

Who Tells One Hand What the Other Is Doing: The Neurophysiology of Bimanual Movements

Minireview

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It is common knowledge that movements of the arms are naturally coupled. For instance, certain modes of temporal coupling are more natural for the system than others. In-phase (clapping) and anti-phase (walking) rhythms can be maintained at higher frequencies than other phase relationships; further, in-phase rhythms are more stable than anti-phase rhythms (Tuller and Kelso, 1989). Spatial coupling of movements also exists: subjects easily produce circles or lines with both hands simultaneously, but when they draw lines with one hand and circles with the other, they make ovals with both hands (references in Franz et al., 1996, and Swinnen et al., 1998).

To a neurophysiologist, these aspects of bimanual movements raise questions. Where is the coupling produced? What neural mechanisms produce it? For instance, does one side of the nervous system control the other, or is there a cooperative interaction of the two sides? What mechanisms accomplish decoupling? Since many bimanual synergies can be achieved with practice—from playing the drums to typing—there must be neural mechanisms that modify default coupling. What are these mechanisms, and where are they localized?

Studies in Humans

The mechanistic questions we raise are difficult to address with human subjects. However, recent progress—strengthened by neuropsychological research and imaging technologies—provides surprising insight. One important result regards the cortical role in mediating temporal coupling: studies of bimanual coordination in people with disconnected cortical hemispheres (split brains) revealed that the temporal coupling is not reduced (Tuller and Kelso, 1989) (Figure 1A).

While this argues against a role for the cortex in coupling, that conclusion may be premature. First, in Tuller and Kelso's results, temporal coupling not only was not reduced, it was enhanced. Second, during bimanual movements the dominant hand leads the nondominant hand by 15–30 ms (Stucchi and Viviani, 1993). Dominance is usually considered a cortical phenomenon, and a PET study showed asymmetric activation of the dominant hemisphere during bimanual movements (Viviani et al., 1998). After considering various alternatives, Stucchi and Viviani concluded that only an asymmetry in cortical

activation would suffice to explain their asynchrony. However, their model does not account for increase of coupling in split brains, so it cannot be complete. Central pattern generators (CPG) are an important alternative source for the coupling. CPGs play a role in the coordination of certain rhythmic, bilateral movements and have been found in the spinal cord (Grillner, 1985). Since CPGs are affected by cortical and subcortical efferents, cortex may modulate temporal coupling through them. For instance, it may control the resonant frequencies of the CPG or modulate limb activation at different phases of the cycle. This would be consistent with the callosotomy results. Loss of interhemispheric communication could disrupt complex patterns and yet leave CPG coupling intact. This is also consistent with the inter-hand time lag: hemispheric dominance might lateralize CPG activation, and lateralized activation could cause asynchrony in the movements. Of course, in some temporal coupling—for example, speech with movement—additional, extra-spinal neural mechanisms would need to be involved.

In spatial coupling, interhemispheric interactions may play a more central role. Split brain subjects are better than normals at decoupling spatial aspects of bimanual movements (Franz et al., 1996) (Figure 1B). It has been suggested that spatial coupling may be a simple by-product of biomechanical coupling of the arms, but two intriguing studies refute this point. Franz and Ramachandran (1998) showed that amputees with phantom limb effects are susceptible to spatial coupling even though the amputated limb cannot move, and there are similar results in normals who are moving one arm and imagining movement of the other (Heuer et al., 1998). A difference between mechanisms underlying temporal and spatial bimanual control makes a variety of neurophysiological explorations possible. In the following sections, we show the modest contributions that have already been made to this field and how novel methodologies may expand that contribution.

Studies in Primates

Before reviewing experimental work in primates, we note that bimanual coordination in animals may be different than in humans. Human motor control is heavily lateralized, and, as we saw, handedness is related to some aspects of bimanual control. While monkeys do display some handedness, significant differences may exist between monkeys and humans regarding the lateralization of control for coordinated bimanual movement. Nevertheless, in monkeys, as in humans, movements of the two arms naturally couple, and monkeys, like humans, can learn to decouple them.

Physiological studies have focused on two cortical areas. One is the supplementary motor area (SMA), and the other is the primary motor area (M1). The SMA is often associated with “coordinating bimanual movements,” but the idea is still controversial. EEG and brain imaging studies in humans demonstrated specific activation of SMA during bimanual movements (see, for example, Lang et al., 1988, and Viviani et al., 1998). SMA lesions caused deficits in bimanual coordination

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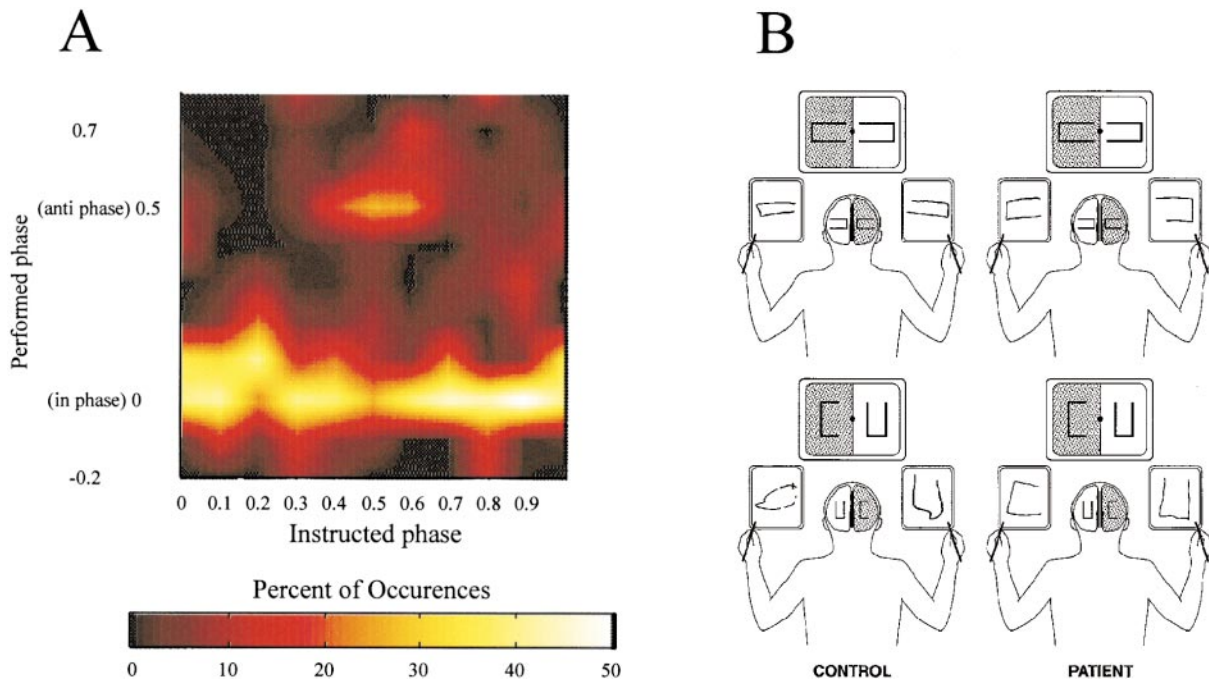


Figure 1. Spatial, but Not Temporal, Coupling Is Reduced in Split Brain Patients

(A) Split brain patients performing rhythmic tapping movements tend toward an in-phase rhythm. The x axis is the relative phase with which subjects were instructed. The y axis shows the phase actually performed. Note the tendency to in-phase performance regardless of the instruction. The only deviation is a limited ability to follow an anti-phase pattern. Adapted from Figure 4 in Tuller and Kelso, 1989.

(B) Split brain patients do not suffer between-hands interference when producing spatially distinct movements. In the panel's top half, both split brain patients and controls produce figures requiring activation of homologous muscle groups in the two arms. In the panel's bottom half, producing a figure with nonhomologous arm activation causes interference in controls; split brains produce the figures more accurately. Reproduced with permission from Franz et al. (1996).

in monkeys and humans (references in Brust, 1996, and Wiesendanger et al., 1996). However, efforts to replicate bimanual deficits in SMA-lesioned monkeys did not find an effect on bimanual coordination (Kazennikov et al., 1998).

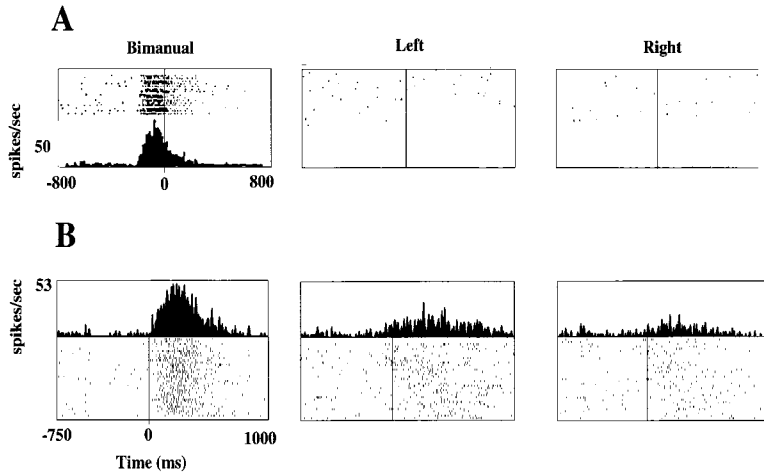
One of the most powerful demonstrations of an SMA role in bimanual coordination came from a single-unit recording experiment (Tanji et al., 1988). Monkeys made restricted finger movements to touch keypads. They used either one hand or both hands while activity was recorded in SMA and M1. Nearly all M1 cells responded during bimanual movements just like they responded during movements of the contralateral hand alone. In contrast, SMA neurons responded differently during bimanual movements than during movements of either hand (Figure 2A). For our purposes, both increased and decreased firing rate during bimanual movements will be called "bimanual related" activity. Recent results from our laboratory using whole arm movements showed similar bimanual related activity in SMA neurons, but in our study M1 cells were also bimanual related (Donchin et al., 1998) (Figure 2B). This seeming paradox can be resolved because converging evidence shows a fundamental difference in control of proximal and distal movements of the upper limb. The two M1 are poorly connected through the corpus callosum for the hand and fingers but well connected for the upper arm (references in Wiesendanger et al., 1996), and neuropsychological studies of ipsilateral deficit confirm that control

of the arms is more bilaterally organized than control of the fingers (Jakobson et al., 1994).

So, results in primates support the involvement of cortex in bimanual control and suggest differences in proximal and distal bimanual control, but they leave many questions unanswered. We know little about the role of each hemisphere and the cooperation between them. We know little about asymmetry in cortical function that causes, among other things, asynchrony in the arm movements. We also do not know what mechanisms modulate bimanual coupling and allow the arms to perform different functions simultaneously. The methods of classical electrophysiology may pose inherent limitations in addressing these issues. In such studies, we record neural response rates during different trials and seek to understand brain function by ascribing roles to neurons on the basis of their pattern of activation. This approach cannot address temporal structure in the neural activity or in the relation of activity to behavior. However, coordination is a temporal phenomenon; even spatial coupling of arm movements depends on simultaneity. Tools that permit analysis of temporal aspects of activity could open a new window on the control of bimanual movements.

Population Vectors in Bimanual Control

Population averages have been used to explore temporal aspects of neural activity and behavior. In these experiments, averaging across neurons (recorded individually) exposes a relationship between the time course



In both studies, bimanual related activity could either increase or decrease during bimanual movements. In the study on finger movements, such activity was found only in SMA; in the study on proximal arm movements, it was found in both M1 and SMA.

Figure 2. Bimanual Related Activity in SMA and M1

The figure shows dot displays (trials centered on beginning of movement) and peri-event time histograms illustrating bimanual related activity.

(A) A bimanual related cell from the SMA hand area during a finger flexion experiment. The left-most display shows bimanual trials, the middle display shows left handed trials, the right-most display shows right handed trials, and the middle display shows left handed trials. The cell is activated during bimanual movements but hardly modulated when each hand moves separately. Figure reproduced with permission from Tanji et al. (1988).

(B) A bimanual related cell from the proximal arm area of M1. Dot displays are arranged as in (A). In this task, the monkey is executing arm movements and not finger movements. Data from Donchin et al. (1998).

of neural activity and behavior. For instance, a data reduction method called the population vector (PV) is commonly used. It is based on the idea that each neuron has a certain “preferred direction” and votes for moving in this direction, with a weight that depends on its momentary firing rate. The PV is given by the vector sum of all single unit vectors and reliably predicts the direction of the upcoming movement. Additionally, the time course of the rotation of the PV seems to be related to the dynamics of a mental calculation required for rotation of the intended direction of movement (Lurito et al., 1991).

Recent results using the PV show that the curvature of the movement is related to the time lag of M1 activity. The lag for highly curved movements is greater than for those that are straight, suggesting that the delay is due to the complexity of the motor control (Moran and Schwartz, 1999).

Can the PV approach contribute to understanding bimanual coordination? Figure 3 shows PVs calculated from bilaterally recorded data from our lab (Donchin et al., 1998) addressing the brains’ decoupling of bimanual movements. The figure shows that cortical activity can represent different combinations of arm movements using the same population of cells. Further research may uncover how neural activity allows this flexibility of coding. Still, cortical activity reflecting spatially decoupled arm movements supports the role of interhemispheric communication in this coupling. Figure 3 also shows

that, during unimanual movements, the nonmoving arm’s PV points in the same direction as the moving arm’s, though it is smaller. This suggests that decoupling of the neural activity is incomplete—an interpretation consistent with the incomplete decoupling of the arm movements themselves.

Neural Interactions in Bimanual Control

Multineuron recording promises even more direct insights into the temporal nature of motor control. Recently, interest in multiple electrode recording has increased because, in part, of temporal structure discovered in neural activity. This structure could contain information beyond what exists in single neuron recordings. For instance, correlation—even between hemispheres—may “bind” visual features to form coherent percepts (Engel et al., 1991). Dynamical modulation of correlation develops within tens of milliseconds and thus may be an indicator for the rapid assembly and dissipation of groups of functionally related neurons (Vaadia et al., 1995).

Simultaneous recording is particularly relevant to bimanual control. Recording in both hemispheres could provide direct evidence of the coupling and decoupling necessary for bimanual movements. Such recording may also supply convergent evidence for asymmetrical cortical activation related to the asynchrony in arm movements.

These ideas are largely unexplored, but not entirely. Simultaneous interhemispheric M1 spiking activity and

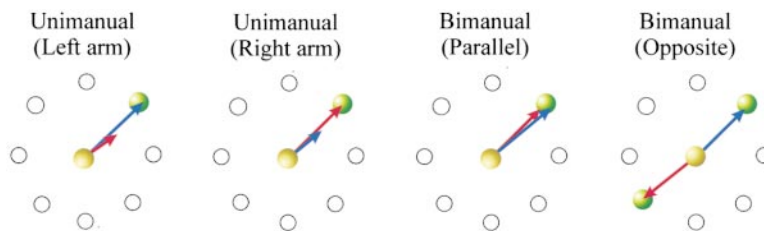


Figure 3. Reconstructing Bimanual Movements by Population Vectors

PVs calculated from both hemispheres describe unimanual movements and different bimanual movements. The monkey performed a bimanual “center-out task” where the left arm, the right arm, or both arms moved. Movements were made from a central location (yellow circle) to either one target (unimanual trials, green circle) or two targets (bimanual trials, green circles). Two popula-

tions were formed by grouping cells most responsive to the left arm (144 cells) and the right arm (166 cells) separately. Blue arrows show the PV for the left arm; red arrows show the PV for the right arm. Data from Donchin et al. (1998).

local field potentials (LFP) were recorded during bimanual and unimanual manipulation tasks (Murthy and Fetz, 1996). The study found interhemispheric synchronization but did not find differences between synchronization in unimanual and bimanual movements. However, LFP oscillations synchronized more during exploratory movements, suggesting a relationship to the level of sensorimotor coordination. It may follow that interhemispheric synchronization is related to complexity of bimanual control. Then, similarity between bimanual and unimanual synchronization implies similar coordination requirements in the two types of movements. This interpretation is consistent with the one we offered for the PV of the nonmoving arm in Figure 3.

One preliminary result from our laboratory is salient in the context of this discussion. We found that M1 interhemispheric LFP correlations were weaker than intrahemispheric correlations. After impairing the motor system by lesions in the two SMAs, interhemispheric correlations were increased, but, after 4 months, returned back to their normal level. Perhaps ablation of a bilaterally connected cortical motor area was compensated by increased interhemispheric interaction in other motor areas. Another possibility is that normally the SMA inhibits excess interhemispheric correlation, so that the increased M1 correlation is pathological and not compensatory. Our data are insufficient to decide between these possibilities, but both of them imply a functional role for interhemispheric correlations.

New bimanual tasks that manipulate the level of bimanual control are necessary to probe this role more directly. To design such tasks, it will be necessary to rely heavily on the psychophysical literature reviewed above.

Conclusion

Research into neural mechanisms of bimanual coordination sheds light on questions raised by psychophysics. While the results we review are merely suggestive, the overall structure of the neural mechanisms may be emerging slowly.

Different mechanisms may serve the spatial and temporal coupling of bimanual movements. Temporal coupling depends on a lateralized pace-keeping mechanism possibly associated with spinal CPGs, is preferentially controlled by the dominant hemisphere, and does not depend directly on the corpus callosum. Spatial coupling, in contrast, arises through interhemispheric interaction. Individual neurons in each hemisphere reflect this interaction, as does interhemispheric synchronization. The interaction allows decoupling of the arms, as substantiated by the PV analysis. Furthermore, bimanual proximal arm movements and finger movements are controlled differently, as shown in differences in the patterns of neural activity in M1 and SMA.

Taken as a whole, the research we review has not yet culminated in a conclusive model. However, by combining psychophysics and neurophysiology, we raise concrete, testable hypotheses that may help realize this goal.

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