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Research Report

DISSOCIATION OF SPATIAL AND TEMPORAL COUPLING IN THE BIMANUAL MOVEMENTS OF CALLOSOTOMY PATIENTS

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Abstract—The neural mechanisms of limb coordination were investigated by testing callosotomy patients and normal control subjects on bimanual movements. Normal subjects produced deviations in the trajectories when spatial demands for the two hands were different, despite temporal synchrony in the onset of bimanual movements. Callosotomy patients did not produce spatial deviations, although their hands moved with normal temporal synchrony. Normal subjects but not callosotomy patients exhibited large increases in planning and execution time for movements with different spatial demands for the two hands relative to movements with identical spatial demands for the two hands. This neural dissociation indicates that spatial interference in movements results from callosal connections, whereas temporal synchrony in movement onset does not rely on the corpus callosum.

A remarkable faculty of humans is the ability to produce coherent actions by coordinating the limbs to achieve a common goal, such as in grasping a jug, tying one's shoelaces, or playing a musical instrument. Although the subcortical and cortical processes that underlie single-limb movements have been studied extensively, the neural mechanisms that govern coordination between the limbs have received relatively little attention. Each cerebral hemisphere exerts primary control of the contralateral limbs, but the spatial and temporal properties of bimanual movements reveal strong interactions between the limbs. It is difficult, for example, to produce different temporal patterns with the two hands. The strong tendency toward synchronous movements (Kelso, Southard, & Goodman, 1979; Klapp, 1979; Schoner & Kelso, 1988; Yamanishi, Kawato, & Suzuki, 1980) is evidence of temporal coupling. It is also difficult to produce different spatial patterns with the two hands, for example, a square shape with one hand and a circle shape with the other. Spatial interference in the trajectories of such tasks is evidence of spatial coupling in coordination (Franz, Zelaznik, & McCabe, 1991).

The corpus callosum is the most direct connection between the cerebral hemispheres (Gazzaniga, 1989). Callosotomy patients, in whom the cerebral hemispheres are surgically disconnected, therefore, provide a model to investigate the neural processes of coordination. Previous research has demonstrated that callosotomy patients produce normal temporal coupling in continuous movement tasks (Preilowski, 1972; Tuller & Kelso, 1989; Zaidel & Sperry, 1977). This tendency toward temporal

synchrony is so powerful that the patients are virtually unable to turn handheld knobs using two different temporal patterns when visual feedback of the limbs is removed. Without such feedback, they resort to moving with identical temporal patterns (Preilowski, 1972). The strong focus on temporal coupling and the limited use of spatially demanding tasks in these investigations have left open the question of whether callosotomy patients demonstrate spatial coupling.

To investigate the neural processes of spatial and temporal coupling, we applied to callosotomy patients a standard paradigm for examining bimanual movements. When normal subjects attempt to produce movements requiring different spatial forms (i.e., lines combined with circles) or directional properties (i.e., horizontal movements combined with vertical movements) for the two hands, spatial interference in the trajectory paths of both hands is exhibited. These tasks prove to be spatially demanding even when subjects move at a preferred rate (Franz et al., 1991). In the present study, a callosotomy patient and normal control subjects were tested on repeated cycles of trajectories that required movements in either the same orientation or orthogonal orientations for the two hands. We also tested complex spatial tasks in a discrete paradigm using control subjects and two callosotomy patients to elucidate whether the observed spatial effects would generalize to a more complex spatial pattern.

EXPERIMENT 1

Subjects

Patient J.W., a 40-year-old man (described in Sidtis, Volpe, Wilson, Rayport, & Gazzaniga, 1981), underwent two-stage posterior-anterior surgical section of the corpus callosum in 1979. During conditions of unrestricted feedback (i.e., normal conditions), he maintains everyday coordinated actions of the limbs, such as in manipulating objects, operating an automobile, and playing board games. J.W. has been tested repeatedly over the past 20 years in experiments that require lateralized visual input. He is experienced in maintaining fixation and shows no signs of extinction when stimuli are presented to the two hemispheres simultaneously.

Three normal males (ages 39, 40, and 43) participated as control subjects. All subjects were right-handed and had normal vision and hearing.

Stimuli

Stimuli consisted of single lines 8 cm or 16 cm long. Lines were oriented either horizontally (along an *x* axis) or vertically

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(along a y axis) on a computer screen with the medial border 2° to the left or right of a fixation point. The stimuli subtended horizontal and vertical visual angles proportional to their sizes (i.e., 8° horizontally for an 8-cm line).

Apparatus and Procedure

The subject was seated at a standard desk on which two Kurta digitizer tablets were placed side by side. Directly behind the tablets, a computer monitor was situated so that its center was aligned with the medial axis of the subject's body. The subject held a digitizer pen in each hand to draw the stimuli that appeared on the computer monitor. The hands were blocked from the subject's view by a paper screen.

So that information would be presented to each hemisphere separately, the stimuli were visually lateralized. On single-hand trials, a single stimulus appeared; on bimanual trials, two stimuli appeared. Stimuli were presented for a brief duration of 150 ms to discourage eye movements. Eye movements were monitored during the entire testing session to ensure that the lateralization of input was successful.

The subject fixated on a central point located at all times on the computer monitor. After a variable interval (500 ms to 1,000 ms), the line stimulus (stimuli) occurred. The subject was instructed to draw the linear trajectory in a back-and-forth or left-to-right manner, depending on the stimulus orientation, at a self-determined pace for a 10-s trial. In single-hand trials, repeated cycles of a single stimulus were to be drawn using only one hand. In bimanual trials, the stimuli to the left and right of fixation were to be drawn repeatedly by the left and right hands, respectively. No instructions were given as to how to coordinate the limbs.

All 16 possible stimulus combinations were employed (2 lengths \times 2 orientations for each limb, combined in all possible bimanual conditions). Four blocks of trials were administered in random order.

Results

All subjects performed single-hand control tasks without difficulty. Because bimanual coupling is the focus of this study, analyses are limited to bimanual tasks. For these analyses, task pairs were categorized into four conditions: (1) same orientation, equal size; (2) same orientation, unequal size; (3) orthogonal orientation, equal size; and (4) orthogonal orientation, unequal size. The time of movement onset and cycle duration were measured for each hand, on each cycle of movement within a trial. The control subjects adopted a movement speed of between 1.1 Hz and 1.6 Hz, and this rate was relatively constant across the four conditions. The speed of movement for the patient was within this range (1.4 Hz).

To assess temporal coupling, we computed the difference in time of movement onset (i.e., time when direction reversed) between the two hands for each line segment and averaged across cycles within blocks of trials. For the callosotomy patient J.W., on more than 95% of the segments, the two hands reversed direction within 10 ms of each other. There was no

consistent tendency for one hand to lead the other, and these effects were identical across the four conditions. Control subjects produced similar results: In all task conditions, the hands reversed direction within 10 ms of each other on at least 90% of the movement segments.

To examine spatial coupling, we plotted and viewed all trajectories on a computer screen. It was immediately obvious that trajectories produced by control subjects exhibited considerable spatial deviations that were not apparent in the trajectories produced by the callosotomy patient. To quantify these effects, we measured the orientation of each segment and computed the angular difference between corresponding segments produced by the two hands. The absolute difference between this value and the target value was then calculated (0° or 180° for the same-orientation condition; 90° for the orthogonal-orientation condition). As expected, normal subjects produced substantial deviations in the trajectories characterized by orthogonal orientations compared with those characterized by same orientations (see Fig. 1). A main effect of line orientation emerged for 1 control subject, $F(1, 58) = 8.57, p < .05$, and approached significance for a 2nd control subject, $F(1, 56) = 7.94, p < .06$. The difficulty in producing lines was quite dramatic for the 3rd control subject, who was virtually unable to produce linear trajectories on 72% of his trials, because of frequent hesitations and multiple direction changes within each segment. The pattern for J.W. was the opposite of the control subjects' pattern: J.W. exhibited better performance in the orthogonal-orientation conditions compared with the same-orientation conditions, $F(1, 57) = 48.13, p < .05$. This unexpected result is consistent with spatial uncoupling in the patient. J.W. is unaware of the spatial

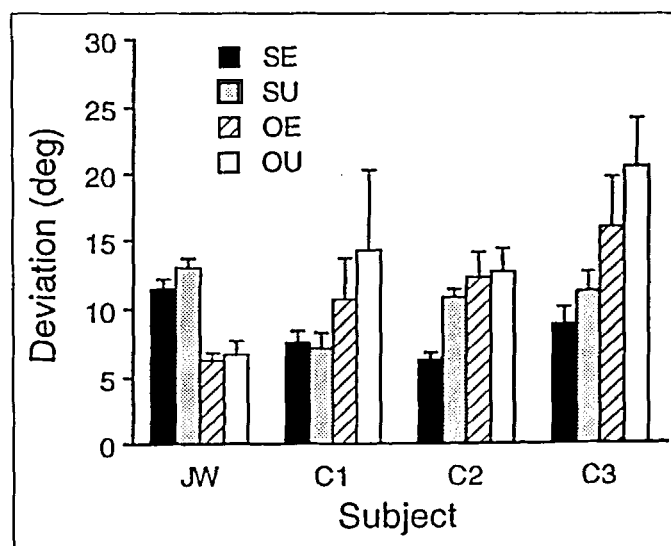


Fig. 1. Spatial deviation in linear trajectories drawn by two hands simultaneously by patient J.W. and 3 age-matched control subjects. Shown on the ordinate is the average deviation from perfect performance in degrees, for each of the four conditions: movements of same orientation and equal size (SE), same orientation and unequal size (SU), orthogonal orientation and equal size (OE), and orthogonal orientation and unequal size (OU).

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compatibility of two lines oriented in the same direction and may be unable to capitalize on the redundancy.¹

These results suggest that although temporal coupling is intact following callosotomy, spatial coupling is greatly reduced. To ascertain the generality of these effects, subjects were tested on a second task that increased the complexity of the spatial trajectories.

EXPERIMENT 2

Method

The subjects and apparatus in Experiment 2 were identical to those employed in the first experiment. The stimuli consisted of three-sided rectangles that appeared in two sizes ($4 \times 8 \times 4$ cm or $8 \times 4 \times 8$ cm) and two orientations (see Fig. 2). As in Experiment 1, the two sizes were crossed with the two orientations to produce four categories of task pairs. Subjects were instructed to begin each movement as soon as possible after presentation of the stimuli, to complete the three-segment movements as rapidly as possible, and to move the hands together rather than staggering the movements. Two blocks of 56 trials each were administered, and trials with discontinuous trajectories (i.e., gaps in the spatial path) were eliminated from analysis.

Results

Reaction time was computed as the time between stimulus presentation and movement onset. All 3 control subjects were significantly slower to initiate trials in which the initial segments required movements along orthogonal axes than trials in which the segments were along the same axis (Fig. 3a): $F(1, 108) = 5.15, p < .05$; $F(1, 107) = 25.58, p < .05$; and $F(1, 103) = 37.25, p < .05$. Averaged over the 3 subjects, the magnitude of this effect was 161 ms. Similarly, reaction time for the control subjects was 124 ms slower, on average, when the corresponding segments were unequal in size than when the corresponding segments were equal in size: $F(1, 108) = 6.65, p < .05$; $F(1, 107) = 14.86, p < .05$; and $F(1, 103) = 17.90, p < .05$. These findings indicate large increases in movement planning time for normal subjects when spatial parameters of direction or size differ for the movements of the two limbs. Reaction time for J.W. was not affected by these variables, $F(1, 110) < 1$.

Response duration was computed as the total duration of the movement. A pattern similar to that obtained for reaction time was evident in response duration (Fig. 3b). Movements involving orthogonal trajectories or segments of unequal sizes did not affect performance of the callosotomy patient, $F(1, 110) < 1$. Response duration increased substantially for 2 control subjects when orientation differed for the two tasks: $F(1, 108) = 36.70, p < .05$; $F(1, 103) = 24.79, p < .05$. For the 3rd control subject, response duration increased when size differed, $F(1, 102) = 96.69, p < .05$.

1. All subjects tended to produce movements with larger amplitudes than required. Thus, because the effects of size were not clear, this variable is left for discussion in the section reporting on Experiment 2.

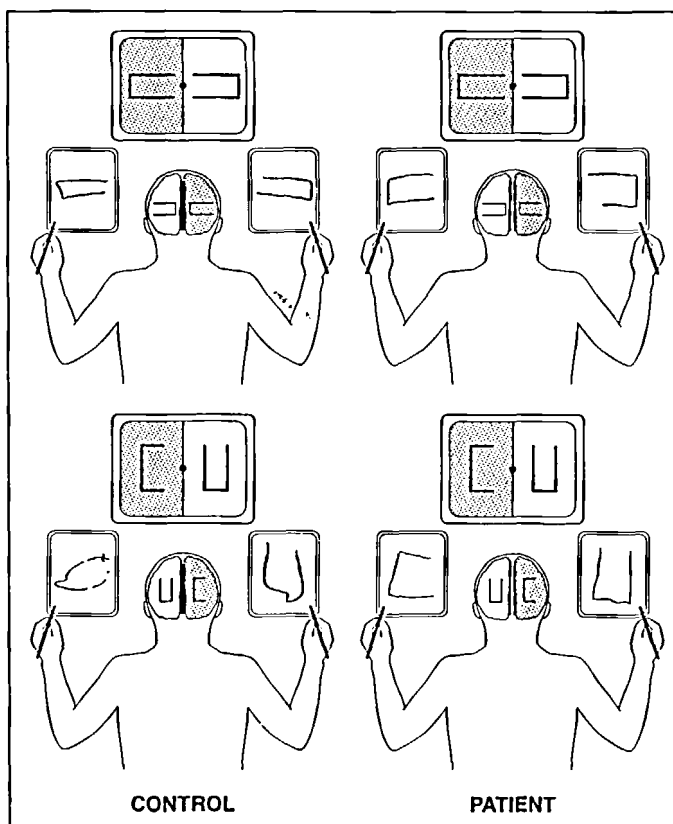


Fig. 2. Schematic of the experimental setup and representative trajectories from Experiment 2. Shading indicates correspondence between the side of presentation on the computer monitor and the cerebral hemisphere receiving the information. On the left is a representative trial for a control subject in the same-orientation, equal-size condition (top) and the orthogonal-orientation, unequal-size condition (bottom). The bar connecting the two hemispheres represents an intact corpus callosum in the control subject. The patient's performance on a trial from each of these two conditions is depicted on the right.

These measures indicate that additional planning before and during movement execution was necessary for control subjects when spatial requirements differed for the two hands. For J.W., all movement combinations were performed with the same amount of planning time. The fact that 1 control subject produced longer reaction times than J.W., and 2 control subjects produced longer durations, indicates that J.W.'s performance was not at ceiling.

Generalizability of Results

To examine the generality of these results, we tested J.W., a second callosotomy patient (V.P., described in Sidtis et al., 1981), and 2 control subjects on complex spatial trajectories. V.P., age 42, underwent anterior-posterior callosotomy in 1979. Temporal coupling in V.P. has been shown to be normal (Tuller & Kelso, 1989). Because our goal was to provide additional evidence of spatial uncoupling across a wide variety of movement demands, a protocol involving 50 unique geometric figures characterized by lines, curves, circles, and squares was ap-

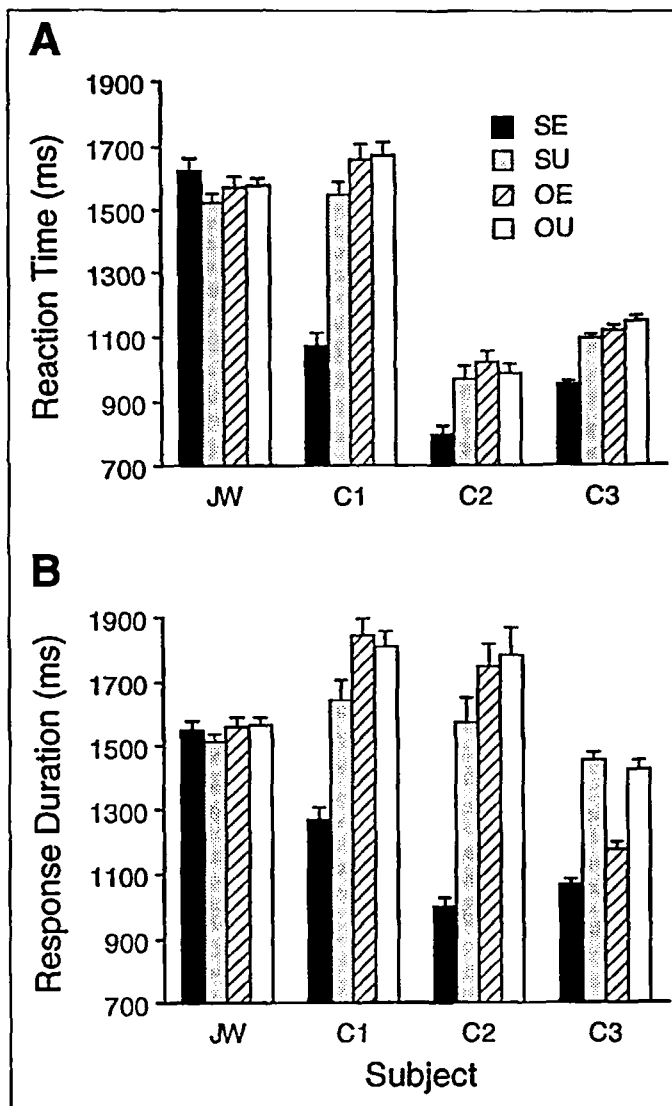


Fig. 3. Reaction time and response duration for J.W. and 3 age-matched control subjects on the complex trajectory task. Average reaction time (a) and response duration (b) and standard errors are depicted for movements of same orientation and equal size (SE), same orientation and unequal size (SU), orthogonal orientation and equal size (OE), and orthogonal orientation and unequal size (OU).

plied. On each of 50 trials, two different figures were presented, one to each hemifield. The subjects were required to draw both patterns simultaneously. Of all the subjects, V.P. produced the most accurate spatial trajectories. To verify these spatial effects, we asked four independent judges to evaluate the spatial characteristics of the drawings in comparison to templates of the target patterns. There was overwhelming agreement across raters that the callosotomy patients' drawings were more spatially accurate than the control subjects' drawings. The average ratings indicated that the patients' performance was better than the controls' on 63% of the trials, equal on 10%, and worse on 27% ($p < .001$ by a sign test). In fact, the drawings of V.P.

ranked the highest of all 4 subjects' drawings. Thus, the strong spatial uncoupling observed in J.W. generalized to another callosotomy patient, and to a variety of spatial tasks.

It should be noted that even with substantial practice, these spatial coupling effects appear to persist in normal subjects.² It is therefore unlikely that spatial uncoupling in callosotomy patients is the result of postsurgical practice.

DISCUSSION

Taken together, the current results reveal an important dissociation in the constraints associated with bimanual movements. Temporal coupling is intact in callosotomy patients despite their ability to simultaneously produce trajectories with different spatial demands. This dissociation indicates that the processes producing spatial and temporal coupling involve separable mechanisms. These findings have profound implications for understanding the way the neural architecture is organized in complex actions.

Temporal coupling occurs even when the primary pathways between the cerebral hemispheres are severed. This result constrains the possible neural bases for temporal coupling. One possibility is that feedback from the moving limbs is projected bilaterally and these signals are used by each hemisphere to adjust the output to the contralateral limb. A second possibility is that temporal coupling arises because a single processor coordinates the final issuance of motor commands, thus synchronizing the actions of the two limbs during bimanual movements (Stucchi & Viviani, 1993). This processor could reside in one hemisphere or the other, and evidence of asymmetric activation is in accord with this hypothesis (Kim et al., 1993). Alternatively, temporal coupling may arise at a level below the cerebral cortex, reflecting subcortical processes. By this hypothesis, each hemisphere may contribute to the control of movements of the contralateral hand, but the signals to the periphery during bimanual movements are issued synchronously (Bullock & Grossberg, 1988; Osman, Kornblum, & Meyer, 1986). It should be mentioned that although the anterior commissure is intact in both callosotomy subjects who participated in these experiments, there is no known role of this structure in motor control. Future research will determine the nature of temporal coupling.

Spatial coupling, in contrast, appears to result from direct interactions between the cerebral hemispheres, via the corpus callosum. There is ample evidence that cortical representations of movement are in terms of spatial parameters such as movement direction and extent (Georgopoulos, Taira, & Lukashin, 1993). In addition, imaging studies have found bilateral activation in cortical representation areas during unimanual movements (Kim et al., 1993; Roland, Meyer, Shibasaki, Yamamoto, & Thompson, 1982; Seitz, Roland, Bohm, Greitz, & Stone-Elander, 1990). A functional consequence of this cortical architecture appears to be that there are interactions between the spatial characteristics of movement plans for the two limbs during bimanual movements. There are at least two hypotheses that may account for these effects. One hypothesis is derived from claims that the contributions of the two hemispheres to

2. The first author has examined people on these tasks for years, and even over repeated testing sessions, the spatial effects remain.

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movement are asymmetric. In particular, the study of apraxic disorders has led to the hypothesis that the left parietal cortex is essential for the spatial representation of complex movements (Heilman, 1979). This asymmetry may be achieved by callosal inhibition of the right hemisphere (Cook, 1986). With these fibers being severed in the patients, the right hemisphere would be released from its inhibition and could assume control of movements of the left hand. An alternative hypothesis is based on the idea that in normal movement, each hemisphere is dominant in the control of the contralateral hand. Viewed this way, the corpus callosum can provide a pathway for integrating processing because the two limbs are usually working to achieve a common goal. In the callosotomy patient, this cross talk is eliminated, and the two hands can follow independent spatial goals. By either hypothesis, the current results demonstrate that interactions in the spatial representations are abolished following callosotomy.

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