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Interhemispheric Integration

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INTRODUCTION

There are two cerebral hemispheres. Each interconnects with the other through the corpus callosum and anterior commissure. These two structures have been studied in detail in recent years from both an anatomical and behavioral perspective. Both types of studies were primarily motivated by concerns that did not address the issue of the nature and logic of interhemispheric integration, the problem of what information and how information is communicated between the two hemispheres. Yet, the structure is of profound importance when considering such issues since it is one of the few identifiable input and output channels of the cerebral cortex that is easily accessible to experimental manipulation. The study of such a message system may well give clues to larger questions of how the cortex is functionally organized. However, since the well known lateralized and specialized processes of the human brain are unique and without precedent in other mammals, what the commissures convey and how they convey it most likely varies from one species to another. As we will see, this compounds the problems of cross-species comparisons and argues for limiting many interpretations of structure-function correlates to within-species observations.

My own current interests center on the human brain, and here the recent observation that MR imaging (MRI), can verify the presence or absence of cortical commissures with great accuracy has provided new insights into the brain and behavioral correlates that the examination of this structure affords in humans. In what follows, I will review studies that suggest (a) the cerebral commissural system is highly specific in the kinds of information it transfers, (b) the commissural system can adapt to early injury, (c) the functional capacity of specific commissural zones varies among species, (d) the transfer of subcortical information is limited to crude spatial information and attentional processes, and (e) a high degree of individual variation exists in the lateralization of cortically specialized processes. Where possible I will try to relate the functional story to current anatomical knowledge. Rubbing these two disciplines together should, at some point, yield new insights into mind–brain relationships.

SPECIFICITY OF COMMISSURAL FUNCTION

Complete commissural section has been attempted in humans in an effort to limit the spread of epileptic activity between the cerebral hemispheres. In the California series both the anterior commissure and corpus callosum were presumed sectioned (Bogen et al. 1965). Twenty-five years of highly productive research has been carried out on a small group of patients from this series (Sperry 1968, 1974; Gazzaniga 1970). When interactions between the hemispheres have been noted, it has always been assumed that the information in question was being integrated subcortically. Until recently, similar assumptions have also been made in the East Coast series (Gazzaniga and LeDoux 1978). With the advent of MRI it has become possible to clarify earlier claims by verifying the extent of the surgical section (Gazzaniga et al. 1984). When the surgery is planned to be limited to a specific commissural area or when surgical mistakes are made, a rare opportunity exists to systematically manipulate neuropsychological tests in an effort to determine the kinds of information that can be transmitted through the spared fiber systems. In this fashion, the degree and extent of specificity of commissural function can be explored. As a rule each patient becomes a unique entity to study. With this development the analysis of any data set requires taking into account the patient's overall neuropsychological status, medical history, and MR image.

Studies on Sensorimotor Integration

The sensorimotor capacities of two disconnection patients have recently been examined. Case E.B., a 26 year old female, underwent partial callosal section for intractable epilepsy in 1983. The posterior one-half of the callosum was sectioned in one operation and the extent of the section was verified with MRI. Prior to her callosal surgery E.B. had undergone, at the age of 19, a right occipital resection in an earlier effort to control her epilepsy. This resulted in a left central hemianopia that has remained static. Because of the preoperative hemianopia, interhemispheric testing of visual function was not attempted; however, interhemispheric tests on tactile function were carried out. Preoperative testing of tactile function was unremarkable. Postoperatively, these tests revealed she was unable to name objects placed out of view in the left hand. Objects placed in the right hand out of view were easily named. She was also unable to transfer stereognostic information from one hand to another, thereby demonstrating that no tactile sensory information was being cross-communicated between the two hemispheres. Additionally, while her left hand was able to retrieve like items in a match-to-sample paradigm, she could not retrieve objects on verbal command with the left hand. The rest of her neurologic history is unremarkable and she currently enjoys good health. The second patient, case J.W., underwent full callosal section in two stages and the extent of his full section has been verified with MRI (Fig. 1). He is in excellent health, has been studied extensively, and a complete medical history as well as other neuropsychological tests are reported elsewhere (Gazzaniga et al. 1985).

The capacity of each patient to carry out a simple tactile-motor task was assessed in much the same manner originally employed for split-brain patients (Gazzaniga et al. 1963). In brief, each finger was touched lightly in either the proximal or distal phalanx. The within-hand task required the subject to touch the point of stimulation with the thumb of the same hand (Fig. 2). Subsequently, the between-hands condition was run. Here a point was stimulated in the same fashion on one hand and the subject was required to find the corresponding point on the opposite hand with the thumb of the opposite hand. The full task was carried out on several occasions in each patient over a period of years. The results reported here were collected two years after surgery on E.B. and five years after the final callosal surgery on J.W. The pattern of response capacity has not changed over either patient's postoperative course.

Both patients responded easily and with high accuracy when stimulus and response were within-hand (Fig. 3). In the between-hand condition case J.W., the fully sectioned patient, was unable to cross-integrate the information in either direction, a result consistent with other fully sectioned patients. Case E.B., however, the patient with only a partial section, showed a unique pattern of results. While she was able to cross-integrate information from the right hand to the left, she performed at chance when trying to cross-integrate information from left to right.

These results confirm and extend earlier findings. The corpus callosum is active in the cross-integration of sensory and motor information. When the structure is completely sectioned, sensory information arriving and being processed in one hemisphere's somatosensory cortex remains isolated to that hemisphere. Further, when information is transmitted to the opposite hemisphere, the present results suggest the transmitted information traverses over highly specific callosal pathways. In case E.B. it appears that the callosal surgery included fibers that were responsible for transmitting motor

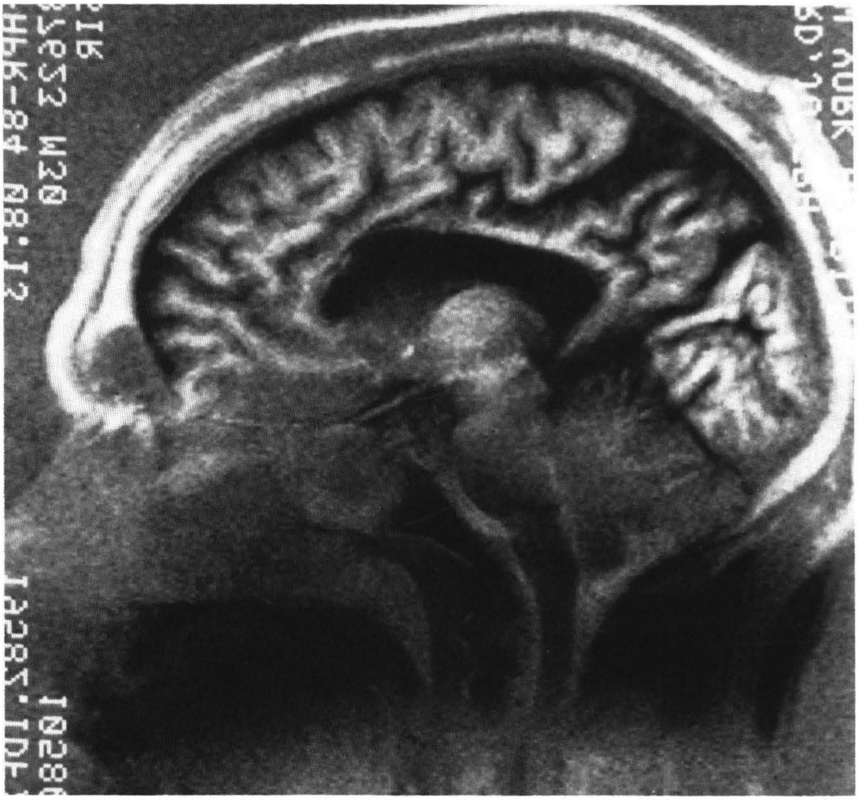


Fig. 1—MRI of case J.W. showing the entire callosum has been successfully sectioned. Note the presence of the anterior commissure.

information from the left hemisphere to the right. At the same time the surgery was not extensive enough to section the fibers that were responsible for allowing integration of motor information from right to left.

Studies on Language and Commissural Specificity

The present study includes two split-brain patients. J.W., as already described, had undergone a complete callosal section. Case V.P., in whom MRI revealed spared callosal fibers, was studied in an attempt to determine whether these remaining fibers were capable of transmitting any kind of perceptual or cognitive information. Her spared fibers were in the region of the splenium and rostrum of the callosum (Fig. 4). In standard tests of perceptual interactions, neither patient showed any indication of perceptual information being transferred between the two hemispheres (Holtzman

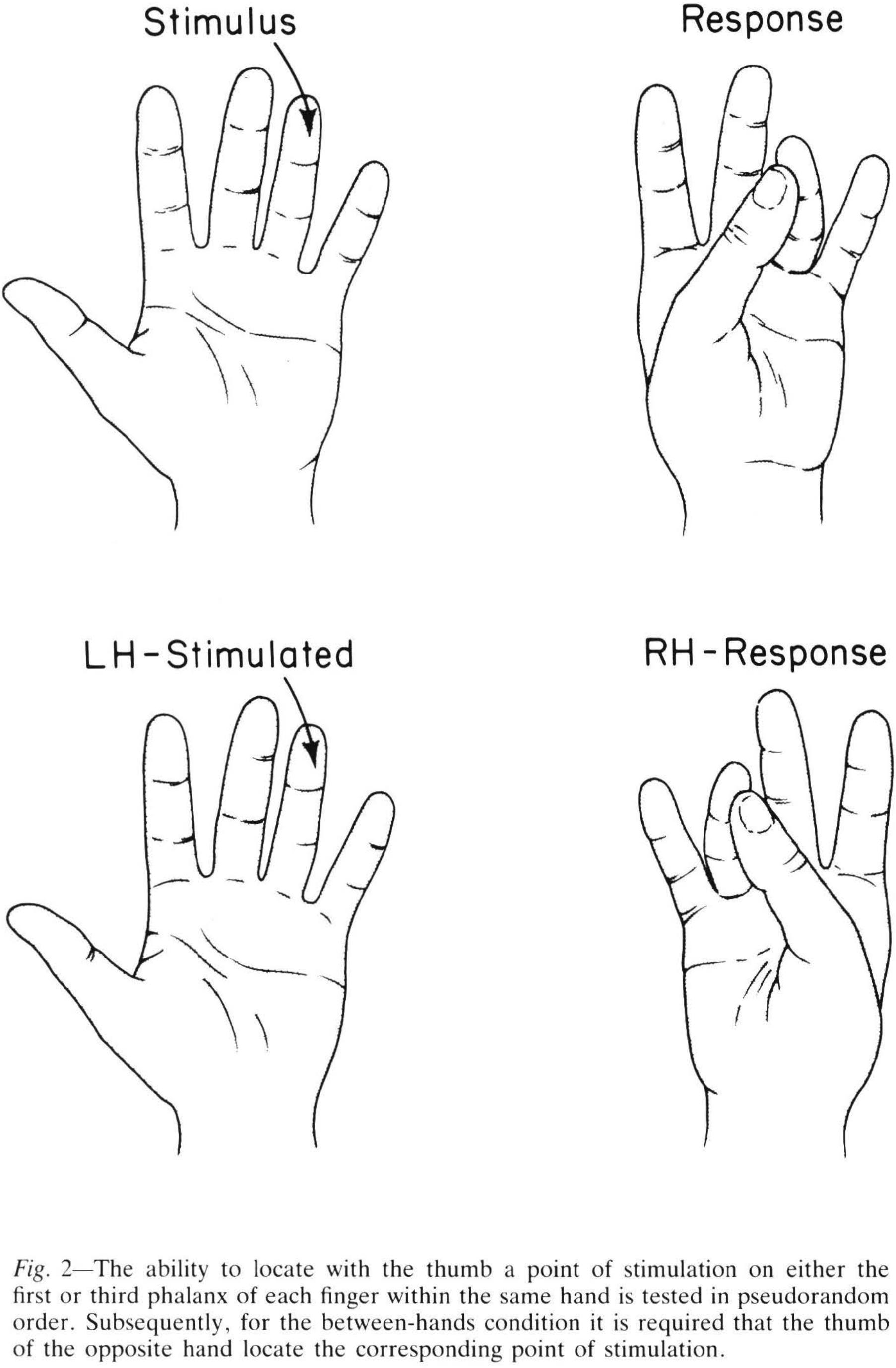


Fig. 2—The ability to locate with the thumb a point of stimulation on either the first or third phalanx of each finger within the same hand is tested in pseudorandom order. Subsequently, for the between-hands condition it is required that the thumb of the opposite hand locate the corresponding point of stimulation.

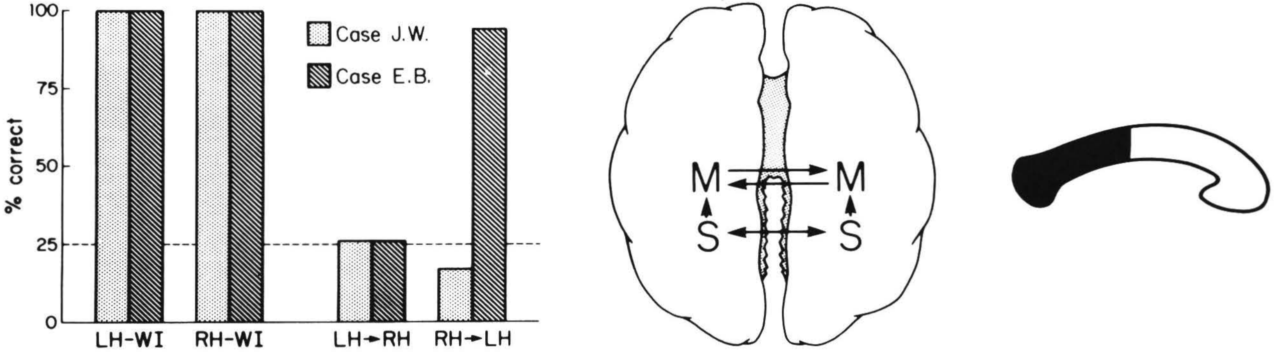


Fig. 3—The results of cases J.W. and E.B. are presented along with a diagram suggesting the probable mechanism of action. The fully sectioned patient was unable to carry out the between-hands task whereas the partially sectioned patient was impaired in only one direction, thereby suggesting the neural fibers involved in transmitting the motor information to the opposite hemisphere were sectioned for only one direction of transfer.

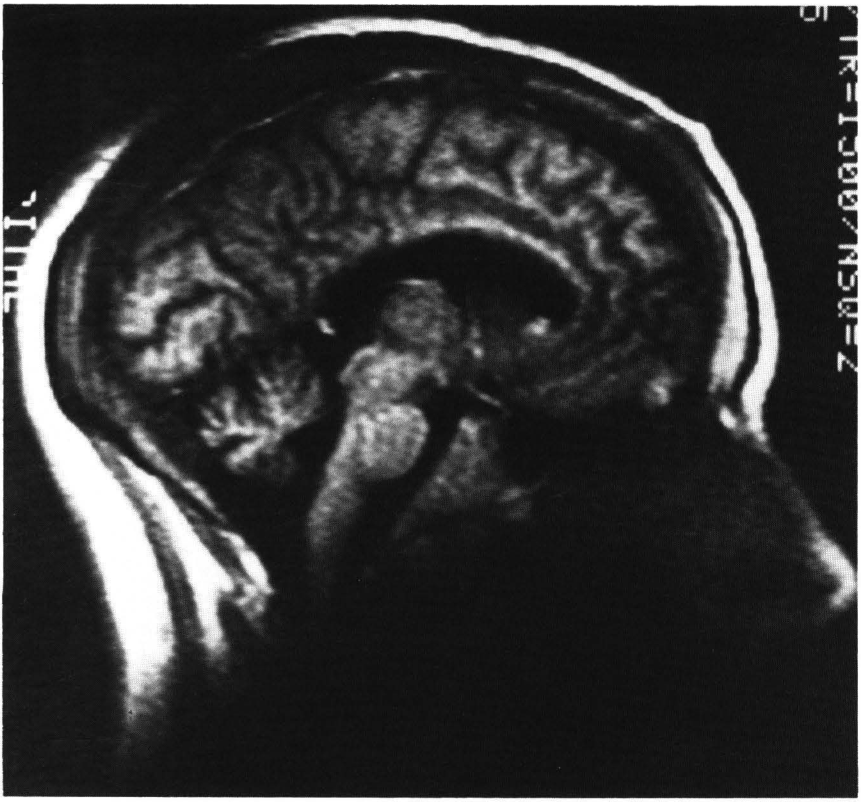


Fig. 4—Case V.P. had fibers inadvertently spared in the region of the splenium and rostrum.

1984). Additional perceptual tests were given to V.P. A series of circles varying in size were presented to either the left or right hemispheres (within-hemisphere) or across the midline (between-hemispheres). Thus, on each trial two circles were presented and the task was to say "yes" they were the same or "no" they were different. When both circles were presented to the left hemisphere, V.P. scored 35/40 and when both were presented to the right hemisphere she scored 30/40. In the between-hemispheres condition, in which one circle went to each hemisphere, V.P. was at chance (45/80). The remaining fibers in V.P. seemed nonfunctional in this test of perceptual interaction.

Since some of the remnant fibers were in anterior regions that might interconnect language areas, an extensive battery of tests was administered to examine the possible role of these fibers in language processes. Results to date are intriguing but incomplete. In one set of studies the ability of these fibers to exchange semantic information was tested (Gazzaniga et al.

1984). In this series of tests a word was presented to one hemisphere and 500 ms later a word was presented to either the same hemisphere or the opposite hemisphere. The various relations of lexical items were examined, e.g., insect-ant versus insect-fish, and the task was to say either "yes" they were related or "no" they were not. Both J.W. and V.P. showed excellent performance within each hemisphere but chance performance across the hemispheres.

However, other tests on V.P., carried out in collaboration with Marta Kutas and colleagues, revealed a different picture. While the fully sectioned J.W. continues to show no interaction between the hemispheres, V.P. shows a different pattern of results (Gazzaniga, Van Patten, and Kutas, personal communication 1987). In this study a large set of carefully graded language stimuli comparisons were presented that varied orthographically and phonologically. In brief, V.P. performed a between-fields comparison in which she judged whether two words, one presented in each half visual field, did or did not rhyme. The stimulus pairs were divided into four experimental conditions on the basis of their phonological (i.e., rhyming [R+] versus nonrhyming [R−]) and orthographic (i.e., look alike [L+] versus nonlook alike [L−]) similarities as follows:

1) R+L+ if words in pair rhymed and looked alike (e.g., look-book, tire-fire);
2) R+L− if words in pair rhymed but did not look alike (e.g., bake-ache, rule-tool);
3) R−L+ if words in pair did not rhyme but looked alike (e.g., near-pear, cough-dough)
4) R−L− if words in pair neither rhymed nor looked alike (e.g., shell-paths, keys-fort).

V.P. showed significantly greater than chance accuracy in one test condition. Only when the words in the two visual fields both looked and sounded alike (R+L+) was V.P. able to judge whether or not they rhymed. Thus, V.P. demonstrated no ability on this test to integrate information from the two visual fields unless there was an overlap of both visual and phonemic information. One possible explanation for these results is that the remaining callosal fiber system seems to honor some domains of information but not others, a notion that is consistent with one last observation on V.P.

In this test on case V.P. two vowels, AA (look and sound alike), or a vowel and a consonant, AB (do not look or sound alike), or two consonants, BB, were presented in both a within and between visual field condition. The task was to simply respond "yes" if they were the same or "no" if they were different. In this test no interactions were seen between the two hemispheres. Within-hemisphere performance was near perfect. This suggests that somehow individual letters do not evoke enough dimensions of "richness," leading to some kind of redundancy that allows for interhemispheric interaction that is somehow supported through these remaining fibers.

From the foregoing, it is clear that a patient with only splenial and rostral fibers spared was able to cross-compare information in only one of the four stimulus conditions, the condition in which words both looked and sounded alike. In sharp contrast, a patient with full callosal section responded on the interhemispheric comparison task at chance for all conditions. Additionally, the remnant fiber systems, that can support the interhemispheric comparison of words that look and sound alike, fail at communicating information when the stimuli are letters that look and sound alike. Unequivocal identification of the callosal areas crucial for the transfer is not yet possible since we have not been able to test a patient with either a similar rostral or splenial remnant intact while the other was absent, and who also has language capacities in the right hemisphere. Additionally, other tests are currently being designed to eliminate possible issues concerning criteria difference for relatedness judgements as opposed to sameness judgments. Nonetheless, since V.P. does not transfer visual or language information in any simple sense, the pattern of results suggests that the splenial (visual) and rostral (phonetic) fiber systems may uniquely combine partial information in order to allow for correct judgments. Additionally, the present results raise the question of how specific information exchange can be for brain based language activities and how callosal fibers may or may not be activated as a function of the psychological dimensions of the stimuli used.

COMMISSURAL PLASTICITY IN THE FACE OF EARLY BRAIN DAMAGE

In recent years there have been several primate studies suggesting that early brain damage may create unique commissural connections that allow for different functions in the adult brain. Much as in the fashion reported by Goldman-Rakic in the monkey (1981), early damage in the human might also allow for formation of aberrant interhemispheric connections that course through the remaining anterior commissure. She showed that, although a consequence of surgical manipulation, callosal fibers may exhibit some rearrangements of their connectivity: if the dorsolateral prefrontal cortex is removed from one hemisphere of the rhesus monkey at a sufficiently early developmental stage, callosal fibers originating from the contralateral principal sulcus will be found to innervate regions not normally receiving this callosal input. In support of this kind of mechanism, thalamic afferents have recently been shown to proliferate and make specific axospinous contacts on neurons in upper cortical layers three months following deafferentation by callosotomy performed on one month old rats (Vaughan and Peters 1985).

We have studied one case where this possibility has become apparent in the human brain. Case P.S., one of the original patients from the Wilson series, has now been studied for 11 years following his full callosal surgery in 1975. His medical history includes clinical notations of early left-sided brain abnormalities as evidenced by clinical EEG at the age of two. He was operated on at the age of 15 and postoperatively has shown an evolving course where interhemispheric communciation of a complex type is now possible (Gazzaniga et al. 1982). In 1984, MRI revealed a full callosal section.

Case P.S. does not transfer sensory information between the two hemispheres. The simultaneous presentation of nonsense figures, one to each half brain, does not find him able to say whether or not the two are the same. This is also true for faces and circles of subtly different size as just described for case V.P. However, P.S. is now easily able to communicate to the opposite half brain the nature of any nameable stimulus whether it be a color, a shape, an object, or a word. Other tests have revealed that this coding ability is dependent on some kind of phonetic mechanism, as P.S. can be easily foiled by using homonyms. Thus, the word "rows" presented to one hemisphere will find the other interpreting the transmitted message as "rose" just as frequently as "rows."

This explicit capacity has not been seen in any other fully sectioned callosal patient. The possibility remains that the anterior commissure in case P.S. has somehow responded to early cortical injury and established connections in temporal or other regions that would allow for this kind of unique capacity. In short, the plasticity that has been reported in the monkey brain may also be apparent in the human brain.

INTERSPECIES VARIATION IN STRUCTURE-FUNCTION CORRELATES

The MRI technique has also allowed for the sharpening of hypotheses about the commissural areas that are critical for modality-specific interhemispheric communication in the human brain. Prior to being able to confirm the actual extent of callosal surgery in humans using MRI, it was necessary to depend on surgical notes. We now know that surgical estimates can be in error. Nonetheless, ten years ago surgical notes served as the basis for proposing certain ideas on commissural localization that now appear incorrect. For example, after presumed full callosal surgery on four patients, we observed that two could transfer visual information (Risse et al. 1975). Two other patients did not show transfer. In an effort to account for this we proposed the remaining anterior commissure could vary in the kinds of information it was able to transfer.

The animal literature clearly pointed the way to the conclusion that the anterior commissure could transfer visual information. It made perfect sense to believe that the same structure could transfer visual information in humans. Although only the callosum was found to subserve interocular transfer in cats, the anterior commissure was found to be involved in visual transfer in chimpanzees (Black and Myers 1964) and rhesus monkeys (Gazzaniga 1966; Noble 1968; Sullivan and Hamilton 1973). Taken together, there was strong evidence that the same might be true for humans.

We now have had the opportunity to give an MR scan to one of those supposedly split patients (Fig. 5). It clearly showed that the splenium had been spared in the surgery, thus explaining the transfer of information. In another series of patients, similar results have been noted (Gates, personal communication). Each time where there is evidence of transfer of visual information that requires exact matching of stimulus features, following supposedly full commissurotomy, there has been sparing of the splenium. This suggests the anterior commissure, a structure that clearly is able to transfer visual information in the monkey and chimp, does not do so in the human. A similar point has been made by McKeever and colleagues (1981).

In searching for an explanation of this interspecies difference in function, only a few facts are known. In humans, the anterior commissure represents approximately 1% of the neural fibers that contribute to intercortical communication, compared to 5% in the rhesus monkey (Foxman et al. 1986). Thus, the human anterior commissure is proportionately much smaller in comparison to the corpus callosum and the extensive cortical territories it serves. In the monkey, between half and two thirds of the temporal lobe transfers information to the contralateral hemisphere exclusively via the anterior commissure. In the human, while the distribution is not fully known, it is thought to be much less.

Additionally, appreciation for the role of the anterior commissure in interhemispheric integration in primates may have been underestimated because of the results obtained by earlier silver degeneration studies, which mapped only the terminal distributions of the anterior commissure (Zeki 1973; Pandya et al. 1971). The terminal fields were found only in the rostral portions of the temporal lobe and an assumption was made that the anterior commissural fields of origin homotopically overlapped the terminal fields. In recent years, the view has arisen that the anterior commissure projects to perhaps only the anterior third of the temporal lobe, in agreement with the earlier studies, while its field of origin extends much further caudally (Zeki 1973; Jouandet and Gazzaniga 1979; Jouandet et al. 1984). Thus, the principle of homotopicality, which holds true for innumerable point-to-point projections between the hemispheres, does not appear to extend to the whole field distributions of the cerebral commissures.

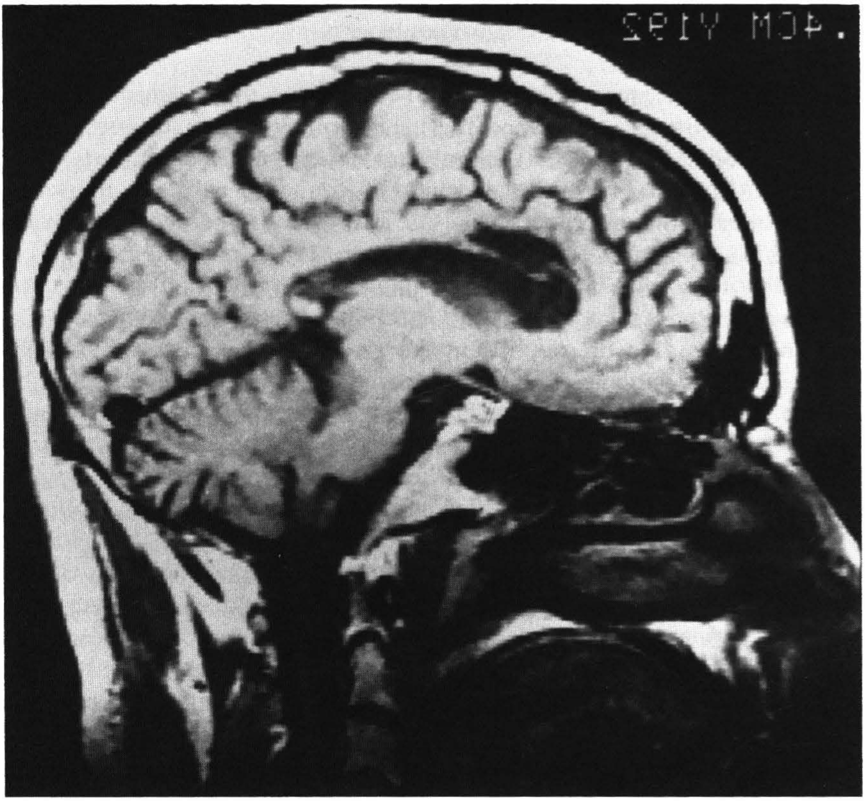


Fig. 5—MRI of case J. Kn. This patient was presumed split until MR imaging revealed a clearly intact splenium. The patient transfers visual but not tactile information between the two hemispheres. (Special thanks to William Abend, M.D. of Harvard Medical School for arranging this scan.)

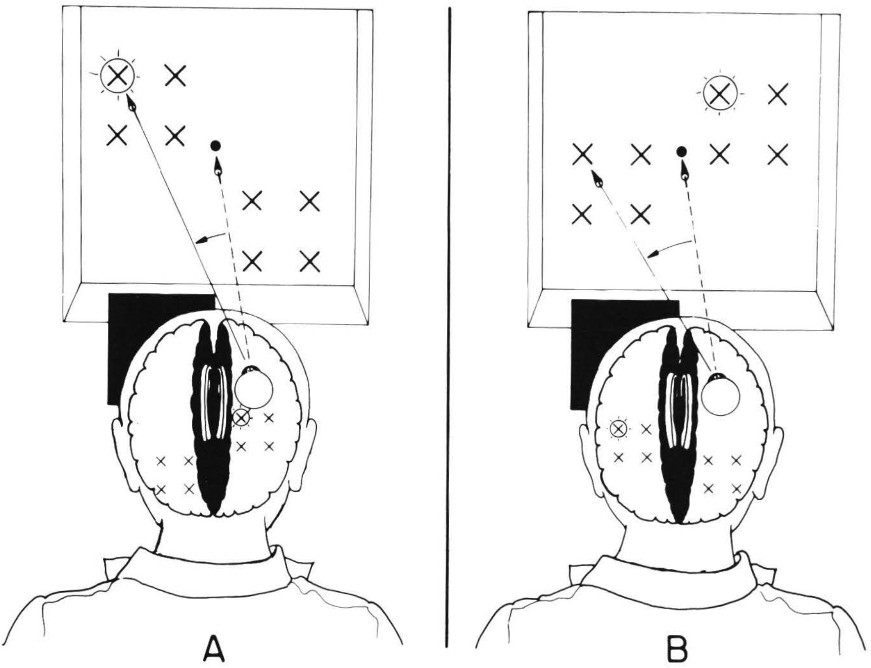
Finally, there is much data to suggest a great interspecies variation in the anatomy of the anterior commissure. For example, the misalignment of the anterior commissural fields of origin and termination seen in primates is even more exaggerated in the cat, where an extensive neocortical field of origin projects contralaterally to only paleocortical areas below the rhinal sulcus (Jouandet 1982). In short, the anterior commissure appears to have undergone very substantial remodeling during the phylogenetic evolution of mammalian species (Jouandet and Hartenstein 1983; Granger et al. 1985).

The clear difference in function seen between monkey and human brains, combined with possible new anatomical correlates supporting these differences, suggests a cautious note when attempts are made to compare the function of similar brain structures across species. It suggests the arguments against such cross-species comparisons are as crucial today as they were when originally presented. A similar difference in function between monkey and humans can be seen in that the superior colliculus is capable of cross-integration between the two half brains.

REMAINING INTERHEMISPHERIC EXCHANGE: CALLOSUM SECTIONED HUMANS TRANSFER ONLY CRUDE SPATIAL INFORMATION

Visual integration of any perceptual, color, or brightness information is not possible following full callosal section. At the same time, it has been determined that crude spatial information can be cross-integrated. In one set of experiments, a 4-point grid was presented to each visual field. On a given trial one of the positions on the grid was highlighted. In one condition of the task the subject moved his eyes to the highlighted point within the visual field stimulated. In the second condition the subject was required to move his eyes to the homologous point in the opposite visual field (Fig. 6). Split-brain subjects were able to do this easily, thereby suggesting some crude cross-integration of spatial information. Once again, however, if the task required the subject to respond to perceptual features, there was no interhemispheric integration. In these experiments the four spatial points were changed to four geometric shapes, each positioned differently in the visual fields. On each trial, target locations were defined by the type of geometric form to which the movement should be directed, rather than by the relative position in the grid. In this condition, eye movements made to a highlighted stimuli could be accurately carried out only within a half brain. These tests show that noncallosal systems are somehow active in the cross-integration of crude spatial information. Since similar findings have also been found in patients with the anterior commissure sectioned as well, it is presumed other brain structures are involved in the mediation of this information.

Although these findings imply that representation of the ipsilateral hemifield is not completely eliminated by callosal transection, they do not necessarily imply that the availability of such information depends on interactions between cortical and subcortical structures. Consistent with the much reported blindsight hypothesis, ipsilateral representation could be provided directly via retino-collicular projections, independent of any cortico-collicular influence. The visual function reported to remain following cortical lesions in the monkey is consistent with this view (Keating 1975). If the human brain were similar, it would be expected that such ipsilateral representation would be unaffected by damage to the occipital cortex and that the performance on these tasks of a patient with occipital damage would be comparable to that obtained from the commissurotomy patients. This possibility was carefully examined by Holtzman (1984). The results of his studies reveal an important observation about cortical-subcortical interactions active in interhemispheric integration.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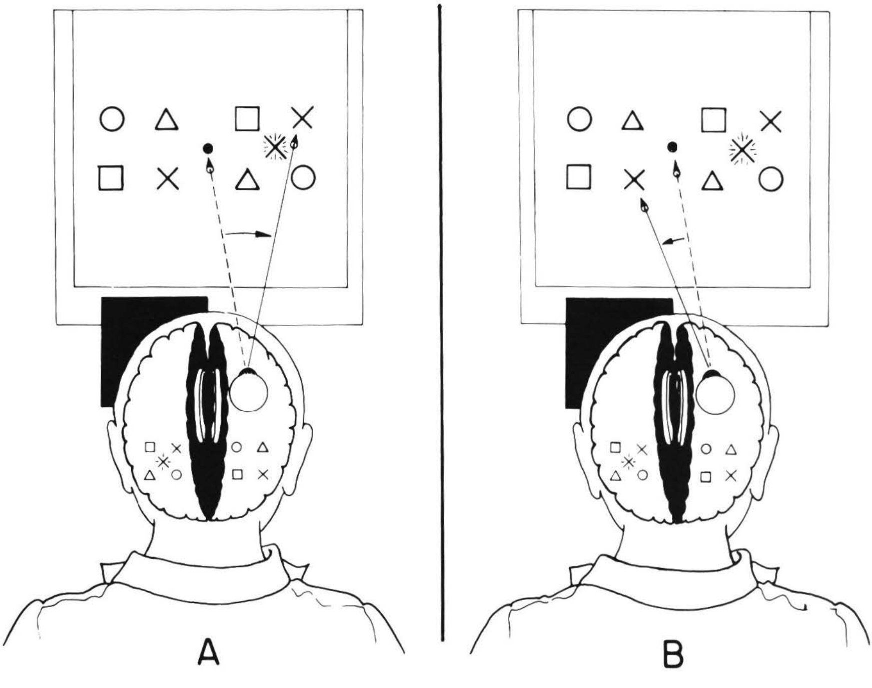
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THERE IS COLLICULAR-CORTICAL INVOLVEMENT IN THE CROSS-INTEGRATION OF SPATIAL INFORMATION FOLLOWING CALLOSAL SECTION

Analysis of possible collicular function was carried out on case B.H., a 34 year old woman who had undergone surgery for an AVM in the right occipital lobe. Postoperatively she had a dense left homonymous hemianopia. She performed quite accurately when required to localize targets in her perceptually intact right visual field, whereas her performance did not exceed chance levels for eye movements into her perceptually blind left visual field. Thus, there is no evidence that these targets could be localized in a visual field rendered blind by occipital damage even though her superior colliculus remains entirely intact. Therefore, the localization of visual stimuli in the ipsilateral hemifield appears to require intact occipital cortices.

This kind of observation suggests that, contrary to monkeys, in humans simple spatial information cannot be managed by an intact collicular (or other midbrain) system in the absence of normal input from visual cortical areas. Cross-integration of such information is only possible when midbrain structures remain connected to cortical processes, as is the case in the split-brain patient.

INDIVIDUAL VARIATION IN LATERAL SPECIALIZATION

It has been well established for dozens of years that language processes can sometimes be managed in the right hemisphere. While the left hemisphere is usually responsible for language, as has been established most elegantly by Milner, there can be some variation in this pattern as evidence by these

Fig. 6—The upper example depicts the spatial tests. On within-field trials (a) the eye moved to the stimulus that was surrounded by the probe, on between-field trials, and (b) the eye moved to the corresponding stimulus in the other hemifield. Each matrix of 4 "X"s subtended 2X2 degree of visual angle; the nearest edge of each matrix was 1.5 degree from the vertical meridian. On each trial the vertical offsets of the matrices varied randomly in 1 degree steps, so that the vertical positions of the matrices were unpredictable from trial to trial.

The lower example depicts the perceptual tests. On the within-field trials (a) the probe appeared centered in one of the arrays and the eye moved to the corresponding stimulus in the field in which the probe appeared, on between-field trials, and (b) the eye moved to the corresponding stimulus in the opposite field. Each matrix of 4 figures subtended 2X2 degree of visual angle; each figure within a matrix subtended approximately 0.25 degree of visual angle. The nearest edge of each matrix was 1.5 degree from the vertical meridian. The matrices were always positioned symmetrically about the horizontal and vertical meridians. On each trial, the 4 figures in each matrix were randomly shuffled so that the position of a particular figure was unpredictable from trial to trial.

right hemisphere cases (Milner et al. 1962). In this context, it should come as no surprise that the cortical lateralization of other mental and cognitive skills might also vary. Additionally, in recent years there has been much evidence from cognitive psychology that mental processes are made up of components and that these components have identifiable and localized brain processes associated with them (Gazzaniga 1985). Gaining evidence for this view is a frequent endeavor when studying patients whose cortical commissures have been sectioned. In the present study, a task requiring a sequencing capacity was studied in two patients, J.W. and V.P.

In brief, subjects were presented with two 9-cell grids, one presented to each half visual field. On any given trial, a series of four of the nine cells was briefly highlighted with an "X" in pseudorandom order. After the stimulus sequence terminated, the subject was required to point with the hand, ipsilateral to the field of presentation, to each highlighted cell in the sequence presented. Thus, a stimulus appearing in the left field was responded to by the left hand and a stimulus appearing in the right field was responded to by the right hand (Fig. 7).

Case J.W. could perform the task with his left hemisphere but not his right. Case V.P., however, performed the task with her right hemisphere but not her left. This variation in hemispheric superiority on the task underlines how the overall cognitive composition of each hemisphere can vary. Additionally, the presence of one kind of skill does not necessarily predict the presence of another. This sequencing task was originally administered with the view that it might be a basic task that would correlate

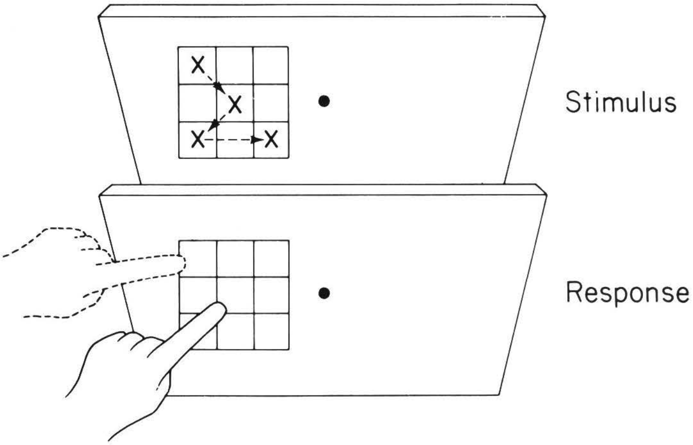

Fig. 7—Sequencing task. A sequence of four of nine cells is illuminated in either the left or right visual field. The task is to retrace the sequence by pointing with the hand ipsilateral to the field stimulated.

with the left hemisphere's superior linguistic skills. Clearly, the capacity for reproducing sequences functions independently of those processes.

EVIDENCE OF BI-HEMISPHERIC INVOLVEMENT IN SPECIALIZED SKILLS

Over the past 25 years of split-brain research it has been difficult to isolate what the potential costs to cognition might be by dividing the human cerebrum. Many earlier studies have shown there is no change in reaction time response to simple discriminations (Gazzaniga and Sperry 1966), in the capacity to form hypotheses (LeDoux et al. 1977); or in verbal IQ (Campbell et al. 1981). There have been some reports that negative effects can be registered on memory function (Zaidel and Sperry 1974), while others have not confirmed this concern (LeDoux et al. 1977). There is data that hemispheric disconnection actually allows each half brain to function without perceptual interference from the other and thereby confers on the whole brain a supernormal capacity to apprehend perceptual information (Holtzman et al. 1984). Taken together, while most prior studies have been carried out in the context that each half brain is an independently functioning system that operates no differently when separated than when connected, new studies are beginning to challenge this original view. The old working assumption was based on the kind of behavioral profile seen in the split-brain cases that possess language in each hemisphere. In this highly select and small group of subjects, each hemisphere seemed capable of responding in its own way to a wide variety of stimuli.

But then there are the other cases where right hemisphere performance after surgery was poor to nonexistent. The question became whether such patients possess right hemisphere skills at all, or are those skills merely "locked in" after disconnection from the dominant left half brain. It is assumed that the perceptual capacity and engrams are there but there is no ability to operate on the perceptual capacity. We plan a large study on this issue and are encourgaed by some early results. Consider cases E.B., D.R., and L.L. Each is different.

Prior to split-brain surgery case E.B. was administered a number of tests including the nonsense wire figure test of Milner and Taylor (1972). This task is believed to tap into right hemisphere specialized systems. Case E.B. was able to perform the task with either hand when the objects were presented out of view. Her intact callosum appeared to assist in distributing the information arriving in her left brain from the right hand, over to the specialized system in the right hemisphere. At least, that is how we have come to think about these kinds of things.

After the posterior half of the callosum was cut, E.B. was unable to name objects placed in the left hand in typical split-brain fashion. The fibers crucial for the interhemispheric transfer of tactile information had been severed and as a result the right hand knew what the left did not. E.B. also proved to be without right hemisphere language. While she was able to find points of stimulation on the left hand by touching them with the left thumb, thereby demonstrating good right hemisphere cortical somatosensory function as already described, she was unable to retrieve with her left hand an object named by the examiner. This task is managed easily by patients with right hemisphere language. Most importantly, however, E.B. could no longer perform the wire figure task with either hand.

Since E.B. could perform the task preoperatively it seems clear that the right hemisphere has the capacity to contribute to solving this kind of task when it is connected to the left. Disconnected from the left, it appears unable to function. Performance on this task with both hands was greatly impaired. As already mentioned, this kind of finding suggests the left hemisphere may normally contribute certain executive functions to specialized systems in the right brain. What was thought to be one integrated system, that is, the capacity to carry out these nonverbal tasks is actually the product of the interaction of at least two systems, each located in a different brain area.

The same general finding was seen in the pre-versus postoperative scores on the Block Design test for E.B. as well as two other patients: cases D.R. and L.L. This test is considered to be a right hemisphere task although there are also several reports suggesting left hemisphere damage can cause deficits in performance of the task. Both patients underwent full callosal section. Case L.L. had a right temporal lobe resection prior to the callosal surgery, carried out in an effort to control his epilepsy. His callosal surgery was done in two stages. Case D.R., a 39 year old woman, had her surgery carried out in one operation. Prior to surgery, each patient's performance on the Block design subtest of the WAIS was fast and accurate, and well within the normal range. The preoperative tests were done with the right hand. Postoperatively, neither the left nor the right hand of either subject could perform the task with ease. The time needed to solve the simpelst patterns doubled and completion of the more difficult patterns became impossible. Case L.L. revealed no other right hemisphere function except for the capacity to locate with the left hand a point of light flashed in the left visual field. He was unable to carry out the simplest pictorial or verbal match-to-sample test with the right hemisphere. Yet, it appears that preoperatively the right hemisphere, when connected to the left participated in the solving of the block design problem. Also, since the postoperative scores for the left hemisphere were down, the left hemisphere obviously benefited from processes located in the right half brain.

Case D.R. had a more responsive right hemisphere. She was able to carry out match-to-sample tasks for lateralized visual but not verbal stimuli. Yet, when two geometric shapes were presented sequentially to the right hemisphere, she was unable to make a same/different judgment, thereby indicating her right hemisphere was not capable of simple problem solving. At the same time, there is some evidence that D.R's right hemisphere understands some simple nouns. Yet, even with the far greater capacity to process information within the right brain, neither the left hand nor the right could perform the block design test as well as the right hand had performed it preoperatively. Here again we see evidence that the normal contribution of the right hemisphere to solving such tasks can be realized only when it is connected to the left. And again, the left hemisphere was also benefiting from the right brain prior to the operation.

For future surgeries, a more comprehensive pre- and postoperative battery of tests is planned. However, when the evidence to date is analyzed it suggests that dissociable factors are active in what appear to be unified mental activities. In short, one can begin to envision "executive controllers" active in manipulating the data of specialized processing systems. These controllers normally tend to be lateralized in the left brain, and when the right brain becomes isolated from their influence its specific functions become hard to detect.

SUMMARY

Sectioning the cerebral commissures for the control of epilepsy in humans has proved beneficial to both the patient and to science. Complete section of the commissure permits individual examination of each separate half brain. When fibers of the callosum are spared, either by design or inadvertently, examination of how specific these cortical routes are in the kinds of functional information they transmit is possible. Studies in both these domains reveal variation in lateral specialization. Lateralized processes are sometimes in the left brain, sometimes in the right, and sometimes both half brains seem active in supporting a particular function via the corpus callosum. Additionally, the callosum appears to be highly specific in the kinds of information it encodes.

REFERENCES

Black, P., and Myers, R.E. 1964. Visual function of the forebrain commissures in the chimpanzee. *Science* **146**: 799–800.

Bogen, J.E.; Fisher, E.D.; and Vogel, P.J. 1965. Cerebral commissurotomy: a second case report. *J. Am. Med. Ass.* **194**: 1328–1329.

Campbell, A.L.; Bogen, J.E.; and Smith, A. 1981. Disorganization and reorganization of cognitive and sensorimotor functions in cerebral commissurotomy: compensatory roles of the forebrain commissures and cerebral hemispheres in man. *Brain* **104**: 493–511.

Foxman, B.T.; Oppenheim, J.; Petito, C.K.; and Gazzaniga, M.S. 1986. Proportional anterior commissure area in humans and monkey. *Neurology* **36**: 1513–1517.

Gazzaniga, M.S. 1966. Interhemispheric transfer of visual learning. *Neuropsycho.* **4**: 183–189.

Gazzaniga, M.S. 1970. The Bisected Brain. New York: Appleton-Century-Crofts.

Gazzaniga, M.S. 1985. The Social Brain. New York: Basic Books.

Gazzaniga, M.S.; Bogen, J.E.; and Sperry, R.W. 1963. Laterality effects in somesthesis following cerebral commissurotomy in man. *Neuropsycho.* **1**: 209–215.

Gazzaniga, M.S.; Holtzman, J.D.; Deck, M.D.F.; and Lee, B.C.P. 1985. NMR assessment of human callosal surgery with neuropsychological correlates. *Neurology* **35**: 1763–1766.

Gazzaniga, M.S., and LeDoux, J.E. 1978. The Integrated Mind. New York: Plenum Press.

Gazzaniga, M.S.; Sidtis, J.J.; Volpe, B.T.; Smylie, C.S.; Holtzman, J.D.; and Wilson, D.H. 1982. Evidence of para-callosal verbal transfer after callosal section: a possible consequence of bilateral language organization. *Brain* **102**: 53–63.

Gazzaniga, M.S.; Smylie, C.S.; Baynes, K.; Hirst, W.; and McCleary, C. 1984. Profiles of right hemisphere language and speech following brain bisection. *Brain Lang.* **22**: 206–220.

Gazzaniga, M.S., and Sperry, R.W. 1966. Simultaneous double discrimination response following brain bisection. *Psychonom. Sci.* **4**: 261–262.

Goldman-Rakic, P.S. 1981. Development and plasticity of primate frontal association cortex. In: The Organization of the Cerebral Cortex, eds. F.O. Schmidt, F.G. Worden, G.F. Adelman, and S.G. Dennis, pp. 69–97. Cambridge, MA: MIT Press.

Granger, E.M.; Masterton, R.B.; and Glendenning, K.K. 1985. Origin of interhemispheric fibers in acallosal oppossum (with a comparison to callosal origins in the rat). *J. Comp. Neurol.* **241**: 82–98.

Holtzman, J.D. 1984. Interactions between cortical and subcortical visual areas: Evidence from human commissurotomy patients. *Vision Res.* **24**: 801–813.

Holtzman, J.D., Volpe, B.T.; and Gazzaniga, M.S. 1984. Spatial orientation following commissural section. In: Varieties of Attention, eds. R. Parasuraman, D.R. Davies, and J. Beatty, pp. 375–394. New York: Academic Press.

Jouandet, M.L. 1982. Neocortical and basal telencephalic origins of the anterior commissure of the cat. *Neurosci.* **7**: 1731–1752.

Jouandet, M.L.; Garey, L.J.; and Lipp, H.P. 1984. Distribution of the cells of origin of the corpus callosum and anterior commissure in the marmoset monkey. *Anat. Embryol.* **169**: 45–59.

Jouandet, M.L., and Gazzaniga, M.S. 1979. Cortical field of origin of the anterior commissure of the rhesus monkey. *Exp. Neurol.* **66**: 381–397.

Jouandet, M.L., and Hartenstein, V. 1983. Basal telencephalic origins of the anterior commissure of the rat. *Exp. Brain Res.* **50**: 183–192.

Keating, E.G. 1975. Effects of prestriate striate lesions on the monkey's ability to locate and discriminate visual forms. *Exp. Neurol.* **47**: 16–25.

LeDoux, J.E.; Risse, G.L.; Springer, S.P.; Wilson, D.H.; and Gazzaniga, M.S. 1977. Cognition and commissurotomy. *Brain* **100**: 87–104.

McKeever, W.F.; Sullivan, K.F.; Ferguson, S.M.; and Rayport, M. 1981. Typical cerebral hemisphere disconnection deficits following corpus callosum section despite sparing of the anterior commissure. *Neuropsycho.* **19**: 745–755.

Milner, B.; Branch, C.; and Rasmussen, T. 1962. Study of short term memory after intracarotid injection of amytal. *Trans. Am. Neurol. Assn.* **87**: 224–226.

Milner, B., and Taylor, L. 1972. Right hemisphere superiority in tactile pattern-recognition after cerebral commissurotomy: evidence for nonverbal memory. *Neuropsycho.* **10**: 1–15.

Noble, J. 1968. Paradoxical interocular transfer of mirror-image discrimination in the optic chiasm sectioned monkey. *Brain Res.* **10**: 127–151.

Pandya, D.N.; Karol, E.A.; and Heilbronn, D. 1971. The topographical distribution of interhemispheric projections in the corpus callosum of the rhesus monkey. *Brain Res.* **32**: 31–43.

Risse, G.; LeDoux, J.E.; Wilson, D.H.; and Gazzaniga, M.S. 1975. The anterior commissure in man: functional variation in a multisensory system. *Neuropsycho.* **16**: 23–31.

Sperry, R.W. 1968. Mental unity following surgical disconnection of the cerebral hemispheres. The Harvey Lecture Series 62, pp: 293–323. New York: Academic Press.

Sperry, R.W. 1974. Lateral specialization in the surgically divided hemispheres. In: The Neurosciences, The Third Study Program, eds. F.O. Schmitt and F.G. Worden. New York: Rockefeller University Press.

Sullivan, M.V., and Hamilton, C.R. 1973. Interocular transfer of reversed and nonreversed discrimination via the anterior commissure in monkeys. *Physiol. Behav.* **10**: 355–359.

Vaughan, D.W., and Peters, A. 1985. Proliferation of thalamic afferents in cerebral cortex altered by callosal deafferentation. *J. Neurocytol.* **14**: 705–716.

Zaidel, D., and Sperry, R.W. 1974. Memory impairment after commissurotomy in man. *Brain* **97**: 263–272.

Zeki, S.M. 1973. Comparison of the cortical degeneration in the visual regions of the temporal lobe of the monkey following section of the anterior commissure and the splenium. *J. Comp. Neurol.* **148**: 167–175.