Article abstract—In patients who have undergone complete section of the corpus callosum for intractable epilepsy, lateralized presentation of visual nonverbal stimulation showed that the coordination of motor acts by either hand is controlled exclusively by the contralateral hemisphere. When two patients had serial operations consisting of an initial division of the splenium and posterior 3 cm, followed by complete callosal division, an opportunity arose to test the explicit cortical pathways involved in ipsilateral control. Between operations, these patients could not coordinate movements of the hand ipsilateral to the hemisphere receiving the command. This suggested that for visual nonverbal stimulation, the posterior 3 cm of corpus callosum is necessary for control of the ipsilateral hand; the rostral callosum cannot transfer sensorimotor commands. Also, contrary to current views, each hemisphere can carry out sequentially dependent motor activity.

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Cortical mechanisms involved in praxis: Observations following partial and complete section of the corpus callosum in man

Bruce T. Volpe, M.D., John J. Sidtis, Ph.D., Jeffrey D. Holtzman, Ph.D., Donald H. Wilson, M.D., and Michael S. Gazzaniga, Ph.D.

Understanding of the brain mechanisms involved in visual-motor control was advanced by the demonstration in a split-brain cat that a disconnected hemisphere could guide and control either paw with equal facility. The results supported views that emphasized subcortical systems in visual-manual control. Studies in primates, 2-5 however, demonstrated impaired ability of a disconnected hemisphere to control the ipsilateral limb. These studies emphasized the cortical components of visual-manual control, with conflicting claims about the ipsilateral hemisphere-hand capacity traced to cross-cuing of the opposite hemisphere by the orienting response of the eyes, head, or neck. 3.6

Concurrently, human studies of praxis were being carried out after complete section of the corpus callosum for control of epilepsy. These studies showed a difference between proximal and distal

control when a visual command was presented to a disconnected hemisphere. Each hemisphere could control the proximal movements of either arm but could control only the distal movements of the contralateral hand. About the same time, Geschwind and Kaplan9 described a patient with a left hemisphere tumor that also thinned the anterior two-thirds of the callosum, causing apraxia of the left arm and hand. Geschwind¹⁰ stressed the importance of verbal command and elaborated the proposed left hemisphere dominance for motor activities. He suggested that the pathways involved in the interhemispheric integration of sensorimotor activity included transfer from the left hemisphere by any one of several interhemispheric callosal connections.

In the Liepmann tradition, other investigators suggested that organized motor acts involved a

From the Division of Cognitive Neuroscience (Drs. Volpe, Sidtis, Holtzman, and Gazzaniga) Cornell University, New York, NY, and the Department of Neurosurgery (Dr. Wilson), Dartmouth-Hitchcock Medical Center, Hanover, NH.

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Address correspondence and reprint requests to Dr. Volpe, Division of Cognitive Neuroscience, Cornell University Medical School, 1300 York Avenue, New York, NY 10021.

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single cortical area outside of the primary motor cortex in one or the other hemisphere. They did not comment on the pathways involved in the interhemispheric integration of motor acts. 11-14 However, studies after surgical commissurotomy did not support these claims; 15 under appropriate stimulus conditions, each hemisphere could organize motor acts, but ipsilateral distal movements were performed poorly.

The present experiments show that the genu or anterior trunk, or both, of the corpus callosum (rostral callosum) cannot transfer critical visual or sensorimotor information necessary for distal motor action and that each hemisphere has the potential to organize a range of sequential distal movements in the contralateral limb without contribution from the opposite hemisphere.

Patients. Three of the four patients-P.S., J.W., and V.P.—were described elsewhere. 16 S.W. is reported below. All patients had section of the callosum to control intractable epilepsy. All were right-handed with left-hemisphere language dominance, and although there appeared to be a variable language ability in the right hemisphere in P.S., V.P., and J.W., 16 there was no comparable language ability in the right hemisphere of S.W. P.S. and V.P. had complete callosal sections in 1976 and mid-1979, respectively. J.W. and S.W. had a two-stage operation with division of 3 cm of posterior callosum (including the splenium), followed 10 weeks (J.W.) or 5 months later (S.W.) by complete callosal section. 17 Section of the callosum in J.W. was complete in late 1979, and in S.W. in 1981. All patients had an intact anterior commissure. Each volunteered for experimental sessions carried out between 1979 and 1981.

Patient S.W., a 22-year-old man at the time of testing, was born after a term pregnancy and normal delivery. He had recurrent febrile seizures complicated by prolonged postictal states at age 6 months. The etiology of the seizures was not found, but he was treated with anticonvulsants. He reached milestones normally until age 6 years, when he had behavior problems and persistent nocturnal seizures. Seizures increased in frequency and severity over the next 5 years.

In 1976, at the age of 16. EEGs recorded irregular anterior and bilateral 4 to 5 and 2 to 3 cps delta activity. Spike discharges were diffusely present, with no lateralized foci. Medical therapy in the next 5 years resulted in brief seizure-free periods. At the time of isolated posterior callosal section in November 1980, examination was difficult because he had frequent absence attacks. Between attacks he was oriented and alert, without aphasia or apraxia. Apart from bilateral horizontal nystagmus, there were no abnormalities of cranial nerves, reflexes, or sensorimotor function. WAIS testing showed a verbal score of 84 and performance of 85. EEG revealed symmetric 7- to 8-cps alpha activity with medium-amplitude semirhythmic 2-cps delta waves and random bilateral bursts of spike and sharp waves. There were

no lateralized foci. CT was normal. After surgery, seizure frequency declined.

General observations of these patients' responses to verbal commands were made periodically. Right hand performance after verbal command was accurate soon after the operation. As recorded in other split-brain patients, 8,15 left hand performance improved. Initially, they all made clumsy movements with the left hand to verbal command, although aspects of the command that required proximal muscle control were performed accurately. The range of verbal commands required symbolic or nonsymbolic movements, imitation of gestures, and demonstration of object use. In the most recent observations, P.S. had no problem performing any verbal command for left hand movement. J.W., V.P., and S.W. made infrequent errors with the left hand but occasionally performed tasks in a clumsy fashion, particularly tasks that required discrete control of the hand muscles. To the command "salute," for example, J.W. partially closed his fingers over his thumb while placing the left hand on his forehead. These clinical observations left unresolved the question whether the right hemisphere had decreased motor ability or the left hemisphere had decreased control over the ipsilateral distal muscles. These possibilities were explored in the present experiments.

Methods. For the observation of tactile localization (experiment 1), the patients sat and extended their hands, palms up and fingers spread, to lie comfortably on a table. Using an anesthesiometer, one of eight specified points on the fingers of one hand was stimulated lightly (7 gm). Before the experiment began, however, the patients saw the stimulation points and viewed their respective responses to each "within" and "between" condition. During the test, the patient remained blindfolded and was required to respond in one of two ways. In one condition ("within the hand"), the subject was asked to use the thumb of the stimulated hand to find the stimulated point. In the other condition ("between the hands"), after point stimulation on one hand, the subject was asked to find the identical point on the unstimulated hand, using the thumb of the other (responding) hand.

For experiments 2 and 3, stimuli were slides that were rear-projected on an opaque screen or were generated on a 48-cm video screen by an Apple II microprocessor. The subject was seated 0.5 m from the display screen and was instructed to fixate on a dot in the center of the screen. Stimuli were presented at least 3° to the right or left of fixation for 150 msec. The slides were 20 line drawings of hand postures. A single posture picture appeared in one or the other lateralized visual field on each trial. After each exposure, the patients were required to mimic the postures with one hand

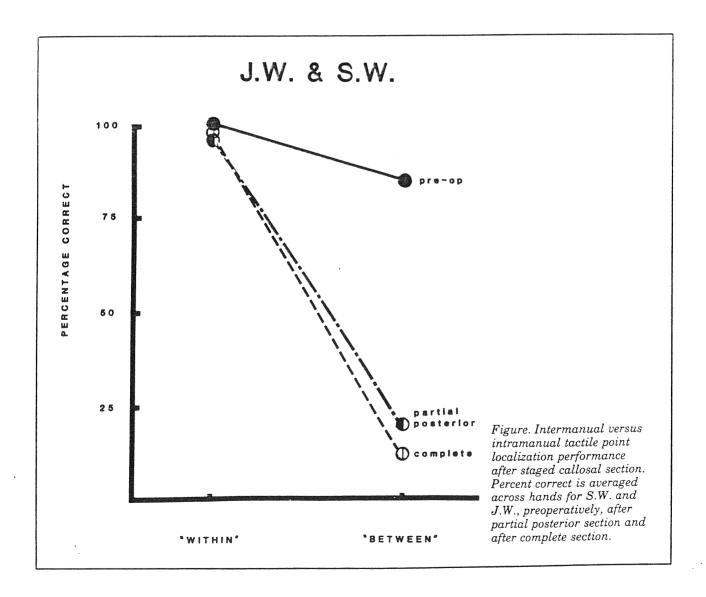
out of vision. Lateralized exposures and hand postures were randomly presented.

Experiment 4 required a computer-generated display that consisted of two grids lateralized in each visual field. The closest edge of each 5×5 cell grid was 4° to either side of a central fixation spot and symmetric about the horizontal and vertical meridians. Each square within a grid subtended 2.4° of visual angle, and all the X's that appeared centered in these cells on experimental trials subtended 1 imes 2 degrees of visual angle.

A metal frame, 15×15 cm, was placed in front of the subject and was thoroughly explored tactually and visually. The frame was divided into a 5 imes 5 grid. The patient was instructed to move his index finger to the location on the metal grid that corresponded to the location of the X that appeared on the screen. On each trial, the subjects started from the center cell of the grid. After five practice trials in each visual field, they had no difficulty with the task. For the experimental trials the grid

and the tested hand were kept out of view, and the patient's forearm was fastened to the table to prevent proximal movement. The patient fixated the central dot, and X flashed randomly in any one of 48 positions.

Results. Experiment 1. This observation directly tested tactile-motor integration within each hemisphere and between hemispheres. 18,19 Preoperatively, all patients performed the "within" task perfectly. The percentage of correct responses on "between" trials was 83% for J.W. and 88% for S.W. Since J.W. and S.W. performed similarly for both conditions at all stages of callosal section, the figure represents average data of both patients' performance. The two response conditions "within" and "between") administered to each hand resulted in four experimental possibilities: within left hand, within right hand, between right and left hands, and between left and right hands. Since the proportion correct for left and right hands did not



differ significantly (p > 0.10), the data were averaged across hand of performance. Each data point represented 40 trials for each condition for each subject.

Performance after partial or complete section was significantly worse than preoperative performance (p < 0.001). Furthermore, the similarity of performance after partial or complete callosal section (p > 0.10) suggests that the partial posterior section was sufficient to disrupt a motor task that required interhemispheric integration. Despite this, there was no disruption of performance in the intrahemispheric task ("within" condition) at any stage of section.

Experiment 2. Slides of hand postures were used to examine visual-motor abilities of the partially disconnected hemispheres. Preoperatively, J.W. and S.W. performed at 85 to 90% accuracy, irrespective of the stimulated hemisphere or responding hand. After posterior section, the responses made by the hand contralateral to the visually stimulated hemisphere remained superior, but the responses of the ipsilateral hand deteriorated (table 1). Patient fatigue did not permit two complete replications of the task, and each value represents the percentage of correct responses on a total of 34 trials. Interaction between hemisphere and hand was significant for both patients (chi-square ranged from 9.9 to 31.1; p < 0.001 for right and left visual field exposure). Since 54% of the correct responses in the ipsilateral hand condition occurred when the stimulus was a fist or an open hand, the betterthan-chance performance may have resulted from ipsilateral control for postures that require minimal finger dexterity.

Experiment 3. After the remaining callosal fibers were sectioned in J.W. and S.W., the same tests of hand postures were used to assess the motor performance of each hemisphere. V.P., who also had complete callosal section, was included for these observations. Forty trials were collected for each condition for J.W. and S.W., and 31 trials for each condition for V.P. Patient fatigue did not permit two complete replications with V.P.

Table 1. Ipsilateral and contralateral hemisphere control of visual-manual hand postures after partial posterior callosal section

		Left visual field		Right visual field	
	Left hand	Right hand	Left hand	Right hand	
J.W.	74	26	29	88	
S.W.	68	23	15	85	

The results after complete callosal section were similar to those after partial section. Each patient could assume a hand posture with the hand contralateral to the stimulated hemisphere, but ipsilateral hemisphere hand performance was severely impaired (table 2). This interaction between hemisphere and hand was significant for each patient (chi-square ranged from 14.7 to 50.1; p <0.0001 for right and left visual field exposure). The decrease in ipsilateral control for J.W. and S.W., particularly in the right visual field, involved fewer than five trials, too few for a determination of hemisphere task superiority.

Experiment 4. Whereas the previous hand posture tasks tested one form of right-hemisphere-directed distal movement, this task explored the ability of a disconnected hemisphere to direct rapid finger movement to a discrete spatial location. P.S. was included with V.P., J.W., and S.W. for this observation. All patients were tested after complete callosal section (table 3). There were 24 trials for each condition for each patient, except for P.S., who became fatigued after 38 trials. The data affirmed the inability of both hemispheres to control distal muscles of the ipsilateral limb; they also demonstrate that the right hemisphere could direct the left hand to a specific spatial location. The interactions in J.W., V.P., and P.S. between visual field and hand were significant (chi-square ranged from 5.8 to 13.8; p < 0.01 for right and left visual field). In S.W., performance after left visual field exposure was superior for the left hand, but performance after right visual field exposure did not differ for the two hands. In view of small differences between the right and left hemisphere performance of the other three patients, this result could not be taken as a measure of generally superior righthemisphere performance on this task. In the main, these data suggested that under visual stimulation conditions, the right hemisphere can direct sequential left-hand motor activity outside of the realm of left-hemisphere influence.

Discussion. In these patients with partial posterior

Table 2. Ipsilateral and contralateral hemisphere control of visual-manual hand postures after complete callosal section

	Left visual field		Right visual field				
	Left hand	Right hand	Left hand	Right hand			
J.W.	83	13	0	80			
S.W.	75	10	0	85			
V.P.	90	19	10	90			
Percentage correct performance.							

Table 3. Visually elicited distal motor control directed to a specific spatial location: Complete callosal section

	Left visual field		Right visual field				
	Left hand	Right hand	Left hand	Right hand			
J.W.	71	13	13	67			
S.W.	58	8	17	21			
V.P.	42	8	25	58			
P.S.	71	26	53	84			
Percentage correct performance.							

callosal section, we attempted to determine a locus of interhemispheric connections that subserves ipsilateral control of distal muscles. Impaired tactile localization and impaired ipsilateral hemispherehand performance after visual stimulation suggest that some sensorimotor information remained inaccessible to the opposite hemisphere. Furthermore, the results suggest that the anterior commissure and the rostral callosum do not transfer either lateralized visual images that elicit motor activity or the specific motor program needed to carry out the appropriate movement. The similarity of performance after partial or complete section suggests that partial posterior section is sufficient for a functional disconnection of distal muscles. These findings stand in contrast to previous views about the cortical pathways that are sufficient for carrying out ipsilateral hemisphere-hand visual motor control, particularly by the proposed rostral callosal pathways connecting the precentral motor areas.²⁰

However, the findings are consistent with impaired tactile transfer after isolated 3-cm midcallosal section. Moreover, in patients with partial surgical section of the anterior callosum (with or without anterior commissure section), either limb could mimic a finger posture after exposure of visual images lateralized to one or the other hemisphere. In these patients, there was no evidence of any of the sensorimotor disorders observed after complete callosal section. In summary, interhemispheric transfer of nonverbal sensorimotor information is dependent on specific posterior fibers of the callosal system.

The integration of these findings with other reports may permit a view of human functional callosal anatomy. If the splenium is sectioned, naming of visual stimuli lateralized to the right hemisphere is disrupted.^{23–26} A 1.5-cm posterior section (including the splenium) does not disrupt sensorimotor integration or tactile naming,²⁷ but the present data suggest that an additional 1.5-cm posterior section disrupts both functions. Rostral callosal interruptions disrupt few tasks that require interhemispheric sensory integration.²² Although

posterior extension of the rostral section for 4 to 5 cm interrupts verbally directed sensorimotor tasks and interhemispheric tactile tasks, 9.28 sensorimotor tasks that are based on visual stimuli remain undisturbed. The posterior 3 cm of callosum may be the structure that is necessary to provide the sensory window through which each hemisphere shares visual, sensory, and motor information from the contralateral field. The anterior callosum may be a cognitive window, insufficient for transfer of sensory information or motor programs, but able to transfer information after some higher-order abstraction. 29

Distal motor control in the hand posture experiments required moving the fingers with continuous proprioceptive afferent information. In contrast, grasping or pointing movements are made to a target defined by the environment and require quick displacement of hand or fingers. After complete callosal section, observations of locating a point in space add to the range of capacities of the nondominant hemisphere that are independent of the dominant hemisphere. With the posture data. these observations are difficult to contain within the theory that motor engrams originate from a discretely lateralized area outside the primary motor cortex in one hemisphere or that the left hemisphere organized the left-hand response.13 However, they are consistent with observations of clinically apraxic patients who display marked independence of right-hemisphere-directed motor activity when tasks are based on visual nonverbal stimulation.9 Our results show that both hemispheres could carry out complex motor acts under proper stimulus conditions, and they support Geschwind's description¹⁰ of apraxia as a nonunitary disorder. If apraxia is the inability to perform a motor act without accompanying weakness or sensory loss, 30 the contribution of the right hemisphere to motor activity may be considerable.31.32

The inability of the right hemisphere to direct a left-hand response in some motor tasks may be based on the linguistic information implicit in asking a patient to perform to command. Evaluation of right hemisphere responses to language stimuli is complicated by rare examples of right-hemisphere language comprehension. and its variability when present. We did not detect consistent differences between right and left hemisphere sensorimotor performance in these four experiments, but other observations suggested that the right hemisphere may contribute uniquely to some visual motor tasks. Action This may not be true for language-motor tasks, but the issues can be tested in split-brain experiments.

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