is completely determined by the output of the samples from the right timer. For *null left,* bimanual tapping would be completely determined by the output of the samples from the left timer. Given that there is no real integration of the different timers, the simulations fail to produce a reduction in variability during bimanual tapping.

The *random* model provides the simplest form of integration. Prior to each response, the output integrator randomly selects one of the two timing signals. This model actually predicts a slight increase in variability, resulting from the fact that the means of the two distributions are not identical.

For the *first* model, the samples of the combined distribution are based on whichever timer provides the first input. That is, central commands to tap are sent to both effectors as soon as one of the timers indicates that the target time has elapsed. The combined distribution will include samples from both the right and left distributions because of their considerable overlap. The *last* model is the converse. In this case, the central command is delayed until both the right and left timers indicate that the target time has elapsed. Interestingly, both models predict reduced central variability during bimanual tapping. However, these models also predict a change in the mean of the intertap intervals. The first model predicts that participants tap faster, and the last model predicts that participants tap slower.

Table 1
Six Models by Which Two Timing Mechanisms Can Be Integrated

Models	Mean interval	Central variability
Null		
Right	392	13.77
Left	389	12.35
First	383	10.94
Last	399	11.28
Random	391	13.68
Waiting		
Right	399	17.11
Left	399	17.43
Average	391	9.41
Experimental results	391	9.68

The *waiting* model is a more complicated version of the first and last models. Rather than have the coupling occur by means of the commands to the periphery, coupling in the waiting model is in terms of the restarting of the two timers. That is, after each timer indicates the target time has elapsed, the associated hand makes a response. Restarting the timers, however, must occur simultaneously and is delayed until both timers have completed timing the previous interval. With this model, separate variability estimates are obtained for each hand. However, neither estimate provides a good fit to the data, both in terms of the means and standard deviations.

The final model discussed in Table 1 is the *average* model. For this model, the intervals in the combined distribution are calculated by taking the average of the two samples for each bimanual response. The simulation of this model provides an excellent fit to the data. First, the mean of the combined distribution falls halfway between the means for the left and right distributions. More impressively, the simulated standard deviation is 9.41 ms. In Experiment 1, the average central variability of the right and left hands during bimanual tapping is 9.68 ms. On the basis of the empirical estimates of central variability, the average model predicts a bimanual advantage of about 29%, a value close to the observed value of 26%. Note that the 29% reduction by the averaging model can be obtained analytically. The standard deviation is reduced by a factor of the square root of 2 (or 29.3%) when a new distribution is formed by averaging two independent samples from a normal distribution.

Large-scale simulations based on the mean data for Experiment 2 also were conducted. The two unimanual distributions were based on the mean finger and forearm estimates. Again, the average model clearly provided the best fit. The simulated central variability in the bimanual condition was 9.7 ms, and the observed value, averaged over finger and forearm, was 9.8 ms.

The average model may seem at first to be implausible in real time. In this model, a sample is taken from each timer, and the integrated central output occurs at the average of these two samples. It seems illogical that an averaged output could be sent prior to the time at which the integrator receives the second input component. How could it be known when this input would arrive?

However, if timing mechanisms are conceptualized as producing a continuous signal, an averaging integrator is not unreasonable. A sketch of how averaging might occur for a single bimanual response is given in Figure 6. The activation of each timing mechanism is represented by a continuous activation function. The peak of this function

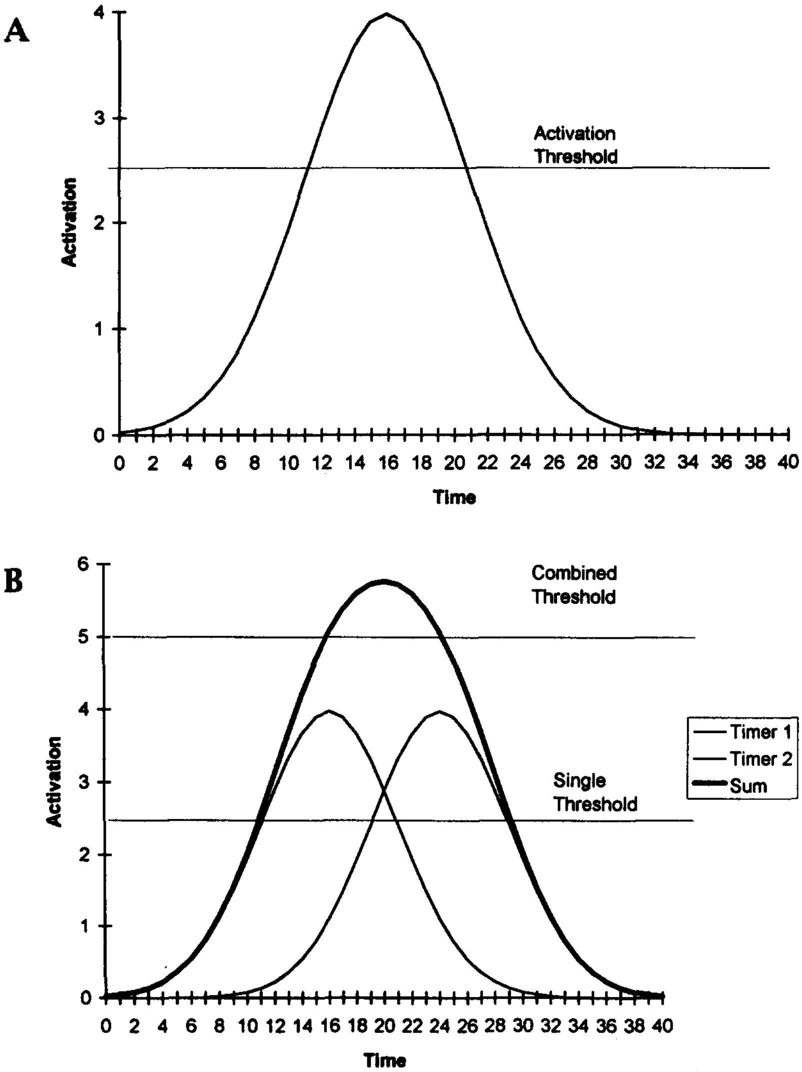

Figure 6. Hypothetical distributions representing the activation of timing mechanisms over time. A: Representation of a single timing mechanism. B: Two timing mechanisms are integrated, leading to a more precise signal.

may be thought of as corresponding to the value for this sample of the target interval. Alternatively, there may be some threshold that corresponds to this value, and the timer signals that the target interval has elapsed once this threshold is crossed.

In the bottom of Figure 6, two activation functions are shown in thin lines. These correspond to two independent samples, one associated with the left timing mechanism and one associated with the right timer. For bimanual tapping, a single, integrated activation function is derived by summing these two activation functions. If the two samples have a reasonable amount of overlap, the peak of this new function will fall between the peaks of the two input functions and will even be at the average if the input functions have the same variance. (In the threshold version of this mechanism, there would need to be an increase in the threshold during bimanual tapping.)

It remains to be seen if the bimanual advantage emerges as a result of some sort of neural averaging process. We offer the current example to demonstrate that this form of coupling could occur in real time.

The idea that outputs from separate timers are integrated is not necessarily at odds with the dynamical perspective of coupled oscillators. Indeed, the output constraint hypothesis could be viewed as one specific version of how coupling arises. However, there are potential areas of difference that can be explored in future research. Theoretical work on coupled oscillators has offered important insights into a number of interlimb phenomena, such as the stability space of different phase relations and hysteresis effects that accompany phase transitions (see Haken et al., 1985). The current focus of the averaging model has been restricted to the effects on within-hand variability (although the model does predict phasing constraints). It will be useful to explore the implications of an output bottleneck on other aspects of bimanual coupling.

Finally, the averaging model makes quantitative predictions concerning the magnitude of the bimanual advantage across different experimental conditions. For example, central timing variability is proportional to the target interval (e.g., Ivry & Corcos, 1993; Wing, 1980). The averaging model predicts that across tapping rates, the standard deviation during bimanual tapping should be reduced by approximately 29%. An experiment to test this prediction would also provide an important test of the generalizability of the bimanual advantage.

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