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Subcortical locus of temporal coupling in the bimanual movements of a callosotomy patient

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Abstract

The timing of repetitive movements was assessed in a callosotomy patient under unimanual and bimanual conditions. Similar to neurologically healthy individuals, the patient exhibited strong temporal coupling in the bimanual condition. Moreover, for both the left and right hands, within-hand temporal variability was reduced in the bimanual condition compared to the unimanual conditions. This bimanual advantage is hypothesized to reflect the temporal integration of separable timing signals, one associated with the left hand and one associated with the right hand (Helmuth, L. L., & Ivry, R. B. (1996). When two hands are better than one: Reduced timing variability during bimanual movements. *Journal of Experimental Psychology: Human Perception and Performance*, 2, 278–293). The fact that it persists following callosotomy is inconsistent with models that attribute bimanual coordination in these patients to the control of a single hemisphere. Rather, the results suggest that motor commands from the two hemispheres are integrated subcortically. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

The study of bimanual movements has provided an important window through which to observe the psychological and neural mechanisms involved in the control of action. While human motor behavior exhibits impressive flexibility, there exist some fundamental constraints in our ability to coordinate the gestures of the two hands. In some situations, these constraints reflect the fact that the two hands are being used to achieve a common goal. For example, skilled rowers seek to produce identical movements with the right and left arms in order to propel the boat forward in the most efficient and fastest manner. However, there are many situations in which the two hands are concurrently used to achieve different actions. While taking a shower, a person may adjust the temperature of the water while simultaneously reaching for a bar of soap or in driving, one hand can be used to control the steering wheel while the other is used to move the stick shift. Despite the fact that the movements of the two hands are directed to distinct targets and serving different (sub)goals, the gestures are not performed independently.

An impressive literature has accumulated over the past two decades characterizing the constraints manifest in the production of bimanual movements. Central to this work is the observation that bimanual movements exhibit strong temporal coupling. This coupling can be observed in both discrete and continuous movements. When reaching for targets at two different distances, people exhibit a strong tendency to initiate and terminate the movements of the two arms in close synchrony to one another (Kelso, Southard & Goodman, 1979; Marteniuk, MacKenzie & Baba, 1984). Even more compelling are the findings from studies of repetitive movements. Most of us have great difficulty producing even the simplest rhythms that do not involve simple ratios (e.g., tap 3 against 2), and even skilled musicians appear to depend on an integrated temporal representation when producing complex rhythms (Jagacinski, Marshburn, Klapp & Jones, 1988; Klapp, Hill, Tyler, Martin, Jagacinski & Jones, 1985; Summers, Rosenbaum, Burns & Ford, 1993).

The ubiquity of temporal coupling has provided the cornerstone for the development of dynamical accounts of bimanual coordination. The work of Kelso, Turvey, and their colleagues (see Kelso, 1995; Kugler & Turvey, 1987) has provided important insights regarding the organization of repetitive bimanual movements, focusing on the coordinative structures that emerge during the production of such movements. This work has emphasized interactions between the two effectors, primarily measured in terms of the

stability of the relative phase. The relative phase between two moving effectors has been related to various factors, including the biomechanics of the task context (Turvey, Rosenblum, Kugler & Schmidt, 1986), frequency (Kelso, 1984), and cognitive factors such as attention (Schmidt, Carello & Turvey, 1990; Peters & Schwartz, 1989). Well-developed theoretical models have been put forth to account for these phenomena, based on the theoretical construct of coupled oscillators. The timing of each limb is described as reflecting the continuous variation of the state of each oscillator, and the interactions between the limbs reflect the coupling of these oscillators. These interactions produce an attractor space in which there is a strong bias for the two effectors to move either in-phase or anti-phase, with a dominance for the former relationship.

In addition to examining the temporal relationship between the two limbs during bimanual movements, one can also look at the timing within each limb. We have recently studied the stability of timing for a single limb, comparing performance between uni- and bimanual conditions (Franz, Ivry & Helmuth, 1996b; Helmuth & Ivry, 1996). Our basic design has used a repetitive tapping task introduced by Wing and Kristofferson (1973). On each trial, a pacing signal is presented, establishing the target movement frequency. The participant is asked to begin tapping with the finger, synchronizing their responses with the tones. After about 10 responses, the tones cease, and the participant continues to tap unaided, attempting to produce a series of periodic responses at the target frequency. Temporal stability is primarily assessed by the standard deviation of the inter-response intervals produced during the unpaced phase. Surprisingly, we observed that the standard deviation for each hand was reduced during the bimanual condition compared to the unimanual condition. That is, the temporal consistency for each hand improved when the person was producing a similar movement with the opposite hand. We refer to this effect as the bimanual advantage.

To account for the bimanual advantage, we propose a model that entails the notion of coupled timing mechanisms. The basic assumption of the model is that, during the course of generating the commands for periodic movements, two timing signals are triggered, one to regulate the movement of the right hand and a second to regulate the movement of the left hand. These timing signals will determine when each response should be initiated. However, we assume that these timing signals do not have direct access to the motor system. Rather, we propose that the implementation of these central commands is constrained by a shared output gate (Fig. 1(a)). This gate provides a mechanism by which all effectors receive central commands in a

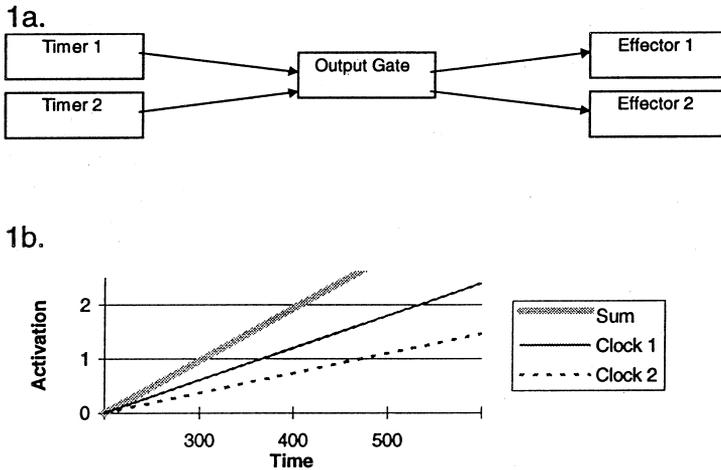


Fig. 1. (a) A common output gate constrains when movement commands are directed to the effectors. Separate timing signals are associated with each effector, but they are integrated before the commands are issued. (b) Movements are initiated when the clock signals reach threshold. Threshold 1 is for unimanual movements. Threshold 2 is for bimanual movements. Summing while doubling the threshold results in a normalization procedure. Averaging results from the fact that the normalized threshold is reached at the midpoint between when the two clocks reach the unimanual threshold. The activation functions continue past threshold in the example to depict the averaging process. In the model, it is assumed that reaching threshold terminates activation for the current cycle and initiates the timing process for the next cycle.

synchronized fashion (akin to the “GO” mechanism in the model of Bullock & Grossberg, 1988). Temporal coupling, according to our model, arises from this gating process.

During unimanual movements, we assume that the gating process is triggered when the activation from an internal timing mechanism reaches threshold. But what about during bimanual movements in which there are two timing signals? How will the gate be triggered? We have explored different integration rules in a series of simulations (Helmuth & Ivry, 1996). In these simulations, we assume that the timing for each response is determined by a random sample from a normal distribution of inter-tap intervals, with identical distributions used for the left and right hands. Rules based on either first in or last in principles predict that the variability for each hand will be reduced compared to unimanual tapping. However, these rules also predict a shift in the mean frequency (e.g., the frequency should be slower for a last-in rule), whereas the experimental results show that frequency is identical for uni- and bimanual tapping. An alternative rule is based on the idea that the gating process performs a form of averaging, triggering at the midpoint of the

time dictated by each timing signal. This rule predicts that temporal variability for each hand will be reduced during bimanual tapping and that the frequency will be unchanged.

The reduced temporal variability can be qualitatively appreciated by considering a simple numeric example. Suppose that the person is trying to produce a response every 400 ms, but due to noise in the timing system, the signals associated with the left and right hands would, for a particular interval, reach threshold at 350 and 450 ms, respectively. If either hand were tapping alone, this would be a substantial deviation. However, if the gating process performs an averaging operation, the commands to both hands will be issued at 400 ms. The magnitude of the expected improvement from averaging can be easily derived; this model is a form of the central limit theorem. If the distributions of intervals for the two hands are equal, then the standard deviation of a distribution formed by averaging two independent samples is equal to the unimanual standard deviation divided by the square root of two. The results of Helmuth and Ivry (1996) are in accord with these predictions.

Averaging, at first blush, does not seem intuitively reasonable in the temporal domain. How could the gate calculate the average of two signals if the second signal does not arrive until some point in the future? The solution is to consider the timing signals as continuous rather than discrete variables. As shown in Fig. 1(b), a simple summation process will produce an averaging operation, given that the threshold is normalized to reflect the number of inputs. Such integration schemes have been proposed for a variety of phenomena in visual perception (e.g., Levi, Klein & Yap, 1987; Tolhurst & Heeger, 1997); here, we extend this idea to the temporal domain.

Our model of the timing of bimanual movements can be summarized as follows. We assume independent timing signals are generated for each hand, but that the implementation of these signals is constrained by a common output gate. In this model, timing and temporal coupling are assumed to reflect the operation of separable processes. Various sources of noise can be expected at different processing stages and will contribute to the observed variability in both the timing of each limb and the relative phase between the limbs. Unlike standard coupled oscillatory models, the interactions between the timing mechanisms are discrete. The resulting coupling is weak in the sense that the outputs from the timing mechanisms only interact at the point of the output gate. The gating process generates the synchronized commands to the periphery and initiates the activation of the two timing mechanisms for the next cycle.

The initial motivation for the temporal integration model came from studies exploring the neural mechanisms of coordination. Patients with cerebellar lesions exhibit increased variability on the repetitive tapping task (Ivry & Keele, 1989). For patients with bilateral pathology, this deficit is observed in the movements produced by either hand. For patients with unilateral lesions, the increased variability is restricted to the ipsilesional hand. This latter group offers an interesting within-subject comparison since performance with their impaired hand can be compared to that obtained when tapping with their unimpaired hand. Wing and Kristofferson (1973) developed a model to decompose the total variability on this task into two component sources: one associated with central planning processes (including timing) and one associated with motor implementation (see Methods). Patients with unilateral lesions in the neocerebellum were found to have increased central variability. These findings, in concert with deficits observed for these patients on perceptual and sensorimotor learning tasks that require precise timing, led us to propose that the cerebellum plays a critical role in the representation of temporal information (see Ivry, 1997).

The fact that timing variability is only increased on the ipsilesional side implies that there must be at least two timing systems, one that is damaged and one that is intact. Our current thinking is more general. We conceptualize the cerebellar cortex as an array of timing elements, with the elements tuned to different intervals that are linked to specific input or output systems. Thus the cerebellum can be considered as providing a near-infinite set of timing elements rather than forming a single internal clock (Ivry, 1996). Indeed, the bimanual advantage is not limited to movements involving the two hands. It is also manifest when participants tap with various effector combinations, either involving limbs on the opposite or same side of the body. Moreover, an additional reduction in variability is observed when three effectors are used on concert (unpublished data). The patients with unilateral cerebellar damage also provide an interesting test of the temporal integration model. These patients should exhibit reduced variability on their ipsilesional side when performing bimanual movements. This result was reported by Franz et al. (1996b) in a study of four patients with unilateral cerebellar lesions.

While numerous studies, including our own, have investigated the neural systems involved in temporal processing, (see reviews by Gibbon, Malapani, Dale & Gallistel, 1997; Hazeltine, Helmuth & Ivry, 1997; Meck, 1996), the neural basis for temporal coupling has received relatively little attention. Studies in animals who have undergone spinal resections demonstrate that

interlimb coordination can persist without any input from the central nervous system (Grillner & Zangger, 1979). However, this work has focused exclusively on locomotion, a behavior for which evolutionary pressures are likely to have favored low-level control mechanisms. The fact that the bimanual advantage is found with non-homologous effectors, including finger–foot combinations, suggests that the hypothesized gating process is supraspinal.

One possibility is that the gating process is subcortical. This hypothesis is supported by research involving patients who have undergone resection of the corpus callosum for the treatment of intractable epilepsy. Despite the lack of direct communication between the two cerebral hemispheres, including those connecting parietal and frontal areas implicating in motor control, split-brain patients continue to exhibit strong coupling during the production of bimanual movements. Tuller and Kelso (1989) tested two callosotomy patients on a repetitive finger-tapping task. The patients' movements were not only temporally coupled, but showed an even stronger bias than the control participants for the two fingers to move either in-phase or anti-phase despite entraining stimuli that were presented over a range of phase relationships.

Franz, Eliassen, Ivry and Gazzaniga (1996a) also reported temporal coupling following callosotomy in a set of drawing tasks. Interestingly, this temporal coupling persisted despite the fact that the patients showed no evidence of cross talk in terms of the spatial trajectories of their movements. Spatial accuracy was comparable when the bimanual movements were made along orthogonal axes as when they followed parallel axes. In contrast, people with an intact corpus callosum have great difficulty when the movements are orthogonal (Franz et al., 1996a; Franz, Zelaznik & McCabe, 1991). Thus, the neural bases of spatial and temporal coupling are dissociable: while the former involves transcallosal pathways, temporal coupling is not dependent on the integrity of the callosum, consistent with the idea of a subcortical locus.

An alternative explanation for the persistence of temporal coupling following callosotomy is that the control system generating the motor commands for both hands is restricted to a single hemisphere. Stucchi and Viviani (1993) observed a consistent right-hand phase lead in bimanual drawing tasks for both right- and left-handed subjects. To account for this result, they proposed that the left hemisphere provides a common command signal to initiate the movements for each hand. This hypothesis is consistent with various lines of evidence demonstrating left hemisphere involvement in the

control of movements produced by both the contralateral and ipsilateral hands. Neuroimaging studies have consistently observed left hemisphere activation during the production of unimanual movements with either the right or left hand (Kim et al., 1993) and patients with apraxia following left hemisphere lesions show bilateral impairments (Heilman & Rothi, 1997).

A study by Kingstone and Gazzaniga (1995) provides strong evidence for the left-hemisphere control of both hands in a split-brain patient. On each trial, two words were presented, one in each visual field. The words were concrete nouns. If linked together, the words formed a new word with a distinct meaning (e.g., fire and arm). The patient was asked to produce a drawing corresponding to his percept. On no trials did the patient produce a drawing corresponding to the integrated meaning (e.g., a gun), indicating a lack of interhemispheric integration. Drawings of integrated meanings were observed when both words were presented to the same visual field. Surprisingly, drawings corresponded to the word presented in the right visual field (left hemisphere) on about half of the trials when the drawings were made with the left hand. When the drawings were made with the right hand, essentially all of the depicted objects corresponded to the word in the right visual field. Thus, the left hemisphere not only guided the actions of the right hand, but also guided the actions of the left hand on a significant proportion of the trials.

We have outlined two models to contrast possible loci of temporal coupling following callosotomy (Fig. 2). One model, the temporal integration model, is based on the idea that, while separate motor plans are generated for each hand, coupling occurs at a subcortical level. The other model, the unilateral control model, is based on the idea that a single hemisphere assumes bilateral control when interhemispheric communication is absent, and coupling arises from a common command being issued to both hands. Both models would predict intact temporal coupling in split-brain patients. For the temporal integration model, coupling emerges from the integration of two signals; for the unilateral control model, coupling results from the expropriation of the ipsilateral effector. The bimanual advantage phenomenon allows a means for comparing the viability of these two models. By the logic underlying the temporal integration model, independent timing signals for both effectors are produced and averaged subcortically, and thus the bimanual advantage should be observed in a split-brain individual. In contrast, the unilateral control model holds that a bilaterally projected movement initiation command arises at the cortex, with this command signal

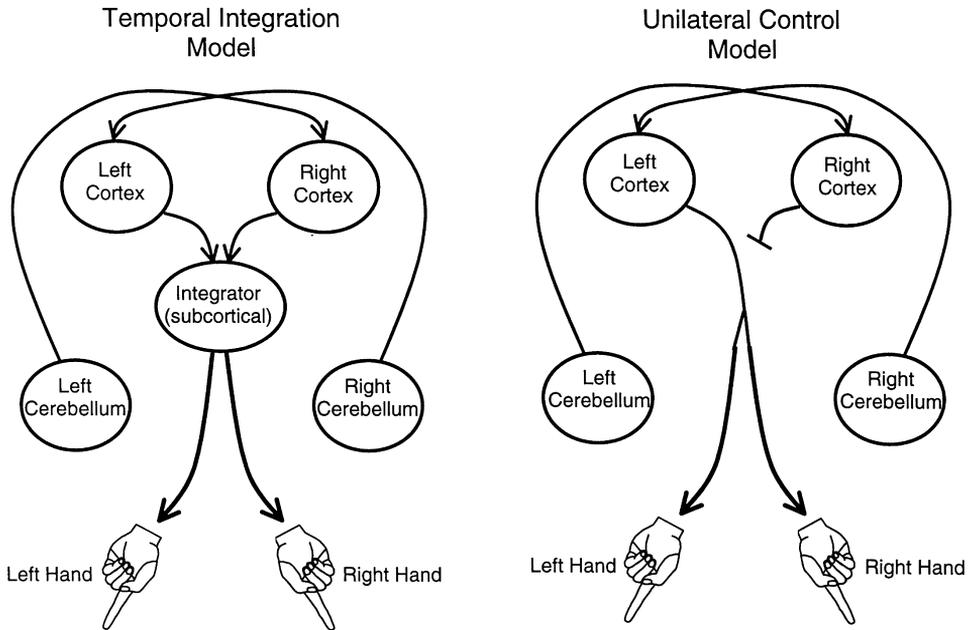


Fig. 2. Two models to account for the persistence of bimanual temporal coupling after callosotomy. In the temporal integration model, a subcortical gate integrates independent commands, each with their own timing signal, in a manner similar to Fig. 1(a). In the unilateral control model, a single hemisphere issues commands to both hands.

reflecting a single timing signal. If this is the case, the bimanual advantage will be absent in the patient's performance despite persistent temporal coupling.

2. Methods

2.1. Participants

Testing was conducted on one callosotomy patient and two control subjects. The patient, VJ, was a 42 year-old left-handed woman. Her childhood neurological profile was normal except for a problem with stuttering. At age 16, VJ began experiencing seizures with no precipitating event. Various medication treatments were administered over the next 20 years with limited success. The patient continued to experience severe seizures characterized by a complete loss of consciousness, incurring several severe injuries from falls.

At age 41, callosotomy was recommended when EEG monitoring was unable to identify a target region for focal resection. VJ underwent a two-stage operation. The first operation was performed in January 1995 and involved resection of the anterior two thirds of the corpus callosum. Nine months later, a second operation was performed during which the remaining posterior callosal fibers were severed. MRI scans confirm that the callosotomy operation is complete with sparing of the anterior commissures.

VJ has experienced moderate success from the procedure. Although she continues to experience seizures, they are largely unilateral, less frequent and considerably milder than prior to the callosotomy. Neuropsychological assessments were performed with various instruments both prior and subsequent to surgery. VJ's full scale IQ as measured by the WAIS-R was 80 prior to surgery and 88 post-surgery. Mild improvement was also observed on the Purdue Pegboard Test, a standardized measure of manual dexterity, although she remained at around the 2nd percentile on this test, a finding comparable to that observed in other callosotomy patients. VJ was able to produce manual gestures to oral commands with either hand prior to surgery and after the anterior callosotomy. However, she made some errors when tested with the left hand after the second operation. Two control subjects, a 48 year-old right-handed woman (MS) and a 47 year-old left-handed woman (KS) were also tested. Both reported no significant neurological histories.

2.2. Procedure

All of the testing was conducted on a PC computer system. The CMOS clock hardware on the motherboard of the computer was used to time all stimulus events and record response onsets, with the sampling rate set to provide millisecond accuracy. The stimuli were square wave tones, generated from the sound generator on the computer. Responses were collected from a peripheral response board linked to the computer through the parallel port. Five keys are mounted on this board, each measuring 10×2.3 cm, aligned to comfortably match the positions of the fingers. A force of approximately 0.33 N is required to activate the response keys. Although the keys do not generate an audible click at the point of contact, sufficient sound is generated to provide auditory feedback with each response.

The basic experiment involved the repetitive tapping task introduced by Wing and Kristofferson (1973). At the beginning of each trial, the computer presented a series of 500 Hz tones. The duration of each tone was 50 ms and the inter-onset interval was 500 ms. The participant was instructed to begin

tapping, synchronizing his or her responses with the tones. All responses were made with the index finger of the designated hand during unimanual blocks, or with both index fingers during bimanual blocks. After the first response was recorded, another 12 tones were presented, allowing the participant to produce approximately 13 paced intervals. At this point, the tones were terminated and the participant was required to continue tapping in an unpaced mode until 23 additional intervals were recorded. The instructions emphasized that the person was to try and maintain a constant pace, consistent with that presented during the synchronization phase. Feedback was provided at the end of each trial, with the mean and standard deviation for both the paced and unpaced phases presented on the computer screen. After a brief rest, the next trial was initiated. Each block consisted of five trials.

In separate blocks, the tapping task was performed with either the right hand alone, the left hand alone, or with both hands. During bimanual tapping, the participants were informed that they should respond so that both fingers pressed the keys simultaneously (in phase mode). Each participant completed five blocks of left, right, and bimanual tapping, with the testing completed over two or three sessions. The blocks were run in triads of the three conditions with the order approximately counterbalanced over the sessions.

2.3. Data analysis

The primary analyses were performed on the last 21 inter-response intervals produced during the unpaced phase of each trial. An error-checking analysis was performed on-line to determine if any of the produced intervals during the unpaced phase were less than 250 ms or greater than 750 ms. Intervals less than 250 ms usually indicate either the detection of a bounce on the response key (with two responses being recorded for one keypress) or a tremor. Intervals longer than 750 ms occur when the person fails to produce sufficient force to activate the response key. Trials with one or more intervals outside these criteria were repeated at the end of a block, producing a primary data set of 25 trials with 21 unpaced intervals for each condition.

The mean and standard deviations were calculated over these 25 trials as was the mean phase difference between the onset of the right and left responses during bimanual tapping. The primary analysis involved an analysis of within-hand variability using the Wing–Kristofferson model. A detailed description of this procedure as well as various tests of the underlying assumptions can be found in other sources (see Wing, 1980; Ivry & Hazeltine, 1995; Ivry, Keele & Diener, 1988). In brief, the Wing–Kristofferson model

assumes that variability on this task arises from noise in two sources. One source is associated with central control processes and includes variability associated with an internal timing process that determines when each response should be initiated. The second source is associated with response implementation processes, noise that arises in the translation of the central commands into an overt response. The model rests on two critical assumptions. First, the two components are independent and thus the total variability is the sum of the contributions of the two components. Second, tapping is assumed to be open loop. Each interval is thus constituted by a random sample from a distribution representing when a response should be initiated and the motor implementation times bounding that interval. Given these assumptions, the covariance between successive intervals provides an estimate of variability associated with motor implementation processes. This covariance is predicted to be negative, a result that has been consistently obtained in numerous experiments (Helmuth & Ivry, 1996; Ivry & Hazeltine, 1995; Wing, 1980). An estimate of central variability can then be obtained via subtraction.

Prior to the calculation of central and motor variability, the series of intervals for a given trial were transformed to remove global drift in the mean tapping rate. For this purpose, a linear regression was performed over the series of 21 unpaced intervals and the data used in the Wing–Kristofferson analysis reflected the difference between the observed intervals and that predicted once the global linear component was considered. This procedure increases the estimate of the implementation component (and correspondingly, decreases the estimate of central variability) given that it reduces the positive correlation between successive intervals that is introduced when a person speeds up or slows down over the course of the 21 intervals. This transformation generally has minimal effect on the component estimates. However, VJ exhibited a consistent speed-up during the unpaced phase in all conditions and thus the use of the transformed scores had a considerable effect on the component estimates for her data.

3. Results

Our focus in this paper centers on the temporal performance of the split-brain patient. In particular, does she show temporal coupling during bimanual tapping, and more important, does she exhibit the bimanual advantage, a reduction in within-hand variability during bimanual tapping

compared to unimanual tapping? As such, we focus on the results for VJ, referring to the data from the healthy participants only when a baseline comparison is required.

VJ was able to perform the repetitive tapping task with little difficulty. She generally began tapping within the first few tones and was able to synchronize her responses with the tones in all three conditions. During unimanual tapping, only two trials were repeated, both with the right hand. During bimanual tapping, eleven trials were repeated due to the fact that she failed to generate sufficient force with one hand to activate the response key on at least one response. Table 1 presents the means and standard deviations of the inter-response intervals for the paced and unpaced portions of the experiment, with the standard deviation scores based on the raw, rather than transformed data. VJ tapped at a rate slightly faster than the tones during paced phase and continued to speed up during the unpaced phase, especially during left-handed unimanual tapping and when tapping with both hands. The reasons for this are unclear, although a similar trend is generally observed with both healthy and some neurologically impaired populations (see Ivry & Keele, 1989). Her mean standard deviation scores are all below 30 ms and generally are less than 20 ms during the unpaced phase. These values fall well within the range for that observed with healthy college-age participants.

To evaluate the data during unpaced tapping with the Wing–Kristofferson model, we first determined the covariance function for each condition over

Table 1
Mean interval and standard deviation for each hand during paced and unpaced phases of the repetitive tapping task

| | | Unimanual | | Bimanual | |
|---------|------------------|-----------|--------|----------|--------|
| | | Left | Right | Left | Right |
| Paced | | | | | |
| | Mean | 497.76 | 491.46 | 492.72 | 487.68 |
| | (Standard error) | (1.38) | (2.95) | (2.04) | (2.58) |
| | SD | 23.08 | 20.49 | 21.23 | 27.78 |
| | (Standard error) | (1.84) | (1.69) | (1.26) | (0.77) |
| Unpaced | | | | | |
| | Mean | 470.70 | 486.62 | 464.98 | 466.14 |
| | (Standard error) | (3.69) | (4.66) | (5.08) | (4.81) |
| | SD | 22.48 | 18.99 | 19.38 | 18.14 |
| | (Standard error) | (1.89) | (1.60) | (0.84) | (1.26) |

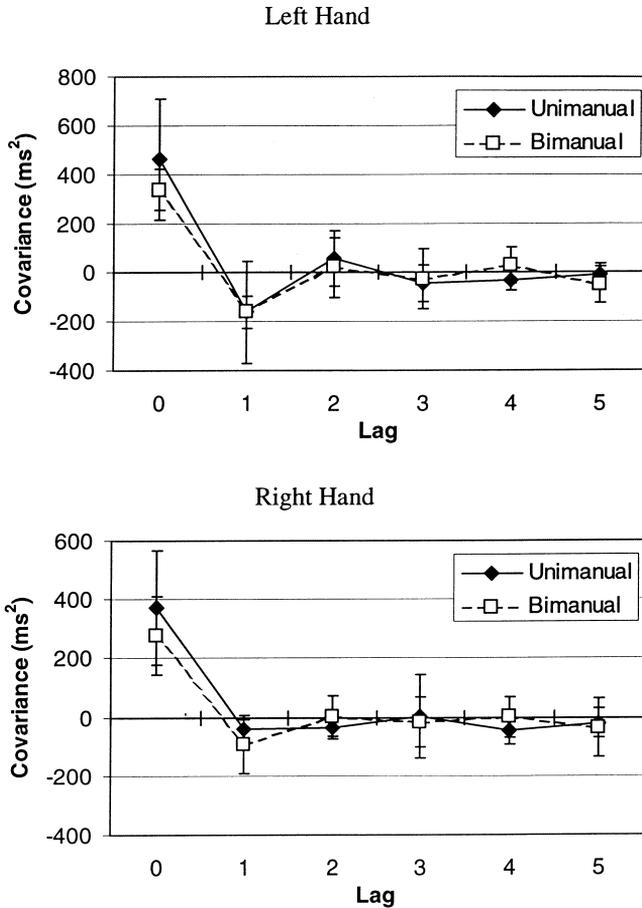


Fig. 3. Covariance functions for the split-brain patient, plotted for lags 0–5.

lags 0–5, using the transformed data as described above (Fig. 3). Lag 0 corresponds to the variance of the intervals. Lag 1 corresponds to the covariance between successive intervals and provides an assessment of the basic prediction of the model, namely that this value should be negative. Lags 2–5 correspond to the covariance between non-neighboring intervals, separated by distances of n intervals. These values provide further tests of the model since they are expected to be zero if the assumption of the independence between the central and implementation variability holds. Both predictions were confirmed in the data for VJ. The lag 1 value is negative in all five blocks for each condition. At higher lags, both negative and positive values were

observed, but these were consistently small, with 95% confidence interval encompassing zero for almost all of the data points.

Using this function, the estimates of the central and implementation sources of variability were calculated from the transformed data. To repeat, the lag 1 covariance provides an estimate of implementation variability and an estimate of central variability is then obtained by subtracting this value from the total variability¹. The overall standard deviation scores along with the component estimates are presented in Fig. 4. Within-hand temporal consistency was better for VJ during the bimanual condition in comparison to the unimanual conditions. The bimanual advantage can be seen in the overall standard deviation scores for both the left and right hands. Moreover, when these scores are partitioned into central and peripheral components, the improvement is restricted to the estimate of central variability². In contrast, the estimate of implementation variability is unchanged for the left hand and shows an increase for the right hand. These results are similar to what we have observed with both normal participants (Helmuth & Ivry, 1996) and patients with cerebellar lesions (Franz et al., 1996b).

These data were statistically analyzed in a series of 2×2 ANOVAs with one factor being hand (left vs. right) and the second factor being mode (unimanual vs. bimanual) with block serving as a repeated measure. The effect of mode was significant for both the overall standard deviation scores, $F(1,4) = 9.05$, $p < 0.05$, and the estimates of central variability, $F(1,4) = 54.48$, $p < 0.005$. The overall variability decreased from 20.1 ms in the unimanual mode to 17.4 ms in the bimanual mode. This effect was more dramatic for the estimate of central variability; it decreased from 13.7 ms in the unimanual mode to 6.4 ms in the bimanual mode. The effect of hand did not reach significance with either measure (overall: $F(1,4) = 3.69$, $p > 0.12$; central: $F(1,4) = 6.25$, $p < 0.07$), although there was a trend for the left hand to be less variable than the right in terms of the estimate of central variability

¹ The correct equation is $\text{variance}(\text{Central}) = \text{variance}(\text{Total}) - 2 * \text{variance}(\text{Implementation})$, where $\text{variance}(\text{Total})$ is the observed variance of the inter-tap intervals, $\text{variance}(\text{Implementation}) = - \text{auto-covariance}(\text{Lag } 1)$. The implementation component is multiplied by two because each interval is bounded by two responses, each with its own implementation noise.

² A similar pattern is observed if the raw data are considered rather than the transformed data. Table 1 provides the total variability scores from the raw data. When analyzed with the Wing-Kristofferson model, the estimates of central variability are 18.3 and 12.4 ms for the left hand in the uni- and bimanual conditions, respectively. The corresponding values for the right hand were 18.4 and 16.7 ms. For both hands, the estimates of implementation variability for the uni- and bimanual conditions were within 1 ms of each other.

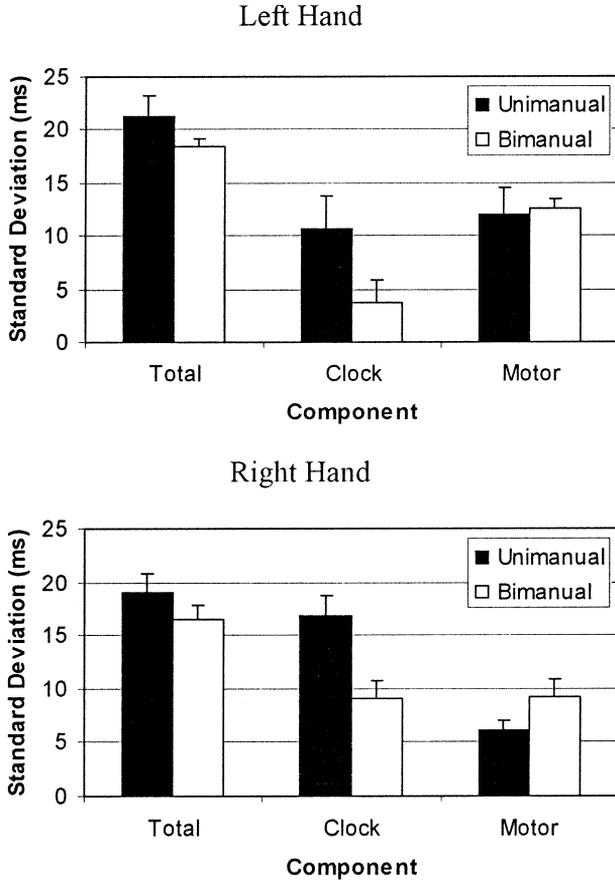


Fig. 4. Overall standard deviation scores for the split-brain patient, plotted along with the component estimates derived from the Wing-Kristofferson model.

(left: 7.2 ms; right: 12.9 ms). The hand \times mode interaction was not significant in any of the analyses.

For the implementation variability, there was a significant effect of hand, $F(1,4) = 13.90$, $p < 0.05$, indicating that the right-hand standard deviation (7.6 ms) was significantly less than the left-hand score (12.3 ms). Neither the effect of mode, $F(1,4) = 4.36$, $p > 0.1$, nor the mode \times hand interaction, $F < 1$, were significant. With right handers, Helmuth and Ivry (1996) had observed lower implementation variability for the right hand, a result similar to that obtained with VJ. However, the current finding is puzzling given that VJ is left-handed.

A quantitative assessment can be made concerning the magnitude of the reduction in variability during bimanual tapping. The averaging model assumes that the improvement arises from the integration by the output gate of the two timing signals. Thus, the reduction will be based on averaging out noise that arises in the central planning processes and will not be influenced by noise associated with implementation processes. As noted earlier, if the central processes have equal noise characteristics, then the observed reduction should be equal to the central standard deviation observed during unimanual tapping divided by the square root of two. However, the unimanual results for VJ indicate that the central noise distributions for the two hands may not be equal. Thus, we ran a series of simulations of the averaging model using the observed values for both the means and standard deviation for the right and left hands.

Averaging over 10 simulations of 25 trials each, we obtained a predicted central estimate of 10.2 ms (due to the issuance of a common “GO” command, the estimate is the same for both hands). This value is slightly larger than the observed value for the right hand (9.5 ms) and considerably larger than that observed for the left hand (4.0 ms). The reason for this is unclear. It may reflect the fact that we are dealing with a relatively small data set consisting of just 25 trials per condition. The observed data for VJ likely underestimates her true central variability. The observed values for her left hand are lower than that found in a group of neurologically healthy participants (Helmuth & Ivry, 1996), resulting from the fact that her lag 1 correlation was greater than the theoretical limit of -0.50 on two blocks (Wing, 1980).

In general, the performance for the two control participants was similar to what we have observed with college-age students (Helmuth & Ivry, 1996). Averaged over the four conditions, the mean produced interval during the unpaced phase was 480 ms for MS and 475 ms for KS. Thus, both controls tended to speed up following the cessation of the pacing signal, similar to what was observed for patient VJ.

The total standard deviation values as well as the component estimates derived from the Wing–Kristofferson model are presented in Fig. 5. MS did not show a bimanual advantage in terms of the total standard deviation scores. However, the estimate of central variability for both the left and right hands was lower during the bimanual conditions, a difference that did not reach statistical significance, $F(1,4) = 3.40$, $p < 0.15$. KS exhibited a robust bimanual advantage in terms of the total variability scores, $F(1,4) = 20.67$, $p < 0.05$. On every block, the observed standard deviation for both the left and right hands was lower during bimanual tapping compared to the

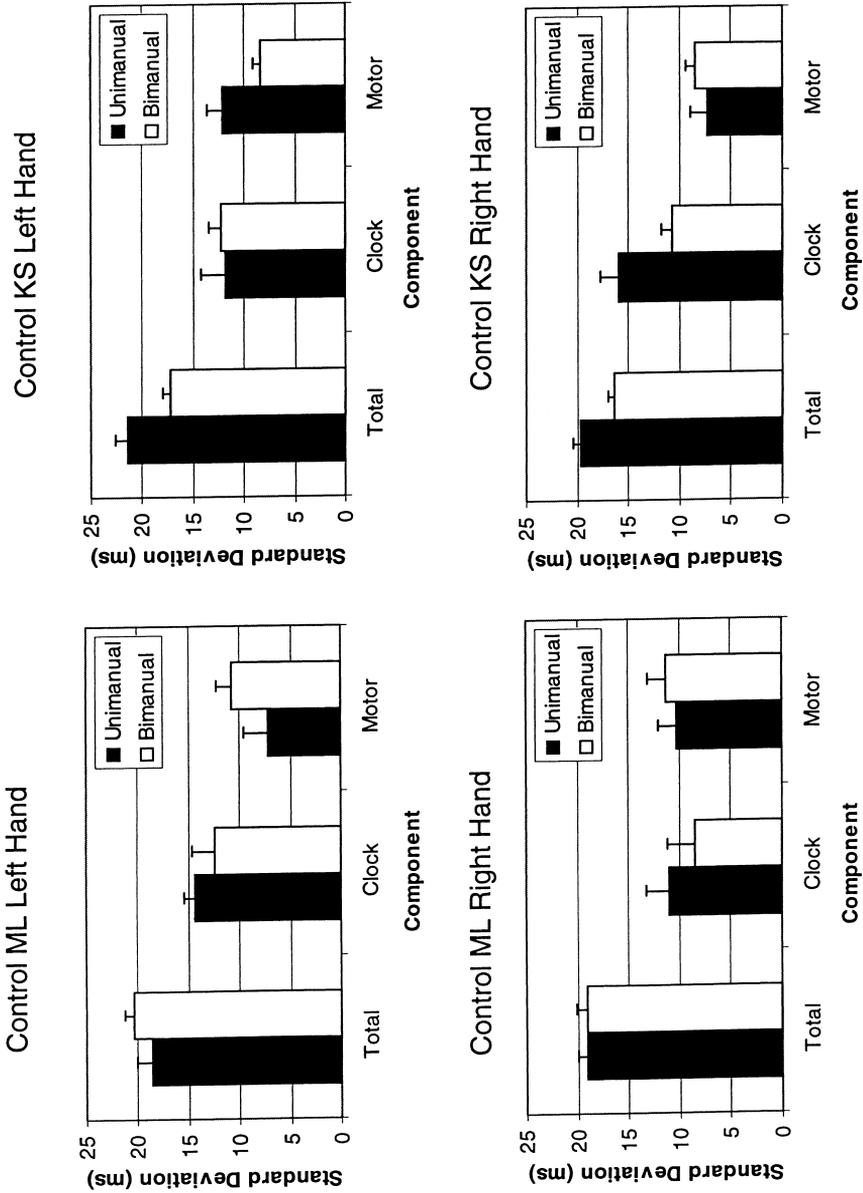


Fig. 5. Overall standard deviation scores for the two control participants, plotted along with the component estimates.

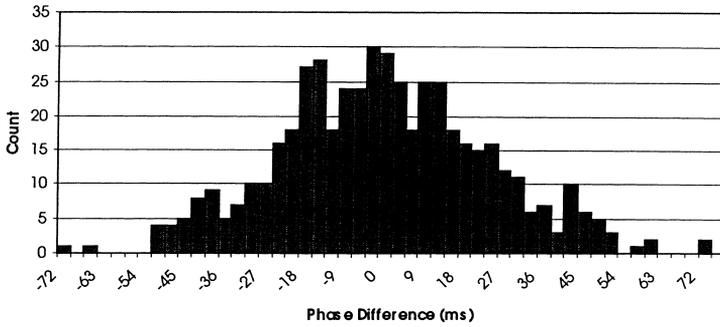
corresponding unimanual blocks. In terms of the component estimates, neither the central nor the implementation estimates showed a significant difference between the bimanual and unimanual conditions (central: $F(1,4) = 1.80$, $p > 0.25$; implementation: $F(1,4) < 1$). However, for both dependent variables, tapping mode interacted with hand (central: $F(1,4) = 7.24$, $p < 0.06$; implementation: $F(1,4) = 32.72$; $p < 0.005$). The improvement during bimanual tapping with the right hand was associated with the estimate of central variability; unexpectedly, the improvement for the left hand was associated with the estimate of implementation variability.

Caution should be exercised in interpreting the component estimates from a study with a small number of participants. While the Wing–Kristofferson model assumes that the two sources of variability are independent, the estimation of these sources is clearly not independent. Any error in the estimate of the implementation variability (via the lag one covariance) will result in an error of the opposite direction for the estimate of central variability. Nonetheless, the results for both VJ and the two control participants are consistent with what we have observed in previous studies with college-age students. The estimate of within-hand central variability was lower during bimanual tapping compared to unimanual tapping. This effect was significant for both patient VJ and one of the controls, MS and was significant for the right-hand performance for control KS.

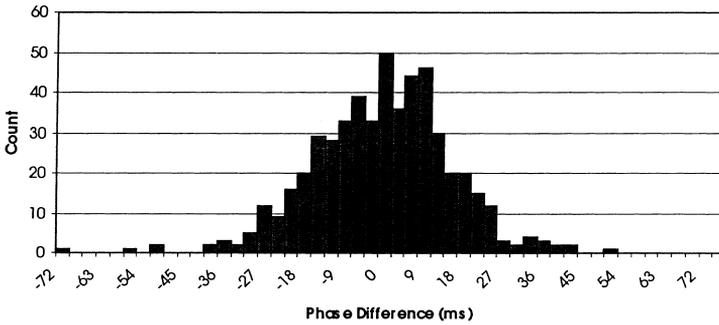
Fig. 6 depicts the distributions of phase differences for the three participants. All three distributions are generally symmetric and centered close to zero. This is what would be predicted if a common gating signal initiated the movements of the two hands, with phase differences resulting from noise that arises in downstream processes related to motor implementation. Overall, VJ's bimanual movements exhibit temporal coupling similar to what was observed in the control participants. Averaged over 504 intervals (one trial was eliminated due to an aberrant interval that fell outside the $\pm 50\%$ cutoff), her mean phase difference was 1.4 ms, with the right hand slightly leading the left.

However, the distribution of phase differences was more disperse for VJ than that observed for the control participants. The standard deviation for VJ is larger (23.4 ms) than that observed for the control participants (ML: 13.3 ms; KS: 15.7 ms). Moreover, the phase difference was greater than 40 ms on 11.3% of the intervals for VJ, whereas the comparable values for the two controls, ML and KS, were 0% and 1.5%. The phase difference results suggest that temporal coupling may not be as strong in VJ. This could reflect the fact that temporal coupling arises at multiple levels. For example, in addition to a

Callosotomy Patient Phase Distributions



Control KS Phase Distributions



Control ML Phase Distributions

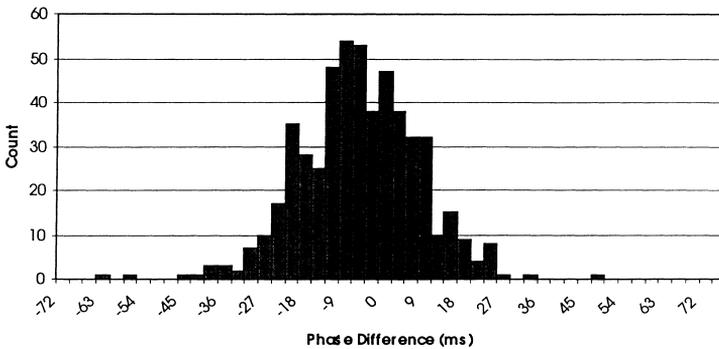


Fig. 6. Distributions of phase differences for the split-brain patient and two control participants.

common gating signal, peripheral cross talk, either at spinal or supraspinal levels might also contribute to temporal coupling. Perhaps these additional sources of temporal coupling are lost following the callosotomy procedure. The current study does not allow an assessment of this hypothesis.

It should be noted that it is possible for two movements to appear temporally coupled even if they are independently generated. For example, if two metronomes were operating at the same frequency, their outputs would show a consistent phase difference even if the signals were uncoupled. In a similar vein, one might argue that VJ's performance only looks temporally coupled because she is complying with our task instructions with both hands. That is, the two hands might be operating independently, but each has been entrained to the pacing signal. There are a number of problems with this argument. First, VJ showed a consistent speed-up during the unpaced phase of tapping, and this speed-up was observed for each hand during bimanual tapping. Thus, at a global level, we observed a deviation in her temporal performance that was similar for both hands, strongly indicative of coupling. Second, temporal coupling has been observed in the performance of other split-brain patients when no explicit instructions are given regarding movement timing (Franz et al., 1996a) and even when an explicit attempt is made to produce uncoupling (Tuller & Kelso, 1989).

To further explore the source of temporal coupling, we tested VJ under a number of other bimanual conditions. We were concerned that she might be using external sources of feedback to entrain the responses of the two hands. Both visual and auditory cues were available during the primary experiment. VJ tapped with her eyes open (although she generally looked at the computer and not her hands). Moreover, the response board produces an audible sound when each key strikes the bottom of the device. We eliminated these cues in two additional blocks of testing. VJ was required to close her eyes during the entire trial. In addition, white noise was played over headphones once the tones were terminated during the paced phase, and VJ reported that this eliminated all sounds from the keyboard. Two blocks of five trials were run under this limited feedback situation. There was minimal difference between her performance here compared with the primary experiment. VJ again exhibited a tendency to speed-up during the unpaced phase with the means for the inter-tap intervals being 477.1 and 478.0 ms for the left and right hands, respectively. As before, the right hand tended to lead the left, although the mean phase difference was quite small, only 3.3 ms (sd = 25.8 ms). Eliminating visual and auditory feedback also has little effect on her temporal consistency. The overall standard deviation scores were 24.5 for the left hand

and 16.1 ms for the right hand and the corresponding estimates of central variability were 3.1 and 12.7 ms. These latter values should be treated cautiously, however, since they are based on only 10 trials.

To further eliminate experimental cues that might facilitate temporal coupling, we also tested VJ on one block in which we eliminated the pacing signal. For this block, VJ was instructed to begin tapping following the presentation of a single tone. She could set her own pace, with the only constraint that she tap with both hands. Visual and auditory cues were again eliminated. Here, too, she exhibited strong temporal coupling. She opted to tap at a faster rate here, choosing a speed closer to 2.5 Hz and, interestingly, there was no evidence of an overall speed-up over the course of the 30-interval trials. The means of the inter-tap intervals were 413.9 and 414.2 ms for the left and right hands, respectively, and as in the other conditions, the distribution of phase differences was relatively close to zero (mean = 13.8 ms, $sd = 22.1$ ms). In a final block, VJ was asked to tap at a much slower pace without visual or auditory feedback. The tones occurred once every 2 s and VJ was asked to synchronize with this signal. We had thought that at such a slow pace, the two hands might become uncoupled since the gating process might be accessed successively for each hand without interference. However, the two hands remained temporally coupled and a pronounced speed-up was evident for both hands. The inter-tap interval means were 1337 and 1335 ms.

4. Discussion

Temporal coupling is perhaps the most distinctive feature of multi-effector coordination. Many of our basic skills are dependent on temporally coordinated gestures including walking, running, bimanual pulling and lifting. Moreover, even in bimanual skills in which the hands perform different gestures, the actions of the two hands must be finely linked in the temporal domain. In pulling open a drawer to extract an object, the temporal regularities are exhibited in terms of the relationship between the grasping, pulling, and reaching components (Kazennikov et al., 1994). Given the ubiquity of temporal coupling, it is not surprising that this phenomenon has been the subject of intense study in the motor control literature.

Previous work had established that callosotomy patients continue to exhibit temporal coupling during bimanual movements (Franz et al., 1996a; Tuller & Kelso, 1989). This result is impressive given that on a host of other tasks, the right and left cerebral hemispheres of these patients exhibit

substantial independence (Holtzman & Gazzaniga, 1985; Luck, Hillyard, Mangun & Gazzaniga, 1989). While one might argue that such coupling implies some sort of integration at the output of mental activity, other aspects of motor control continue to demonstrate reduced bimanual interactions. For example, in striking contrast to individuals with an intact corpus callosum, split-brain patients are able to produce conflicting trajectories with the two hands (Franz et al., 1996a). This spatial uncoupling in the face of persistent temporal coupling underscores the fundamental nature of the latter aspect of coordination.

The current study was designed to explore different models of how temporal coupling might occur in callosotomy patients. In the Introduction, we outlined two models that would produce temporal coupling (Fig. 2). Both models share the feature that commands to the periphery are issued from a common source. Indeed, this is assumed to be the source of temporal coupling. Where the models differ is in terms of the source of the inputs to the effectors. In the temporal integration model, the inputs arise from two separate control systems, one associated with the movements of each hand. These inputs include the temporal information regarding when the next movement in a periodic series should be initiated. In the unilateral control model, the input is restricted to a single controller following the callosotomy operation. By this model, one hemisphere is assumed to be critical for the production of bimanual movements in this population. While both models predict temporal coupling, only the temporal integration model predicts a reduction in within-hand variability during bimanual movements. This bimanual advantage reflects the statistical benefit conferred on the gating process from the fact that it is receiving two independent timing signals (Helmuth & Ivry, 1996).

The results for the split-brain patient are in accord with the temporal integration model. The patient not only exhibited pronounced temporal coupling, but the temporal consistency of each hand was better when the two hands moved together. At the very least, these results indicate interactions of distinct temporal signals associated with the two hands. Our working hypothesis is based on the idea that the command to initiate movements for each response during the repetitive tapping task is controlled by an internal timing mechanism which we associate with the cerebellum (Ivry, 1997). Each half of the cerebellum is assumed to provide these timing commands for movements on the ipsilateral side of the body (Franz et al., 1996b; Ivry et al., 1988). However, we propose that these central commands are constrained by an output gate and it is at this output gate that the temporal interactions

between the two timing signals occur. Support for this conceptualization was obtained by partitioning the variability scores into two component sources, one associated with central control processes and the other with motor implementation processes (Wing & Kristofferson, 1973). The improvement was attributed solely to the central component.

4.1. Neural locus of temporal coupling

The current results place some constraint on the locus of the putative gating process. The split-brain patient exhibited a bimanual advantage, a result we take as indicating that the timing signals for the left and right hands continue to interact following callosotomy. Given that this surgical procedure severs all of the callosal fibers between the two hemispheres including those between motor regions of the parietal and frontal lobes, it seems unlikely that the gating process is cortical. There remain at least two possible ways in which the cortex might integrate motor commands in these patients. The anterior commissure is intact in VJ. However, this pathway primarily involves interhemispheric connections between limbic and anterior temporal lobe regions (Klingler & Gloor, 1960). Second, timing signals might interact in one hemisphere via crossed subcortical connections.

A subcortical locus of temporal coupling seems more tenable. At present, we can only sketch out some possibilities. For the most part, the required physiological and anatomical studies have not been conducted. We limit our discussion to three loci: spinal cord, the cerebellum, and basal ganglia. This should by no means be taken to mean that other structures are not viable. Our selection here is based on the fact that, while admittedly speculative, each structure has been studied in terms of contributing to the temporal control of actions.

Simple spinal mechanisms of temporal coupling in locomotive behavior have been identified in a number of species including both invertebrates and vertebrates (see Grillner, Wallen, Brodin & Lansner, 1991; Schoener & Kelso, 1988a). For example, simple networks involving reciprocal inhibition can produce the oscillatory activity required for swimming or walking. While it is possible that a similar form of integration is responsible for the bimanual advantage, the fact that it is observed with various limb combinations leads us to suspect that the gating operation is part of a more centralized process involved in movement initiation (see below).

The cerebellum would be one possible structure. In our earlier study (Franz et al., 1996b) involving patients with unilateral cerebellar lesions, we

were impressed by the dissociation between timing and temporal coupling. The patients exhibited poor timing when tapping with their ipsilateral hand. When tapping with their impaired and unimpaired hands, they not only exhibited a bimanual advantage but their movements were highly coupled. This led us to propose that the cerebellum generated the timing signals, but that the integration of these signals occurred at some other site. However, this conclusion was premature. It is possible that the cerebellum not only provides the requisite temporal representation for these tasks, but also allows for the coupling of separable timing signals generated for different effectors. The neural basis for such coupling is not clear at present. Descending inputs to the cerebellum are projected bilaterally, at least in the visual modality (Glickstein, 1990). But the temporal integration model as sketched in Fig. 1 requires that the integration occur on the output side. That is, the two timing signals should remain independent until they are integrated by the gating mechanism. Little is known, both in terms of anatomy and physiology, concerning interactions between the two halves of the cerebellum and whether their outputs are projected bilaterally.

A second possible subcortical locus is the basal ganglia. There are a number of provocative reasons to suspect that this structure might play a role in temporal coupling. This structure is clearly associated with movement initiation. One of the cardinal features of Parkinson's disease is an inability to initiate movement. One might hypothesize that this symptom is reflective of a "stuck" gate and that dopamine modulates the threshold of different movement patterns, favoring those that have been associated with positive rewards. Moreover, lesions of the subthalamic nucleus, another component of the basal ganglia complex, produces hemiballism, a debilitating disorder in which the patient produces the same ballistic movement over and over. This symptom could be viewed as a "broken" or leaky gate. In both cases, the basal ganglia is viewed as interacting with other structures in the motor pathway, helping to select and initiate a desired movement. Physiological studies have indicated that the mechanism here is one of disinhibition. For example, in preparing a saccade, activity in the superior colliculus corresponds to the desired eye movement well in advance of the actual initiation of the movement. The movement is held in check by inhibitory signals from one of the output nuclei of the basal ganglia, released only when this signal is disinhibited (Chevalier & Deniau, 1990). Berns and Sejnowski (1996) have proposed a generalized model of selection by disinhibition, arguing that the double inhibitory links of the striatal–pallidal–thalamic pathway are ideal for implementing a winner-take-all network.

Anatomically, each half of the basal ganglia has been shown to be bilaterally innervated by premotor and prefrontal cortex (McGuire, Bates & Goldman-Rakic, 1991). This would seem to provide the critical ingredients for a gating process that integrates two timing signals. One might imagine that each half of the cerebellum provides an input to the contralateral motor areas of the cortex that increases in intensity as the target time approaches. A record of this activation would be projected to both halves of the basal ganglia, triggering the gate when threshold is achieved, with selected movement patterns in both hemispheres being implemented in a synchronized fashion. However, there is one serious problem with this scheme. The contralateral projection from frontal cortex to the basal ganglia crosses via the corpus callosum (Goldman-Rakic, personal communication). If temporal integration was dependent on this pathway, we would expect it to be absent in the split-brain patient. Other pathways for bilateral integration within the basal ganglia remain to be explored. It is unclear if other projections to the basal ganglia (e.g., to the subthalamic nucleus) involve crossed as well as uncrossed pathways or if there are anatomical connections between the two halves of the basal ganglia.

4.2. Alternative accounts of temporal coupling

We have considered alternative ways in which temporal information might interact between the movements of the two hands. One possibility is that, during bimanual movements, feedback generated from each hand provides a salient cue that can be used to adjust the timing of the other hand. During unimanual movements, such feedback would not be available and thus there would be no opportunity for these corrections. We do not believe that visual or auditory cues provide relevant feedback cues. First, neurologically healthy people show greater temporal variability when tapping with a pacing signal than when tapping in an unpaced mode. This is likely due to the fact that, even when the pacing signal is present, timing is primarily dependent on an internal process (Wing, 1980) with the pacing signal used as in intermittent reference. We have also found that the bimanual advantage continues to hold even when we provide a pacing signal, implicating other sources of temporal interaction (Helmuth & Ivry, unpublished). Second, although we did not assess the bimanual advantage during the blocks in which the split-brain patient tapped without visual or auditory feedback, her performance appeared unchanged from that exhibited during the basic task. Moreover, the bimanual advantage is absent when the two movements are performed by

different individuals, despite the fact that temporal coupling can be sustained from visual feedback (Helmuth & Ivry, 1996).

We did not, of course, eliminate feedback related to proprioception and tactile sources. Ideally, one would like to see if the bimanual advantage is obtained with patients who are deprived of such feedback sources, either due to an experimental manipulation or neurological disease. To date, we have not had such an opportunity. However, we have explored in simulation studies various feedback-based models. In these simulations, the timing of response n is a function not only of an internal timing process, but also the asynchrony of the two hands on response $n-1$. That is, we use the asynchrony error to adjust the timing for the response of each hand. In models using single timing mechanisms as well as those in which there are separate timers, the models have always predicted an increase in total variability during bimanual tapping. It appears that any feedback-based model will have to allow the corrections to occur within an interval rather than across intervals.

4.3. The gating process as a component of movement initiation

Our interpretation of the bimanual advantage has been framed by a generalization of the Wing–Kristofferson two-component model in which we postulate separate timing mechanisms for each hand. An alternative conceptualization of the control of rhythmic movements is based on dynamical systems analysis. At an abstract level, rhythmic movements can be characterized as reflecting coupled oscillators (Kelso, 1984; Schoener & Kelso, 1988b). The dynamic properties of such a system define a limit cycle, an attractor that defines a state of coordinative stability. This dynamic attractor stabilizes behavior by offsetting perturbations from the limit cycle. However, a second source of variability can occur from perturbations along the limit cycle (e.g., speeding up or slowing down). During unimanual tapping, there is no compensation for perturbations along the limit cycle since performance is stable at all points on the attractor. However, during bimanual movements, two oscillators are assumed to move along the limit cycle, one corresponding to the movements of one hand and the other to the movements of the second hand. When these attractors are in phase with one another, they can provide a corrective force for perturbations along the limit cycle. Thus, from a dynamic systems perspective, the bimanual advantage might arise because of this additional source of stability – the attraction between each point on the limit cycle.

At present, the relationship between these different conceptualizations is unclear. The dynamic systems view provides an elegant description of the temporal dynamics of bimanual movements. However, the mapping between abstract entities such as coupled oscillators and limit cycles and psychological and neural processes is murky at best. Rather than emphasize the continuous interactions between oscillators, the temporal integration model suggests relative independence of the control processes associated with the two hands. The point of interaction in our model occurs at the gating process, when central commands are issued to the periphery and the next processing cycle for each timer is initiated. The temporal integration model is explicit in terms of the component processes involved in producing temporally coordinated actions, either with one hand or two hands.

As a process model, the temporal integration model allows us to generate predictions concerning both the proposed psychological and neural components. The square root of two prediction is one such example. A second relates to the hypothesized operation of the output gate. Implicit in the model is the idea that the gating process infers some level of discrete control over the effectors. In a task such as repetitive tapping, there is a defining point within each cycle that psychologically corresponds to the division between one response and the next. For example, when tapping on a key, this might correspond to the key press itself (Billon, Semjen & Stelmach, 1996) or the point at which the downward movement begins. When the wrists are rotated back and forth, this point would likely correspond to the position on the extreme left or right of the cycle. The gating process is assumed to correspond to these points, providing the motor commands for the next response. This discrete form of control has the computational advantage in that central control processes are not taxed by the requirements of continuous control. Such a strategy would be especially advantageous for a system with the substantial inherent delays that are found in biomechanical systems. On the other hand, it also entails a cost in that there are constraints on when movements can be initiated, a form of a refractory period.

A refractory period would place limits on the speed with which interesting implications for one of the best-described phenomenon regarding bimanual motor control. People are able to perform in-phase movements at higher frequencies than anti-phase movements. When the frequency exceeds a critical point, the anti-phase pattern can not be maintained and a transition is observed to the in-phase pattern. We assume that during in-phase tapping, the gating process operates simultaneously for the two hands. However, during anti-phase tapping, the gating process may have to operate twice per

cycle, opening once for each hand. As the frequency of periodic movements is increased, interference will occur when the interval between successive gating operations approaches the duration of the refractory period. Thus, this interference would be observed much earlier during anti-phase tapping than during in-phase tapping due to the double gating requirement. In this way, the temporal integration model can offer a process-based account of the greater stability of in-phase movements.

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