Exp Brain Res
DOI 10.1007/s00221-006-0640-2

RESEARCH ARTICLE

Intermanual interactions during initiation and production of rhythmic and discrete movements in individuals lacking a corpus callosum

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Received: 20 March 2006 / Accepted: 13 July 2006

Abstract Three individuals lacking a corpus callosum, two due to callosotomy and one agenesis, and three age-matched healthy controls were tested on a bimanual task in which a discrete or rhythmic arm movement was initiated following a visual signal while the other arm produced continuous, rhythmic movements. The control participants initiated the secondary, rhythmic movement in phase with the ongoing rhythmic base movement and the two limbs were coupled in an inphase mode across the duration of the trial. In contrast, the acallosal individuals failed to show phase entrainment at the initiation of the secondary, rhythmic movements. Moreover, the callosotomy patients exhibited weak coupling between the rhythmically moving limbs while the individual with callosal agenesis consistently synchronized in an antiphase mode. The control participants exhibited increased perturbation of the ongoing base movement when initiating a discrete movement; for the acallosal participants, the base movement was similarly perturbed in both secondary movement conditions. These results are consistent with the hypothesis that intermanual interactions observed during bimanual movements arise from various levels of control, and that these are distinct for discrete and rhythmic movements. Temporal coupling during rhythmic movements arises in large part from transcallosal interactions between the two hemispheres. The imposition of a secondary movement may transiently disrupt an ongoing rhythmic movement even in the absence of the corpus callosum. This may reflect subcortical interactions associated with response initiation, or, due to dual task demands, a transient shift in attentional resources.

Keywords Bimanual coordination · Rhythmic movements · Discrete movements · Corpus callosum · Subcortical coupling · Interhemispheric connection

Introduction

When people produce rhythmic bimanual movements, the left and right limbs exhibit strong spatiotemporal coupling (Amazeen et al. 1998; Cohen 1970; Kelso 1995; Swinnen and Carson 2002). This coupling is manifest in two ways: first, the movements are produced at a common frequency; second, only two-phase relationships, inphase and antiphase, are spontaneously stable. Other phase relationships require extensive training (Zanone and Kelso 1997) and/or augmented perceptual feedback (Puttemanns et al. 2004; Swinnen et al. 1993). Coupling is also present when the two arms produce non-rhythmic, i.e., discrete

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movements. For instance, when reaching to two targets at different distances and with different target widths, the movements of each arm are initiated in a near-synchronous manner (Kelso et al. 1979; Marteniuk et al. 1984). Similarly, the two hands tend to produce similar forces with near-identical temporal profiles when attempting to generate isometric forces of different magnitudes (Diedrichsen et al. 2003; Rinkenauer et al. 2001; Steglich et al. 1999).

While such kinematic and kinetic coupling is a prominent constraint for both rhythmic and discrete movements, there are notable differences between these two classes of actions. Rhythmic movements tend to be continuous with an invariant period and amplitude, commonly produced without explicit targets in extrinsic space. Discrete actions, on the other hand, are characterized by well-defined initiation and termination landmarks. Termination is frequently associated with a spatial target in extrinsic space. From a dynamical systems perspective, discrete movements can be interpreted as fixed-point attractors (Schöner 1990); rhythmic movements and the coupling of two or more cyclic movements have been modeled as limit cycle attractors coupled to each other (Kay et al. 1987; Sternad et al. 1996). As these two attractors are the two main stable attractors in nonlinear dynamical systems, it has been proposed that rhythmic and discrete movements form two basic units of action, or movement primitives (de Rugy and Sternad 2003; Sternad et al. 2000). A related distinction suggests that even within the domain of rhythmic movements, the control operations differ depending on whether the movements are produced in a smooth continuous manner, or are marked by discrete salient events (Spencer and Ivry 2005). Evidence consistent with both of these views has been obtained in neuroimaging (Lutz et al. 2000; Schaal et al. 2004; Yu 2005) and neuropsychological studies (Spencer and Ivry 2005; Spencer et al. 2003).

If the control of discrete and rhythmic movements involves distinct neural mechanisms, the question arises as to how we produce actions that combine discrete and rhythmic components. Many actions require this form of integration. While walking or running, we may impose a discrete action either with the foot (e.g., kick a ball) or with the hand (e.g., point to an interesting landmark). Within the domain of bimanual movements, we may stir the soup with one hand and use the other to pick up a salt shaker. Given the neural and behavioral dissociations between rhythmic and discrete movements, it is reasonable to hypothesize that the different actions of the two hands would be relatively independent, or exhibit attenuated forms of coupling compared to conditions in which both hands produce either rhythmic movements or discrete movements, the conditions typically examined in studies of bimanual coordination.

To explore this issue Wei et al. (2003) tested neurologically healthy individuals in a novel bimanual task. Participants performed rhythmic movements about one elbow at different periods (base movement). Following the presentation of an imperative signal at a random phase, they were required to initiate a movement with the contralateral hand while maintaining the base movement. This secondary movement was either rhythmic or discrete. The results showed a clear distinction between the two secondary movement conditions. While the initiation of the secondary rhythmic movement was generally in phase with the base movement of the other arm, the initiation of the discrete movement was independent of the phase of the base movement. Moreover, the reaction time for rhythmic initiation was directly related to the period of the base movement (i.e., shorter RTs for faster base movements), whereas the discrete reaction time was invariant across the different base movement rates.

These results indicate that coupling was considerably stronger in the rhythmic-rhythmic condition. Nonetheless, other aspects of the results indicate that the discrete movements were not performed independently of the base movement. First, the initiation of either rhythmic or discrete secondary movements led to a transient perturbation of the base movement (phase advance), as well as a transient increase in the rate of the base movement, especially in the discrete condition. Second, the peak velocity of the discrete movement scaled with the rate of the base movement. Thus, there was evidence of intermanual coupling even in the discrete condition, although the form of these interactions was different from that observed in the rhythmic condition. The present study further investigates the issue of bimanual coupling in tasks involving discrete and rhythmic movements by examining acallosal patients, i.e., individuals that lack the connection between the two hemispheres.

Individuals lacking the corpus callosum provide an interesting opportunity to study bimanual coordination given the absence of direct communication between the cerebral hemispheres. For instance Tuller and Kelso (1989) tested a callosotomy patient on a bimanual rhythmic tapping task. Interestingly, the patient exhibited a strong tendency to produce in- and antiphase movements, similar to those observed in control participants, even when lateralized visual metronomes were used to specify the target timing of the responses for each hand. Ivry and Hazeltine (1999) also reported strong temporal coupling during rhythmic tapping in another callosotomy patient, even when the task was performed without an external metronome. Note that both of these studies examined finger tapping where a salient event, the finger contact with the table surface, marked each cycle in synchronization with a metronome.

In contrast, Kennerley et al. (2002) tested three callosotomy patients on a bimanual circle drawing task. Under such conditions, spatiotemporal coupling was greatly attenuated; in fact, in some trials, the two limbs moved at different rates. As circle drawing involves multijoint coordination and cannot be directly compared to tapping, a second experiment was conducted in which all of the movements involved rhythmic finger movements. Rhythmic performance with smooth transitions between flexion and extension were compared to intermittent or discrete-like movements that involved a pause before each flexion phase. This relatively subtle distinction led to a marked difference in performance: coupling was much more pronounced in the discrete condition compared to the continuous condition.

Thus, the processes underlying spatiotemporal coupling observed during continuous movements appears to involve cortical mechanisms that interact through signals communicated across the corpus callosum (Ivry et al. 2004). In contrast, a subcortical locus is indicated for spatiotemporal coupling associated with discrete movements, either produced in isolation (Franz et al. 1996) or as part of a rhythmic pattern. These subcortical connections, linked to the timing of certain events such as the onset or offset of the movements, would provide a pathway through which signals to the two hands could interact in the absence of the corpus callosum.

Prior studies with callosotomy patients have generally involved tasks in which both hands produced similar movements and in which the two actions were initiated at the same time (e.g., both drawing circles or both tapping; but see Franz et al. 2000. In the current study, we test three acallosal individuals on the bimanual tasks introduced by Wei et al. (2003). For these tasks, the focus is on constraints that arise when a secondary movement is introduced during the course of an ongoing rhythmic movement. Moreover, the key comparison is between conditions in which the secondary movement is also rhythmic or when it consists of a brief, discrete movement.

From the extant literature, the three hypotheses can be formulated: first, differences between the two groups should be seen in the constraints on initiation of the secondary rhythmic and discrete movements. As the onset of a discrete secondary movement is independent of the phase of the rhythmic movement in control participants (Wei et al. 2003), we expect the same pattern to be present in the acallosal participants. More interestingly, initiation of a secondary rhythmic movement can conceivably lead to different expectations: while control participants will show marked spatiotemporal coupling between the two limbs which persists over subsequent movement cycles, as seen by Wei et al. (2003), for acallosal participants, two results are plausible: Given the assumption that a subcortical mechanism is required to initiate the secondary movement, this mechanism may have information regarding the current state of the ongoing base movement of the other hand. As such, the secondary movement would be constrained to start inphase with the base movement, with uncoupling emerging over subsequent cycles. Alternatively, phase information may be limited to the hemispheric representation of the ongoing movement. In this case the initiation of the secondary rhythmic movement should be independent of the phase of the base movement. Once the secondary movement has become established, we expect to observe attenuated or absent coupling between the two continuous movements, similar to what was reported by Kennerley et al. (2002).

A second set of hypotheses can be formulated with respect to perturbations of the base movement induced by the initiation of the secondary movement. If the onset of a secondary movement, either discrete or rhythmic, constitutes an event that is accessible via subcortical pathways to both hemispheres, we would expect to observe similar perturbations in the base movement around the time of initiation in both healthy and acallosal individuals. In the healthy individuals of the study by Wei et al. (2003) these perturbations were most prominent when the secondary movement was discrete, probably because the onset was not in phase with the rhythmic base movement. This difference between rhythmic and discrete initiation may be absent in the acallosal group assuming that the phase of the rhythmic base movement is communicated via the corpus callosum.

A third focus is on the difference between acallosal individuals: two individuals were surgical callosotomy patients and one individual had callosal agenesis. Agenesis individuals have received relatively little attention in previous work on bimanual coordination. In studies of hemispheric specialization involving perceptual studies, agenesis individuals perform similar to control participants, suggesting extensive reorganization, either within each hemisphere or in the communication paths between the hemispheres (e.g., Barr and

Corballis 2002). However, in a study of bimanual force production, an agenesis patient exhibited relative independence of the two hands when asked to produce isometric forces of different intensities (Diedrichsen et al. 2003). Hence, bimanual coupling in steady state rhythmic performance may reveal differences.

Methods

Participants

Three acallosal individuals were tested. JW (age 48, male, right-handed) and VP (age 49, female, right-handed) underwent surgical resection of the corpus callosum in 1979 as part of their treatment for intractable epilepsy (for details see Sidtis et al. 1981). While the callosotomy was complete in JW, a sparing of the most ventro-rostral fibers of the corpus callosum remained present in the patient VP, providing inter-hemispheric connection between the two cingulate gyri and other prefrontal areas (Corballis et al. 2001). The third participant RU (age 58, male, right-handed) lacked the corpus callosum congenitally. His condition was accidentally discovered during a precautionary MRI following a headache episode. He did not report any unusual problems with coordination during development.

Three neurologically healthy control participants (two males, one female) were matched to the acallosal group with respect to age (54 vs. 52 years, control range of 47–59 years), education (control mean = 16 years; acallosal mean = 15 years) and handedness (all right-handed). All the participants gave informed consent following a protocol approved by the Committee for the Protection of Human Subjects (CPHS) at the University of California, Berkeley.

Materials and procedure

Participants were seated at a table with a smooth, wooden surface. The shoulders were abducted to approximately 45° and the fingers were curled, with the lateral surface of the arms resting lightly on the table surface. Rhythmic movements of the forearm were executed by flexion/extension of the elbow joint. Three-dimensional position data was sampled with an Ascension mini-bird system at a rate of 140 Hz and recorded on an IBM-compatible PC. The position sensors were taped to the tip of the left and the right index finger (Ascension Technology, Burlington, VT, USA). A computer monitor was placed at eye level, approximately 80 cm in front of the participant.

During each trial, a small cross was presented on the center of a computer screen positioned 80 cm in front of the participant. At the beginning of the trial, the participant rested both arms on the table, positioned to extend perpendicular to the body axis with elbows extended to approximately 170°. The trial began with the presentation of a cross on the computer monitor and the participant was instructed to maintain fixation on this stimulus throughout the trial. When the participant was ready, the experimenter started an auditory metronome. This consisted of 12 pacing tones (1,000 Hz, 30 ms duration), with a period of either 300 or 550 ms. In separate blocks, the participant was required to make oscillatory movements (base movement) with either the left or right forearm, one full oscillation per pacing tone. The experimenter indicated that the movement amplitude should span approximately 80°, with maximum flexion of 90°. However, this aspect of the task was not emphasized because one goal of the study was to observe how the introduction of a secondary movement influenced the amplitude of an on-going base movement. The participant continued to perform the rhythmic base movement after the pacing tones ended. Vision of the arm producing the base movement was prevented with a screen.

At a random interval (3–5.5 s) after the last pacing tone, a white circle (0.5° diameter) was displayed on the screen, 6° lateral of the fixation cross on the side of the resting arm. This stimulus served as the imperative signal for the secondary movement. In the discrete initiation condition the cue signaled the participant to flex the resting forearm towards the body while continuing to make the rhythmic base movement with the other arm. The trial ended 10 s after the auditory metronome was terminated, providing between 4.5 and 7 s of data after the initiation of the secondary movement. In the rhythmic initiation condition, the cue signaled the participant to begin rhythmic movements with the resting arm while maintaining the base movement. The instructions emphasized that the secondary movements should be performed at the same speed and amplitude as the base movements, but no instructions were given regarding the phase relationship between the two arms. In this condition, data collection continued for 15 s after the start of the continuation phase, providing 9.5–12 s of data after the initiation of the secondary movement. In both the discrete and rhythmic conditions, participants were instructed to begin the secondary movement as soon as they saw the imperative signal. However, the experimenter did not place a strong emphasis on initiation speed since this appeared to confuse the first patient tested during practice trials. Rather, the experimenter continually re-emphasized that the participant should continue to produce the base movement.

The experiment for each participant consisted of eight blocks with 20 trials in each block. The first four blocks were performed at a pace of 300 ms, the second four blocks at a pace of 550 ms. For each rate, two blocks were performed with the discrete condition, followed by two blocks with the rhythmic condition. For each of the four conditions (2 periods × 2 secondary movements), the base movement was performed with the right arm in one block and the left arm in the other block. The same order of presentation was used for all six participants. Two practice trials were included at the start of each block. The experiment lasted approximately one hour, excluding the time required to set up the equipment.

Data analysis

For the analysis, we ignored the z-coordinate (height over table) as participants maintained light contact with the table surface throughout the trial. From the movement trajectories for each arm in the horizontal plane (x, y), we extracted the main axis of movement using a principal component analysis on the spatial data (Fig. 1). This convention was adopted because the axis of rotation was not fixed by a device. All movement data was projected onto this axis and were measured in units of cm. Zero was defined to be at the center of mass of all data points, calculated over the entire trial. Positive values of the position record indicated extension of the elbow joint and negative values indicated flexion. To compute velocity, the position time series was numerically differentiated and smoothed with a zero-lag sixth-order Butterworth low-pass filter with a cutoff frequency of 5 Hz.

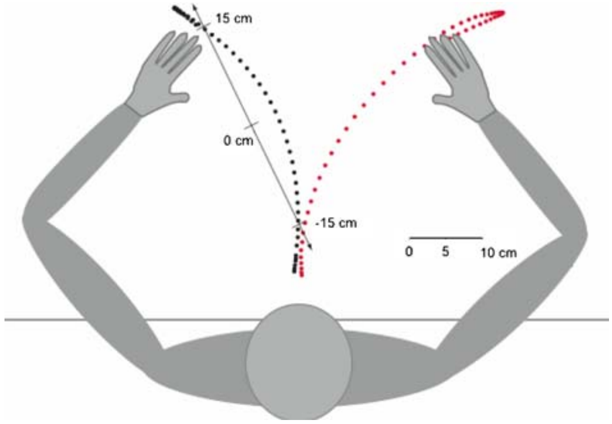

Fig. 1 Experimental setup and coordinate definitions for the data analysis. The participants were seated at a table, both elbows resting on the table surface. Movements were executed by flexion and extension about the elbow joint. For data analysis, the movement data was projected onto the best fitting line that describes the main movement orientation

Calculation of dependent measures

Three exemplary trials for the rhythmic and the discrete conditions are shown in Fig. 2. In Fig. 2a, callosotomy participant JW initiates a rhythmic movement with his right arm, while maintaining the oscillatory base movement with his left arm. In Fig. 2b, the same individual initiates a discrete movement. Figure 2c shows a discrete initiation trial where the patient had severe difficulties in performing the task. Instead of the instructed discrete movement he performed one movement cycle. In parallel, he stopped the base oscillation for several cycles. This trial was eliminated from the regular analysis as detailed in the following.

To calculate period and amplitude of each cycle, the times and positions of the extrema of the position signals of the continuous base movement were determined. Cycle period (T) was calculated as the temporal interval between two successive maxima, cycle amplitude (A) as the difference in position between maxima and the successive minima. These measures were averaged across all cycles before the onset of the imperative signal to obtain T_{pre} and A_{pre}. Equivalent averages were calculated to obtain post-initiation measures, T_{post}, and A_{post}, of the rhythmic base movement. The two cycles during and immediately following the initiation of the secondary movement were excluded in order to avoid transient effects.

The onset of the secondary movement t_{init} was defined as the time at which the velocity of the secondary movement exceeded a threshold of 0.14 m/s. Initiation time (IT) was calculated as the difference between the onset time of the imperative signal t_{imp} and the onset time of the secondary movement t_{init}.

Calculation of phase variables

In order to analyze the relative timing of events between the two arms, t_{init} and t_{imp} were converted into phases. The initiation phase of the secondary movement φ_{init} was calculated as:

$$\phi_{\mathrm{init}} = 2\pi(t_{\mathrm{init}} - t_{\mathrm{peak}})/T_{\mathrm{pre}},$$

where t_{peak} is the last peak in the position signal of the base movement before the onset of the secondary movement. The phase of the imperative signal φ_{imp} was calculated accordingly:

$$\phi_{\mathrm{imp}} = 2\pi(t_{\mathrm{imp}} - t_{\mathrm{peak}})/T_{\mathrm{pre}}.$$

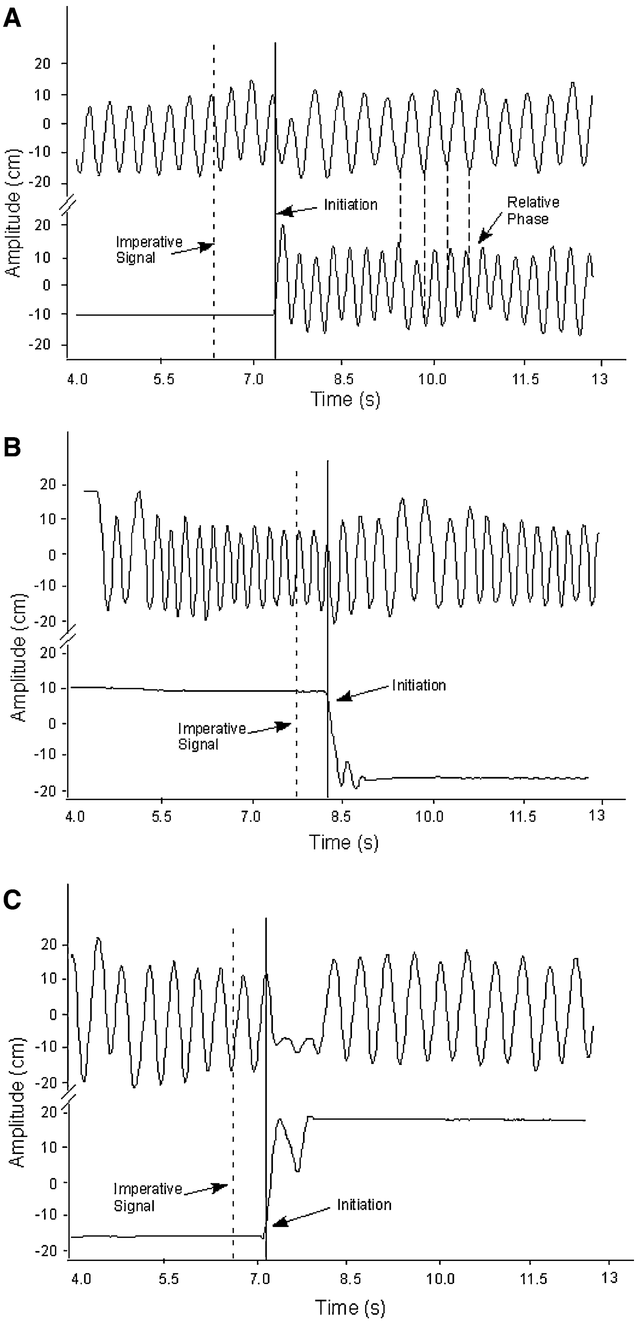

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Fig. 2 A segment of the time series of three exemplary trials with rhythmic and discrete initiation. **a** Rhythmic initiation trial performed by callosotomy patient JW. The *upper trajectory* shows the cycles of the rhythmic base movement produced by the left arm and the *lower trajectory* shows the cycles of the secondary movement produced by the right arm. The imperative signal and initiation time of the secondary movement are marked by *vertical lines*. The *vertical dotted lines* during the bimanual movement epoch are aligned to peak flexion of the left arm and illustrate the wandering relative phase between the two arms. The metronome pacing period was 300 ms in this trial. Note that the period of the participant's movements was slightly slower than the target pace both before and after the imperative signal. **b** Discrete initiation trial of the same acallosal patient. **c** Unsuccessful trial where the acallosal patient failed to perform the instructed discrete movement and simultaneously stops the continuous movement. This trial was eliminated from the regular analyses

where t_{peak} is the last peak in the position signal of the base movement before the imperative signal.

These phase calculations assume sinusoidal trajectories, a reasonable approximation of the pre-perturbation segment of the trial (see Fig. 2).

Peak velocity of the secondary movement after initiation

Peak velocity during the first flexion phase of the secondary movement was calculated. For this measure, the angular position was first differentiated with a two-step difference algorithm, and the maximum was identified using a standard peak-picking algorithm. Peak velocity was measured in meters per second.

Perturbation due to initiation

To capture perturbations of the base movement that might occur as a result of the secondary movements, the base movement was analyzed in phase space, i.e., the space spanned by position and velocity. Compared to deviations in timing only, we expected a spatio-temporal measure to be more sensitive. As shown in Fig. 3, prior to the onset of the secondary movement, the base movement traverses a cycle in phase space. The perturbation is visible as a deviation in the radius and phase velocity. To compute the radius r and the phase angle θ, the position trace was first high-pass filtered to eliminate slow drifts that would introduce periodic changes in the radius (sixth-order Butterworth, 0.5 Hz cutoff). Subsequently, position and velocity were normalized to one by dividing the time series by its mean half-amplitude. Note that the normalization was based on the time series *before* the trigger. The phase θ was then calculated as the arctangent of velocity over position. The radius r was computed from position and velocity using Pythagoras. The derivative of the angular position $\dot{\theta}$ was then computed by a two-time step differentiation of θ.

For a sinusoidal signal, r and $\dot{\theta}$ would be constant. Therefore, perturbations were indicated by deviations in r or $\dot{\theta}$ from the stationary signal. To capture the perturbation of the base movement induced by the initiation of the secondary movement, the root mean square deviation from this mean $\mathrm{RMSD}_{\mathrm{init}}$ was calculated beginning with the cycle peak before t_{init} and terminating with the second peak following t_{init}

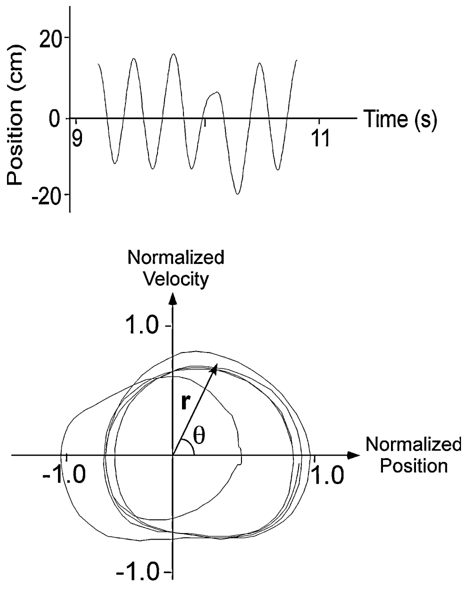

Fig. 3 Calculation of radius r and phase θ at the initiation of the secondary movement. The *top panel* shows five cycles around the time of initiation. A pronounced perturbation in the base movement is evident at the onset of the secondary movement. The *bottom panel* shows the phase portrait across this epoch with normalized position and velocity (for details see text)

(Fig. 5a) (Given the different phases of t_{init} this leads to asymmetrical centering of the window of calculation around t_{init}). To obtain a baseline measure characterizing behavior before the perturbation, RMSD was calculated over all cycles of the trial preceding the peak before t_{init}. The two RMSD measures before and during initiation were normalized by the respective duration over which they were calculated. Subsequently, they were compared by t tests to evaluate whether the base movement was perturbed by the initiation of the secondary movement.

Relative phase

In order to assess the degree of synchronization between the two oscillatory movements in the rhythmic initiation condition following the initiation, a discrete phase estimate was computed as:

$$\varphi = 2\pi(t_{\mathrm{B}} - t_{\mathrm{S}})/T_{\mathrm{pre}},$$

where t_{B} and t_{S} are the times of two adjacent minima of the base and secondary trajectories. For this calculation the first two minima in the oscillating and the initiating arm following t_{init} were paired and then all subsequent minima were paired (see Fig. 2). Inphase behavior, i.e., $\varphi = 0$ rad, corresponds to the situation in which the two arms move in a mirror-symmetric fashion. Note that the pairing was maintained even if the two trajectories drifted apart, i.e., if the hands moved at different frequencies leading to phase wrapping. To capture this information, we opted to not apply a 2π modulo operation and, thus, values larger than 2π rad indicated phase wrapping with one cycle corresponding to 2π.

Statistical analyses

Analyses of variance with a fully crossed fixed effect design were conducted with the following factors: task (rhythmic initiation vs. discrete initiation), oscillation period (300 or 550 ms), arm of initiation (left or right), and participant group (acallosal or control). Due to the small number of acallosal individuals, we conducted a five-factor ANOVA with participant as a fixed effect. Therefore, generalizations to a theoretical population of acallosal individuals should be made with caution. Tests of the distribution properties of the phase of initiation against a uniform distribution were conducted on onset phase using the Rayleigh tests for circular variables (Fisher 1993). Paired t tests with Bonferroni corrections were conducted for comparisons of dependent measures within a trial. The significance level was set at $P = 0.05$ for all analyses.

Results

Prior to analysis trials in which the basic task instructions were not followed were excluded from further processing. Typical cases were when participants started the secondary movement before the imperative stimulus or when they failed to maintain the base movement following the onset of the secondary movement. Only four such trials were excluded from the control participants or the individual with acallosal agenesis. For the two callosotomy patients JW and VP 18 and 12 trials, respectively, were eliminated based on these criteria. For most of these trials, the patients failed to maintain the rhythmic base movement at the onset of the secondary movement as illustrated in Fig. 2c (19 discrete; 11 rhythmic). We also excluded trials in which the latency of the secondary movement was greater than 1,000 ms; this value was roughly equivalent to two standard deviations above the mean initiation time. This procedure excluded another 2% of the trials.

Figure 2a and b illustrates two successful trials of callosotomy patient JW. These two trials exemplify a number of phenomena quantified below: The secondary rhythmic and discrete movements do not begin inphase with the base movement; despite this independence of initiation phase and period, the base movement shows a transient perturbation at the time of the onset of the secondary movement; once established, the two rhythmic movements do not exhibit a stable phase relationship, oscillating at different periods. Following the initiation of a discrete movement the base oscillations change in both amplitude and period: the periods become slower and the amplitudes become larger. Note that the amplitudes were not explicitly prescribed. Figure 2c illustrates one trial where the participant had trouble executing the required pattern: the rhythmic base movements were interrupted and the discrete movement showed an additional cycle. This trial was eliminated from regular analysis.

Kinematics of the base movement

To capture the rhythmic performance of the base movement, the average periods and amplitudes before (T_{pre}, A_{pre}) and after (T_{post}, A_{post}) the onset of the secondary movement were computed across the 20 trials per condition and per participant. The means and standard deviations of the periods for the rhythmic and the discrete initiation conditions are summarized in Tables 1 and 2, with the data pooled over the two arms. From inspection of the variability measures shown in parentheses, the participants were able to oscillate at a fairly stable rate, although the callosotomy patient VP was considerably less consistent than the other participants.

To compare how the two participant groups responded to the initiation of the secondary movement a 2 (group) × 2 (arm) × 2 (period) × 2 (task) × 2 (epoch: pre-post) repeated-measures ANOVA was conducted on period with participants as a random factor within the group. As expected, period differences were highly significant, $F(1, 1732) = 6015$, $P < 0.0001$, indicating that the participants did adopt different rates for the slow and fast conditions. More interesting, we observed main effects of group, $F(1, 1732) = 85.86$, $P < 0.0001$ and epoch, $F(1, 1732) = 38.49$, $P < 0.0001$. These main effects were qualified by a group by epoch interaction, $F(1, 1732) = 8.39$, $P < 0.001$, reflecting the fact that the acallosal individuals slowed down more than controls after the initiation. Note, though, that the means for the two groups were more similar in the post-perturbation phase due to the fact that one of the controls, C2, was markedly slower than all others in the pre-perturbation phase. There was also a task by period interaction, $F(1, 1732) = 138.23$, $P < 0.000$, revealing that for both groups, the period of the base movement was slower after initiation for the rhythmic task compared to the discrete task. Finally, there was also an interaction of arm by task by period, with the right arm movements slower than the left arm movements at the 550 ms condition for the discrete task.

Table 1 Mean cycle durations (ms) of the base movements in the condition with initiation of a rhythmic movement

Participants	T_{pre}		T_{post}	
	300 ms	550 ms	300 ms	550 ms
JW	335 (15)	568 (22)	377 (22)	608 (18)
VP	353 (35)	562 (71)	381 (33)	582 (67)
RU	318 (9)	609 (16)	323 (11)	651 (27)
Average	335 (30)	580 (37)	361 (22)	613 (37)
C1	324 (20)	617 (25)	337 (22)	643 (23)
C2	466 (25)	650 (22)	469 (21)	652 (22)
C3	337 (12)	567 (11)	337 (11)	555 (14)
Average	375 (19)	611 (20)	381 (19)	617 (20)

Participant averages were calculated for the interval before (T_{pre}) and after (T_{post}) the initiation of the secondary movement. The results for each participant are presented separately for the two period conditions (300 and 550 ms). Acallosal patients are identified by their initials and the symbol C refers to control participants. The standard deviations across 20 trials are listed in parentheses

The amplitudes in the different conditions showed relatively large differences across participants but these differences showed little pattern. This was not surprising as amplitudes were not specified in the task. On average amplitudes were 33 cm for both acallosal and control with a range between 21 and 40 cm.

Phase of the initiation of the secondary movement

A central question was whether the initiation phase of the secondary movement φ_{init} was constrained by the phase of the rhythmic base movement. Due to the random length of the foreperiod, the phase of the imperative signal φ_{imp} was distributed approximately uniformly across the cycle. Thus, if the secondary movement was initiated independent of the base

Table 2 Mean cycle durations of the base movements in the discrete condition (see Table 1 for details)

Participants	T_{pre}		T_{post}	
	300 ms	550 ms	300 ms	550 ms
JW	352 (18)	508 (33)	368 (23)	529 (27)
VP	429 (35)	560 (66)	461 (45)	589 (80)
RU	338 (8)	585 (16)	348 (12)	589 (11)
Average	373 (20)	548 (38)	392 (26)	569 (40)
C1	402 (36)	582 (26)	369 (39)	591 (26)
C2	501 (43)	614 (14)	516 (45)	627 (26)
C3	331 (15)	537 (14)	352 (20)	532 (12)
Average	395 (31)	578 (18)	412 (35)	584 (21)

movement, the initiation of the secondary movement with respect to the ongoing base movement should be also uniformly distributed. Figure 4 shows the distributions of φ_{init} pooled for the period and hand conditions and separated for control and acallosal individuals. For the discrete initiation condition neither of the two groups showed distributions of φ_{init} that were significantly different from a uniform distribution. In contrast, the rhythmic initiation was significantly constrained in controls to occur at around $0/2\pi$ rad of the ongoing rhythmic movement. The acallosal group showed no such constraints.

Rayleigh tests performed on the individuals' data confirmed this impression statistically. For the discrete initiation condition the distributions for all six participants were not significantly different from a uniform distribution. For the rhythmic initiation condition, the results for the control participants differed from those for the acallosal patients. All three control participants showed distributions of φ_{init} that were significantly different from a uniform distribution with increased frequencies for φ_{init} to be at 0 or 2π ($P < 0.0001$). For the acallosal group, the initiation of the secondary rhythmic movement was not similarly constrained. The distributions for two of the acallosal individuals were not different from uniformity. For JW, the distribution was not uniform: there were two modes at approximately π and 2π rad, a pattern not seen in control participants.

Latency and peak velocity of the secondary movement

The mean initiation latencies IT of the secondary movements are presented in Table 3, with the data again pooled over the two arms. A 2 (group) × 2 (arm) × 2 (period) × 2 (task) ANOVA performed on mean values revealed significant differences between the two groups, $F(1, 862) = 52.31$, $P < 0.0001$. Acallosal participants had a significantly longer IT than controls, although the effect was small (454 vs. 443 ms). Importantly, the latencies for the rhythmic and discrete conditions did not differ for both groups, $F(1, 862) = 2.90$, $P = 0.089$, nor were there any significant interactions.

Interestingly, the peak velocity of the first flexion phase of the secondary movement was influenced by the period of the base movement, $F(1, 862) = 91.42$, $P < 0.0001$. This effect was observed in both the controls (2.12 vs. 1.73 m/s for the 300 and 550 ms

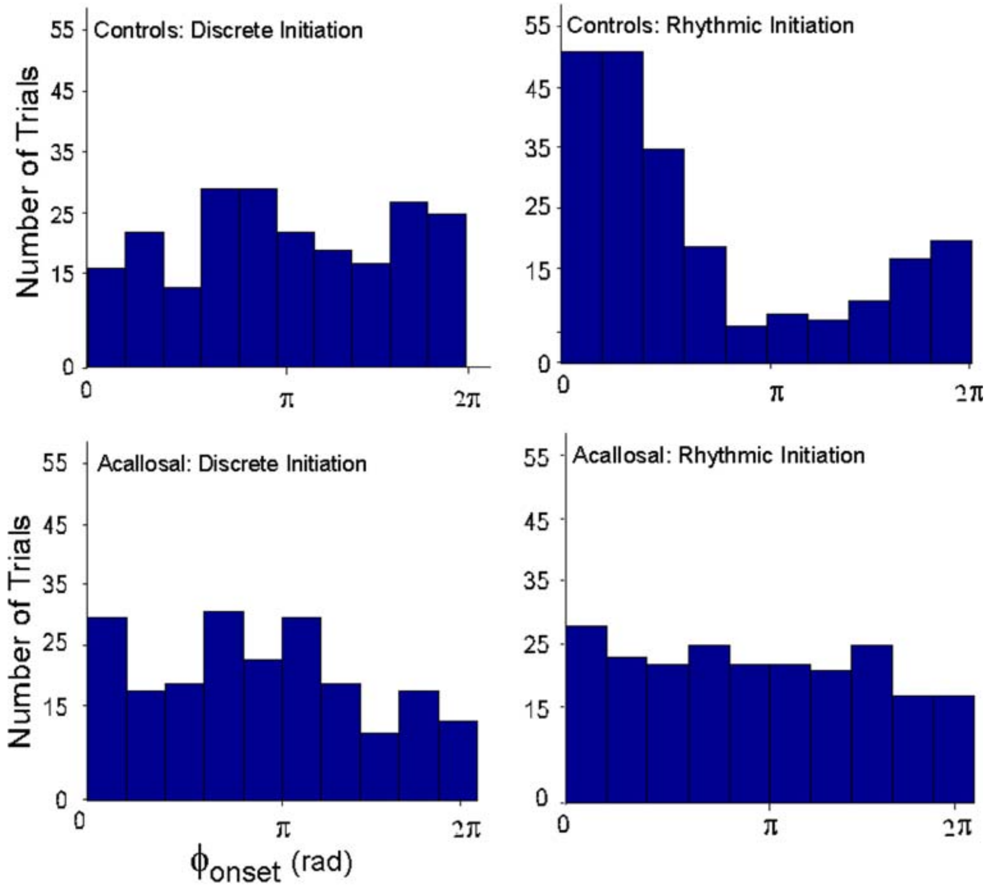

Fig. 4 Histograms for the phase of initiation φ_{init}

Table 3 Mean initiation times (IT, ms)

Participants	Rhythmic initiation		Discrete initiation	
	300 ms	550 ms	300 ms	550 ms
JW	483 (94)	483 (115)	471 (140)	434 (72)
VP	513 (125)	617 (150)	679 (118)	507 (118)
RU	375 (88)	379 (99)	320 (84)	331 (53)
Average	457 (102)	493 (121)	490 (114)	424 (81)
C1	433 (90)	488 (141)	379 (63)	432 (90)
C2	349 (86)	407 (100)	485 (154)	418 (105)
C3	464 (119)	462 (144)	467 (135)	507 (115)
Average	415 (98)	452 (128)	444 (117)	452 (103)

Standard deviations across 20 trials per condition are presented in parentheses

conditions, respectively) and acallosal participants (2.30 vs. 1.95 m/s), regardless of the type of secondary movement. The effect of group was also significant, $F(1, 862) = 34.20$, $P < 0.0001$, with the acallosal participants reaching higher peak velocities than the control group, although this was mainly caused by the large values from RU (Table 4).

Perturbation of the base movement by the initiation of the secondary movement

Figure 5a shows the time series of phase velocity $\dot{\theta}$ and position of the rhythmic base movement over a segment spanning the time of initiation of the secondary movement ($t_{\mathrm{init}} = 0$). In this example, the callosotomy patient shows a transient perturbation in $\dot{\theta}$ of the base movement around t_{init} (Fig. 5b).

To quantify these perturbations, we calculated the RMSD for $\dot{\theta}$ over an interval delimited by the peak before and the second peak after the onset of the secondary movement (the hatched area in Fig. 5a). The pattern of results of the mean values of RMSD of $\dot{\theta}$ is summarized in Fig. 6. The grey solid line shows the grand average of the RMSD value prior to the initiation of the secondary movement, presenting a baseline measure of the stability of the base movement. (These RMSD values calculated over the pre-initiation interval did not differ between the two groups. Therefore, the grand average was used for comparison.) A first statistical analysis compared the RMSD estimates of before and during initiation of the secondary movement by paired t tests for each of the 16 conditions. With one exception all t tests yielded a significant difference ($P < 0.0001$, with $\alpha = 0.0003$ after Bonferroni correction, one condition was significant at $P < 0.0005$), indicating that the initiation of the secondary movement produced a perturbation in the ongoing base movement larger than fluctuations in the pre-initiation phase. On average, the RMSD values were about twice as large as those obtained prior to the perturbation. Similar effects were observed when the

Table 4 Mean peak velocity (m/s) of the secondary movement during the discrete movements and initial cycle of the rhythmic movement

	Rhythmic initiation		Discrete initiation	
	300 ms	550 ms	300 ms	550 ms
JW	1.77 (0.55)	1.44 (0.33)	1.79 (0.37)	1.88 (0.32)
VP	2.33 (0.87)	1.79 (0.71)	2.22 (0.38)	1.66 (0.79)
RU	2.84 (0.31)	2.31 (0.35)	2.90 (0.42)	2.61 (0.62)
Average	2.31 (0.58)	1.85 (0.47)	2.30 (0.39)	2.05 (0.58)
C1	1.84 (0.52)	1.99 (0.25)	2.30 (0.67)	1.98 (0.36)
C2	2.47 (0.45)	1.79 (0.37)	1.79 (0.50)	1.36 (0.39)
C3	2.11 (0.25)	1.50 (0.21)	2.21 (0.26)	1.74 (0.29)
Average	2.14 (0.41)	1.76 (0.28)	2.10 (0.47)	1.69 (0.35)

Standard deviations are presented in parentheses. Since there was no difference between the left and right arm, the data from these conditions were pooled

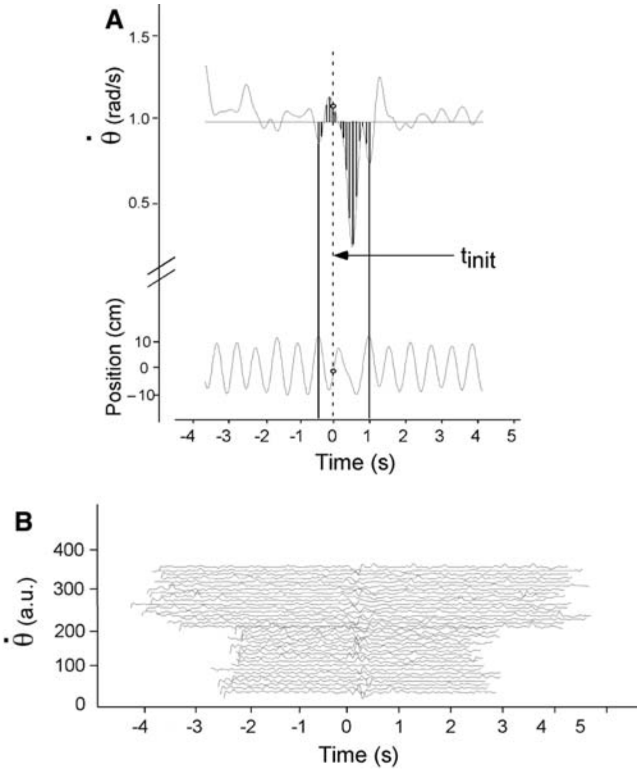

Fig. 5 **a** Segments of the time series of $\dot{\theta}$ and position around the initiation time t_{init}. The hatched area illustrates the RMSD measure for $\dot{\theta}$ that quantifies the magnitude of the perturbation. The trace is from a trial when the callosotomy patient JW was producing rhythmic movements with the right arm at target rate of 550 ms with a discrete secondary movement. **b** All 20 of the trials from the condition depicted in **a**, aligned at Time 0, the initiation time of the secondary movement, t_{init}. The time series of phase velocity $\dot{\theta}$ are stacked on top of each other separated by a constant interval. Hence, the units of the y-axis are arbitrary

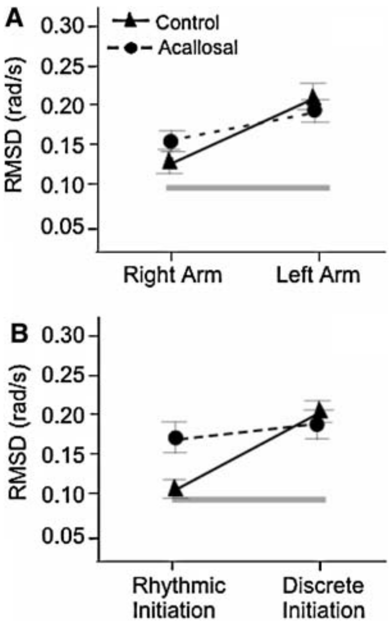

Fig. 6 **a** Average perturbation, measured by RMSD of $\dot{\theta}$ for base movement performed with either the right or left arm. The *grey solid line* indicates the grand average RMSD score prior to the initiation of the imposed movement. The *triangles and circles* indicate this measure for controls (*solid line*) and acallosal (*dotted line*). The error bars indicate standard deviations. **b** Average perturbation separated by the conditions of discrete and rhythmic initiation in the secondary movement

RMSD measure was based on deviations in the radius, *r*, and hence are not reported here.

To compare the effect of the perturbation across conditions, the mean RMSD values were entered into a 2 (group) × 2 (task) × 2 (period) × 2 (arm) ANOVA. Significant main effects were obtained for arm, $F(1, 862) = 27.30$, $P < 0.0001$, and task, $F(1, 862) = 40.62$, $P < 0.0001$. The first effect was due to the fact that perturbations were larger when the left arm performed the base movements (Fig. 6a), an effect that was more pronounced in the control group (group × arm interaction: $F(1, 862) = 9.52$, $P < 0.005$). The second main effect of task revealed that, overall, the two groups showed significantly larger perturbations of the base movement when the secondary movement was discrete compared to when it was rhythmic, $F(1, 862) = 40.62$, $P < 0.0001$ (Fig. 6b). More important, group and task also interacted, $F(1, 862) = 21.22$, $P < 0.0001$. For the acallosal group the perturbations in the discrete and rhythmic initiation tasks did not differ significantly, $F(1, 433) = 1.23$, $P = 0.268$, while this difference was highly significant for the control group, $F(1, 433) = 6.92$, $P = 0.001$. The two-way interaction between group and period was also significant, $F(1, 862) = 25.37$, $P < 0.0001$. The acallosal group showed larger perturbations for the 550 ms period condition compared to 300 ms; the reverse was observed for the control participants.

We also examined whether the magnitude of the perturbations were dependent on the phase at which the imposed movement was initiated. Inspection and correlation analyses showed that RMSD did not systematically depend on the phase.

Rhythmic synchronization

The tendency to synchronize the rhythmic movements of both arms was assessed in the post-initiation interval for the imposed rhythmic condition. For each trial, point estimates of relative phase φ were determined for all cycles following initiation and pooled into histograms based on 10 trials per condition with at least 10 data points per trial. While the data of the control group were pooled in Fig. 7a, the data of the three acallosal participants are shown separately in Fig. 7b–d. Inspection of these histograms illustrate that the three control participants showed a sharp peak around $\varphi = 0$ and smaller ones at -2π and 2π rad, indicating frequency-locked movements in which the arms maintained a mirror-symmetric inphase relationship. Note, that there was no instruction whether inphase or antiphase should be adopted. Negative phase values correspond to cycles in which the secondary movement lagged behind the base movement.

While the two callasotomy patients JW and VP also show a peak at $\varphi = 0$, their distributions are much broader with values ranging from -5π to 20π rad. As detailed in the methods, relative phase was not adjusted with modulo 2π in order to identify drifts and phase wrapping. Typically, the secondary movement oscillated at a faster rate than the base movement (see Fig. 2 for an example).

The congenital acallosal participant RU showed a distinct pattern with peaks centered around π and $-\pi$ rad. For most of the cycles, this participant exhibited an antiphase relationship between the two oscillations. The negative φ values signaled that there was a tendency for the base movement to be performed faster.

Entrainment to bimanual rhythmic coordination

While Fig. 7 gives a clear indication that callosotomy participants show reduced phase- and frequency-locking when the two arms were performing rhythmic movements, the histograms obscure the time course of relative phase, i.e., whether the two cyclic movements were entrained in the beginning and drifted apart, or whether there was no phase locking from the initiation of the secondary movement. To address this question,

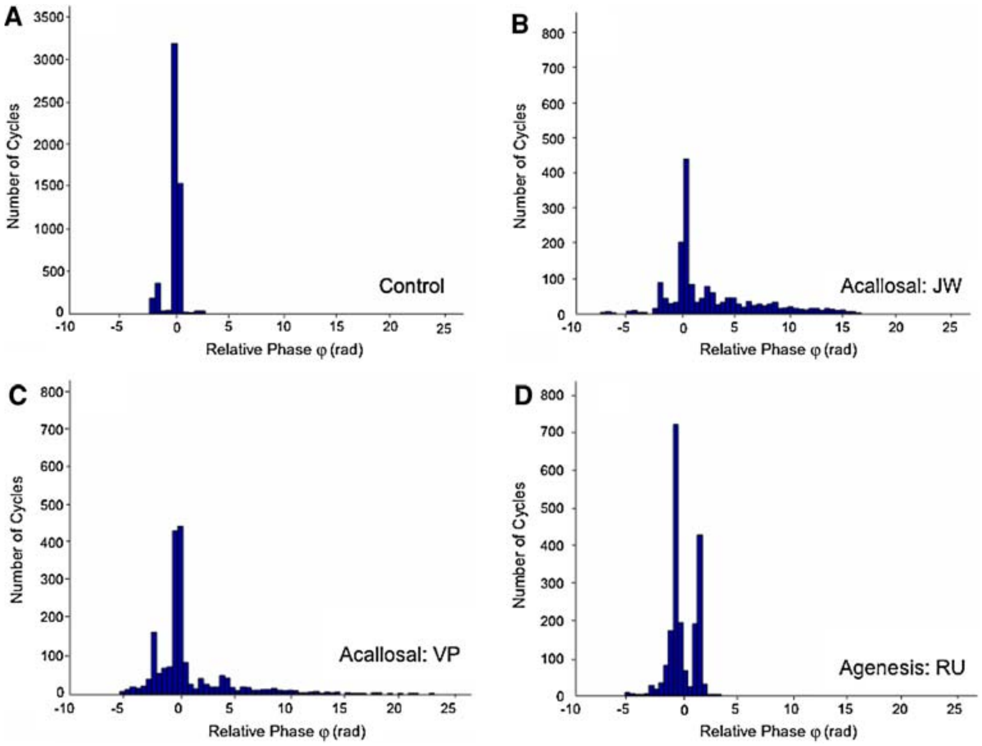

Fig. 7 Histogram for relative phase φ between the two arms after the secondary rhythmic movement has been initiated. The data of all three participants of the control group are pooled given their overall similarity. The data for the three acallosal participants are graphed separately. Relative phase is calculated in a cumulative fashion. Drifts and loss of cycles are indicated by *values* larger than 2π. *Positive values* indicate that the base movement leads the secondary movement. *Values greater or less than* 2π indicate that the movement of one arm lapped the other arm by one or more cycles

φ of the first four cycles following t_{init} were plotted as a function of cycle number (Fig. 8). The control participants show a relatively tight clustering around 0 rad at cycle 1, directly following initiation, and this coupling became increasingly tighter and after four cycles. The movements were either inphase or antiphase, with the former dominating in most trials. In contrast, the callosotomy individuals JW and VP show φ-values at cycle 1 that were spread out and even increased across the successive cycles. The agenesis participant RU shows a different picture: while the initiation φ is spread out following the imperative signal, there is a tendency toward antiphase movements with each cycle.

Discussion

A substantial literature has accumulated over the past two decades demonstrating that during bimanual movements there are marked spatiotemporal constraints between the two limbs. These studies have generally focused on symmetric rhythmic actions, identifying the contribution of biomechanical, neurophysiological, and perceptual factors that may underlie interlimb coupling. Considerably less attention has been dedicated to bimanual movements in which the task demands are distinct for the two hands even though these types of actions are more prevalent in daily behavior (Obhi 2004). In the present study, we compared the interactions that occur when an ongoing rhythmic movement is combined with either a similar, rhythmic movement or a discrete action (Wei et al. 2003). In particular, we explored how these interactions were affected in individuals lacking the corpus callosum. The comparison of healthy participants and acallosal individuals should provide insight into how direct interhemispheric communication across the corpus callosum contributes to spatiotemporal constraints that occur when a new movement is initiated with one arm when the other limb is producing an ongoing rhythmic movement. Moreover, by requiring either discrete or rhythmic secondary movements, we sought to further examine whether these two movement classes are associated with distinct neural systems.

Constraints on the initiation of a rhythmic or discrete secondary movement

Healthy participants exhibited strong spatiotemporal coupling when initiating a secondary rhythmic movement against a background of another rhythmic movement. Phase entrainment was evident at the moment of movement initiation, indicating that coupling was already present before the preparation of the secondary movement. This coupling was absent when a discrete movement was initiated, consistent with the findings of Wei et al. (2003) in healthy adults. In con-

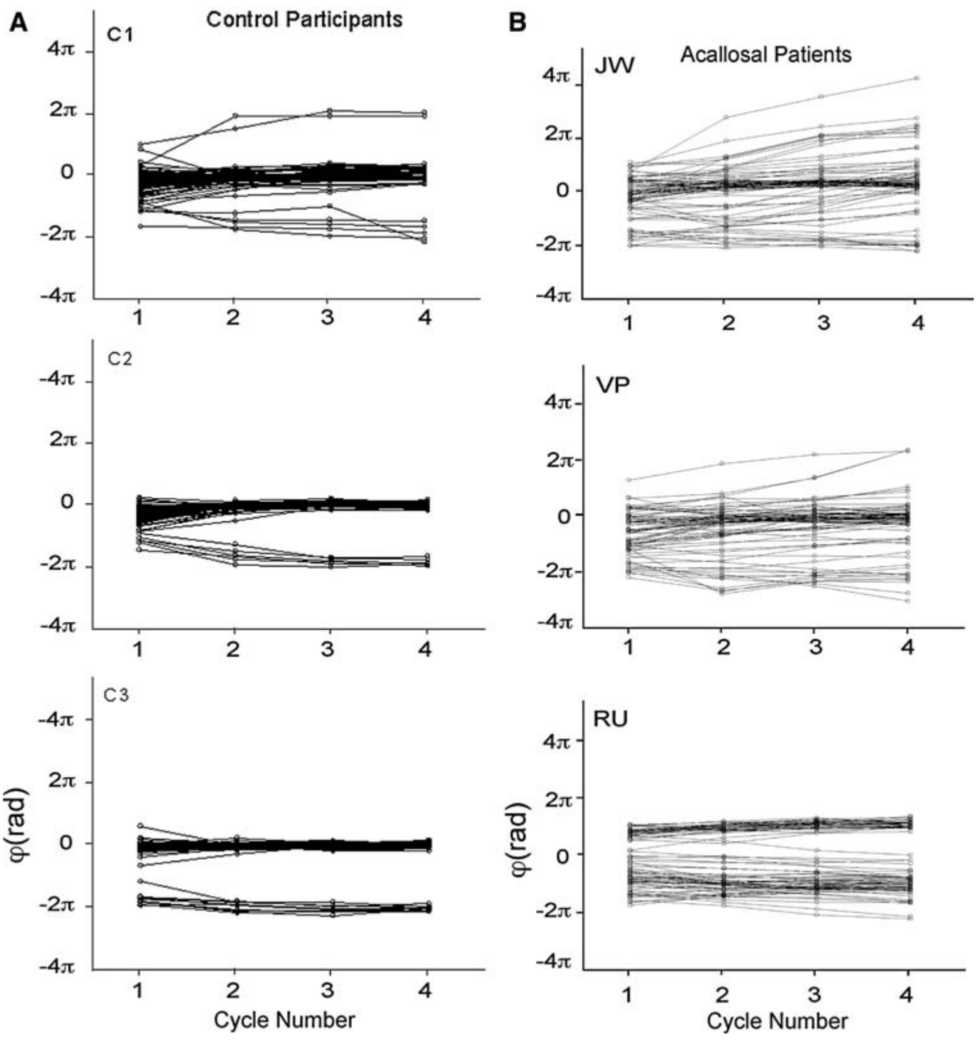

Fig. 8 Relative phase φ evaluated for the first four cycles following the initiation of the secondary movement for the control (**a**) and acallosal (**b**) participants

trast, this phase entrainment at movement initiation was absent in the acallosal participants for both discrete and rhythmic secondary movements. Moreover, these participants exhibited attenuated coupling during the bimanual phase of the rhythmic task, although the degree of this uncoupling varied across the three individuals. Taken together, the results from the control and acallosal groups indicate that spatiotemporal constraints observed during bimanual rhythmic movements are highly dependent on communication across the corpus callosum (Kennerley et al. 2002).

While the results point to a cortical locus of these interactions, the requisite neural regions remain unclear. Neuroimaging studies of bimanual interlimb coupling have revealed activation of premotor and posterior parietal cortex during rhythmic movements which increased when the coordination requirements were more challenging (Wenderoth et al. 2004, 2005). Similarly, interference arising during the planning and execution of spatially conflicting discrete reaching movements activates posterior areas of the parietal cortex (Diedrichsen et al. 2006). Moreover, in a patient undergoing a two-stage callosotomy operation, spatial uncoupling only became evident after the second, more posterior resection (Eliassen et al. 1999, 2000). Hence, we have proposed that the intermanual constraints in symmetric actions are due to the activation and transcallosal interactions supported by the parietal lobes (Ivry et al. 2004).

The lack of coupling between the two limbs when the secondary movement entails a discrete movement, in both the controls and acallosals, suggests that there is little confluence from the control signals for rhythmic and discrete movements. This hypothesis is further supported by imaging studies indicating the differential engagement of cortical and subcortical areas for these two classes of movements (Schaal et al. 2004). The results of the acallosal participants are especially informative. Previous studies have indicated that temporal coupling persists in callosotomy patients for discrete movements, regardless of whether these movements are made in isolation (Franz et al. 1996) or in a repetitive manner as occurs during finger tapping (Ivry and Hazeltine 1999; Tuller and Kelso 1989), although the variability of the inter-tap onsets may increase (Eliassen et al. 2000). In contrast, loss of temporal coupling is observed when rhythmic movements are produced in a continuous manner; that is, without any salient events such as contact or synchronization points (Kennerley et al. 2002). This dissociation has led to the hypothesis that a subcortical mechanism is engaged during movement initiation (Ivry et al. 2004). The lack of coupling in the current study would indicate that the initiation of a discrete movement does not require coordination with, or modification of the command signals for an ongoing rhythmic movement.

Perturbation of an ongoing rhythmic movement by the initiation of a secondary movement

The observed lack of phase entrainment during the initiation of the secondary movement, however, does not mean that the two actions were produced independently. Perturbations of the base movement were generally observed, and these effects were even more pronounced in the acallosal group. While the coupling of the two rhythmic movements in normal adults had less effect on the base movement, the initiation of a discrete movement introduced a transient perturbation in the ongoing rhythmic movement (also reported in Wei et al. 2003, although in different measures). Moreover, this perturbation was greater when the base movement was produced by the left hand. Keeping in mind that all participants were right-handers, this finding suggests a higher degree of stability for the dominant arm (Byblow and Goodman 1994).

The asymmetric nature of these perturbations suggests several interpretations. First, the asymmetries may be related to hemispheric specializations for motor control. For example, it has been proposed that the hemisphere contralateral to the dominant hand is more adept in the open-loop control of the trajectory of a movement, whereas the contralateral hemisphere is more adept in controlling endpoint locations (Serrien et al. 2006). The greater stability of the dominant hand in the current study follows if we assume that the continuous nature of the rhythmic movements emphasizes trajectory control over endpoint control (Wang and Sainburg 2005). Alternative asymmetric control hypotheses rest on the idea that the dominant/left hemisphere plays an essential role in skilled movements (see Serrien et al. 2006) or bimanual coordination (Viviani et al. 1998). As such, the left hemisphere would be more strongly involved in controlling both hands and the initiation of a secondary movement with the right arm could have a stronger perturbing effect on the non-dominant arm than vice versa.

Second, the asymmetry may reflect the demands on attentional resources. Initiating a secondary movement requires a shift in attention that may result in a transient reduction of resources devoted to the baseline task. An exemplary trial illustrates this reading: In Fig. 2c the participant fails to perform the instructed discrete movements and performs a cycle similar to the base movement. At the same time, he stops the base movement, potentially due to a shift of attention to the secondary movement. The effect of this is conceivably more pronounced when the baseline task is being performed by the non-dominant limb (Amazeen et al. 1997, 2005). Perturbations of the baseline movement were also observed for the acallosal participants and were, in fact, even higher than in controls. However, the perturbations were similarly high for discrete and rhythmic secondary movements, unlike in control participants where perturbations were modulated by the task demands of the secondary task.

One interpretation of these perturbations is that a subcortical mechanism associated with initiating the secondary movement influences the ongoing base movement. That is, the transient signal required to initiate the secondary movement may broadcast to descending commands for both hands (Ivry and Hazeltine 1999). The fact that this perturbation is similar for the discrete and rhythmic secondary conditions is consistent with the notion that this subcortical process is independent of the specific movement commands associated with the base movement.

The attentional hypothesis suggests an alternative interpretation. That is, the initiation of the secondary movement created a transient reduction in attentional resources devoted to the base movement. Such resource sharing effects between hemispheres are frequently observed in studies of callosotomy patients, even in the absence of task-specific interactions (reviewed in Gazzaniga 2000).

The present data sets do not allow us to make strong evaluations of the different hypotheses proposed for the observed perturbations of the baseline movement in the controls and acallosals. However, two aspects of the results are consistent with the attentional hypothesis. First, in a significant number of trials, the callosotomy patients showed a prolonged disruption of the rhythmic base movement (Fig. 2c). Indeed, the occurrence of these led the experimenter to provide occasional reminders prior to the start of each trial that the base movement should always be maintained. Second, the perturbation effect was reduced for the control participants when the secondary task was rhythmic. In this condition, the movements of the two arms can be integrated into a unified coordination pattern, or what might be viewed as a single task. For the acallosals, the perturbation effect was independent of whether the secondary movement was discrete or rhythmic, consistent with the hypothesis that for the acallosal individuals, the movement patterns associated with each hand are independent (Franz et al. 1996; Kennerley et al. 2002).

Differences between individuals lacking a corpus callosum due to agenesis or callosotomy

The rhythmic-initiation condition also contained a relatively long episode in which both arms moved rhythmically, revealing further interesting findings especially in acallosal individuals. First, continuous bimanual coupling was severely compromised in the callosotomy patients, similar to that reported by Kennerley et al. (2002). Second, the performance of the acallosal agenesis individual deviated from that observed in the other participants. Unlike the surgical callosotomy patients, he did not adopt different frequencies (and hence phase wrapping) for the two rhythmic movements. Nonetheless, his performance was distinct from the controls in that he generally adopted a predominantly antiphase coordination pattern. These results demonstrate that temporal coupling during continuous movements can become established in individuals who have always lacked a corpus callosum. This coupling could arise if a single hemisphere controls bimanual actions or due to the functional recruitment of an expanded anterior commissure (Serrien et al. 2001).

Differences in bimanual coupling between agenesis and callosotomy patients have also been reported by Serrien et al. (2001). Using a drawer opening and grasping task, individuals with acallosal agenesis synchronized the movements of the two hands at the start and end of the action. Callosotomy patients, however, lacked this synchronization with a complete uncoupling apparent in two of the patients when vision was absent. A similar pattern is evident in the current results with the stronger temporal coupling in the agenesis individual compared to the callosotomy patients. Note, though, that the performance of the agenesis individual differs markedly from the controls, both in the onset of the rhythmic movement (no phase entrainment) and the adopted phase. Thus, while agenesis individuals show greater intermanual constraints than those in whom this fiber tract was resected later in life, the communication over the corpus callosum underlies many of the constraints observed during bimanual rhythmic movements.

In conclusion, interhemispheric coupling and the role of the corpus callosum was further elucidated in a complex asymmetric bimanual task. While initiation of a secondary movement is mediated by callosal connections, leading to spatiotemporal independence of the two hands without the corpus callosum, perturbations exerted by secondary movements appear to be mediated through subcortical structures. Spatiotemporal coupling in bimanual rhythmic movement is significantly deteriorated without corpus callosum, but life-long experience can restore the coupling. For neurologically healthy humans the differences between tasks that involve discrete and rhythmic components are congruent with the hypothesis that discrete and rhythmic movements constitute two different movement types.

Acknowledgments This research was supported by the National Science Foundation (BCS-0096543 and PAC-0450218), the Tobacco Settlement Funds 4100020604, and the National Institutes of Health (HD045639, NS30296, NS40813).

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