

- early September 1980 have been fixed in glutaraldehyde and are presently being prepared for observation by T. Bargar, Electron Microscopy Laboratory, University of South Carolina.
14. J. O. Young, *Hydrobiologia* 45, 373 (1974).
15. In September 1980 we initiated an experimental and regular sampling program to examine the causes of encystment and excystment and to determine the seasonal patterns of cysts at the intertidal site.
16. We thank D. Brambilla, J. Christy, R. Feller, P.

Montagna, M. Palmer, S. Stancyk, J. Vernberg, D. Wethey, and S. Woodin for comments on earlier drafts of the manuscript and T. Bargar for assistance with the electron microscopy and photomicrography. This research was supported in part by NSF grant OCE78-09450. Contribution 382 from the Belle W. Baruch Institute for Marine Biology and Coastal Research, University of South Carolina.

31 October 1980; revised 23 December 1980

Cognitive Interaction After Staged Callosal Section: Evidence for Transfer of Semantic Activation

Abstract. *Sensory and cognitive functions were assessed in a right-handed male before and after partial and complete callosal commissurotomy. After the initial posterior section was made, there was no evidence of interhemispheric sensory transfer, although the left hemisphere did have access to stimulus-related semantic and episodic information from the right hemisphere. After the callosum was completely sectioned, this exchange was no longer observed.*

The splitting of mental unity following surgical section of the corpus callosum for seizure control demonstrates the importance of this fiber system for the normal interaction among the cortical areas subserving sensory, perceptual, and cognitive activity in each cerebral hemisphere (1). At the sensory level, a callosal "window" provides each hemisphere with a representation of the ipsilateral hemifield not available through primary afferent projections, which are almost exclusively contralateral (2). As sensory information undergoes further processing, it may gain access to referents in memory that contribute to recognition, comprehension, and a sense of episodic context. While internally represented referential information provides a basis for cognition in either hemisphere, the interhemispheric availability of such higher-order information has not been described under conditions in which the sensory window has been eliminated. Because of the recent modifications in the microsurgical technique of commissurotomy, the effects of partial as well as complete callosal section can now be examined in the same patient (3). The topology of callosal projection makes it possible to sever the interhemispheric connections between posterior cortical sensory areas while sparing the connections between more anterior areas that may be involved in cognition (4). We now describe what we believe to be the first observations of interhemispheric availability of higher-order information in the absence of sensory transfer after selective posterior callosal commissurotomy.

The patient, J.W., is a bright 26-year-old right-handed male with a history of staring spells, reportedly since grade

school. After his first grand mal seizure at age 19, seizure frequency increased and remained intractable. Midline section of the corpus callosum was performed in two stages by D.H.W. The posterior half of the corpus callosum including the splenium was sectioned first, with the remaining anterior portion sectioned in a second operation approximately 10 weeks later because of a recurrence of seizures (5).

During the interoperative period, J.W. was evaluated for evidence of sensory transfer and for the status of perceptual and cognitive functions within each hemisphere (6). Tests for transfer indi-

Table 1. J.W.'s left-visual-field performance (percent correct responses) on picture- and word-naming tests administered at each operative stage. The interoperative period refers to the interval following section of the posterior callosum but preceding complete section, which is represented at the postoperative stage. The initial surgery was performed on 10 August 1979, and the section was completed on 16 October 1979. The 20-questions interaction yielded above chance performance on pictures presented at the first interoperative session and aided both picture and word naming at the second interoperative session. By session 3, J.W. was using a self-generated inferential process.

Stage	Stimuli	
	Pictures	Words
Preoperative (8 August 1979)	93	63
Interoperative I (24 August 1979)	28	13*
Interoperative II (15 September 1979)	67	42
Interoperative III (27 September 1979)	83	58
Postoperative (9 November 1979)	20*	0*

*Not significantly better than chance.

cated that after the initial posterior section, the primary visual, auditory, and somatosensory systems of the right hemisphere were disconnected from the expressive language system of the left hemisphere. For example, whereas J.W. named words presented to his left visual field with 63 percent accuracy before surgery, left-visual-field performance on this test (13 percent) was not significantly different from chance after posterior callosal section (7). In contrast, right-visual-field accuracy was unchanged after the initial surgery (93 percent preoperatively, 91 percent postoperatively) (8). Disconnection was also demonstrated on an interfield comparison test that required a same-different judgment of the simultaneous presentation of stimuli to each visual field. Although performance was nearly perfect (98 percent) before posterior section, it did not differ from chance (50 percent) after the initial surgery.

The second phase of our evaluation revealed that although stimuli lateralized to the right hemisphere could neither be transferred to the left hemisphere for naming nor compared with left-hemisphere stimuli, they were being correctly interpreted within the right hemisphere. When the required response was pointing with the left hand rather than naming, the right hemisphere was 92 percent accurate at indicating picture-word correspondence for left-visual-field stimuli. Although unable to provide a spoken description, J.W.'s ability to comprehend the meaning of words and pictures in the left visual field indicated the presence of a right-hemisphere semantic system, thus strongly suggesting that he could be included among the small subset of commissurotomy patients with language in the right hemisphere (9).

Despite the sensory disconnection that resulted from the posterior section, left-hemisphere verbal responses following right-hemisphere stimulation were unlike those of patients with a complete callosal section. While such stimuli could not be named, he did not deny having "seen" something. Instead, naming failures were accompanied by apologies for a poor memory and on occasion, an agitated state like that described in the tip-of-the-tongue phenomenon (10). At such times, the patient claimed to "see" the stimulus in his mind but was unable to name or describe it.

After several such incidents, the investigators initiated a game of "20 questions" whenever the patient felt that he had some sense of the left-visual-field information. This interaction would be-

gin with the question "Is it an object or a living thing?" and would include questions about form (for example, large or small), function (for example, used in the home) and class (for example, animal or vegetable). These questions did not always aid the patient in naming the left-visual-field stimulus, but they were required for correct naming of such stimuli during each of the first two interoperative test sessions. One such interaction occurred after a black-and-white line drawing of a hunter's cap was presented in the left visual field. After indicating that the stimulus represented an object, J.W. was queried about a number of object classes such as vehicles, tools, and housewares, rejecting each until clothing was offered. The patient was then able to recognize the associated sex of the usual wearer, the season in which it was worn, and its usual color before finally naming the stimulus correctly.

Left-visual-field performance on picture- and word-naming tests administered before, between, and after successive operations is contained in Table 1 (11). Right-visual-field naming remained highly accurate (> 90 percent) at each session. At the first interoperative testing, J.W.'s left-visual-field picture naming was slightly, but significantly, better than chance (binomial $P < .02$), by virtue of the 20-questions interaction with the investigators. His naming of the left-visual-field information improved throughout the interoperative period, and by week 7 (the third interoperative session), he had adopted a self-generated inferential strategy based on his description of a mental image. For example, the word *stove* elicited descriptions of a hardware store and an aunt's kitchen, with the latter leading to the correct response. On another trial, the word *onion* elicited a description of the family garden. J.W. described these experiences as follows: "It's like things are moving around constantly, and I'm trying to narrow it down to something that will just stop. I'm seeing a whole general picture but one thing is almost right in the middle."

Although the patient described the transferred information in pictorial terms, the initial description was rarely that of the stimulus itself but more likely of a context in which it might be found, or of some associate. Moreover, the specificity of the transferred information allowed him to avoid synonymous substitution errors (for example, reading the word *cap* as *hat*, *auto* as *car*, or *boat* as *ship*), which might be expected if only referential "pictures" were being trans-

ferred. Homophonic errors were also largely avoided after left-visual-field presentation (75 percent accuracy). Of the four errors made on this test, two were unrelated to the original stimuli, and two consisted of the incorrect spellings (for example, *tail* for *tale*) although in one of these, subsequent usage indicated that the correct meaning had been preserved (12). No errors were made on right-visual-field homophones.

The inference process was not always lengthy, nor was it always vocalized. Even in the tenth interoperative week, however, the naming of left-visual-field stimuli was rarely immediate, occurring quickly only for stimuli associated with some strong personal interest (such as *car*). After the callosum was completely sectioned, left-visual-field naming did not differ significantly from chance. The

inference strategy was no longer attempted and the patient denied any experience following left-visual-field stimulation. Figure 1 presents a schematic representation of J.W.'s naming ability at each operative stage (13).

Our observations, then, indicate that the anterior portion of the corpus callosum plays a role in the interaction between cognitive rather than sensory systems in each hemisphere. In J.W., this interaction was based on stimulus-related semantic and, to a lesser extent, episodic information transferred between the hemispheres. After right-visual-field stimulation in the interoperative period, the expressive language system of the left hemisphere had direct access to both the sensory and higher-order information extracted from memory. After left-visual-field stimulation, however, there was

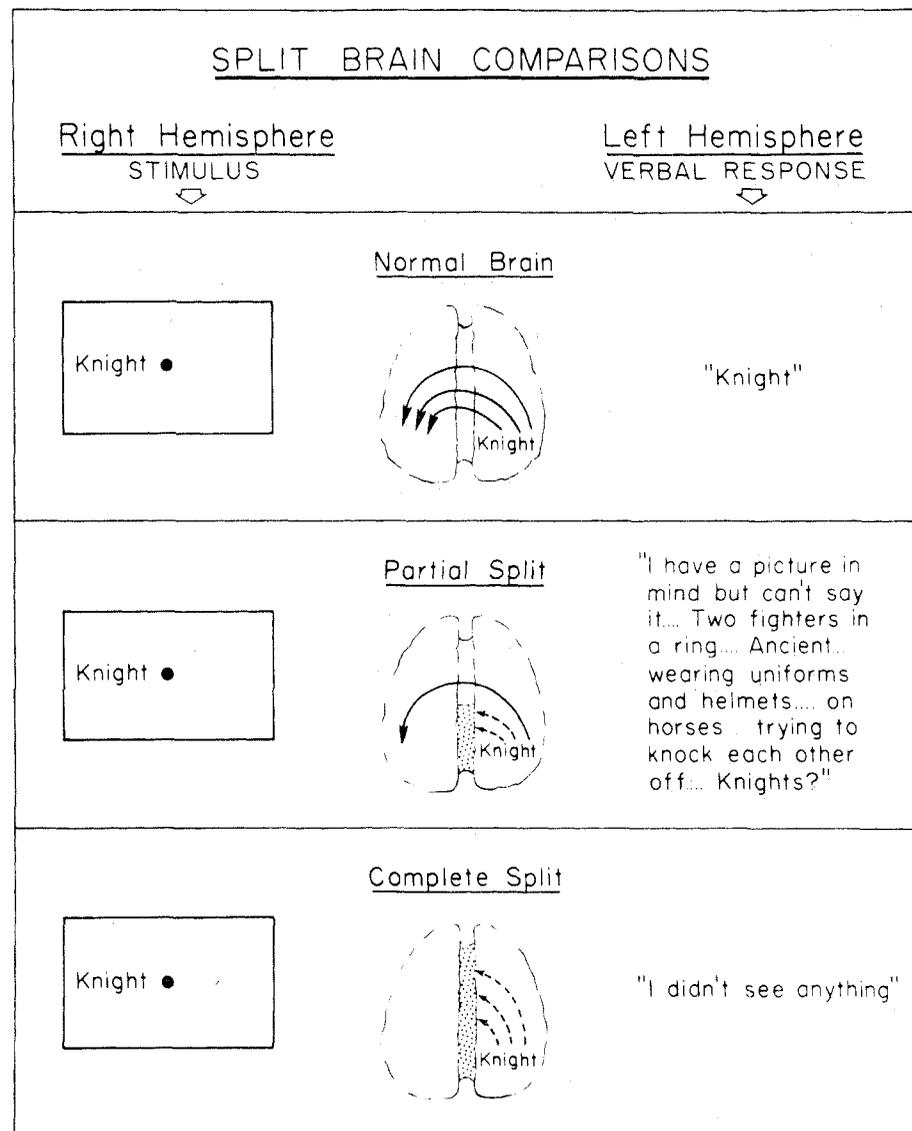


Fig. 1. Schematic representation of J.W.'s left-visual-field naming ability at each operative stage.

no sensory transfer and thus, only the activated memory referents were initially available. On such trials, recognition occurred in reverse: The inferential process appeared to reflect a search through an already activated semantic field for the identity of the original stimulus (14). When the callosum had been completely sectioned, neither sensory nor higher-order information was available to the expressive language system after stimulation of the right hemisphere.

JOHN J. SIDTIS, BRUCE T. VOLPE
JEFFREY D. HOLTZMAN

Division of Cognitive Neuroscience,
Department of Neurology,
Cornell University Medical College,
New York 10021

DONALD H. WILSON

Department of Neurosurgery,
Dartmouth-Hitchcock Medical Center,
Hanover, New Hampshire 03755

MICHAEL S. GAZZANIGA

Division of Cognitive Neuroscience,
Department of Neurology,
Cornell University Medical College

References and Notes

1. M. S. Gazzaniga, *The Bisectioned Brain* (Appleton-Century-Crofts, New York, 1970); _____ and J. E. LeDoux, *The Integrated Mind* (Plenum, New York, 1978).
2. M. S. Gazzaniga, J. E. Bogen, R. W. Sperry, *Brain* **88**, 221 (1965); *Neuropsychologia* **1**, 209 (1963); S. P. Springer and M. S. Gazzaniga, *ibid.* **13**, 345 (1975).
3. Case reports of lesion and surgical section of the anterior callosum [M. S. Gazzaniga, G. L. Risse, S. P. Springer, E. Clark, D. H. Wilson, *Neurology* **25**, 10 (1975); N. Geschwind and E. Kaplan, *ibid.* **12**, 675 (1962); H. W. Gordon, J. E. Bogen, R. W. Sperry, *Brain* **94**, 327 (1971); W. H. Sweet, *Arch. Neurol. Psychiatry* **45**, 86 (1941)] as well as the posterior callosum [D. N. Levine and R. Calvanio, *Neurology* **30**, 21 (1980); M. S. Gazzaniga and H. Freedman, *ibid.* **23**, 1126 (1973); A. F. Wechsler, *ibid.* **22**, 628 (1972); M. Sugishita, M. Iwata, Y. Toyokura, M. Yoshioka, R. Yamada, *Neuropsychologia* **16**, 417 (1978); P. E. Maspes, *Rev. Neurol.* **80**, 100 (1948); J. H. Trescher and F. R. Ford, *Arch. Neurol. Psychiatry* **37**, 959 (1937)] have been published. In many of these cases, the extent of the lesion was unspecified, and in others, the surgical notes indicated that some of the fibers in the ostensibly sectioned area had been spared.
4. N. Geschwind, *Brain* **88**, 237 and 585 (1965).
5. Using the estimating procedure of C. L. Oon [Am. J. Roentgenol. **92**, 1242 (1964)], D.H.W. sectioned approximately the posterior 3 to 4 cm of the callosum in the first operation. For a description of the microsurgical procedure, see D. H. Wilson, A. Reeves, and M. S. Gazzaniga [*Neurology* **28**, 649 (1978)].
6. For visual testing we used standard tachistoscopic techniques to present stimuli briefly (generally for 150 msec), thus ensuring lateralization to a single hemisphere via its contralateral visual field. Auditory testing consisted of a dichotic speech sound identification test, and tactile tests required manipulation outside the field of vision [M. S. Gazzaniga et al. in (3); S. P. Springer, J. J. Sidtis, D. H. Wilson, M. S. Gazzaniga, *Neuropsychologia* **16**, 305 (1978)].
7. Preoperative and postoperative accuracy scores (percentages) on left-sensory-field naming tests are as follows: visual words, 63, 13; tactile objects, 100, 20; and dichotic consonant-vowel syllables, 67, 23. None of the postoperative scores differ from chance.
8. Preoperative and postoperative accuracy scores on right-sensory-field naming tests are as follows: visual words, 93, 91; tactile objects, 100, 90; and dichotic syllables, 77, 100.
9. J. J. Sidtis, B. T. Volpe, D. H. Wilson, M. Rayport, M. S. Gazzaniga, *J. Neurosci.* **1**, 323 (1981).
10. R. Brown and D. McNeill, *J. Verb. Learn. Verb. Behav.* **5**, 325 (1966).
11. Although the data in Table 1 represent performance on repeated administrations of the same picture and word tests, the improvement in performance based on the inference strategy was evident with novel stimuli as well. For example, in the tenth interoperative week, left-visual-field naming of novel words occurred on 71 percent of the trials, whereas right-visual-field performance was at 92 percent.
12. The specificity of the higher-order information available from the right hemisphere suggests that deep dyslexia may not represent right-hemisphere reading.
13. While the transfer of higher-order information may have occurred in both directions, it was not feasible to evaluate transfer from left to right hemispheres (9).
14. Retrieval from memory has been characterized as a spreading activation process [A. M. Collins and E. F. Loftus, *Psychol. Rev.* **82**, 407 (1975)] in which information adjoining the initial referent in memory shares its activation. In somewhat different but compatible terms, the activated field upon which the inference is based can be seen as a memory description constructed by the right hemisphere but evaluated by the left hemisphere [D. A. Norman and D. G. Bobrow, *Cognit. Psychol.* **11**, 107 (1979)].
15. Aided by PHS grant 2 R01 NS15053-02, the Alfred P. Sloan Foundation, the McKnight Foundation, and RR001-02 to Rockefeller University Hospital.

4 June 1980; revised 1 December 1980

Hinged Teeth in Snakes: An Adaptation for Swallowing Hard-Bodied Prey

Abstract. Six genera of snakes, representing at least three lineages, possess teeth that fold backward against the jaws rather than being firmly ankylosed. This condition, effected by a connective tissue hinge at the base of each tooth, is associated with suites of cephalic modifications that enable the snakes to grasp and to swallow hard-bodied prey.

The teeth of most snakes are sharp, curved, and firmly ankylosed to the jaws. Such teeth are ideal for piercing and grasping, but are ill-suited for dealing with hard-bodied prey. Thus, durophagic adaptations (that is, those related to feeding on hard-bodied prey) in snakes have been thought to be limited to reduction of tooth size and number [in the egg-eaters *Dasyplectis* and *Elachistodon* (1)] and to modifications facilitating the extraction of soft parts from mollusk shells [in dipsadine and pareine snakes (2)]. I report here a previously unrecognized durophagic adaptation in snakes: hinged teeth (3). Although viperid snakes have fangs capable of considerable movement, this action results from motion between cranial bones, especially the maxillae (to which the fangs are affixed) and the prefrontals. The viperid system is therefore simply an extension of the advanced cranial kinesis typical of snakes. In sharp contrast, six genera have teeth that are attached to the dentigerous bones by flexible connective tissue fibers (4, 5). Typically these teeth are small, numerous, distally flattened, and extremely smooth on their leading surfaces. Although hinged teeth are known in a variety of fishes (6) and lissamphibians [in which the tooth itself is divided into an ankylosed pedicel and a crown which may be movable (7)], hinged teeth have not been reported in amniote vertebrates.

Other changes have accompanied the development of hinged teeth in snakes. Differences in cephalic structure correspond to distinctive tooth morphologies

and permit the recognition of three groups of hinged-toothed snakes. Group 1 includes only the primitive Indomalaysian genus *Xenopeltis*. Group 2 contains three genera of colubrid snakes: the Malagasian *Liophidium*, the northern neotropical *Scaphiodontophis*, and the Indomalaysian *Sibynophis*. These three genera have frequently been united as the subfamily Sibynophiinae; however, their structural similarities pertain largely to the feeding apparatus and may have been derived in parallel (8). Group 3 includes the related African colubrids *Lycophidion* and *Mehelya*.

In group 1, the base of each tooth is expanded and enveloped in a connective tissue sheath. The hinge fibers run from the distolingual quadrant of that sheath to the adjacent bone (Fig. 1, B and C). Opposite the hinge, the bone slopes to form a pedicel. The teeth of small and moderate-sized (\leq approximately 700 mm, snout-vent length) *Xenopeltis* are distinctly bicuspid (Fig. 1A). The leading surface of each tooth is broad, almost flat, and curved at its tip. Distal to that surface and slightly offset is a pointed cusp. The flat surface is extremely smooth, showing only a fine vermicular ornamentation at approximately $\times 10,000$ magnification. The teeth of larger individuals are unicuspid, sharp, and strongly recurved. The teeth are numerous (approximately 40 on each maxilla), and almost all tooth positions are occupied simultaneously, indicating an abandonment of the alternate tooth replacement scheme characteristic of other snakes (9).