

Research Report

THE EFFECT OF CALLOSOTOMY ON NOVEL VERSUS FAMILIAR BIMANUAL ACTIONS: A Neural Dissociation Between Controlled and Automatic Processes?

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Abstract—*The corpus callosum is the large band of fibers that connects the two cerebral hemispheres of the brain. Individuals who have had the fibers of these tracts surgically severed by callosotomy are able to draw two different spatial figures simultaneously using the left and right hands, without evidence of interactions in the spatial planning processes. Paradoxically, tasks (e.g., tying shoes) that appear to depend on spatial interactions between the left and right hands, each of which is controlled by a separate cerebral hemisphere, pose little difficulty. How can this be? In the study reported here, we observed that well-learned cooperative actions of the hands remain intact in 2 callosotomy patients, whereas actions novel to these patients are virtually impossible for them to produce without visual guidance. We infer that duplicate memory engrams of well-learned actions can be accessed by both cerebral hemispheres without callosal mediation, whereas callosal interactions are necessary for precise cross-matching of sensory information during spatial planning or perceptual-motor learning.*

When asked to tie her shoes, callosotomy patient V.J. was able to do so with remarkable ease, even in the absence of visual guidance, when tested at the earliest opportunity following her recovery from surgery. When asked how she was able to perform the action, she replied in a joking fashion, "I've been doing it since I was 5 years old!" Similar performance was demonstrated by J.W., a callosotomy patient since 1979. Tested years following his surgery, J.W. tied his shoes with eyes closed and showed no fumbling whatsoever.

J.W. and another callosotomy patient (V.P.) were participants in an earlier bimanual study in which visually lateralized bilateral stimuli presented on a computer screen were to be drawn as quickly and accurately as possible using the left and right hands. Control participants were virtually unable to draw two different figures with the left and right hands concurrently. Spatial interactions were readily observed in the trajectories of the two hands, and reaction time to draw was much longer than when control participants drew the same shape with the left and right hands simultaneously. These findings are in strong contrast to those observed in callosotomy patients: Spatial accuracy and reaction time were virtually identical whether these patients drew two copies of the same figure or two entirely different figures. These findings revealed that spatial interactions normally observed between the limbs during the planning of bimanual actions depend on the intact corpus callosum (Franz, Eliassen, Ivry, & Gazzaniga, 1996).

Given that the sensory information from the fingers of the hands is projected to separate cerebral hemispheres that separately control the contralateral hands (Brinkman & Kuypers, 1973), it is unclear how the

two hands can cooperate to perform a task like tying shoes with the corpus callosum severed. V.J.'s comment that she had years of experience tying shoes prior to surgery led to our hypothesis: Controlled processes that mediate the learning of new bimanual tasks depend on the corpus callosum, whereas well-learned bimanual actions are stored or accessed without dependence on an intact corpus callosum.

THE EXPERIMENT

Our hypothesis was directly put to test using a task in which 2 callosotomy patients and 4 control participants were asked to perform complex skills by producing pantomime gestures following verbally given commands. With eyes closed, participants were asked to perform a gesture that would most closely resemble the way a verbally instructed action would be performed in a real situation. For example, a participant was asked to "pretend you are pouring water from a cup." The participant would then hold up one hand as though supporting a cup, and gradually pronate the hand at the wrist as though pouring liquid out of the cup. Participants were first pretested with eyes open on unimanual tasks to ensure that the verbal commands were understood and the pantomime tasks were achievable. These pretests revealed that neither patient experienced difficulty in understanding and responding to the verbal instructions. In addition, no participant showed an exclusive preference to use one hand or the other on unimanual tasks.

Method

Subjects

V.J. is a 44-year-old, left-handed female with left-hemisphere language representation who underwent two-stage callosotomy in January 1995 (see Baynes, Eliassen, Lutsep, & Gazzaniga, 1998, for details). J.W. is a 43-year-old, right-handed male who underwent two-stage callosotomy in 1979. Four control participants recruited from the University of Otago Psychology Department were matched with the patients on the basis of gender, handedness, and approximate age (left-handed male, age 38; right-handed male, age 36; right-handed female, age 33; left-handed female, age 43).

Procedures and apparatus

The formal experiment consisted of tasks that were carefully chosen to elicit either a unimanual action (as in the pretests) or a bimanual action. Ten unimanual tasks (e.g., "Please show me how you would pick up an orange") and 40 bimanual tasks were included. Bimanual tasks were of primary interest because they depend on control mechanisms from both cerebral hemispheres. For bimanual tasks, instructions were intended to elicit bilateral cooperative actions (e.g., "Please show me how you would put toothpaste on a toothbrush," "Please

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show me how you would open a jar"). Note that the imagined objects to be manipulated were familiar (most people brush their teeth and open jars). Participants performed 40 bimanual tasks with eyes closed. Data were collected using a Panasonic BP314 (50-Hz) camera, and then digitized off-line to assess spatial and temporal variables.

After each attempt to produce the gestures, participants were asked how much experience they had with the particular task. They were queried with some variant of the question, "How often do you [do the task]?" A task was included in the statistical analysis only if the response indicated no familiarity with the task (e.g., "I have never played golf," "I honestly do not wash dishes") or everyday familiarity with the task (e.g., "I brush my teeth every day," "I practice the piano regularly").

Preliminary analyses on unimanual tasks included both novel ($n = 5$) and familiar ($n = 5$) tasks. We focus here on a subset ($n = 16$) of the 40 original bimanual actions that could be classified as being well learned prior to surgery ($n = 8$) or that had never been performed in a real situation by the participant ($n = 8$).

Dependent variables

Processing time was assessed as the latency between the end of the verbal instructions and the onset of movement. We refer to this variable as processing time rather than reaction time because subjects were not explicitly instructed to perform the actions as quickly as possible, although they were encouraged to maximize accuracy. Movement time was measured as the duration of the action, from onset to offset of movement. This variable was calculated from the first movement onset (regardless of which hand) to completion of the pantomime task. Processing time and movement time were digitized to the nearest 0.1 s.

Spatial accuracy was assessed by independent raters' evaluations of performance. Two observers blind to condition independently rated each participant's performance on each task using a 5-point Likert scale. Interrater reliability ($r = .90, p = .037$) and intrarater reliability across two independent rating sessions (Rater 1: $r = .71, p = .01$; Rater 2: $r = .92, p < .001$) were both significant.

Results

Preliminary within-subjects analyses on group (J.W., V.J., control), task (novel, familiar), and condition (unimanual, bimanual) revealed a significant Group \times Task \times Condition interaction for accuracy, $F(5, 4) = 37.09, p < .01$. Follow-up analyses on unimanual tasks only produced no significant effects, $F(2, 7) = 0.91, p > .05$, whereas analyses of bimanual tasks revealed that callosotomy patients were significantly more accurate on familiar tasks than novel tasks, $F(2, 13) = 5.22, p < .05$. The results for processing time are consistent with these findings: There were no significant differences in processing time for novel and familiar unimanual tasks performed by control participants (novel: $M = 0.88, SD = 0.40$; familiar: $M = 0.60, SD = 0.29$) or by callosotomy patients V.J. (novel: $M = 1.31, SD = 0.92$; familiar: $M = 2.10, SD = 1.06$) and J.W. (novel: $M = 0.77, SD = 0.71$; familiar: $M = 0.93, SD = 0.49$) (all $ps > .05$). Because floor and ceiling effects were not apparent from the unimanual tasks, nor were significant differences found across unimanual familiar and novel tasks, we focus on the bimanual tasks for the remainder of this report.

Nonparametric Wilcoxon signed-ranks tests revealed that both V.J.

($W = 48, p < .05$) and J.W. ($W = 36, p < .001$) were significantly less accurate on novel tasks than familiar tasks. Figure 1 depicts this clear reduction in spatial accuracy for novel bimanual tasks performed by both callosotomy patients compared with control participants.

Processing time and movement time for bimanual tasks were subjected to separate Group (J.W., V.J., control) \times Task (familiar, novel) repeated measures analyses of variance. Analyses of processing time revealed a significant main effect of group, $F(2, 28) = 5.79, p < .01$, and a significant Group \times Condition interaction, $F(2, 28) = 3.15, p = .05$. Analysis of simple effects revealed that V.J. was significantly slower to respond to novel tasks ($M = 2.84, SD = 1.83$) than to respond to familiar tasks ($M = 1.32, SD = 1.02$), $F(1, 14) = 4.21, p < .05$. Figure 2 depicts the clear lengthening of processing time for V.J. relative to all other participants on the novel bimanual tasks only. Processing time for familiar bimanual tasks was virtually identical across all participants. There were no differences between groups in the movement times (not shown).

These results indicate that V.J. was both slow to respond and poor in terms of spatial accuracy on novel tasks, whereas J.W. responded quickly but produced spatially inaccurate (or incorrect) actions on novel tasks. No such effects were observed in familiar tasks.

DISCUSSION

A comment on an anecdotal finding may be worthwhile. One bimanual task was to "pretend you are threading a needle." V.J. was able to pantomime this action without hesitation by producing a pinchlike gesture with the right hand, as though she were holding a needle, followed by a small horizontal motion with the left hand, as though she were putting the thread through the eye of the needle. When asked to put a fishing hook on a line, a task that requires an almost identical action but a different verbal description, V.J. was virtually unable to produce the gestures. She then indicated that she had never fished. Exactly the opposite was observed in J.W., who was able to produce the correct gestures for putting a hook on a line, but unable to perform the needle-threading task. His answer to the queries afterward indicated that he does not sew, although he has fished on

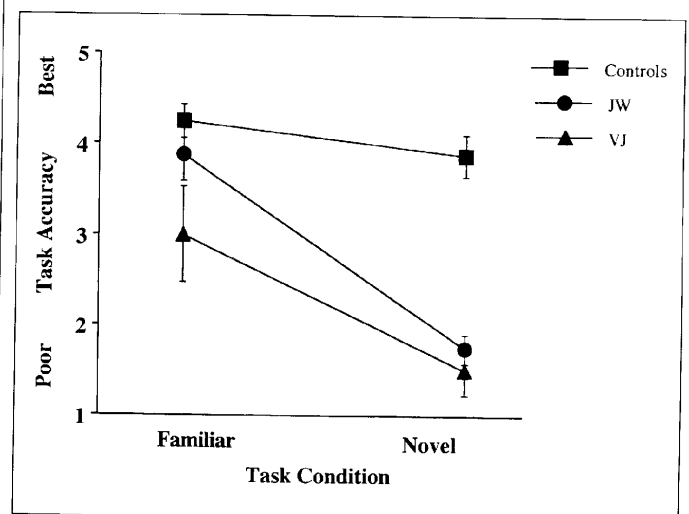


Fig. 1. Average scores for spatial accuracy (1 = poorest performance, 5 = best performance) and standard errors on bimanual tasks.

Novel Versus Familiar Bimanual Actions

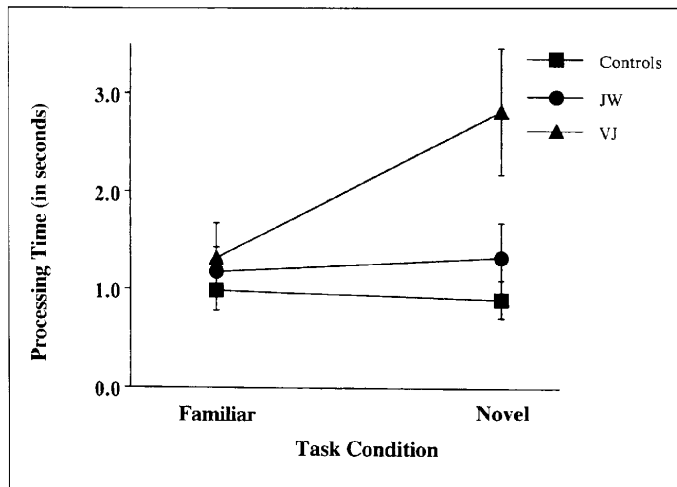


Fig. 2. Average processing time and standard errors (to the nearest 0.1 s) on bimanual tasks as a function of task familiarity.

occasion. Subsequent conversation with these participants revealed that they had both seen such tasks performed by other people in real-life situations or in films, although they had not themselves performed the novel task. This observation leads to the inference that although the actions required for the two tasks are nearly identical, similarity of actions alone does not provide for direct transfer of their word labels. Memory storage for actions, therefore, appears to be related to the self as performer. Notably, this dissociation is anecdotal, given there is only a single example. Admittedly, finding a task that was well learned prior to surgery for 1 participant but not the other was purely fortuitous.

Our main findings provide strong evidence that representation of well-learned action consists of the procedures of the action together with their symbolic codes (in this case, verbal). Consistent with this hypothesis, studies of apraxia and aphasia (Efron, 1963) suggest that the brain mechanisms for general language processes overlap extensively with those for skilled motor action. Brain-imaging studies have demonstrated activation of left dorsolateral prefrontal cortex (Peterson & Fiez, 1993), supplementary motor area (Ojemann et al., 1998), and superior temporal gyrus (Weiller et al., 1995) during verb generation. The same frontal areas are also known to be activated in skilled motor actions. In addition, performance on a memory test for verbal phrases describing simple actions improves if encoding involves enactment of the motor actions (Kormi-Nouri, Nyberg, & Nilsson, 1994).

Our findings also provide a clear dissociation between performance on novel and well-learned bimanual actions in patients with callosotomy. Earlier work supports the claim that the integrity of the corpus callosum is essential for the learning of new bimanual actions (Preilowski, 1972; Zaidel & Sperry, 1977). Visual guidance appears to enable unification of the cerebral hemispheres in the case of callosotomy, so learning can occur. Our results suggest that well-learned actions are stored and accessed in association with their verbal (symbolic) codes, and therefore no longer rely on on-line visual information initially required for learning. Consistent with this claim, functional magnetic resonance imaging studies have shown a decrease in activation in the prefrontal cortex with learning of a complex motor task (Karni et al., 1995), which suggests that the neural representation of motor memory changes over time. Recent findings

also indicate that neural activation from prefrontal cortical regions shifts to premotor, posterior parietal, and cerebellar structures following only 6 hr of practicing a new motor task (Shadmehr & Holcomb, 1997).

A novel contribution of the present results comes from the manipulated bimanual component inherent in the tasks. Recall that each cerebral hemisphere controls movements of the contralateral hand. Both cerebral hemispheres must therefore be involved in execution of a bimanual action. The present findings lead to the novel claim that well-learned actions can be accessed by both cerebral hemispheres without callosal connections.

Subcortical processes are likely to mediate the memory storage or access of well-learned actions. The subcortical basal ganglia complex has been implicated in the memory storage of well-learned sequences in animals (Aldridge, Berridge, Herman, & Zimmer, 1993; Berridge & Whishaw, 1992). The basal ganglia have also been shown to play a role in the programming of sequential actions in humans (Jones, Phillips, Bradshaw, Iansek, & Bradshaw, 1992; Mushiaki & Strick, 1995), as well as some aspects of speech processing (Brunner, Kornhuber, Seemuller, Suger, & Wallesch, 1982). This evidence is consistent with the possibility that the basal ganglia are involved in both the memory storage of well-learned action codes and the temporal streaming of those codes to the elaborated patterns of muscle sequences that reside as memory engrams in both cerebral hemispheres. Alternatively, a single cerebral hemisphere may store the well-learned action codes, which are then transferred via ipsilateral and contralateral (subcortical) projections to motor output mechanisms of both hands.

In summary, the present findings provide important implications for understanding the neural representation of skilled action. First, patients with completely severed callosal connections are unable to perform novel actions using the two hands, although they perform well-learned bimanual actions with no difficulty, even without visual monitoring. This suggests that the neural processes of visual guidance, visual imagery, and attentional demands associated with perceptual-motor learning are distinct from the processes of memory retrieval of a well-learned action. Second, well-learned actions appear to be stored and accessed in association with distinct symbolic codes.

We pose the question of whether these results point to a more general neural dissociation between controlled and automatic processes (e.g., Shiffrin & Schneider, 1977). If these terms are redefined with respect to the present tasks, controlled processes require precise cross-matching of sensory information, whereas automatic processes utilize symbolic codes that allow for direct access to information stored elsewhere in the brain. In the case of well-learned bimanual actions, there appears to be direct access to memory engrams in both cerebral hemispheres, presumably via subcortical circuitry. In our earlier study using drawing movements (Franz et al., 1996), one task was to draw visually lateralized lines in a continuous fashion as accurately as possible. Though not instructed to do so, the patients produced a close temporal coupling of movements of the two hands. This occurred without evidence of spatial coupling. It remains to be determined whether or not it is important that temporal coupling was not an explicit requirement of the task, and that the primary demands were placed on spatial accuracy. Together, these findings lead to the conclusion that both spatial planning and perceptual-motor learning of bimanual actions require controlled processes that depend on callosal interactions, whereas temporal coupling and accessing codes of well-

learned actions occur relatively automatically via subcortical processes. Identifying the precise mechanisms involved in automatic processes is a challenge for future work to address.

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