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9

Bimanual Action Representation: A Window on Human Evolution

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9.1 Introduction

A remarkable feature of humans is our hands. Whether to quench our thirst or to write down our thoughts, our hands readily translate our ideas into action. Indeed, the first species of humans was named *"habilis"* (handy) after its "handmaking" of stone tools (Eccles, 1989, p. 23), which required, at the very least, coordination of both hands.

This chapter describes research by my colleagues and me into bimanual representation, a process critical to human evolution. Focusing on how different forms of abstract spatial coupling may reflect representational processes in the brain, it considers possible links with research using other experimental approaches, with the greater goal of promoting discussion across what appears to be an emerging multidisciplinary area of study.

The timing properties of unimanual movements provided the initial impetus for present-day research on bimanual actions. Studies using the Fitts task (see Fitts, 1954) demonstrated that a highly reliable relationship exists between movement difficulty and movement time in unimanual movements to targets. Whereas the original Fitts task was performed by tapping repetitively between two targets, the relationship generalized reliably to discrete aiming movements (Fitts and Peterson, 1964) as well as to a host of other unimanual tasks (e.g., Langolfet al., 1976; Jagacinski et al., 1978).

In the early 1970s, investigators were beginning to examine the temporal properties of interlimb coordination tasks. For example, Cohen (1971) observed that homologous muscles (identical sequences) and nonhomologous muscles (opposite sequences) often moved with temporal synchrony. Somewhat earlier, Wyke (1967) had begun pioneering work on the effects of brain damage to speed of unimanual and bimanual movements.

Adding another interesting twist to history, Kelso and colleagues (1979) combined two Fitts's aiming movements in a bimanual task. When they changed the difficulty of the two tasks by varying distance, target width, or both, they observed that the two hands of subjects initiated and terminated movements in a much more coupled fashion than Fitts's law would have predicted. Kelso and colleagues concluded that in bimanual tasks of this type, the hands operate as a "functional synergy," a term borrowed from the earlier writings of Bernstein (1967).

About the same time as the study by Kelso and colleagues, another influential approach was developed by Klapp (1979) and by Peters (1977), among others. Time patterns were manipulated by requiring subjects to tap in rhythms with simple harmonics or complex nonharmonic relations. Demonstrating that, in the absence of considerable practice, subjects could not produce two distinct timing patterns without interference, Klapp (1979) concluded that the movement system is constrained to produce a single timing pattern. Effects of attention were also found to influence bimanual temporal coupling (Peters, 1981). Numerous studies have now identified specific properties of temporal coupling in bimanual movements (discussion of which is beyond the scope of this chapter). Some compelling evidence comes from tasks of bimanual tapping (Yamanishi et al., 1981), pendula swinging (Turvey et al., 1986), flexion-extension movements of the limbs (Swinnen and Walter, 1991), and continuous drawing of curved trajectories (Semjen et al., 1995). These and other investigations illuminate the importance of temporal compatibility and phase relations as constraining features in bimanual movements.

Studies on temporal coupling led my colleagues and me (Franz et al., 1991) to investigate spatial coupling to determine whether there was a constraint in the spatial domain similar to the one operating in the temporal domain. Subjects asked to draw circles with one hand while drawing lines with the other tend to produce curved lines and linelike circles, which has been taken as evidence of spatial coupling (Franz et al., 1991; Franz, 1997; Chan and Chan, 1995).

Spatial coupling also generalizes to discrete bimanual tasks, such as drawing squares combined with circles. Figure 9.1 shows examples of some bimanual drawing tasks, illustrating the extreme forms of interference that result from spatial coupling of complex shapes. Findings on spatial coupling seemed to reveal constraints that cannot be accounted for by timing or phase relations alone. A task such as drawing circles or



Figure 9.1

(*Bottom*) Basic experimental setup to examine spatial coupling effects in discrete drawing tasks. One stimulus is presented on each side of a visual monitor to instruct what each hand should draw. (*Top*) When identical figures are produced by the two hands, the bimanual task is easy to perform; however, when distinct figures are presented, neurologically normal individuals experience extreme spatial interference of the type shown, whereas split-brain patients do not.

squares requires movements with many degrees of freedom that the limb's extremities are specialized to produce. The ability to move in directions and orientations away from the body midline appears to be an evolutionary development unique to primates. This provides one clue that the spatial constraints under investigation are most likely a phylogenetically recent development (for additional evidence, see Franz, 1997).

Accomplished musicians are able to finger a rhythm with one hand while playing a melody with the other (see Shaffer, 1981). What are the mechanisms of learning two tasks at once? Must the whole brain focus on one task at a time? What are the neural mechanisms that make it difficult to produce two different spatial tasks simultaneously?

9.2 Neural Processes of Spatial and Temporal Coupling

For the past nine years or so, I have had the privilege of working daily with people who have rare neurological conditions, and who have educated me about bimanual actions in ways that textbooks or scientific studies could not.¹ These individuals have provided reallife demonstrations of how remarkably resilient people are in their compensatory abilities that often hide in the shadow of deficits. Although I cannot document all of the insights I have gained, I can at least illustrate some that led my colleagues and me to our laboratory studies. The first set of studies examines the neural processes of spatial and temporal coupling in patients with callosotomy (surgical section of the corpus callosum). The initial question was whether the neural processes that underlie spatial planning and temporal coupling of hand actions could be dissociated. If so, it might be possible to perform two different tasks at once, provided certain neural processes of the two tasks are confined to separate cerebral hemispheres. This set of experiments has led to follow-up studies investigating well-learned versus novel bimanual actions in patients with callosotomy and in those with callosal agenesis.

The second set of studies, which focuses on the existence of phantom limb movement after amputation, investigated whether forms of central representation may result in spatial coupling even when no peripheral feedback is possible. Such evidence would suggest that there exist forms of spatial processes that depend on information already within the brain (i.e., a representation), rather than depending on on-line information from the periphery. The third set of studies focuses on congenital mirror coupling that occurs in the distal extremities of some people. Its findings suggest some intriguing possibilities about development and perhaps even about human evolution. These three sets of studies will be discussed in turn.

Callosotomy Patients

A surgical procedure that severs the corpus callosum, the main commissure between the two cerebral hemispheres, callosotomy ("split brain") is applied in severe cases of uncontrollable epilepsy. The operation is believed to leave subcortical structures intact. An extensive database exists on this topic from decades of influential research by Gazzaniga, Sperry, and others, showing that in the split brain, perceptual, cognitive, and memory processes can be carried out in each cerebral hemisphere separately—without awareness of the other hemisphere (for review, see Gazzaniga and Sperry, 1967). This apparent split in processing led my colleagues and me to wonder whether each hemisphere could operate separately and simultaneously in the processes of motor planning of actions that require *both* hemispheres to act in concert to orchestrate distinct drawing movements of the two hands. We hypothesized that spatial coupling between the limbs would be eliminated with callosotomy, but that temporal coupling would not. These two facets of coupling will be discussed in turn.

Spatial Coupling Because each hemisphere issues motor commands to the opposite hand (Brinkman and Kuypers, 1973), we were able to capitalize on the procedure of visual lateralization (Gazzaniga et al., 1965) by presenting shapes to each hemisphere and asking subjects to draw them. These stimuli could be presented one at a time for unimanual trials, or bilaterally for bimanual trials. Bimanual trials consisted of identical or distinct stimuli. One version of the task presented combinations of curved and straight trajectories similar to those shown in figure 9.1. Another version consisted of three-sided rectangles that were either identically aligned for the tasks of the two hands, or orthogonally oriented (rotated) with respect to one another. The stimuli were presented for a brief duration (<150 ms), and eye movements were monitored. Participants *were* instructed to draw the stimuli as quickly and accurately as possible. Reaction time and movement properties were recorded and analyzed off-line.

To our delight, callosotomy patients were able to draw two different trajectories simultaneously without the spatial interference demonstrated by controls with intact

callosi. Moreover, the reaction time for patients drawing with both hands was the same when they drew two distinct shapes, as when they drew identical shapes. In contrast, the reaction time for control participants was considerably longer when they drew distinct shapes than when they drew identical shapes, indicating substantial spatial interference. We inferred from these findings that the corpus callosum provides for interactions in the spatial plans of movements. With callosotomy, each hemisphere appears to be able to separately orchestrate a spatial plan into action, and the two hemispheres do this simultaneously for motor systems of the hands (Franz et al., 1996a).

A follow-up study of spatial coupling after each stage of two-stage callosotomy surgery provided some evidence that spatial coupling was less affected by anterior surgery than by posterior surgery (Eliassen et al., 1999). This result might suggest that posterior regions of the corpus callosum produce the interactions that underlie normal spatial coupling processes. Other studies have shown evidence of a lack of functional disconnection in some cognitive processes with posterior sparing of the callosum. Findings on monkeys with partial commissurotomy also support the role of the splenium in the transfer of visual information associated with limb movements (Brinkman and Kuypers, 1973).

Little is known about the possible role of other callosal regions in interlimb coupling. In a study that examined a patient's bimanual performance before and after surgical resection of the center section of the corpus callosum due to an angioma (Dimond et al., 1977), the bimanual task consisted of drawing repeated semicircles from the top to the bottom of a page with both hands simultaneously and with mirror symmetry. Unlike in the aforementioned studies of spatial coupling where the hands were obstructed from the participant's view, here it appears they were not. Although the authors reported that the subjects' performance was unimpaired following the surgery, because the tasks were mirror symmetrical, perfect performance may indicate complete spatial independence rather than the elimination of spatial coupling. Future studies on the effects of central callosal section on bimanual coupling would indeed be valuable in producing convergent results.

Redundant pathways of spatial information transfer across the corpus callosum may exist in the normal brain. Indeed, neurons with directional properties have been found in posterior (parietal) as well as anterior (motor cortical) regions in reaching tasks performed by a single limb (Georgopoulos et al., 1982; Kalaska et al., 1983). Through corticocortical pathways, this information may transfer between anterior and posterior regions within each hemisphere, and between hemispheres at more than one possible callosal region. If this is so, partial callosal section would not completely eliminate interhemispheric spatial interactions, whereas complete section would. Testing the effects of partial callosal section with the order of the two-stage callosotomy reversed may be one way to examine this issue. Examining patients with callosal tumors may provide additional information.

Although the above findings consider spatial coupling in direction, coupling in amplitude may also occur. Franz et al., 1996a, manipulated amplitude as well as direction in the task of discrete drawing. Like differences in direction, differences in amplitude between the tasks of the two hands elicited increases, albeit smaller increases, in reaction time and spatial interference in control subjects. Moreover, the effects of spatial coupling in amplitude were much less apparent in the callosotomy patients, suggesting that callosal connections may play a less important role in normal coupling of movement amplitude than of movement direction. In control participants, it appears that when two movements of different amplitudes are paired, the shorter movement becomes slightly longer, and the longer movement becomes slightly shorter (Franz, 1997). Error in endpoint accuracy has also been demonstrated using target aiming tasks to different amplitudes (Martenuik et al., 1984).

It is not clear to what extent amplitude coupling reflects planning versus execution processes. Amplitude accommodation tends to occur when the temporal requirements of bimanual movements demand different movement patterns, as in pairing a single flexion movement with more than one flexion movement performed simultaneously by the opposite limb (Swinnen and Walter, 1991). Spijkers and Heuer (1995) have recently begun to distinguish between programming and execution forms of coupling in amplitude. They demonstrated that amplitude coupling occurs when different but constant amplitudes are assigned to the two limbs. This form of execution coupling becomes more prevalent with increases in movement speed. Spijkers and Heuer also investigated amplitude coupling using movements that alternated between small and large amplitudes, a manipulation believed to reflect programming demands. This manipulation also produced amplitude coupling, but the degree of coupling did not increase with a faster movement speed. Clearly, amplitude coupling effects may reveal operations of complex neural processes that remain to be elucidated. **Temporal Coupling** To investigate whether temporal coordination of the hands is affected by callosotomy, Tuller and Kelso (1989) examined relative phase in semidiscrete tapping movements in callosotomy patients and in two groups of control participants, those with no musical training and skilled musicians. Brief lateralized visual pulses indicated the time to tap each hand, and the relative phase between movements of the two hands was varied across trials. In all groups, performance was least variable when movements were either in phase (0°) or antiphase (180° phase shifted) relative to other nonharmonic phase relations. Because vision was used in this task, Tuller and Kelso concluded that absence of the corpus callosum does not affect visuomotor coordination of the hands. Notably, because there were no explicit spatial demands, the task they employed focused primarily on temporal properties.

Based on Tuller and Kelso, 1989, my colleagues and I had no reason to suspect that temporal coupling would be eliminated after callosotomy. We therefore hypothesized that temporal coupling would be maintained on a version of a continuous drawing task, even though spatial coupling was predicted to be eliminated. Callosotomy patients were asked to draw linear trajectories with each hand in a continuous fashion. The lines were to be drawn either in the same orientation (both horizontal or both vertical) or in an orthogonal orientation (one vertical and the other horizontal). As in the experiment using discrete shapes described above, stimuli were lateralized using a brief duration. In this case, the stimuli were single lines. Subjects were instructed to draw continuous repetitions of the visually presented lines at a preferred pace in the orientation indicated. No specific instructions were given about coupling the hands.

Consistent with the primary findings of Tuller and Kelso (1989), temporal coupling of these movements was no different between the callosotomy patients and the control subjects. In fact, participants from both groups tended to begin and end the cycles of movements of both hands within approximately 20 ms of one another. In addition, there was no evidence of spatial coupling in the trajectories of callosotomy patients, whereas there were severe spatial deviations in the orthogonal trajectories drawn by control subjects. These results led to the inference that the neural mechanisms of spatial and temporal coupling are dissociable. Spatial coupling in the abstract plans for action relies on the corpus callosum. In contrast, temporal coupling of the hands appears not to depend critically on callosal connections (Franz et al., 1996a).

It is possible that temporal coupling, phase locking, or both depend on subcortical circuitry such as the basal ganglia, cerebellum, thalamus, or a combination of these. With respect to the basal ganglia, synchronization could occur between both halves of the basal ganglia, which could result in a coordinated "go" signal to both sides of the cortex (see also Graybiel, 1995). With respect to the cerebellum, coupling between the two sides could be mediated by the cerebellar commissures or the red nucleus. Patients with unilateral cerebellar lesions display a marked increase in timing variance across repetitive cycles of tapping movements by the ipsilesional versus the contralesional hand (Ivry and Keele, 1989), whereas they display a decrease in timing variance in the impaired hand on bimanual tasks, as though movements of the unimpaired hand somehow facilitate performance of the impaired hand (Franz et al., 1996b). It would appear that, although the timing processes themselves may be affected by cerebellar damage, the temporal coupling processes exist outside of the cerebellar circuitry; otherwise, a unilateral lesion might be expected to influence both hands in the same way. Notably, temporal coupling may occur through cerebellar commissures that operate on cerebellar output.

Other possible influences on temporal coupling are the central spinal generators (Grillner, 1985), which may be modulated through cortical and subcortical input (Donchin et al., 1999). If movements consist of a proximal component, coupling between the two sides may be accomplished through contributions of ipsilateral and contralateral projections emanating from the same hemisphere (Gazzaniga and Sperry, 1967).

In summary, results on bimanual coupling tasks in callosotomy patients indicate that spatial coupling in the planning of bimanual actions relies on callosal interactions in the normal brain. Temporal coupling of the limbs appears to rely much less, or not at all, on callosal connections. The next section provides additional evidence that some spatial coupling processes operate on central representations.

Phantom Limbs

Following amputation of a limb, some individuals report experiencing residual sensations of the missing limb. The "phantom limb" phenomenon has been documented since the "writings of Descartes (see Corballis, 1991, pp. 6—11). The sensation may range from a light pain to a very vivid sensation of the actual experience of movement, referred to as "phantom limb movement" (Ramachandran and Hirstein, 1998). People

with vivid sensation of phantom limb movement often claim that they can elicit the sensation of movement through their own volition. We were interested in whether spatial coupling would occur between an intact limb and a phantom limb.

Franz and Ramachandran (1998) applied an adapted version of the circle-line bimanual task to patients who had one arm amputated, with a stump extending 4—6 inches from the shoulder. We were interested in whether vivid experience of movement associated with a phantom limb would result in bimanual spatial coupling of a form similar to that observed in people with two intact arms. If so, we could conclude that at least one form of residual spatial coupling is a central phenomenon, rather than a result of biomechanics or peripheral sensation.

We asked the amputated patients to draw linear segments in a continuous fashion with the intact arm on a drawing tablet, while performing either a spatially compatible or an orthogonal task with the phantom arm. For the task of the phantom arm, participants were instructed to activate the "arm" in the instructed manner by eliciting the experience of movement. In the parallel (spatially compatible) task, tapping movements of the phantom index finger were to be performed as vividly as possible. These movements were linear-like, just as the line drawing movements of the intact arm. In the orthogonal task, twirling movements of the index finger were to be performed as vividly as possible. This task is similar to the circle-line task that resulted in substantial spatial interference in our previous studies. One can illustrate this form of interference by simply trying the task. If you draw lines with one hand while twirling the index finger of your other hand, you most likely will experience spatial coupling, and neither task will be performed in the instructed manner.

Of note, the insertion of fiber tracts controlling movement of the finger was below the level of the amputation for all participants with a missing arm. Therefore, any residual motor signals through the stump would not be able to directly influence finger movements. Of course, because performance of only the intact arm was directly measurable, comparisons were made on performance of the intact arm across all experimental conditions. The findings from these individuals were clear. An amputee with vivid sensation of phantom limb movement produced spatial coupling in the line drawing tasks when imagined twirling movements were performed by vivid imagery of movement of the phantom. These effects were similar to those observed in control participants with two intact arms during actual bimanual performance. Spatial

interference effects of this type were not observed in the direction-compatible parallel tasks performed by either group.

Control participants with single arm amputation but no phantom limb sensation were also tested for imagery effects. When asked to perform the same set of tasks using actual movement of one arm and vivid imagery of the amputated arm, no evidence of spatial interference was observed. That is, vivid imagery without a phenomenal sensation of movement did not produce the degree of spatial coupling that occurred when the sensation of movement was more vivid. This latter finding was verified by asking control participants to perform the same set of tasks using actual movement of one arm combined with vivid imagery of movement of the other. This task also did not produce the degree of spatial coupling demonstrated on the orthogonal task with actual bimanual movements. Notably, there were no apparent differences in mean duration or its standard error across bimanual conditions or between groups. These findings suggest that the phenomena] experience of movement is necessary for spatial coupling to occur.

Given imagery alone did not result in the same degree of spatial interference as the phenomenal experience of movement, it is possible that an efference copy of the movements may mediate spatial coupling effects. Early investigators of visual processes coined the term *efference copy* to refer to a duplicate copy of the motor commands of eye movement sent somewhere else in the brain to be evaluated (von Holst, 1954; Sperry, 1950). Although difficult to directly investigate, it is possible that a form of efference copy of the limb commands may result in spatial coupling effects of the type we observed (Franz and Ramachandran, 1998). Our hope is to investigate this issue further using functional imaging.

Together, the bimanual effects demonstrated in callosotomy patients and in patients with the sensation of phantom limb movement are suggestive of some properties of spatial coupling. First, at least one form of spatial coupling appears to reflect central rather than peripheral influences. Second, because it occurs even when completely different muscle groups are used to perform the tasks, spatial coupling appears to refer to an abstract form of coupling, as opposed to one that is effector specific.

The hypothesis that spatial coupling across the corpus callosum involves abstract, as opposed to muscle-specific, processes gains support from other findings. Direct callosal connections between cortical hand representation areas in the two cerebral hemispheres are believed to be sparse or nonexistent (Weisendanger et al., 1996; for a concise review of relevant studies, see Jakobsen et al., 1994). Perhaps a separate circuit produces coupling between homologous muscles of the distal extremities on both sides of the body. Interoperative recordings of cells in the hand area have demonstrated some evidence of ipsilateral connections from the motor cortex to the index and middle fingers of the hands, in addition to the normally observed contralateral connections (Goldring and Ratcheson, 1972). With respect to coupling in volitional movements, studies on tapping have revealed evidence of coupling between the same fingers of the two hands (Rabbitt and Vyas, 1970). The next subsection explores a neural process that results in homologous finger coupling which appears to be distinct from the callosal processes that result in abstract spatial coupling.

Congenital Mirroring

Suppose a person had an innate neural "wiring" of the hands that resulted in a complete coupling of movements, in apparent contrast to the spatial uncoupling observed in callosotomy patients? There do exist people having congenital mirror movements in their hands and fingers. With each volitional movement of the distal extremities, there is a mirror movement of the respective muscles on the opposite side. Thus volitional movements of the right index finger also result in precisely mirrored left index finger movements, although the mirror movements tend to occur with smaller amplitude than the volitional movements. Although there is some debate as to the cause of this mirroring; one account is that people with congenital mirroring have abnormally dense ipsilateral projections from the brain to the spinal cord that transmit a motor signal not only to the hand contralateral to the stimulated hemisphere (as in normal movement), but also to the hand ipsilateral to the stimulated hemisphere.

Some direct ipsilateral control of the distal extremities appears to be present in the normal population, which may in part account for the difficulties beginning musicians have in producing different sequences of finger movements with their two hands. Moreover, because postures of the distal extremities can be mimicked following lateralized visual presentation to the cerebral hemisphere ipsilateral to the responding hand in callosotomy patients (Trope et al., 1987), it is possible that redundant pathways become active following the surgical procedure.

The extreme form of homologous muscle coupling observed in people with congenital mirroring appears to be abnormal. Cohen and colleagues (1991) applied

transmagnetic stimulation to the hand representation area of one motor cortex of people with normal movement and people with congenital mirror movement. The stimulation in normal controls resulted in localized muscle activation in the hand contralateral to the stimulus. The same stimulation applied to individuals with congenital mirroring resulted in muscle activation of the hand contralateral as well as the hand ipsilateral to the stimulus. These responses occurred at approximately equal latency, which suggests that the signals for movement were not transmitted across the corpus callosum. In addition, an early report of a person with congenital mirror movements who suffered stroke to one motor cortex documented a persistence of movement in the hand contralateral to the damage due to stroke (Haerer and Currier, 1966). These findings suggest that the mirror movements result from extra ipsilateral corticospinal projections emanating from the undamaged hemisphere.

I have had the good fortune of being introduced to a family six of whose members have congenital mirror movements: a father, his two sons, the father's sister, and her son and daughter. Tracing the family tree suggests that the mutation is autosomal dominant. There are no other known neurological disorders associated with this form of congenital mirroring. Moreover, certain tests rule out the possibility that the mirror coupling is due to fusion at the spinal level (a cause of other types of mirroring). Since meeting them, I have met yet another, unrelated family with the same disorder, living across the world in another country. Both families are now part of our research program.

Because the mirroring occurs predominantly in the distal extremities, these subjects afford the opportunity to examine the neural circuitry underlying the vast majority of intricate movements involved in bimanual skilled actions unique to humans. It is known that surgical lesions to descending projections on one side of the spinal cord in primates initially result in paralysis of the limb on that side. Gradual recovery of function is eventually observed in the proximal muscles of the limbs, presumably due to bilateral innervation from interneurons in the ventromedial zone of the spinal cord, although recovery is limited in the distal extremities innervated by contralateral projections whose spinal terminals are not coupled via spinal interneurons (Lawrence and Hopkins, 1976; Tower, 1940).

Figure 9.2 depicts a simple schematic of three types of descending pathways. The normally observed contralateral projections to distal extremities are labeled "contralateral C.S. [corticospinal] tracts." Also shown are the ventromedial pathways



Figure 9.2

Schematic diagram of proposed homologous finger coupling process distinct from the abstract coupling of the corpus callosum. Three descending projections are shown. The contralateral and ipsilateral projections to the distal extremities are shown as one possible mechanism of muscle coupling (proposed to be active in congenital mirroring). The ventromedial projections innervate interneurons at the spinal level, enabling for bilateral control of proximal muscles. Note that, though distal projections do not innervate spinal interneurons, distal coupling may occur due to a common origin. C.S., corticospinal.

that project ipsilaterally to the spinal cord, where they connect to spinal interneurons, which are known to innervate proximal muscles bilaterally (Porter and Lemon, 1991). In addition, a pathway labeled "ipsilateral C.S. [corticospinal] tracts" illustrates the proposed uncrossed projections to distal extremities. Because these proposed projections innervate the same distal extremities as those that are crossed, the pathways are drawn with the same spinal sites of termination as the crossed pathways. Note that the diagram shows projections from only one side of the brain, although they project from both.

In our initial investigations, my colleagues and I asked people with congenital mirroring to draw circles with one hand and lines with the other, as in our studies on abstract spatial coupling. Provided the proximal muscles are used to perform the tasks, these individuals produce patterns of behavior that are neither better nor worse than those

of control subjects, although they are not able to even begin to perform the bimanual task of twirling the finger of one hand and tapping the finger of the other. Mirror coupling of the muscles is so severe that sustained cocontraction tends to occur. Clearly, the processes that result in forms of abstract coupling appear to be intact (corpus callosum), and the mirror coupling produces an additional source of bimanual interaction in movements of the distal extremities. Through their normal compensatory behaviors, these individuals must work to inhibit the unwanted movements.

Interestingly, the corticospinal tract that transmits motor signals to muscles of the distal extremities is a circuitry most phylogenetically recent neural in humans. This circuitry is unique to primates; its density of projections increases throughout phylogeny from monkeys to chimpanzees to humans (Porter and Lemon, 1993, p. 94). The extra density in the human over other species points to neural mechanisms that may have facilitated the emergence of bimanual skills.

Subjects with congenital mirror movements show a remarkable ability to compensate for the mirroring through deliberate control of their actions. For example, the eldest son of one of the families being tested has learned to ride a motorcycle. This skill requires that the fingers of one hand control the throttle at the same time that fingers of the other hand produce an entirely different sequence of actions to control the brake. He would have to be adept at this task, given the cost associated with error. Another member of the same family has taught himself to play a twelve-string guitar marvelously. Is this evidence of extraordinary levels of expertise? One is led to wonder whether, just as advanced forms of compensation may be examples of perturbations in human evolution, so too may deficits. These issues form the basis of ongoing research in our laboratory. One aspect of these investigations is to consider how skilled bimanual actions rely on higher-order representations.

9.3 Representation of Cooperative Bimanual Actions

The aforementioned tasks employed procedures in which a specific task is assigned to each hand, and the processes of coupling between the hands are studied. In this sense, there exist two tasks—one for each hand. Bimanual studies have demonstrated that at least two forms of coupling occur in dual-task procedures of this type: One involves spatial coupling, and the other, temporal coupling. Spatial coupling comes in at least two forms— coupling of direction and coupling of amplitude—both of which appear to rely on the corpus callosum.

This section considers situations in which the two hands cooperate to perform a unified task, such as opening ajar or tying shoes. Little is known about the neural processes underlying these types of bimanual skills and how they are represented in the brain. Interestingly, it may be the case that the task itself defines the binding properties of such bimanual actions.²

Effects of Callosotomy on Novel versus Well-Learned Tasks

Given that abstract forms of spatial coupling between the hands appear to rely on interactions provided by callosal connections, it is astonishing that callosotomy patients are so capable of performing coordinated actions, as noted by Zaidel and Sperry (1977) in their comprehensive study of a large group of patients with full or partial callosotomy tested at least five years after surgery. These and other investigators (e.g., Preilowski, 1972) have noted, in particular, the importance of vision in the learning of bimanual actions. Mark and Sperry (1968) examined the performance of split-brain monkeys in a task of retrieving a food pellet by pushing it with one hand through a hole, and catching it with the other. There was some evidence that the monkeys' performance, after extensive practice on this task using vision, was not completely impaired, in some cases, even without vision. Little is known, however, about the storage of already-learned bimanual skills in humans, who have the capacity to utilize symbolic codes for actions (see also Geffen et al., 1994).

In our research, my colleagues and I had the opportunity to test a patient on novel and well-learned bimanual tasks just following callosotomy surgery. During an initial visit to this patient following her recovery from surgery, we observed that she was able to tie her shoes, rather spontaneously, without the use of vision. Indeed, Zaidel and Sperry (1977) reported that a buttoning task performed by a callosotomy patient in full vision took approximately 150% longer than the same task performed by controls, which suggests that vision may actually slow an already-learned task that otherwise might be performed relatively automatically. The patient we observed appeared able to tie her shoes virtually automatically when no vision was used. This observation and helpful comments offered by the patient have led to a series of studies in which we are examining well-learned and

novel bimanual actions both with and without vision. A clear result emerged from an initial investigation in this series of experiments.

Two callosotomy patients and a small group of control participants were asked to pantomime certain movements in response to oral commands, while blindfolded. The commands were worded in the form "Please show me how you would ...," and the command was completed either by a phrase describing a task requiring one hand ("Reach for a cup"), or a bimanual action ("Peel an orange"). In this study, objects were not shown. Subjects were free to pantomime single-hand actions with whichever hand they preferred (so that apraxia would not be a limiting factor). Given that both hemispheres comprehend speech input, instructions were presented aloud (Gazzaniga and Sperry, 1967). Subjects were queried afterward about the extent of their experience on each task, and family members were consulted to verify these answers when necessary. Results of this study showed a clear difference in the latency to respond and accuracy in performance on well-learned tasks versus tasks never learned before the surgery. Performance on novel tasks was much less accurate than on well-learned tasks in the patients but not in the controls. Similarly, one of the patients produced an increased latency to respond on novel versus well-learned tasks, whereas the second patient responded quickly but incorrectly on novel bimanual tasks. There were no differences in spatial accuracy or response latency on well-learned tasks between patients and controls (Franz et al., 2000).

These findings suggest that well-learned cooperative actions remain intact following callosotomy in humans, and can be performed even without the guidance of vision. Consistent with Zaidel and Sperry, 1977, unfamiliar bimanual actions could not be performed without the aid of vision. One model for these findings is that well-learned tasks are represented in areas of the brain directly accessible to the motor systems of both cerebral hemispheres.

Because verbal codes were used in our study, it seems reasonable to suggest that well-learned behaviors become stored in action codes that no longer require the on-line cross-matching of perceptual information that is necessary during the processes of learning (Franz et al., 2000). Evidence from functional magnetic resonance imaging (fMRI) is consistent with this claim. For example, Kami and colleagues (1995) showed a decrease in activation in the prefrontal cortex in subjects learning a complex motor task. Shadmehr and Holcomb (1997) have shown shifts in neural activation from prefrontal

cortical areas to premotor, posterior parietal, and cerebellar areas in subjects after only hours of practice on a motor task.

Synchronous activity across neurons in the striate cortex of cats has been demonstrated during what appears to be binding processes in visual perception (Engel et al., 1991; Gray et al., 1989, 1992). Synchronous activity across visual areas of both cerebral hemispheres, followed by the elimination of interhemispheric synchrony with callosal section, has also been demonstrated in cats (Engel et al., 1991). Based on such findings, it is reasonable to suggest that a similar form of synchronous activity may occur across the corpus callosum in humans during the learning of bimanual tasks.

Andres and colleagues (1999) examined learning-related changes in the coherence of neural activity across sensorimotor systems of the cortex during a bimanual task. They recorded scalp activity using surface electrodes during performance of an 8-key sequence. The sequence was first over-learned in unimanual blocks of trials, with each hand trained separately. The task was then tested under bimanual conditions in which overlearned sequences of the left and right hands were combined so that the key presses alternated to form a 16-key bimanual sequence. The highest coherence between left and right cerebral cortices occurred during bimanual learning. This coupling was higher than in unimanual control trials. After bimanual performance became stable through practice, the level of coherence returned to that observed in unimanual control trials. This evidence strongly suggests that synchronous activity across the corpus callosum occurs with learning of a cooperative bimanual task. After the task is well learned, synchronous activity is reduced.

Given that the motor cortices of both hemispheres must be active to project movement signals to the two hands, how are well-learned cooperative bimanual tasks accessed by both cerebral hemispheres? One possibility is that one hemisphere controls both hands, even if the movements involve the distal extremities to some extent. Accordingly, the codes for action may reside in one hemisphere (probably the left), and movement commands would project from that hemisphere to both the contralateral and ipsilateral hands (Gazzaniga and Sperry, 1967). A second possibility is that action codes of the well-learned bimanual task are stored in subcortical loci, namely, the cerebellum or basal ganglia. These codes would then be accessed by both cerebral hemispheres, each of which channels the appropriate movement commands to the hand it controls. This possibility would be difficult to differentiate from one in which the two cerebral hemispheres each contain action codes of the bimanual task.

Evidence on the functional role of the supplementary motor area (SMA) in bimanual actions may be interpreted as consistent with the hypothesis that duplicate codes become mirrored in the two hemispheres during learning. Early studies on the SMA indicated that this structure is bilaterally organized (Travis, 1955) and connections between the two sides are "callosal" (DeVito and Smith, 1959). Investigating the role of the SMA in an adapted version of the task in Mark and Sperry, 1968, Brinkman (1984) reported that small unilateral SMA lesions produced minor and transient effects on bimanual performance, whereas larger lesions extending into more anterior regions produced an abnormal form of mirror movements during a bimanual task. Specifically, monkeys were trained to obtain a small food reward by pressing the food pellet through a hole in an upright board with one hand, and catching the pellet with the other. Following unilateral lesions of considerable size, the animals attempted to perform the bimanual task by simultaneously pressing the finger of each hand through the hole. Brinkman attributed this mirroring (not related to the type of congenital mirroring described earlier) to the bilateral projections from the SMA to both sides of the motor cortex. It seems possible that the SMA mediates the duplication of action codes to the other hemisphere via intact callosal projections. Given that the basal ganglia are known to project to the SMA, it is possible that action codes in these subcortical structures (i.e., the striatum) mediate the performance of well-learned bimanual actions in humans (Franz et al., 2000). However, recent investigations have reexamined issues related to SMA function in the bimanual performance of monkeys, suggesting that earlier findings may have been a result of compensatory processes (for a thorough study, see Kazennikov, 1998). More evidence of SMA involvement is discussed below.

Egocentric versus Allocentric Influences and the Acallosal Brain

Preilowski (1972) examined performance of patients with anterior callosal section on a bimanual task that required turning a left-hand held knob to control vertical movement of a cursor and a right handheld knob to control horizontal movement of the same cursor. Production of linear movements along a perfect diagonal (45° orientation) required left-and right-hand knob turns at the same rate. Performance of patients revealed a larger degree of spatial deviation for lines slanted more vertically than horizontally with respect

to the 45° diagonal. To account for these effects, the investigators suggested that the right-hand (left-hemisphere) contribution is more difficult to inhibit than the left-hand (right-hemisphere) contribution. Thus, there was an alleged left-hemisphere dominance in performing the bimanual task.

My colleagues and I have begun to explore possible hemisphere asymmetries in spatial control on bimanual tasks when instructions are not lateralized. One of our primary issues of interest concerns how the brain organizes bimanual actions into the separate requirements of each hand. We began to address this issue using a drawing task in which the precise assignment to each hand was unspecified. This idea will be described more thoroughly below. First, I will introduce under group of participants who have graciously volunteered to participate in our studies.

When testing callosotomy patients, one cannot help but wonder whether similar behaviors would be observed in people born without a corpus callosum. It seems reasonable to assume that vast forms of neural reorganization may be apparent in them. I recently had the good fortune of being introduced to a family consisting of three females with callosal agenesis. All three are able to run around and kick a ball, throw and catch, carry on normal conversations, and perform the other routine daily activities that most people do. Watching the remarkable ability of these individuals to perform these actions normally, or at least apparently so, one wonders how their brains have compensated for the lack of interhemispheric connections.

In our preliminary studies, my colleagues and I found that all three individuals from this family demonstrated a right-hemisphere dominance in their motor actions, as revealed by standardized tests in which stimuli were presented to both hemispheres simultaneously and errors in responding were recorded. In right-handed callosotomy patients, such tests often reveal evidence of extinction of the stimulus presented to the right hemisphere, indicating a left-hemisphere dominance. Similar (and other) tests performed on our callosal agenesis subjects revealed just the opposite— a right-hemisphere dominance for motor actions. This finding led us to begin a set of studies on bimanual processes in the absence of a corpus callosum in two groups of subjects with opposite cerebral dominance: callosotomy participants with left-hemisphere dominance, and callosal agenesis participants with right-hemisphere dominance.³

Our initial experimentation has focused on task selection properties in bimanual actions. Our primary interest is in the way bimanual actions are organized so that each hand is instructed to perform its respective action, especially in tasks that pose more than one possible performance solution. Do there exist asymmetries in control that result in one cerebral hemisphere performing the role of arbiter? If so, do the two hemispheres show biases in the types of information they predominantly process? In our initial investigations of these issues, we chose the task of bimanual circle drawing, a task well studied in neurologically normal individuals, and one used to quantify phase differences between the hands under different movement conditions (Carson et al., 1997; Semjen et al., 1995; Stucchi and Viviani, 1993; Swinnen et al., 1997).

When drawing circles with both hands, there are four different performance solutions that fit into a classification scheme consisting of two basic coordination modes: The first is referred to as "mirror symmetrical" because the two hands draw circles in a mirror-symmetrical fashion with respect to the body midline; and the second, as "parallel" because the two hands draw circles in the same direction with respect to external space. According to Swinnen and colleagues (1997), these two general categories of movement have been used to illustrate, respectively, egocentric and allocentric processing. *Egocentric* refers to movements that occur with respect to a body coordinate frame. Mirror-symmetrical circle drawing tends to be characterized as "egocentric" because the movements do not rely on external information, but only the relative position of the two hands with respect to the body. In contrast, *allocentric* refers to parallel movements, given the two hands must move in the same direction with respect to external space.

To give each hemisphere an equal chance of taking control, rather than lateralizing input, my colleagues and I orally instructed participants. With oral information, both cerebral hemispheres have access to the instructions. People were simply instructed to draw circles with both hands, and data were recorded using digitizer tablets (see figure 9.3). We first thoroughly examined performance of a large group of right-handed participants with intact corpus callosi and no known neurological problems. We recorded kinematics of the circle trajectories, in addition to two other forms of information. The first was to record the probability of selecting the mirror versus parallel coordination mode. We could then compute the conditional probability of selecting either of the two



Figure 9.3

Kinematic data in a bimanual symmetrical circle task. (A,B) Displacement data (x-axis versus yaxis) for the left and right hands, respectively. (C,D) Displacement data for each dimension separately for each hand. (E) Accumulated angular distance across time during the trial, for both hands (closely time locked). (F) Instantaneous differences in phase between the two hands through time. Note that the average phase difference is negative, showing that mirrorsymmetrical tasks are usually performed with a right-hand lead, and suggesting a left-hemisphere organization. direction modes, given each choice of coordination mode. The second variable was whether one hand tended to lead the other, and if so, which one. The purpose of this second manipulation was to access the degree to which the choice of lead hand was related to the choice of coordination mode.

Our control participants demonstrated an overwhelming bias to select the mirrorsymmetrical over the parallel mode (approximately 90% chose the mirror-symmetrical mode). When subsequently instructed to perform the less-chosen parallel mode, approximately half of the control participants chose the clockwise direction, and half chose the counterclockwise mode. Interestingly, clockwise parallel drawing was characterized by a right-hand lead in approximately 80% of the trials, whereas counterclockwise parallel drawing was characterized by a left-hand lead in approximately 80% of the trials.

We applied identical procedures to callosotomy and callosal agenesis participants, with the goal of examining how different cerebral dominance would influence task selection. We were surprised to find that the two groups spontaneously selected different coordination modes. Callosotomy participants chose to draw mirror-symmetrical movements, and were unable to draw in the parallel mode without the use of vision. In contrast, callosal agenesis participants selected the parallel mode (counterclockwise), and were unable to draw in the mirror-symmetrical mode without the use of vision. One inference of these findings is that the corpus callosum provides for the flexible allocation of dominance, given that neither group could perform one category of tasks (Franz, 2000a, 2000b; Franz et al., forthcoming).

These findings are also suggestive of biases in the type of spatial information predominantly processed in each cerebral hemisphere. Note that the callosotomy patients with left-hemisphere dominance for motor actions performed only the mirrorsymmetrical task. Conversely, the right-hemisphere-dominant acallosal participants performed only the parallel task. Although speculative at this time, our findings may link these two types of the processing to different cerebral hemispheres. Accordingly, in the normal brain, the corpus callosum allows for flexible allocation of dominance to either hemisphere, depending on task demands. It is possible that for this reason, the left hemisphere is usually the dominant hemisphere in speech output. Speech, like mirrorsymmetrical movements, requires precise processing of the relative relations among articulators. In contrast, the right hemisphere tends to be more facile at processes related to information from outside of the organism. Of course, because these tentative conclusions are based purely on performance of a bimanual task (Franz, 2000a, 2000b), they remain subject to rigorous experimental testing.

Recent neurophysiological, neuropsychological, and functional imaging evidence indicates that some neurons respond to bimanual related activity. In a single-unit study, Tanji and colleagues (1988) demonstrated changes in neural response patterns of SMA neurons when comparing bimanual to unimanual performance on a task requiring finger flexion movements in monkeys. Donchin and colleagues (1998) recorded neuronal responses of the supplementary motor area (SMA) and primary motor cortex (MI) in homologous sites of the two hemispheres during a bimanual task performed by rhesus monkeys. The task consisted of moving two arm manipulanda to achieve target locations with both arms, which would involve proximal as well as distal muscle contributions. The locations required movements either in the same direction (leftward or rightward) or in mirror-symmetrical directions (one to the left and the other to the right). Movements of the two arms were to be performed simultaneously. Donchin and colleagues presented data of both SMA and MI neurons firing vigorously for bimanual movements. These findings indicate that both cortical areas contain bimanually sensitive neurons, at least for movements involving some proximal contribution. In a compelling demonstration presented by Donchin and colleagues, a right SMA neuron fired vigorously when both hands moved together in the leftward (parallel) direction, but fired much less vigorously when both moved in the rightward direction, and virtually not at all when the two hands moved in mirror-symmetrical directions. This demonstration is consistent with our own claim that there may be a hemispheric dominance in the organization of bimanual tasks, particularly with respect to mirror-symmetrical versus parallel bimanual movements.

Sadato and colleagues (1997) recorded cerebral blood flow during unimanual and bimanual sequences of finger movements in right-handed subjects. Bimanual movements consisted either of mirror-symmetrical sequences of the two hands, in which homologous fingers moved together, or of parallel sequences in which nonhomologous fingers moved together. These investigators found that both types of bimanual tasks activated areas of the parietal lobe, sensorimotor, and premotor areas, and subcorticol structures of the cerebellum, putamen, and thalamus bilaterally. In addition, the dorsal premotor area and the supplementary motor area of the right hemisphere demonstrated a significantly higher level of activation in parallel compared to mirror-symmetrical tasks. These findings are consistent with our thesis that the right hemisphere plays a dominant role in the organization of parallel movements and the left hemisphere plays a dominant role in the organization of mirror-symmetrical movements.

Other compelling evidence consistent with the proposal of hemispheric asymmetries in the organization of mirror-symmetrical and parallel bimanual movements comes from neurological patient studies. Chan and Ross (1988) reported a patient with a righthemisphere ischemic infarction that involved a large region of the right hemisphere including anterior cingulate, the medial prefrontal region, and the SMA. This patient presented an inability to perform bimanual tasks that required nonmirror movements, although he was much less impaired in the performance of mirror-symmetrical movements.

In our ongoing studies, my colleagues and I are investigating the properties of reorganization that may influence representation of bimanual actions in people with callosal agenesis. It is not clear whether the right hemisphere dominance we observed in our small group of these participants reflects reorganization. It also remains to be determined whether the hemispheric asymmetries we observed between the two groups of acallosal participants reflect differences in the way space is represented in the two hemispheres (egocentric versus allocentric).

9.4 Conclusions

It seems clear that the representation of bimanual actions can be studied at many levels of the cognitive and motor systems. The hands and fingers are represented in motor representation areas of each cerebral hemisphere, among other areas in the brain. Callosal connections appear to produce abstract forms of spatial coupling between tasks that are lateralized to separate hands (i.e., separate cerebral hemispheres). If a bimanual task is merely assigned to the performer, but contributions of the two hands are not specified as distinct tasks, the brain must organize which action goes with which hand. It appears that higher-order forms of spatial representation may influence this organization, and the intact corpus callosum may enable flexible allocation of cerebral dominance. When cooperative bimanual tasks of the two hands become well learned, the unitary task may become represented in a different form than in the learning stages. Our most recent work examines the way conceptual representations may be used to unify separate tasks of the two hands. The use of such conceptual representations during performance may allow for a reduction in the interference that would otherwise occur in the dual-task situation. This may be one example of how a dual-task becomes a single task (Franz et al., 2001).

Although we are far from understanding either how the human brain manufactures tools or how representations occur there, the representation of bimanual actions may provide a valuable window on the emerging picture of our evolution.

Notes

1. I wish to acknowledge that all participants in these and all our experiments are volunteers who receive no material benefits of any kind. Their generosity and willingness to educate others, while remaining completely anonymous, is indeed a rare find.

2. I borrowed this idea from Daniel Gopher during a discussion at the Attention and Performance XIX meeting in Kloster Irsee, Germany in July 2000.

3. We were surprised to find evidence of right-hemisphere dominance in these individuals. I am not of course suggesting that this is a hallmark of callosal agenesis because any number of factors may be contributing; indeed, our initial findings may provide more clues about cerebral dominance than they do about callosal agenesis per se.

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