A Cognitive Neuroscience Perspective on Bimanual Coordination and Interference

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Abstract

We argue that bimanual coordination and interference depends critically on how these actions are represented on a cognitive level. We first review the literature on spatial interactions, focusing on the difference between movements directed at visual targets and movements cued symbolically. Interactions manifest during response planning are limited to the latter condition. These results suggest that interactions in the formation of the trajectories of the two hands are associated with processes involved in response selection, rather than interactions in the motor system. Neuropsychological studies involving callosotomy patients argue that these interactions arise from transcallosal interactions between cortically-based spatial codes. The second half of the chapter examines temporal constraints observed in bimanual movements. We propose that most bimanual movements are marked by a common event structure, an explicit representation that ensures temporal coordination of the movements. The translation of an abstract event structure into a movement with a particular timing pattern is associated with cerebellar function, although the resulting temporal coupling during bimanual movements may be due to the operation of other subcortical mechanisms. For rhythmic movements that do not entail an event structure, timing may be an emergent property. Under such conditions, both spatial and temporal coupling can be absent. The emphasis on abstract levels of constraint makes clear that limitations in bimanual coordination overlap to a considerable degree with those observed in other domains of cognition.

keywords: bimanual coordination, spatial coupling, temporal coupling, response selection, event timing, callosotomy, cerebellum, neuropsychology

I. Introduction

A cardinal feature of human behavior is the generative capacity we have for using our upper limbs in the production of voluntary actions. With practice, we master the most complex skills-- the elegant scripts of the calligrapher, the lightning quick movements of the concert pianist, the life saving maneuvers of the heart surgeon. Even those of us who claim to be "all thumbs" are vastly superior to all other species in our ability to produce purposeful, manipulative actions.

We frequently speak of a person as being either left- or right-handed, implying that the dominant hand is more skilled than the non-dominant. Yet casual observation convincingly demonstrates that most actions are bimanual: Typing, using a fork and knife, and buttoning a shirt all require the integrated actions of the two hands. Thus, handedness may be more concisely thought of as describing the typical role-assignment of the hands (Guiard 1987). Of the skills that are included in assessments of handedness, many have a bimanual component (Oldfield 1971). For example, writing or cutting paper with scissors are essentially bimanual actions, with the non-dominant hand serving an essential support, or postural role. In sum, evolution is exploitive: Bipedalism has liberated our upper extremities and we take full advantage of this in our interactions with the world.

While the coordination of our two limbs in most tasks feels effortless and beneficial, much of the motor control research has focused on limitations, or constraints on coordination. By determining these constraints, fundamental principles governing the coordination of actions can be identified. This approach may also provide insight into the degrees of freedom problem articulated in the classic writings of Bernstein (see Whiting 1984), namely, how efficient control is achieved given the redundancy inherent in the motor system.

Limitations in the ability to coordinate bimanual movements have been widely studied with tasks requiring rhythmic, repetitive movements. One appeal of this approach is that tasks bear a similarity, at least superficially, to the most fundamental of multi-limb coordination tasks, locomotion. For example, it is assumed that our ability to produce rhythmic movements with the two upper limbs likely shares some of the constraints defining stable modes of locomotion, and indeed, may reflect the operation of similar neural mechanisms. The preference to move the two limbs in either an in-phase relationship (with the left and right arms moving in the same direction at the same time) or an anti-phase relationship (with the left and right arms moving in opposite directions at a given time) may stem from the fact that locomotion typically involves similar coordination modes. Given that these phase relationships are typically maintained between homologous effectors, researchers looking for the neural correlates of coordination have focused their attention on interactions along the motor neuroaxis (e.g., interneurons in the spinal cord or callosal connections between homologous cortical motor regions).

While recognizing the appeal of evolutionary arguments that attempt to establish common principles shared by locomotion and bimanual coordination, we believe that the two phenomena reflect fundamentally different forms of interactions between limbs (see also, Peters 1994; Semjen 2002). Whereas the motions of the limbs during locomotion are integrated to produce rhythmic, stereotyped movement patterns, the pattern of coordination in two-handed activities can be much more complex. In bimanual actions, the hands often perform distinct movements, whose relationship only becomes apparent when one considers the external goal of this action. For example, when tying shoelaces each hand follows a complex spatiotemporal pattern such that the movement onsets and trajectories for the two hands have no immediate symmetry relationship, but are nonetheless highly coordinated.

Recognition of this difference has led us to re-examine the constraints associated with bimanual coordination. Traditional studies of bimanual coordination have used tasks that mimic the rhythmicity and phase-relationships of locomotion. These approaches have led to a formulation of a set of constraints on bimanual movements arising from the interaction of the two movement patterns. In this chapter, we will review evidence demonstrating that many of these constraints have little to do with the motor system per se. Rather, they reflect limitations associated with processing at abstract, conceptual levels of the cognitive architecture. Our intent is not to discount the relevance of other sources of constraint. However, we believe that these more conceptual sources of constraint have been neglected in the literature on bimanual coordination. Appreciating the fact that many limitations of motor behavior reflect more general features of our cognitive architecture can also help us understand and explain our extraordinary ability to perform complex manual actions involving multiple effector systems.

II. Model tasks for exploring sources of constraint on bimanual movements

As noted above, the study of rhythmic, bimanual movements has been a very productive area of work in the motor control literature; indeed, one could say that the popularization of such tasks in the 1980's represented a true paradigm shift in the field (Kelso 1984). The rich data sets provided by such tasks were refreshing in contrast to the limited movement repertoire (button pressing and highly constrained movements) that characterized traditional studies of motor programming. By studying complex, repetitive actions, the researchers struck on an experimental procedure that was amenable to concepts and analytic tools emerging in other disciplines of the biological and physical sciences. Moreover, this approach held the promise of being applicable to more ecologically valid tasks that demanded the continuous coordination of the two hands for long periods of time.

Consider one variant of these tasks, coordination of wrist flexion and extension movements of both hands. The marked preference for certain phase relationships, the dependency of pattern stability on movement rate, and the asymmetry in the transitions between different stable states are characteristic of certain classes of dynamical systems. The behavior can be formally captured with a component model, in which the movement of each limb is represented by a non-linear oscillator, with its stability described in terms of limit cycle dynamics. Interactions between the limbs arise due to non-linear coupling terms that connect the dynamics of the oscillators (Haken et al. 1985).

While this component model provides an elegant account for the emergent properties of the dynamical system, its formulation is, in essence, abstract. On a representational level it remains unclear whether the component oscillators refer to the position and velocity of a limb, the contraction of agonist and antagonist muscles or more abstract spatial codes. In a similar vein, the theory remains neutral in terms of the neural implementation of its components.

This work emphasized the prominent temporal constraints associated with bimanual movements. People have great difficulty producing movements in which the limbs are not moving at identical or integer ratio frequencies (1:1, 1:2). Even skilled musicians are subject to this constraint, limited in the manner in which they produce complex polyrhythms (e.g., Klapp et al. 1985; Krampe et al. 2000). While these powerful temporal constraints are most evident in repetitive movements, they can also be seen in simpler contexts. A hallmark of bimanual reaching movements is the tendency for the two arms to initiate and terminate at approximately the same point in time, even if the movements span different amplitudes (Kelso et al. 1979).

Other constraints in the production of bimanual movements can be observed on purely spatial measures. Consider the task of simultaneously drawing two shapes, either two lines or a circle with one hand and a line with the other (Figure 1). Spatial assimilation effects are readily observed in the incongruent condition with each shape becoming more elliptical compared to when both hands produce lines or circles (Franz et al. 1991). Similar assimilation effects are observed when people attempt to draw lines of unequal amplitude (Heuer et al. 1998) or produce isometric forces of unequal intensity (Steglich et al. 1999). In all of these conditions, the interference between the two actions occurs on a background of tight temporal coupling between the hands (i.e., similar frequency and stable phase relationship for the repetitive movements).

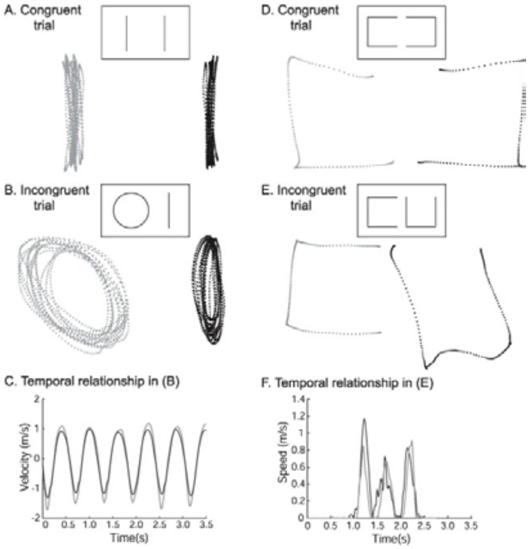


Figure 1. Spatial interference in two bimanual drawing tasks. A, B: In the line-circle task, participants are instructed to simultaneously draw two lines (congruent movements) or a circle and line (incongruent movements). The trajectories reveal greater variability in the incongruent condition. C: movement velocity along the y-direction for the left hand (gray) and right hand (black). D, E: In the three-sided figure task participants are instructed to simultaneously draw three-sided figures that are either congruent (symmetric) or incongruent (successive sides are orthogonal). Neurologically healthy participants exhibit interference in the incongruent condition. F: Temporal coupling is strong during the incongruent three-sided drawing task. The data are plotted as the tangential velocity of each hand over time. Adapted from Franz et al. 1991, 1996.

It has been hypothesized that these temporal and spatial interactions arise on separable levels of the control hierarchy (e.g, Heuer 1993). A study involving split-brain patients also suggests that these sources may be separable in terms of their neural implementation (Franz et al. 1996). These patients have undergone resection of the corpus callosum as part of a radical treatment for severe, chronic epilepsy. The procedure eliminates the primary pathway of communication between the two cerebral hemispheres. In this study, the patients and controls were required to simultaneously draw two three-sided boxes, one with each hand. The target shape for the left hand was presented in the left visual field while the target shape for the right hand was presented in the right visual field. The critical comparison was between conditions in which the orientation of the two shapes was either congruent or incongruent. For the congruent conditions the two shapes were mirror symmetric, for the incongruent condition, one shape was rotated by 90 degrees with respect to the other (Figure 1d,e). ,

For the control participants, the incongruent condition was quite taxing. Compared to the congruent condition, reaction times and movement times were inflated, and spatial assimilation effects were frequently observed. In contrast, the split-brain patients performed similarly on the congruent and incongruent conditions. There was no evidence of any spatial interactions in the productions of the two hands. Interestingly, the patients' bimanual movements remained temporally coupled. Similar to the control participants, the patients initiated each of the three sub-movements in close synchrony. Thus, the patients exhibited persistent temporal coupling in the face of complete spatial uncoupling.

The lack of spatial interactions indicates that spatial cross-talk arises from interactions that involve the corpus callosum. Two neurological accounts have been offered to explain the persistent temporal coupling in the face of spatial uncoupling. First, a single hemisphere may control movement initiation for both hands (Stucchi and Viviani 1993). Alternatively, a subcortical mechanism with access to both effectors may gate the implementation of cortically-generated motor commands (Ivry and Hazeltine 1999; Ivry and Richardson 2002).

The study of split-brain patients by Franz et al. (1996) demonstrates that, at least under certain conditions, constraints associated with trajectory formation can be dissociated from those associated with temporal coordination. This should not be taken to imply that the spatial and temporal aspects of movement can always be decomposed; indeed, later we will argue that for certain types of movement, temporal constraints are an integral part of spatial constraints. However, the dissociation does make clear that constraints on bimanual coordination have multiple sources. In the following sections, we explore these constraints, focusing first on an account of the spatial interactions observed during bimanual movements and then returning to the issue of temporal coupling.

III. Representational basis of spatial constraints

Why do bimanual movements exhibit profound spatial interactions in normal participants? The performance of split-brain patients indicates that these interactions result from interhemispheric communication across the corpus callosum. But between which cortical areas and at which level of representation do these interactions occur? The neural locus was examined by Eliassen et al. (1999) who tested a patient on the three-sided figure task over the course of several months. During this period, the patient underwent two successive operations, the first involving resection of the anterior region of the corpus callosum and the second in which the remaining callosal fibers were cut. It was only after the second operation that the patient became spatially uncoupled. This led the authors to suggest that the critical spatial interactions are a reflection of communication between parietal regions, that is, between regions that play a role in the planning, rather than in the motor execution, of spatial trajectories (see also Serrien et al. 2001). Single cell recordings in primates indicate that neural coding of movement in the parietal cortex is best described in terms of spatial direction, rather than in terms of dynamical properties such as force (Kalaska et al. 1990). Thus, evidence from split-brain studies speaks against the possibility that interactions occur between regions associated with activation of homologous muscles.

This conclusion is further supported by studies that have tried to distinguish between symmetry defined in terms of muscular activation and symmetry defined in terms of movement direction. One of the most robust phenomena in rhythmic studies is that symmetric movement patterns are more stable than asymmetric patterns. For example, with the forearms pronated, wrist flexion/extension is more stable when the movements are symmetric. However, in this situation the symmetric pattern involves both symmetric movement directions and homologous muscle activation. If one hand is oriented with the palm facing down and the other hand with the palm facing up, these two factors can be dissociated. In this condition, performance is stable when the hands move up and down together, even though one wrist is flexing while the other is extending. A more compelling preference for common directional coding occurs when the effector combination involves an arm and a leg (Baldissera et al. 1982, 1991). Thus, cross-talk can occur at a level in which movement direction is represented rather than patterns of muscular activation (Swinnen et al. 2002; but see Riek et al. 1992).

III.1 Direct reaching

The observed bias towards movements that are symmetric with respect to the body axis seems counterintuitive when considering how we typically use our limbs. Consider someone clearing the dinner table after a meal, using the right hand to pick up a glass and the left hand to pick up a plate. The movements that bring the hands towards the objects are likely to be asymmetric as the objects are located in different directions and at different distances. Two different grasps have to be shaped and very different grip and lift-forces have to be applied to the objects. If the actions of each hand were subject to strong assimilation effects, we might expect to see that one or both objects would be missed, or the hand shapes would be inappropriately formed. However, we seem to be able to perform this task effortlessly.

These considerations led us to explore spatial interactions for bimanual movements under different movement cueing conditions (Diedrichsen et al. 2001). In these experiments, people were instructed to make two reaching movements on each trial, one with the left hand and one with the right hand. The movement amplitudes could be either short or long. Thus, the bimanual combination could be classified as congruent (i.e., both long or both short) or incongruent (i.e., one short and one long). The critical manipulation centered on the manner in which the movement directions were cued (Figure 2). In the symbolic cueing condition, the four possible target locations (two end locations for each hand) were visible at all times, and the letters "S" and "L" were used to indicate the target locations. One letter was presented in the left visual field to indicate the left-hand movement and the other letter in the right visual field to indicate the right-hand movement. In the direct cueing condition, the target locations were cued by the onset of the target circles, one appearing on each side.

Dramatic differences were observed between the two cueing conditions. In the symbolic condition, congruent responses were initiated much faster than incongruent responses. This result is consistent with previous findings of a preference for symmetric bimanual movements. However, when the movements were directly cued, people were much faster to initiate their movements and, more importantly, there were no differences in reaction time. A similar dissociation was found for movements made in mirror-symmetric or orthogonal directions. On congruent trials, the required movements were either both in the lateral or both in the forward direction; on incongruent trials, the movement directions were orthogonal to each other. Again, reaction time costs were completely eliminated when the target directions for each hand were directly cued by the onset of stimuli at the two target locations. In addition, the initial direction of the movement was in the wrong direction on a significant percent of the trials in the symbolic, but not in the direct condition. The absence of any cost in the initiation of asymmetric movements in the direct condition is underscored by the fact that reaction times on the bimanual direct cueing conditions were similar to those observed in a control condition in which only unimanual reaches were performed.

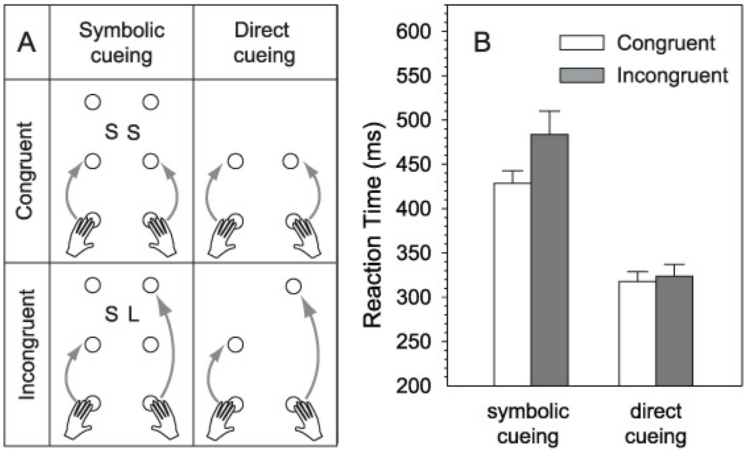


Figure 2. Direct reaching experiment. A: In the symbolic condition, the letters indicate the movement amplitude for the hand on the corresponding side (S=short amplitude; L=long amplitude). In the direct condition, the amplitudes were indicated by the appearance of the target circles. Movements could be either congruent (same amplitude) or incongruent (different amplitudes). B: Average reaction times for congruent and incongruent trials for the direct and symbolic conditions, averaged over the two hands. Error bars indicate between-subject standard error. Adapted from Diedrichsen et al. 2001.

The costs observed in the symbolic condition are manifest prior to the initiation of the actions. For both the direct and symbolic conditions, we did not observe assimilation effects in terms of movement amplitude or increased endpoint error in the incongruent condition. Once the movement targets were selected and the movements initiated, even asymmetric movements proceeded with minimal interference. These results stand in drastic contrast to studies that have used fast reversal movements to study amplitude assimilation effects during bimanual movements (e.g. Spijkers and Heuer 1995). The differences in results between these and our studies may be due to the fact that the movements in our experiment (Diedrichsen et al. 2001) were executed towards visual targets, while in latter studies the movements were produced to match a internally specified amplitude.

III.2 Conflict resulting from the interaction of abstract spatial codes

The contrast in performance between symbolic and direct cues suggests that the constraints associated with spatial interactions during bimanual movements have little to do with the characteristics of the movements per se. The required movements under the symbolic and direct cueing conditions are identical-- participants move from a starting circle to target circles in both conditions. Except for errors in the initial trajectory in the symbolic conditions, the movements themselves are quite similar. Given these observations, we assume that processes involved in motor programming, defined as the specification of motor commands and motor execution, are highly similar in the two cueing conditions. If a preference for producing symmetric bimanual actions was a property of the motor system-- for instance, resulting from a bias to activate homologous muscles or plan movement trajectories of a common direction-- then we would have observed congruency effects in both the symbolic and direct cueing conditions.

If the preference for congruent movements is not associated with the motor system, how should we characterize the psychological operations that underlie the spatial interactions during bimanual movements? One possibility is that the interactions arise at a perceptual level. Mechsner, Prinz, and their colleagues (Hommel et al. 2001; Mechsner et al. 2001) have favored this interpretation, arguing that the actions are coded in terms of expected sensory consequences. In a series of elegant experiments, these researchers demonstrated that the two hands can produce stable asymmetric movements when the feedback conditions are altered such that the sensory signals are symmetric. They propose that the coding of the expected sensory consequences plays a critical role in the selection and planning of the movements. Given that the perceptual system is highly sensitive to symmetry, movements resulting in symmetrical visual feedback might be supported by more stable representations.

One perception-based explanation for the costs observed in the symbolically cued bimanual movements centers on processes involved in identifying the various cues. The stimuli are identical in the congruent condition (e.g., “SS”), whereas they are different in the incongruent condition (e.g., “SL”). However, in a follow-up experiment we eliminated the cues altogether and let participants point to colored circles. The color assigned to each hand was constant within each experimental session. Although there was no need to identify a symbolic cue, participants were much slower to select targets of different colors than to select targets of the same color (Diedrichsen et al. 2003). In a different study, arrows and letters were used to cue the movements for the left hand and right hands, respectively. Thus, nonidentical stimuli were used to cue the congruent and incongruent conditions. Nonetheless, the reaction time cost for incongruent movements was similar to that observed when the same set of symbolic cues was used for both hands (unpublished observations).

Together, theses results suggest that the primary source of spatial interactions during bimanual movements is associated with an intermediate level of processing. On this level the action is represented in relatively abstract terms, without explicit reference to the eliciting stimulus or the execution-related details of the response. Consider a symmetric trial when each hand draws a three-sided square with the open side on the top. Each segment involves the specification of common trajectories for each hand: down, inward, up. Now consider the planning requirements for an orthogonal trial, one in which the open side for the left hand is on top and the open side for the right hand is on the right side. The situation here requires the generation of multiple, spatial codes. The initial movement for the left-hand involves a downward trajectory; for the right hand, a leftward trajectory. For the second segment, the left hand must move rightward and the right hand downward. We hypothesize that the costs observed on orthogonal trials arise from interactions between these various spatial codes. Not only are there conflicts between the component trajectories for each hand, but the spatial trajectories are presented on the left and right sides of the screen and must then be assigned to the left and right hand (Diedrichsen et al. 2003). The overlap between the codes defining the target trajectories and effectors is a ripe source of interference (see Kornblum et al. 1990).

In contrast, action goals for directly cued movements are unlikely to be specified in terms of trajectories or movement paths. Rather, the goals are likely to be related to the endpoint locations. As such, the degree of conceptual overlap is similar for congruent and incongruent movements. Both require the representation of two distinct locations. The lack of a cost on bimanual trials suggests that the representation of multiple locations can be generated and maintained as well as that of a single location.

Support for this hypothesis comes from a recent study, in which we compared different types of cueing when performing the three-sided box tasks (Figure 3). In the symbolic condition, the two target shapes were presented above the drawing surface and the participants reproduced the shapes. In the direct reaching condition, two target lights appeared, one on the left and the other on the right. The participants reached to these locations. As soon as their hands entered these target locations, new targets appeared indicating the next locations. The participants were instructed to immediately continue on to the next pair of targets. In this manner, the participants produced the three-sided trajectories, but only by moving from one direct cue to the next. For the tracing condition, the target shapes were presented directly on the drawing surface and the participants were asked to simply trace the two shapes simultaneously.

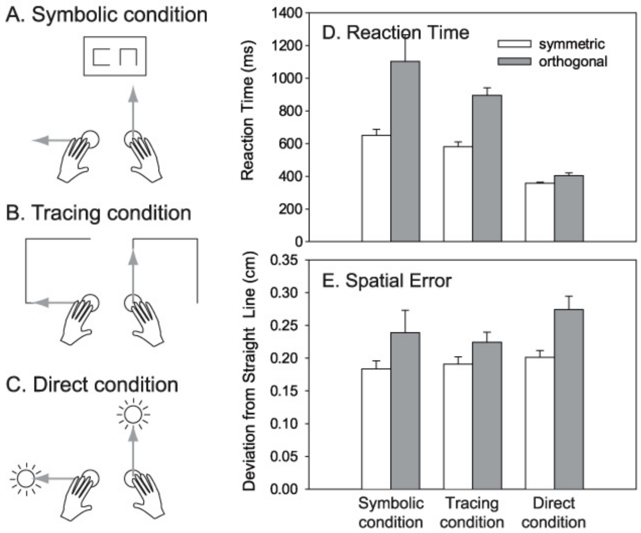


Figure 3. Three-sided figure drawing task with three different cueing conditions. A: In the symbolic condition the movements were instructed by small pictures of the target patterns, presented at the top of the table surface. B: In the tracing condition, the target patterns were presented in full size and the participants were instructed to trace these templates. C: In the direct condition, the movements were cued by the successive illumination of each corner location; the complete pattern was never visible. D: Reaction time results for the three conditions. E: Spatial error, calculated as the average deviation of for straight-line trajectories (Diedrichsen, Hazeltine, & Ivry, unpublished data).

As instructed, the participants initiated the movements with each hand in a near-simultaneous fashion. Thus, the effects of bimanual interference are most evident in the initial reaction times, although a similar pattern was evident in the pause between the first and second segment. As can be seen in Figure 3, the direct reaching condition was much easier than the other two conditions. Minimal RT differences were observed in the symmetric and orthogonal conditions. In fact, informal observation suggests that the participants were typically unaware of whether a particular trial had required a symmetric or orthogonal stimulus. Most interesting was the performance of the participants in the tracing condition. One might suppose that this condition would be similar to the direct cueing condition since participants simply have to move from one visible target location to the next. However, there was a clear cost on orthogonal trials compared to the symmetric trials. We assume that, by presenting the full shape prior to the initiation of the movements, the participants code the stimuli as target shapes composed of a series of directional vectors. When represented in this manner, interactions between varying spatial codes occurs.

Interestingly, we did not find systematic differences between the conditions on measures of movement accuracy. Figure 3e shows the deviation from a straight-line path averaged over the three segments. The spatial costs for the asymmetric shapes were significant in every cueing condition. As these spatial costs persist even after extended preparation time and independent of cue, they likely constitute static, execution-related sources of inference (Heuer 1993; Heuer et al. 2001).

This experiment demonstrates again that bimanual interference results from interactions of codes on multiple levels (Cardoso de Oliveira 2002) and that the manner in which actions are conceptualized may have a dramatic influence on whether or not spatial interactions are manifest in the preparation of bimanual movements. With direct cues, the actions are specified in terms of target locations. For symbolical cues, the translation of the cues into actions entails a direction-based representation. This distinction touches on a long-debated issue in the motor control literature, namely whether movements are specified in terms of endpoint locations or movement trajectories (e.g. Abrams and Landgraf 1990). Our conjecture is that both of these forms of coding may be relevant, with the form of representation dependent on how the task is conceptualized.

III.3 Neural systems for direct and symbolic actions

It is interesting to consider the relationship between direct and symbolically cued movements and the dichotomy that has been made between the dorsal and ventral visual pathways in the cerebral cortex (reviewed in Goodale and Milner 1992). In simplest form, the dorsal stream across occipital-parietal cortex is hypothesized to be essential for visually guided actions. For example, reaching towards directly cued targets is impaired after lesions to the superior parietal lobe (Perenin and Vighetto 1988; Rushworth et al. 1997). Process-based accounts of the computations subserved by the dorsal stream include the representation of location-based codes and the coordinate transformations required for the translation of sensory information into reference frames useful for action (e.g., Flanders et al. 1992; Cohen and Andersen 2002).

The lack of bimanual interference observed in our reaching studies is in accord with observations that representations within the dorsal pathway are relatively immune to illusions associated with object recognition processes. For example, distortions induced by contrast effects are absent when perceived size is inferred by the aperture of a grasping action or the endpoint location of a pointing response (Goodale and Milner 1992). Correspondingly, the lack of cross-talk between the two limbs in bimanual reaching movements suggests that processing within the dorsal stream of each hemisphere is relatively immune to processing within the other hemisphere, even when these processes are used for the online control of movement.

We have tested this idea in a reaching task in which the target locations were perturbed right around or just after movement onset. Such perturbations are readily accommodated: Adjustments of the movement trajectories occur rapidly and in a smooth fashion. They can typically be detected in the movement kinematics 150-200 ms after the target has been displaced (Goodale et al. 1986; Prablanc and Martin 1992). The high processing speed of the system that allows for closed-loop control even during quick movements (Desmurget and Grafton 2000) has led to its characterization as an "auto-pilot" system that automatically guides the hand towards a visual target without intervention of consciousness. As such, involuntary adjustments can be observed in situations in which a target is displaced but participants are instructed not to adjust their movement (Day and Lyon 2000; Pisella et al. 2000).

In the bimanual version of this task (Nambisan et al. 2002), either one or both of the targets were displaced at the time of movement onset. The results suggest that the reaching movements of each hand are controlled by independent on-line control mechanisms when the targets are directly specified. Performance on trials in which both targets were displaced was very similar to performance on trials in which only one of the targets was displaced and, in fact, similar to that found on unimanual trials. However, there were some small signs of cross-talk between the two hands during the adjustments. Specifically, when the right hand adjusted to a rightward jump, the trajectory of the left hand was also transiently perturbed to the right, a perturbation that was quickly corrected for, before the hand reached the target. Most importantly, this perturbation was in the direction of the displacement of the other target in terms of exocentric coordinates. Spatial interference occurring during non-visually guided movements is usually manifest in egocentric coordinates (Swinnen, et al. 2002). Thus the perturbation found in this situation seems to arise from retinal or eye-movement related signals, and may be fundamentally different from the interference underlying the preference for symmetric movements in the context of non-visually guided movements.

While the dorsal stream may be sufficient for directly cued movements, symbolically cues would seem to require the involvement of more ventral visual pathways. In the initial formulation of the dorsal/ventral dichotomy, the ventral stream was considered as part of the perceptual pathways, and in particular with higher-order object recognition. More recently, the role of such processes in the control of action have been acknowledged. For example, with symbolic cues, ventral areas are likely necessary to identify the stimuli and associate them with the appropriate motor output, perhaps in conjunction with premotor cortex. By this hypothesis, we would assume that symbolically mediated actions entail an additional processing stage, one in which the abstract symbols are mapped onto action codes.

There are a number of reasons why bimanual interference might be observed for actions that engage the more cognitive operations associated with the ventral pathway. Psychologically, the response selection processes required for linking abstract stimuli to intended actions pose a prominent bottleneck in multi-task performance (reviewed in Pashler 1994). Moreover, such interference is likely especially pronounced when the tasks require overlapping representations as we hypothesize is the case for the abstract, trajectory-based codes we associate with symbolically cued actions. On the neural level, we assume that such interactions occur across callosal pathways given the absence of such interference in the split-brain patients (see also, Ivry et al. 1998).

Does this mean that callosal fibers are more prominent for regions within the ventral pathway compared to the dorsal pathway? Indirect support for this conjecture can be found in the physiological literature. While receptive field size increases as one progresses along either the dorsal or visual pathway, a hallmark of inferotemporal cortex is that these neurons respond to stimuli from either visual field. Such neurons must have access to the output from upstream cells in either hemisphere. Alternatively, the lack of interference found with directly cued movements may not reflect a dearth of callosal connections along the dorsal pathway, but rather reduced representational overlap between such actions. As noted above, a location-based code entails two distinct target locations for both congruent and incongruent movements.

A different account of why bimanual interference is restricted to symbolically cued movements comes from recent elaborations of the two visual stream model. It has been proposed that the dorsal and ventral streams sandwich a third stream involving the inferior parietal cortex and that this pathway is highly lateralized (Johnson-Frey in press). Damage to inferior parietal cortex in the left hemisphere in humans leads to the severest forms of apraxia (Leipmann 1907; Heilman et al. 1982) and imaging studies show pronounced activation of this region for actions requiring the representation of complex object properties, for example when interacting appropriately with tools (Johnson et al. 2002). Furthermore, the role of the inferior parietal lobe appears to be most prominent in the planning of actions rather than their on-line control (Glover in press). Taken together, the functions associated with this lateralized region would seem to match those we assume are required in the translation of symbolic cues into actions (see also Schluter et al. 1998; Schluter et al. 2001).

From this perspective, the left inferior parietal cortex would be expected to play a prominent role whenever actions are planned on the basis of internal goals or symbolic cues; that is, without the affordance of direct targets. Notably, this hypothesis would assume that these operations are required for symbolically cued movements produced with either hand. Interference would be expected to arise when a single processor is trying to plan two incompatible actions. By this hypothesis, bimanual interference for symbolically cued movements reflects a functional hemispheric asymmetry for the mediation of symbolically cued actions. The lack of interference for directly cued movements is attributed to a more symmetric brain organization for regions involved in visually-guided actions.

It is difficult to assess the relative merits of these neural conjectures at present. An appealing feature of the laterality account is that it acknowledges the prominent role for the left hemisphere in the representation of complex, abstract actions. The laterality hypothesis would suggest that split-brain individuals should show a selective impairment in producing symbolically-cued movements with the left hand. While this has not been apparent in our bimanual studies, a recent study reports a left-hand apraxia in some of these individuals (Johnson-Frey, Funell, & Gazzaniga, submitted). Moreover, the apraxia symptoms were especially pronounced for symbolically-mediated actions, for example, when the eliciting cues were pictures rather than real objects. In addition to behavioral tests, physiological studies should prove useful for evaluating the neural hypotheses sketched above. To date, few neuroimaging studies have focused on the manner in which actions are cued, especially with respect to bimanual coordination.

III.5 Spatial constraints revisited

To summarize, we posit that the ease and proficiency with which different bimanual actions are performed is largely determined by the manner in which the tasks are represented and controlled. The issue of task representation has received little attention, yet provides a powerful account of situations that produce spatial interactions during bimanual movements and, as important, situations in which such interactions are essentially absent.

In much of our work we have focused on the preparation phases of the movements. These phasic constraints are clearly influenced by the way the task is cued and conceptualized. However, many constraints on bimanual movements seem to be static in the sense that they do not change with more or less preparation time (Heuer et al. 2001). These have been attributed to lower levels of the motor system, evident during movement execution.

However, recent work has shown that cross-talk during the execution of repetitive movements is also dominated by the manner in which the movement goal is represented. (see Mechsner et al. 2002; Weigelt and Cardoso De Oliveira 2003). Franz et al. (2001) provide a particularly telling example in a study in which each hand traced a semi-circle. In one condition, the two movements started and ended at the same locations, creating an overall shape of a circle. In the other condition, the starting and ending points were spatially displaced, creating an overall shape of two inverted semi-circles that approach each other at the midpoint (Figure 4). Although the two target patterns are both symmetric and involve similar combinations of muscular actions, people were more adept in the former condition. This result was attributed to the fact that the circle is a simpler and more familiar pattern. We note, though, that both combinations of the semi-circles were symbolically cued. Thus, as with our pointing studies, the degree of conflict appears to depend on goal-based representations that govern the action. Swinnen and colleagues (e.g., Swinnen et al. 1997) have made a similar point, demonstrating that the profound interference observed during the production of complex bimanual trajectories can be rapidly overcome when visual feedback requires the participants to focus on an integrated representation of the action goal.

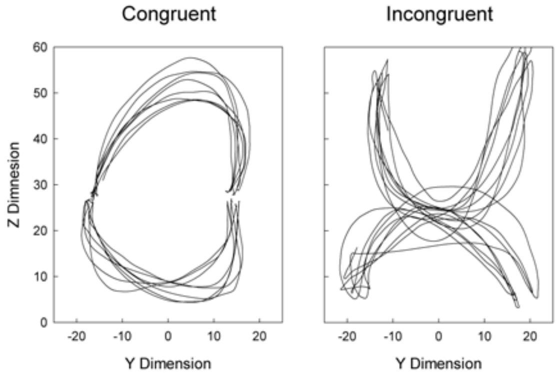


Figure 4. Familiarity of target shape influences the extent of bimanual interference. For both conditions, the participants produced two semi-circles in mid-air, one with each hand. In the congruent condition, the circles were aligned such that the hands were closest at the endpoints. In this way, the hands traced a circle. In the incongruent condition, the hands were closest at the midpoint. The patterns were drawn repetitively. Variability is higher for the unfamiliar curved X's. Adapted from Franz et al. 2001.

What has been underappreciated in the bimanual literature is the extent with which researchers have relied on movements that are symbolically cued and often executed without a visual external goal. Even when templates are provided, they are used to provide a general trajectory reference and as such, are another form of a symbolic cue. We believe that the reliance on tasks that entail symbolic representations has led to the general impression that interference between the movements always occurs in a muscle-related or egocentric coordinate frame and that our ability to produce asymmetric bimanual movements is highly constrained. Our work with directly cued movements leads us to conclude otherwise, at least in terms of spatial constraints. Interference in this situation may be minimal and often occur in an exocentric reference frame (Nambisan et al. 2002).

As noted in the Introduction, studies of bimanual coordination have tended to not use tasks that require the two hands to operate in a synergistic fashion. We would argue that when the actions of two hands are conceptualized as reflecting independent goals, the limitations on performance reflect constraints similar to those identified in the dual-task literature (Duncan 1979; Hazeltine et al. 2003; Pashler 1994) rather than processes that are engaged specifically during bimanual movement.

IV. Representational basis of temporal constraints

We now turn to the second major group of constraints, those between temporal features of the movements. When making discrete bimanual reaching movements, people tend to initiate and (approximately) terminate the movements of the two hands in synchrony (Kelso et al. 1979; Marteniuk and Baba 1984). This coupling is even more prevalent during rhythmic movements. We adopt a common frequency for each limb and, without extensive practice, are limited to only two stable phase relationships, in-phase and anti-phase. Even skilled musicians are limited in the flexibility with which they time the movements of their two hands, with their performance generally indicative of an integrated temporal representation rather than a situation in which the timing of each hand is independently controlled (Klapp et al. 1985; Krampe et al. 2000).

Temporal coupling has provided a cornerstone for the dynamic systems approach to the study of motor control. Our movements involve effectors that are physical entities. As such, movements must respect the laws of gravity, inertia, and mechanics (Kugler and Turvey 1987). This approach has produced rigorous formalisms to describe and predict motor behavior across a wide range of situations including unimanual movements, bimanual movements produced by a single person, or the interactions that occur between the movements of different individuals (Kelso 1995). These models have been expressed in terms of abstract dynamics, prompted by the desire to provide a description at a general level. With their focus almost completely on movement trajectories, these general formalisms have failed to provide process models, a description of the neural and psychological representations and processes that might underlie the observable coordination phenomena.

In this section, we review our recent work on this problem. Similar to what was described in the discussion of spatial constraints, we will argue that the manner in which action goals are represented strongly influences temporal constraints (Semjen 2002), as well as the neural correlates driving these phenomena.

IV.1 Phase stability and the representation of rhythms

A common formalism for describing temporal constraints associated with rhythmic bimanual movements is that of coupled oscillators. Each limb is described as a limit-cycle oscillator with the interactions between two such oscillators captured by a coupling term (e.g., Haken et al. 1985). When expressed in this manner, a concise description of the dynamics can be obtained. The interactions between the oscillators allow the limbs to maintain a common frequency, even when they have different preferred frequencies (e.g., Turvey 1990). Moreover, the abstract dynamics dictate that certain phase relationships will serve as attractors, with the specific strength of such attractors frequency dependent.

Yamanishi et al. (1980) provided one of the first studies to explore the utility of the coupled oscillator model. They used a simple bimanual finger-tapping task. Each hand was required to tap at 1 Hz. The critical independent variable was the target inter-tap interval (ITI) between successive taps of the two hands. In separate blocks, the ITI ranged from 0 ms to 900 ms in steps of 100 ms. Expressed in terms of relative phase, an ITI of 0 ms corresponds to in-phase tapping and an ITI of 500 ms corresponds to anti-phase tapping. The other target ITI's correspond to more complex target phases (e.g., an ITI of 100 ms is a target phase of 36 degrees).

As predicted, participants were readily able to perform the task when the target ITI was 0 ms or 500 ms. Performance for the other ITI's was less stable and there was a pronounced tendency for the produced phase to be attracted to either the in- or anti-phase pattern. For example, when the target ITI was 400 ms or 600 ms, the participants tended to produce ITI's with mean values closer to 500 ms. On various measures, the coupled oscillator model provided a good account of the data. The model captures the attraction towards the in-phase and anti-phase patterns, as well as the dependency of pattern consistency (e.g., variability of relative phase) as a function of the target phase.

While a coupled oscillator model provides an elegant description of performance in this task, an alternative process model should be considered. When viewed as an integrated pattern, the alternating taps define subintervals that divide the 1000 ms within-hand ITI. These subintervals constitute a rhythmic pattern. The 0 ms and 500 ms ITI conditions create simple rhythms, with subinterval durations of 1000 ms and 500 ms in the in-phase and anti-phase patterns, respectively. The subintervals for the other target ITI's define much more complex rhythmic patterns. For example, for the 600 ms ITI, the successive subintervals are 600 ms and 400 ms, forming a pattern in which the ratio of the longer to shorter interval is 3:2. In the 800 ms ITI, the ratio would be 4:1. Perhaps people represent the temporal goal in this task to create subintervals that match the target ratios. Many studies have shown that people have a strong bias to perceive/reproduce temporal patterns that form simple ratios (Collier and Wright 1995; Essens 1986; Povel 1981). When seen from this perspective, the attraction to in-phase and anti-phase patterns might reflect a bias to the simplest of ratios, the 1:1 ratio created by the isochronous patterns.

To compare the coupled oscillator and simplified rhythm representation hypotheses, Semjen and Ivry (2001) replicated the Yamanishi et al. study with one critical difference; In addition to the bimanual condition, participants were also tested in a unimanual condition. For this condition, a single finger was used to make all of the responses and, the conditions varied in terms of the target durations for the subintervals. The in-phase condition (0 ms ITI) could not, of course, be tested in the unimanual condition.

Consistent with the predictions of the rhythmic representation hypothesis, performance in the unimanual and bimanual conditions was essentially identical (Figure 5a). Regardless of whether the participants tapped with one or two fingers, the deviations from the target intervals were essentially identical. Moreover, when the produced subinterval ratios were calculated, there was a clear attraction towards simple ratios (e.g., 1:1, 2:1, or 3:1). The participants were unable to produce the target durations in the most complex conditions, demonstrating a bias to produce subintervals that yielded relatively simple rhythms.

Interestingly, for one condition, the results of our study appeared at odds with that reported by Yamanishi and colleagues. In the 600:400 (or 400:600 since performance is roughly symmetric), Yamanishi et al. had reported an attraction towards anti-phase tapping: The long interval was shortened and the short interval was lengthened (i.e., bias to produce a subinterval ratio of 1:1). In our study, the bias was in the opposite direction. The long interval tended to be lengthened and the short interval shortened, resulting in a produced ratio close to 2:1.

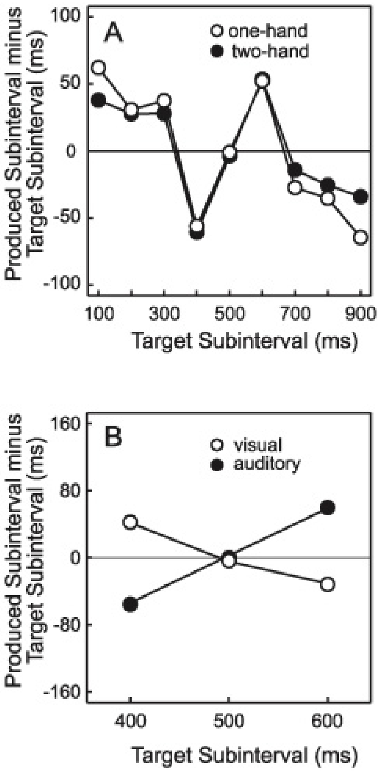


Figure 5. A: Participants tapped temporal patterns created by the division of a 1000 ms interval into two subintervals. Successive taps are made with alternating hands (two-hand) or by a single hand (one-hand). The results are plotted as the difference between the produced subinterval and the target subinterval. The produced subintervals tended to conform to simple rhythmic ratios (e.g., 1:1, 2:1), and most important, were the same in the one- and two-hand conditions. B: One-hand tapping was paced by either a visual or auditory metronome. The metronome had a marked effect for the conditions in which the target subintervals were 400 and 600 ms (or 600 and 400 ms). Adapted from Semjen and Ivry (2001).

The key to this discrepancy provides further support for the rhythmic representation hypothesis. Whereas Yamanishi et al. had used a visual metronome to signal the target subintervals, we used an auditory metronome. Temporal acuity is higher in the auditory domain (Allan 1979). As such, participants were likely more attuned to the large difference between the 600 and 400 ms subintervals with the auditory metronome, and due to the bias to simplify the ratio representation, produced subintervals that approximated a 2:1 ratio. To test this hypothesis, visual and auditory metronomes were directly compared in a second experiment. As expected, the 600/400 target subintervals were distorted towards a 1:1 ratio with the visual metronome and towards a 2:1 ratio with the auditory metronome (Figure 5b).

The Semjen and Ivry (2001) study demonstrates how temporal constraints in bimanual movements may reflect the manner in which the task goals are represented. We have emphasized that the key constraint involved the manner in which the target subintervals were represented. Consonant with the music cognition literature, naïve participants exhibited a strong bias towards rhythmic representations involving simple ratios. While the same constraints were operative for visual- and auditory-paced performance, the differential sensitivity of the two modalities resulted in different patterns of distortion.

It is difficult to envision how a coupled oscillator model could be adopted to account for the results of our study. How would one characterize the two oscillators in the unimanual condition? Certainly not in the manner the oscillators are characterized by Yamanishi et al., that is, as two oscillators set to a common frequency of 1 Hz. The modality effect might be accounted for by postulating that coupling strength varies with modality. But even this hypothesis fails to account for the tendency for the perturbations to go in opposite directions for the visual and auditory conditions. We believe that the most parsimonious account of the temporal constraints is given by the rhythm representation hypothesis. Indeed, the key constraints on temporal performance appear to have little to do with the fact that two limbs were used. Rather, these constraints reflect general limitations in our ability to represent complex temporal relationships.

IV.2 Probing the event structure of rhythmic movements

The rhythm representation hypothesis can account for the bias people show towards certain phase relationships. In-phase and anti-phase patterns entail especially simple temporal representations given that they result in isochronous subintervals. With more complex ratios, we posit that temporal relationships are organized hierarchically. A fundamental timing unit is established and the hierarchy is used to specify which response to produce and when it should be emitted. These temporal representations define an event structure for the action (Semjen 2002).

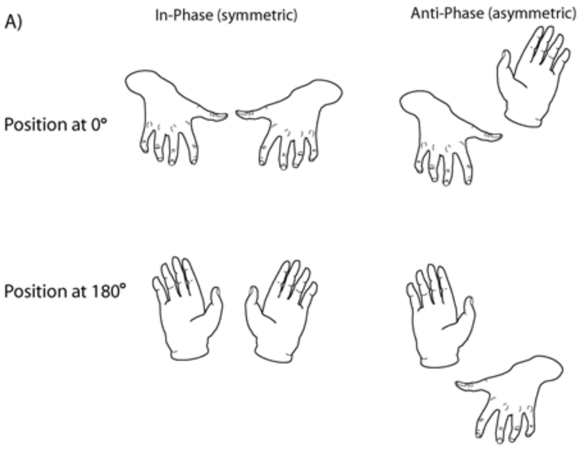
To this point, our discussion of temporal constraints has not addressed why in-phase movements are more stable than anti-phase movements. We offered one explanation with respect to spatial constraints; we proposed that in-phase patterns entail more congruent trajectories than anti-phase patterns. However, we also believe that these two patterns may, under certain conditions, be guided by qualitatively different temporal representations, or event structures.

Consider again the example of wrist flexion and extension, taking the situation in which both palms face downwards. When performed repetitively, these movements can be considered as continuous oscillations. However, synchronization studies have shown that certain points in the cycle are more salient than others. If the movements involve contact with an external surface as in table tapping, synchronization with an external metronome will be organized such that the table is contacted coincident with the beat of the metronome (or more accurately, slightly ahead of the metronome, see Vos, Mates and van Kruysbergen 1995). If there is no external surface, most people synchronize with the initiation of each flexion cycle.

Our hypothesis is that the event structure differs for the in-phase and anti-phase patterns. For in-phase movements, a common event defines the cycle initiation point for each hand. In contrast, anti-phase movements entail two events per cycle, one associated with flexion onset of each hand (Figure 6). According to this hypothesis, the event structure for anti-phase movements is more complex than that associated with in-phase movements and stability will be inversely related to complexity.

We have only begun to test the event structure account of the preference for in-phase movements. The goal in our initial studies was to demonstrate that, under conditions of minimal external constraint, people do indeed conceptualize different event structures for in-phase and anti-phase movements. To this end, participants were instructed to perform continuous wrist flexion and extension movements, either in-phase or anti-phase. At the beginning of the first block, participants were instructed to choose their own pace. Once the participant was accurately producing the desired pattern, in subsequent trials they were instructed to "say the word 'BA' repeatedly as you move". We did not give any indication as to when in the cycle the vocalizations should be made nor were any demonstrations provided that might bias performance. In subsequent blocks, the task was repeated but the movements were now made at different paces. Rate-based feedback was given after each training trial (e.g., "Go faster" or "Go slower") until the participant approximated the target rate. At this point, the BA instruction was added.

We expected that the vocalizations would be temporally coupled to "significant" events during the movements. In other words, we used the BA's as a window on the participant's conceptualization of the event structure of each task. The results showed a striking difference between the two tasks. in the in-phase hand movement condition, on 61% of the trials, participants emitted one "BA" for each cycle and the vocalizations tended to occur around the time of flexion onset. In contrast, in the anti-phase hand movement condition, two BA's were vocalized on 100% of the trials, emitted close to the points at which the hands were at maximum flexion and extension.



B)

	Ba : Hand Cycle Ratio		
	1:1	2:1	Other
In-phase hand movements	61%	31%	8%
Anti-phase hand movements		100%	

Figure 6: Probing the event structure of in- and anti-phase movements. A) Participants were instructed to move in-phase (left column) or anti-phase (right column). Once performance was stabilized, they were required to simultaneously articulate the syllable "BA". B) Although no instructions were given, the vocalizations were usually produced in a fixed temporal relationship with the wrist movements. Participants always vocalized twice per cycle in the anti-phase condition. In contrast, they generally vocalized once per cycle for the in-phase movements, suggesting a simpler event structure for the in-phase pattern. (Spencer, Semjen, & Ivry, unpublished data).

We had also expected to see that the occurrence of BA's would vary with movement frequency. In particular, we had expected that, as rate increased, there would be a transition in the anti-phase condition from two BA's per cycle to one BA per cycle. However, such transitions were not observed in the anti-phase condition. In the in-phase condition, one participant (17% of the trials) said 2 BA's for every movement. Interestingly, this participant adopted the slowest spontaneous hand movement rate in the first block. The failure to observe a change in the number of BA's per cycle may have been due to the fact that we failed to include rates at which the wrist movements themselves underwent a phase transition. Nonetheless, the study does support the basic tenet of the event structure hypothesis: As measured by the occurrence of BA's, a difference is observed in the temporal representation of in-phase and anti-phase movements. Moreover, if we assume that complexity is related to the number of salient events, anti-phase movements are more complex than in-phase movements (see also, Wimmers et al. 1992).

In a sense, the event structure model is a generalization of the rhythm representation hypothesis. The core idea is that temporal constraints may reflect the manner in which the temporal goals of the task are represented. As these representations become more complex, pattern stability suffers. Complex rhythms such as tapping four against three represent an extreme case. Most of us lack the experience necessary to develop the representations for proficient production of such rhythms. Repetitive movements involving isochronous intervals are, obviously much easier. But, as shown by the BA experiment, differences may exist in the representational structure of even simple rhythms, and these likely have consequences in terms of pattern stability.

IV.3 Neural dissociations in the control of continuous and discontinuous movements

Recently, Zelaznik and colleagues (Robertson et al. 1999; Zelaznik et al. 2000; Zelaznik et al. 2002) presented evidence that the temporal control of unimanual movements may vary as a function of task requirements. Participants were required to produce rhythmic movements, either by finger tapping or circle drawing. On measures of variability, performance across the two tasks was expected to be positively correlated (e.g., Keele et al. 1985). To their surprise, temporal variability in tapping and circle drawing were not correlated (Robertson et al. 1999; Zelaznik et al. 2000). These results suggested that different processes were engaged for controlling the timing of these two tasks.

What could account for these null results? We have proposed that the representation of the task goals, or at least the manner in which these goals are achieved may be fundamentally different for tapping and circle drawing, with these tasks being representative prototypes of two different classes of movements (Ivry et al. 2002; Kennerley et al. 2002). Repetitive tapping can be conceptualized as the concatenation of a series of discrete events, with discontinuities observed either when the finger contacts the table surface or just prior to the onset of flexion when people typically make a brief pause. The goal for such tasks is to separate each successive event by the target interval; that is, timing is an explicit part of the action goal with an internal timing being used to control the movements of each cycle.

In contrast, circle drawing involves continuous movements. People can, of course, vary the cycle duration of these movements with the same flexibility as for tapping. However, this does not mean that the on-line control of these movements requires the operation of an internal timer. Rather, temporal regularities might be achieved by optimizing some other variable such as maintaining constant angular velocity, perhaps by the continuous modulation of joint stiffness over a targeted range. We refer to this form of timing as emergent, to contrast with the event timing required for tasks that involve discontinuities (see Zelaznik et al. 2002).

The notion of emergent timing has been espoused previously by proponents of the dynamic systems approach, usually in reference to the idea that there is a preferred frequency for repetitive limb movements (reviewed in Amazeen et al. 1998). We share this view of how temporal regularities may be maintained for continuous movements. However, to account for the fact that these movements are not constrained to a particular frequency, we propose that the control system can determine the mapping between a temporal goal and certain control parameters. In this manner, the goal in a task like circle drawing undergoes a translation. Initially, the goal is of a target cycle duration, similar to the event timing representations for tapping. But because of the continuous nature of the movements and their lack of salient events, the goal can be achieved in an emergent manner by controlling other parameters to optimize performance. Thus, emergent timing tasks have a different form of representation; they lack an event timing structure.

Converging evidence in support of the event/emergent distinction comes from two sets of neuropsychological studies. Various lines of evidence suggest that the cerebellum is essential for tasks that require the precise representation of temporal information, the form of representation that we hypothesize is essential for event timing tasks (reviewed in Ivry et al. 2002). To test this idea, patients with cerebellar damage performed continuous and discontinuous repetitive movements (Spencer et al. 2003). As predicted, the patients exhibited increased temporal variability on various discontinuous movement tasks. These included both tapping tasks and a modified circle drawing task in which the participants were required to insert a pause prior to the onset of each drawing cycle.

Most striking was their performance on the continuous circle drawing task. The movements for this task are considerably more complex than those required for tapping, involving 2-dimensional spatial trajectories that involve multiple joints and interactional torques. Based on conventional neurological thinking concerning the role of the cerebellum in coordinating such movements, one would have expected the patients to be at least, if not more impaired, on the circle drawing task. However, the patients were unimpaired on the continuous circle drawing task: no increase in temporal variability was evident on this task when performing with their impaired limbs. This dissociation is consistent with the idea that the timing of continuous movements does not require continuous control from an internal timing system.

The second neuropsychological dissociation was obtained in studies with callosotomy patients and brings us back to the topic of bimanual coordination. As part of our research on spatial cross-talk, we tested three split-brain patients on the bimanual circle drawing task (Kennerly et al. 2002). The initial goal of the study was to compare their performance when circling in a symmetric mode (one hand clockwise and one hand counterclockwise) versus an asymmetric mode (both clockwise or both counterclockwise). Unimpaired individuals exhibit more stable performance in the symmetric condition (Semjen et al. 1995). The patients failed to exhibit this form of spatial coupling. Their movements were no more accurate in the symmetric condition and phase transitions were observed from the symmetric to the asymmetric mode as often from the asymmetric to the symmetric mode. More striking, however, was that the split-brain patients' movements were frequently temporally uncoupled. On many trials, the hands adopted completely different frequencies, a phenomenon that is never spontaneously observed in normal participants.

The temporal uncoupling during circle drawing was puzzling given previous reports, including our own, that split-brain patients exhibit strong temporal coupling (Franz et al. 1996; Ivry and Hazeltine, 1999; Tuller and Kelso 1989). Interestingly, these previous studies involved tasks associated with an event-based representation. Either the movements were discrete or required tapping-like movements. Thus, we reasoned that the uncoupling during continuous circle drawing may provide another indication that the representational basis of these types of movements is quite different.

To test this idea, we created two hybrid tapping tasks involving flexion-extension movements of the index fingers. In the continuous condition, the participants were instructed to make flexion-extension movements with their index fingers, attempting to move the fingers in a smooth, continuous manner. In the discrete tapping condition, the participants were instructed to insert a brief pause prior to each flexion phase. It is important to note the overall similarity between the two conditions. All movements were made in free space without contacting an external surface, and we did not pace the movements with a metronome or give any instructions regarding synchronization.

Despite this similarity, a dramatic difference was seen in the performance of the split-brain patients (Figure 7). In the air tapping condition, the patients' movements were strongly coupled. A common frequency was adopted for the left and right hand movements, and as measured by the phase difference distribution, the strength of coupling was similar as that found in the control participants. However, in the continuous condition, performance was much more variable. While there were epochs in which the movements were coupled, there were also epochs in which the two hands became temporally uncoupled, similar to what we had observed during the bimanual circle drawing task with these patients. Again, at least parts of the trials, the two hands moved at different frequencies.

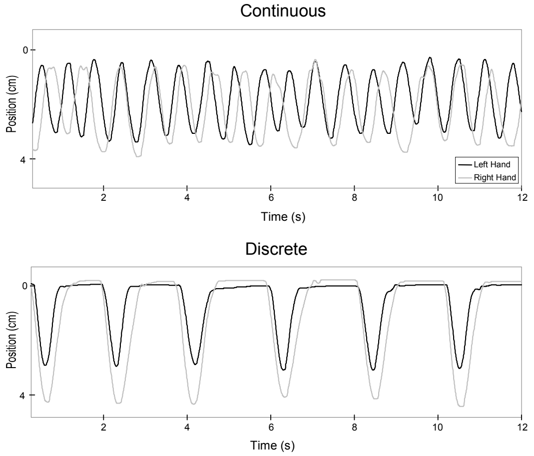


Figure 7. Representative trials of temporal coupling in a split-brain patient during continuous and discontinuous movements. Movements involved flexion-extension of the index finger in midair (flexion is portrayed upwards). In the discrete condition, the patient was instructed to insert a brief pause prior to each flexion phase. While control participants exhibit strong coupling in both conditions, the coupling is weaker, and occasionally absent for the split-brain patients. (based on Kennerley et al. 2002).

This dissociation provides converging evidence concerning representational differences between continuous and discontinuous movements, and emphasizes that bimanual coupling arises from a varied set of constraints associated with these representations. First, consider repetitive, continuous movements. We have argued that the event-based representations provided by the cerebellum are not essential for such tasks (Spencer et al. 2003). While normal participants exhibit strong temporal coupling when making continuous movements, this constraint is absent in the split-brain patients. Based on our earlier considerations about spatial coupling, we hypothesize that temporal coupling for continuous, repetitive movements arises from dynamic interactions between time-varying representations of the abstract spatial goals for these actions. For circle drawing, symmetric patterns appear to be more congruent than asymmetric patterns; for one-dimensional movements, congruency is generally associated with movements along the same direction of rotation. When viewed from this perspective, the absence of temporal coupling in the split-brain patients is another manifestation of the fact that interactions between these abstract spatial codes is mediated by communication across the corpus callosum.

The close relationship between the coupling of spatial and temporal characteristics in the context of continuous movements is also demonstrated by the fact that neurologically healthy individuals show an attenuation of temporal coupling when producing asymmetric (i.e., spatially incompatible) movements at fast rates (Carson et al. 1997; Semjen et al. 1995). Moreover, a complete breakdown of temporal coupling can occur when the spatial overlap between the two tasks is reduced; for example, when the movements are made with non-homologous limbs of very different masses (Jeka and Kelso, 1995).

In contrast, temporal coupling appears to be much more robust for discontinuous movements. We hypothesize that this is because the two movements share a common event structure, a representation of the temporal goals. Stability here is dictated, not in terms of the congruency of spatial relations, but rather in terms of temporal economy. Our movements are biased towards patterns that specify temporal events in a concise and simple manner. In-phase patterns entail a simpler event structure than anti-phase patterns. Both of these patterns are more stable than other phase relations because they entail simple rhythmic representations (e.g., small ratios).

We have argued that the cerebellum is essential for the temporal representations embodied in an event structure (Ivry et al. 2002). We see this structure as one part of a distributed system for controlling actions (and mediating perceptions) that entail complex temporal relationships. For example, a rhythm can be described abstractly-- a drummer can produce a 3:2 bimanual tapping pattern at different speeds. Our expectation is that the abstract level of representation is cortical; the cerebellum is engaged when this abstract pattern is instantiated as a specific action, one that requires the real-time coding of an event structure.

The idea of an event structure for both unimanual and bimanual movements is a powerful tool to understand the temporal coordination of more complicated bimanual actions. For example, when opening a drawer with one hand to grasp an object with the other hand, the timing of the two hands is stereotypically organized (Perrig et al. 1999). However, the phase relationship of the two movements is much more complicated than in simple repetitive tasks. Importantly, the movements in such tasks are part of a generalized motor program, one that specifies the successive events of the two hands to achieve a common goal (Schmidt et al. 1998). We hypothesize that the cerebellum provides the fine temporal resolution necessary for the success of many bimanual actions. Consistent with this idea, cerebellar patients show deficits in the temporal aspects of such a complex bimanual motor tasks (Serrien and Wiesendanger 2000).

Interestingly, split-brain patients are still subject to the temporal constraints imposed by the representation of an event structure. Furthermore, they do not report drastic deficits in many well-learned bimanual skills, even if these require detailed coordination of the hands (Franz et al. 2000; Serrien et al. 2001). We believe this reflects the operation of a mechanism required for the implementation of the actions specified by the event structure. Such a process could ensure that the action codes specified by the cerebral hemispheres are implemented in an efficient manner, an operation that has been likened to a neural gating process. However, we do not wish to imply that this gating process is performed by the cerebellum. At present, our speculations on the localization of such a process are guided by two considerations. First, it should have access to the output from the cerebellum specifying the event structure. Second, it should be capable of initiating actions in a relatively generic manner (e.g., bilaterally). We believe the evidence points to a subcortical locus, perhaps the basal ganglia but it is also possible that a single cerebral hemisphere might meet such requirements (see Ivry and Richardson 2002).

V. Final comments

The study of bimanual coordination has provided an important tool for exploring the cognitive neuroscience of motor control. Central to this work has been the elucidation of the many ways in which our ability to produce bimanual movements is constrained. We have focused on two primary classes of constraint, those associated with the interactions observed between the two limbs in the spatial and temporal domains, similar to what Semjen (2002) referred to as trajectory-level and event-level constraints. We do not wish to imply that a clean division, either psychologically or neurologically, can always be made between the manner in which the spatial and temporal features of movements are represented and controlled. Nonetheless, neuropsychological evidence demonstrates that the two types of constraint can be dissociated (Franz et al. 1996). Indeed, there are notable differences in our accounts of these sources of constraint. Spatial interference effects, at least in terms of response planning, are limited to situations in which the movements are symbolically cued, suggesting that the primary constraint arises with response selection rather than motor programming or execution. The neuropsychological evidence points to a cortical locus for such effects, with candidate areas including ventral visual processing pathways and inferior parietal and premotor cortices. Temporal interactions generally reflect the operation of a unified temporal representation, one in which the timing of salient events is explicitly controlled, a process associated with the cerebellum.

A common theme in our analysis, however, is that the way in which the task goal is conceptualized will play a central role in determining patterns of interference between the two movements. We attribute the difference between symbolically- and directly-cued movements to a difference in task conceptualization, with the former involving goals defined as movement trajectories and the latter involving goals defined as target locations. Similarly, we hypothesize that while an event-based representation is essential for discontinuous movements, this form of representation is not essential for continuous movements. The emphasis on task conceptualization also leads to the conclusion that many of the constraints underlying bimanual coordination arise at an abstract level, one that can be divorced from processes devoted to motor execution. Acknowledging the limitations imposed by our cognitive architecture should also hold promise for understanding and appreciating the extraordinary flexibility with which humans use their two hands.

Acknowledgements

Preparation of this chapter was supported by Grants NS30256, NS40813, NS17778, and NS33504. We are grateful for discussions with Scott Grafton, Scott Johnson, and Winston Byblow. Correspondence should be directed to R. Ivry, Department of Psychology, MC 1650, University of California, Berkeley, CA 94720 USA, or email at ivry@socrates.berkeley.edu.

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