Callosotomy patients exhibit temporal uncoupling during continuous bimanual movements

Steven W. Kennerley[1], Jörn Diedrichsen[1], Eliot Hazeltine[2], Andras Semjen[3] and Richard B. Ivry[1]

[1] *University of California, Berkeley, 3210 Tolman Hall #1650, Berkeley, California 94720, USA*

[2] *NASA Ames Research Center, Mail Stop 262-4, Moffett Field, California 94035, USA*

[3] *Centre de Recherche en Neurosciences Cognitives, CNRS, 31 Chemin Joseph Aiguier, 13402 Marseille Cedex 20, France*

The first two authors contributed equally to this work

Correspondence should be addressed to R.B.I. (ivry@socrates.berkeley.edu)

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Rhythmic bimanual movements are highly constrained in the temporal domain, with the gestures of the two hands tightly synchronized. Previous studies have implicated a subcortical locus for temporal coupling based on the observation that these constraints persist in callosotomy patients. We now report that such coupling is restricted to movements entailing a discrete event (such as a movement onset). Three callosotomy patients exhibited a striking lack of temporal coupling during continuous movements, with the two hands oscillating at non-identical frequencies. We propose a subcortical locus of temporal coupling for movements involving discrete events. In contrast, synchronization between the hands during continuous movements depends on interhemispheric transmission across the corpus callosum.

Research on bimanual coordination has highlighted a number of fundamental constraints that are manifest in both the temporal and spatial domain. When reaching for two targets at different distances, temporal coupling is evident in the strong tendency to initiate and terminate the movements in close synchrony[1,2]. Spatial coupling can be demonstrated when one of the limbs is required to clear an intervening hurdle. The spatial trajectory of the unobstructed limb follows a path similar to that of the obstructed limb[3–5].

Patients who undergo resection of the corpus callosum for intractable epilepsy provide a unique opportunity for exploring the neural bases for intermanual coordination. Although their bimanual movements remain temporally coupled, intermanual spatial interference is abolished[6,7]. For example, when drawing patterns composed of three sides of a square, callosotomy patients are equally facile when the two hands follow orthogonal trajectories compared to when they follow mirror-symmetrical trajectories. In contrast, the latter task is much easier for control participants. Nonetheless, the transition points during these movements are closely synchronized for the patients. Similarly, temporal coupling during repetitive finger tapping is also preserved in callosotomy patients[8–11]. These results suggest that spatial coupling involves interhemispheric communication via the corpus callosum, whereas temporal coupling arises subcortically.

To date, the study of temporal coupling in callosotomy patients has been confined to tasks involving discrete events, such as contact with a surface during repetitive tapping or turning points during linear movements. However, distinct mechanisms are associated with the temporal control of continuous and discrete movements[12]. One account of this difference is that continuous tasks, such as circle drawing, require the specification of a continuous temporal-spatial movement signal, whereas tapping tasks entail a series of discrete signals related to initiation or transition points. In the current study, we test the hypothesis that temporal coupling during continuous movements depends on communication across the corpus callosum.

Circle drawing tasks have provided insight into the spatial constraints associated with continuous bimanual movements. This work has focused on the comparison of two modes of coordination[13,14]. In the symmetric mode, the two hands cycle in opposite directions, maintaining symmetry with respect to the body midline. In the asymmetric mode, the two hands move in the same direction, and the phase relationship between the two hands is less stable than the symmetric mode[15]. As the circling rate increases, the non-dominant hand often demonstrates large deviations from circularity and involuntary transitions from the asymmetric to the symmetric mode.

The instability of the asymmetric condition has been attributed to activation of homologous muscles by ipsilateral descending corticospinal pathways[16]. In this model, each effector receives signals from both contralateral and ipsilateral descending pathways. Because the symmetric condition requires activation of homologous muscles, the signals on both pathways are always congruent. The asymmetric condition requires that non-homologous muscles be activated, and thus conflict between crossed and uncrossed corticospinal pathways may arise. An alternative account of the instability of the asymmetric mode centers on interhemispheric interactions. For example, the population code in parietal, premotor, and motor cortex corresponds to the direction of movement of the contralateral hand[17]. Callosal connections between these areas may result in the reinforcement of mirror-symmetrical patterns.

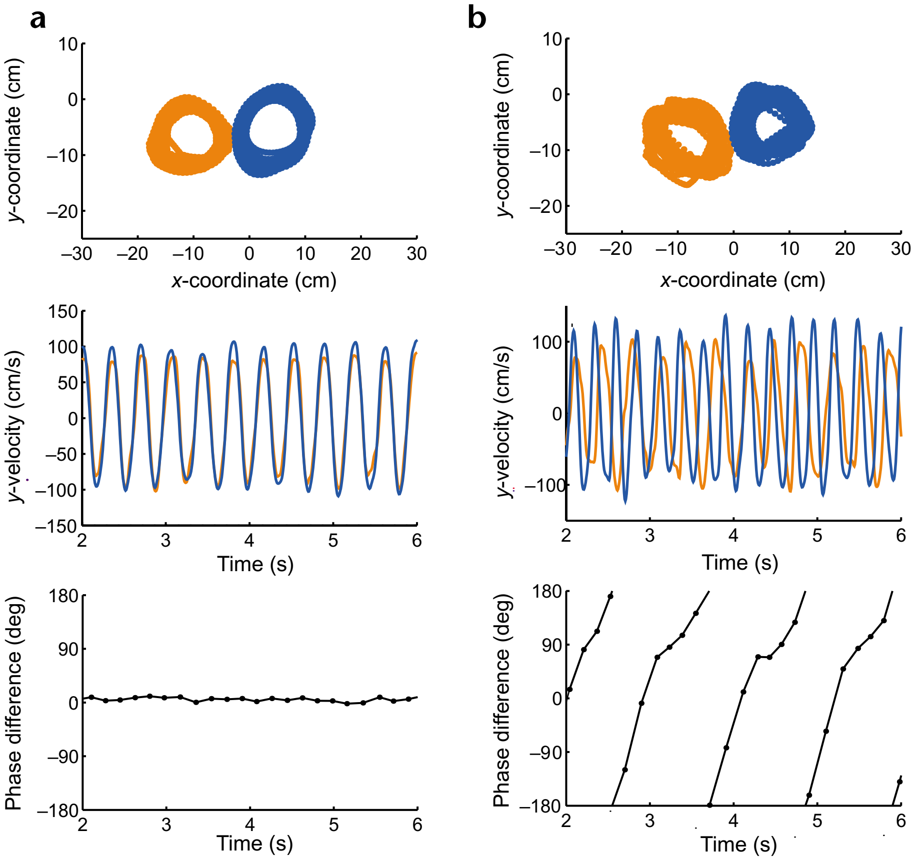


Fig. 1. Temporal uncoupling during a single trial of symmetric, maximum rate circling in a patient. (**a**) Control subject. (**b**) Callosotomy patient VP. Position (top) and velocity along the *y*-axis (middle) of all the cycles within a single trial for the left (red) and right (blue) hands. Bottom, relative phase relationship between the two hands. Point estimates of relative phase were calculated by determining the time of occurrence of every North/South point of the non-dominant hand relative to two successive North/South points of the other hand. Negative values indicate a left-hand lead. The control participant shows synchronous movements with a stable phase relationship. For the patient, the right hand cycles at a higher frequency, causing a continuous drift in the phase relationship (that is, phase wrapping).

To investigate spatial and temporal constraints during continuous bimanual movements, we tested three callosotomy patients in two experiments. In the first experiment, we tested bimanual circle drawing, performed under both symmetric and asymmetric conditions. If spatial coupling results from interactions involving ipsi- and contralateral corticospinal projections, then the patients should also show greater stability during symmetrical circling, similar to controls. Alternatively, if spatial coupling depends on interhemispheric interactions involving callosal fibers, the patients should not exhibit performance differences between the two conditions. Both patterns of movements in this experiment provide a measure of temporal coupling during continuous movements. In the second experiment, a modified finger-tapping task was used to allow a direct comparison of temporal coupling during continuous and discrete movements. The results support the hypothesis that the neural components underlying bimanual coordination differ for these two types of movements.

RESULTS

Sample trials from a control participant and a callosotomy patient on the circle drawing task demonstrate a marked difference in temporal coupling (**Fig. 1**). The patient's hands cycle at different speeds, whereas the control participant's hands remain tightly synchronized. We examine temporal coupling by looking at frequency and relative phase. By comparing the symmetric and asymmetric conditions, we also evaluate spatial coupling. For all dependent variables, separate ANOVAs for the callosotomy and control groups were conducted on the data of individual trials, with the participants included as a factor.

Fig. 2. Callosotomy patients exhibit a large difference in cycling rate between the two hands. (**a**) Mean cycling rate averaged over the two hands; error bars indicate between-subject standard error. Controls are slower during asymmetric movements at preferred rate ($F_{1,90} = 45.8$, $p < 0.001$) and maximum rate ($F_{1,276} = 238.5$, $p < 0.001$). The callosotomy patients maintain a similar rate for symmetric and asymmetric movements at both rates (preferred, $F_{1,120} = 2.6$, $p = 0.11$; maximum, $F_{1,278} = 2.1$, $p = 0.15$). (**b**) Mean absolute difference in cycle duration between the two hands, calculated on a trial-by-trial basis. For both the controls and patients, the rate by mode interaction was significant (controls, $F_{1,177} = 9.3$, $p < 0.005$; patients, $F_{1,193} = 4.2$, $p < 0.05$). However, whereas the controls showed less stability for the asymmetric mode at both rates, the absolute difference in cycle duration for the patients goes in opposite directions for the two rates.

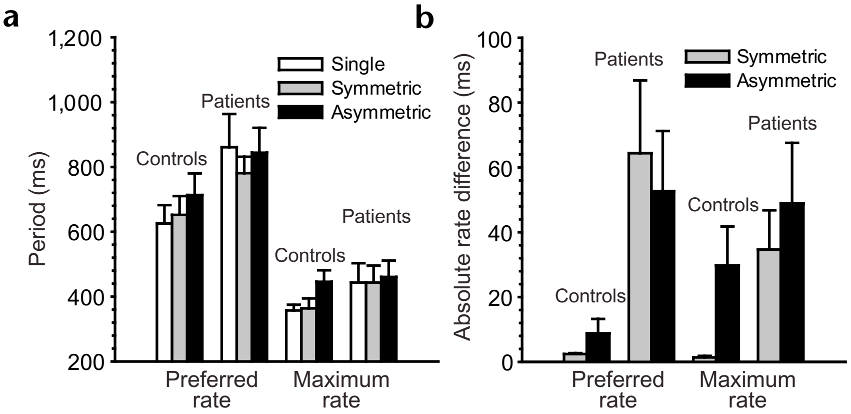
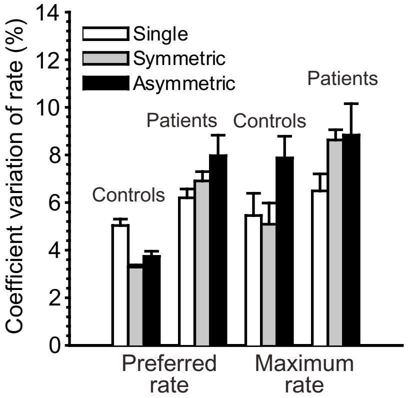


Fig. 3. Increase in instability during asymmetric circling at maximum rate is only found in performance of control participants. The coefficient of variation is a normalized measure of rate variability and is calculated by dividing the within-trial standard deviation by the mean cycle duration.



Circling frequency

The duration of each cycle was defined as the time between two successive south point crossings. The control participants and callosotomy patients performed the tasks at comparable rates (**Fig. 2a**). To assess frequency coupling, we calculated the absolute difference in mean cycle duration between the two hands for each trial (**Fig. 2b**). For the controls, frequency coupling during symmetric movements is indicated by the finding that the difference in cycle duration was less than 3 ms for both preferred and maximum rate conditions. In the asymmetric conditions, the mean absolute difference increased, reaching 29 ms for circling at maximum rate. In contrast, the callosotomy patients showed a pronounced difference between the two hands in cycle duration for all conditions, indicating some degree of frequency uncoupling. This was also evidenced by the finding that in 29% of the preferred rate and 64% of the maximum rate trials, one hand lapped the other at some point of the trial (**Fig. 1b**). Lapping was only present for the controls on 2% of the preferred rate trials and 21% of the maximum rate trials.

We assessed the effects of spatial coupling by comparing performance in the symmetric and asymmetric modes. The control participants circled more slowly during asymmetric movements for both rate conditions (**Fig. 2a**). In contrast, the patients showed no difference between the symmetric and asymmetric conditions when circling at maximum rate. A pronounced difference in the maximum rate condition between the controls and patients was also observed in terms of rate variability (**Fig. 3**). The controls became much more variable in the asymmetric mode ($F_{1,275} = 65.5$, $p < 0.001$). Whereas the callosotomy patients were more variable during bimanual circling, they were equally variable in both modes of bimanual coordination ($F_{1,278} = 0.17$, $p = 0.68$). Thus, the patients failed to show an increase in either the mean or variability of cycle duration in the asymmetric condition.

Relative phase

The phase relationship between the two hands provides a finer-grained analysis of temporal coupling (**Fig. 4**). This control subject's performance showed strong phase coupling during symmetric movements, with only a slight lead of the dominant hand. The variability of the relative phase distribution increased during asymmetric circling, especially in the maximum rate condition. Moreover, the right hand led the left hand by an average of 35° in the latter condition. Similar results were obtained for the other two control subjects.

The histograms for the callosotomy patient, JW, demonstrated considerable phase uncoupling. In all four conditions, the distribution of phase differences was widely dispersed. The results for a second callosotomy patient, VP, were similar. VJ showed greater temporal coupling than the other two patients. The mean rate for the two hands was within 16 ms in all bimanual conditions, and her phase difference distributions were less dispersed. Nonetheless, these distributions were more variable than those observed in the controls.

The group analyses of the variability of relative phase (**Fig. 5**) mirror what was found for the rate difference (**Fig. 2b**), indicating that the fluctuations in relative phase result in large part from the differences in rate. Within the control group, the circular standard deviation increased from the symmetric to asymmetric mode for preferred rate ($F_{1,42} = 50.3$, $p < 0.001$) and maximum rate condition ($F_{1,135} = 92.4$, $p < 0.001$). Phase coupling during symmetric movements was largely unaffected by rate; the sharp loss of phase stability became manifest during asymmetric movements at maximum rate. The callosotomy patients showed a higher variability of the relative phase than the controls in all conditions, consistent with a lack of phase coupling. Whereas the standard deviation of relative phase for the patients was similar for the symmetric and asymmetric mode in the preferred rate condition ($F_{1,57} = 0.98$), they showed greater variability for the asymmetric

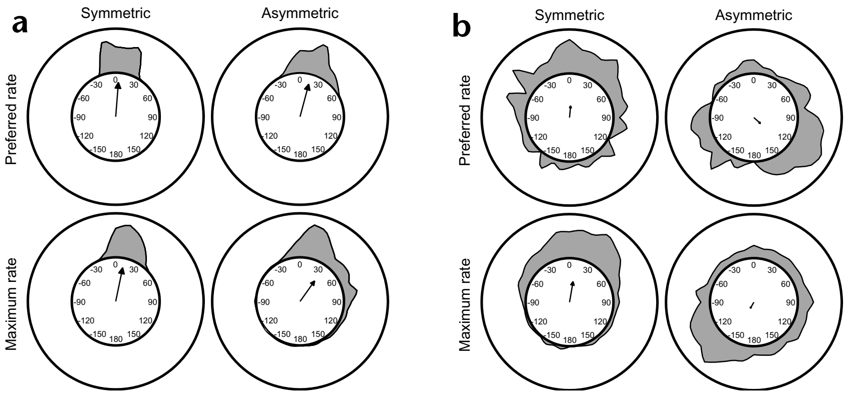


Fig. 4. Increased dispersion of relative phase in a patient. (**a**) Control participant; (**b**) callosotomy patient JW. Top, preferred rate; bottom, maximum rate. Left column, symmetric condition; right column, asymmetric condition. Within each histogram, the arrows ($\vec{M}$) indicate the mean of N relative phase estimations, averaged over all trials and cycles,

$$\vec{M} = \frac{\sum_{i=1}^{N} \vec{P}_i}{N}$$

where $\vec{P}_i$ is a unit-length vector in the direction of the i^{th} estimation of relative phase. The direction of the arrow indicates the mean relative phase, whereas shorter length indicates greater dispersion of relative phase.

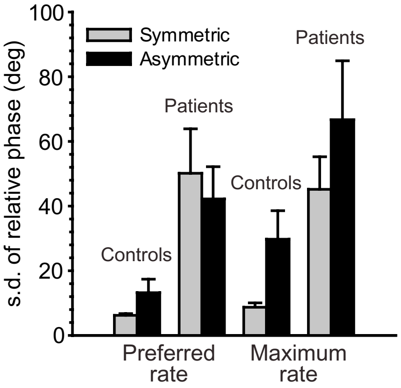


Fig. 5. Summary of relative phase variability for controls and callosotomy patients. Circular standard deviation[32] of relative phase within each trial. $s.d. = \sqrt{-2 \log R}$, where R is the length of the mean vector $\vec{M}$ (**Fig. 4**).

condition than for the symmetric condition when performing at maximum rate ($F_{1,136} = 31.1$, $p < 0.001$).

Phase transitions

Phase transitions provide an important indicator of pattern instability. These were defined as reversals in direction for one hand that remained stable for at least one cycle. In accord with previous findings[14], the controls had such transitions only during asymmetric circling, and of the seven observed transitions, six occurred during the maximum rate condition. In contrast, phase transitions were evenly distributed across symmetric ($n = 6$) and asymmetric ($n = 7$) modes for the callosotomy group. For both groups, the reversal in direction was associated with the non-dominant hand (100% for controls; 77% for callosotomy patients).

Continuous versus discrete finger movements

Given the surprising lack of temporal coupling demonstrated by the patients in the circle drawing task, a second experiment was conducted in which we directly compared continuous and discrete repetitive movements. Bilateral index finger movements were produced under two types of instructions: continuous, in which there should be a smooth transition between flexion and extension phases, and discrete, in which a brief pause should be inserted before each flexion phase. To minimize external constraints, all movements were performed without the fingers contacting the table surface, with eyes closed, and at a self-selected pace. The controls and callosotomy patients adopted a similar pace during the continuous condition (mean cycle durations of 596 and 559 ms, respectively). The insertion of a pause in the discrete movement condition led to longer cycle duration for both controls (904 ms) and patients (1,580 ms). The difference is primarily due to one patient who inserted an average pause of 1800 ms between each cycle.

Temporal coupling was assessed by identifying the onset of the downward movement of each tap and defining cycles as the interval between successive onsets. The callosotomy patients and controls showed similar temporal coupling between the two hands in the discrete tapping condition (**Fig. 6**). However, the callosotomy patients showed a substantial reduction of temporal coupling in the continuous condition ($F_{1,42} = 226.0$, $p < 0.001$). For the individual patients, the increases in the standard deviation of relative phase were 190% (VJ), 229% (VP) and 434% (JW). The controls showed no difference in temporal coupling between the two condition ($F_{1,42} = 0.06$). Thus, despite the general similarity of the movements required for both conditions, the callosotomy patients became essentially uncoupled when the movements were performed continuously.

DISCUSSION

In the first experiment, we investigated the role of the corpus callosum in spatial and temporal coupling during continuous bimanual circle drawing. Spatial coupling is inferred by the reduced stability observed when the circles are produced asymmetrically (non-homologous movements) compared to symmetrically (homologous movements). The results from our control group are consistent with previous reports[13,14]. In the asymmetric condition, the control participants moved at a slower rate, exhibited increased variability in rate and relative phase, and showed occasional phase transitions toward the more stable symmetric mode. In contrast, with the exception of the increased variability in phase coupling during maximum rate performance, the callosotomy patients group did not exhibit differences between the symmetric and asymmetric modes of coordination. Moreover, they were equally likely to exhibit phase transitions in the symmetric condition as in the asymmetric condition.

The spatial trajectory of continuous movements has been hypothesized to result from the output of two oscillators, one for the y- and the other for the x-component[18]. Spatial coupling during bimanual movements can be attributed to cross-talk between the x- and y-oscillators associated with each hand. In the symmetric mode, both pairs of oscillators are in-phase; in the asymmetric mode, the y-oscillators are in-phase, and the x-oscillators are in opposite phase. The neural locus of these interactions has been hypothesized to occur at a spinal level, resulting from the integration of contra- and ipsilateral corticospinal projections[16]. Support for this hypothesis comes from the finding that individual differences in the degree of instability are related to the magnitude of ipsilateral evoked motor potentials following transcranial magnetic stimulation (F.A. Kagerer, J.J. Summers, S.A. Wilson & A. Semjen, *Soc. Neurosci. Abstr.* **30**, 553–554, 2000).

However, our results challenge an account based on ipsilateral corticospinal projections, given that these remain intact in callosotomy patients. Rather, it seems that spatial interactions reflect communication across the corpus callosum. Following resection of these fibers, the patients show little evidence of a difference between the symmetric and asymmetric modes of coordination during biman-

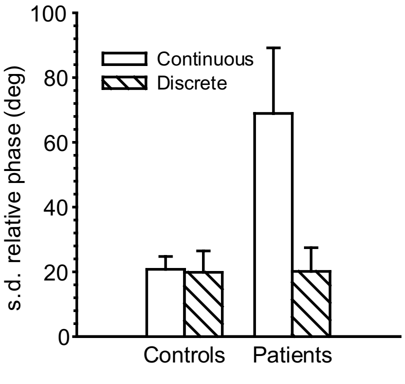


Fig. 6. Dissociation of temporal coupling during continuous and discrete movements in a modified tapping experiment. Circular standard deviation of relative phase in the continuous and discrete conditions.

ual circle drawing. This finding is similar to what has been reported during bimanual movements of orthogonal lines[6] and even in more abstract tasks involving spatially incompatible stimulus–response mappings[19]. A cortical locus of spatial coupling may involve neural codes related to movement direction[17,20] or muscle activity[21]. Neurons in the left and right hemispheres with mirror-symmetric directional tuning or associated with homologous muscles could reinforce each other[22]. Conflict between neurons with different directional or muscular tuning would be generated in the asymmetric condition, resulting in greater instability. Without the callosum, these interactions are absent. Given that the patients studied in the present report have undergone a complete resection of the callosal fibers, we can not infer which cortical areas are involved in such interactions, although several studies point to a critical role for the parietal cortex[7,23].

Callosotomy patients show temporal coupling during bimanual production of relatively discrete spatial patterns[6] or finger tapping[8,10], movements in which a discrete event (e.g., table contact) defines each cycle. Even when producing self-initiated or visually triggered single responses with the two hands, movement initiation times are closely synchronized, although variability may be higher than in control participants[24]. The current results provide the first demonstration that temporal coupling can also be markedly reduced during continuous bimanual movements. This was shown both in the frequency differences between the hands and the high variability of relative phase. The latter effect could be the result of high levels of noise in motor implementation processes, in which a high degree of asynchrony arises following a common input signal to the two hands. However, as indicated by the absolute rate difference, the two hands moved at different frequencies on many trials.

A direct comparison of continuous and discrete movements in the second experiment confirmed that temporal uncoupling in the callosotomy patients was limited to continuous movements. This finding is consistent with recent studies that have shown a dissociation between the temporal control of discrete and continuous movements. Measures of temporal consistency during unimanual tapping and continuous circle drawing are not correlated in normal individuals[12,25]. Moreover, whereas patients with unilateral cerebellar lesions exhibit increased temporal variability when tapping with their impaired, ipsilesional hand, no differences are found between the impaired and unimpaired sides on similar measures obtained during continuous circle drawing (R.M. Spencer, R.B. Ivry & H.N. Zelaznik, *Ann. Meeting Cogn. Neurosci. Soc.*, **152**, 2001).

These results have been interpreted to indicate that the timing processes involved in discrete and continuous movements are distinct, with the cerebellum especially important for event timing, conditions in which the temporal goal is part of the movement representation. The cerebellar contribution to event timing is in terms of absolute timing, serving, for example, to ensure that a series of movements consistently matches the target interval during repetitive tapping. During continuous movements, such control may be achieved indirectly. In circle drawing, a constant rate can be achieved by maintaining a constant angular velocity. In our modified tapping task, in which the fingers did not contact an external surface, temporal consistency could be achieved by maintaining a smooth transition between flexion and extension. This form of control is not possible when pauses are inserted before each flexion cycle, or as in previous experiments, the movements are perturbed by contact with an external surface. Under such conditions, we assume temporal control is achieved by representing the target intervals between successive events.

It has been suggested that for discrete movements, temporal coupling arises through a common gating mechanism that constrains movement initiation to occur simultaneously for both hands[26,27]. Because such temporal coupling persists in callosotomy patients[6], this gating mechanism has been hypothesized to be subcortical. Continuous movements do not seem to require this gating mechanism once the movement is initiated. Nonetheless, as seen here, such movements remain tightly coupled in normal individuals. A single mechanism is likely sufficient to account for both spatial and temporal interactions during continuous movements in normal participants. For instance, coupling of motor commands or proprioceptive inputs from the two limbs[28] could maintain a stable phase relationship and support symmetric movements. Evidence favoring a common mechanism comes from the finding that temporal coupling in healthy control participants is tighter for symmetric movements[14]. Both spatial and temporal coupling of continuous movements is greatly attenuated in callosotomy patients, indicating that these forms of coupling reflect neural communication across the corpus callosum.

METHODS

Participants. Three callosotomy patients (45–48 years old) completed both experiments. The operations were performed for JW and VP in 1979 (ref. 29) and for VJ in 1995. MRI has confirmed complete resection of callosal fibers for JW[30] and VJ[7]. VP has some remaining fibers in the ventrorostral portion of the corpus callosum[31]. JW and VP are right-handed; VJ is left-handed. Four right-handed control participants (43–55 years old) were also tested, with two of them completing both experiments. The experimental protocol was approved by the Committee for Protection of Human subjects at UC Berkeley.

Procedure. In the first experiment, two circles, 10 cm in diameter, were displayed on a table surface in front of the participants. Participants were tested under uni- and bimanual conditions. On each trial, the participants continuously traced the designated circle(s) for 8 s. Within each condition, the participants were required to move in the clockwise direction for one block of trials and in the counterclockwise direction for a second block. Thus, in the bimanual conditions, the factorial combination of the two directions resulted in two blocks of symmetric circling and two blocks of asymmetric circling. All conditions were tested at preferred and maximum rate. Subjects set their own criterion for the preferred rate. For the maximum rate, they were instructed to go as fast as possible while still being able to execute the task. The instructions indicated that the hands might become unstable during a trial and that they should not resist changes in movement direction.

A tone was used to indicate the start and end of each trial. Before the start of the trial, the subjects placed their index finger(s) on the circle(s) at the farthest point. Each block consisted of four trials. For the first sixteen blocks, each movement type was performed first in preferred rate and immediately followed by maximal rate. The last 12 blocks were all performed at maximal rate, with each bimanual condition performed twice.

A modified tapping procedure was used in the second experiment. The subjects positioned themselves so that their wrists were raised about 20 cm above and parallel to the table surface. In the continuous condition, the subjects were instructed to make continuous flexion-extension movements restricted to the left and right index fingers. In the discrete condition, they were required to insert a brief pause before the onset of each flexion cycle. The structure of the trials and test blocks was as in the first experiment, except that each trial lasted 12 s. All movements were made with the eyes closed.

Data acquisition and analysis. Movements were recorded at 137.6 Hz with a miniBIRD magnetic tracking system (Ascension, Burlington Vermont), with receivers attached to the tip of each index finger. Based on the zero crossings in the instantaneous velocity along the *x* and *y* directions (**Fig. 1**), the circles were divided into four quadrants separated by the four cardinal points (labeled north, south, west, east). All analyses were based on these points[14]. The individual trial data were used in the statistical analyses given the small sample size per group.

For a cycle to be considered valid, an orderly sequence of cardinal points was required. Parts of trials where changes in direction or other disruptions occurred were excluded from quantitative analyses, but were further examined for phase transitions. We excluded trials in which a stable movement pattern never developed. This criterion resulted in the exclusion of 6 patient trials and 2 control trials.

For the tapping experiment, the analysis was restricted to instantaneous velocity in the cardinal direction of the tap. Tap onsets were identified as the first point at which the velocity was greater than 5.6 mm/s in the downward direction, and this velocity was maintained or exceeded for at least 35 ms.

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Competing interests statement

The authors declare that they have no competing financial interests.

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