CURRENT PROBLEMS IN RESEARCH

# Cerebral Organization and Behavior

The split brain behaves in many respects like two separate brains, providing new research possibilities.

R. W. Sperry

The control centers of the brain, including the cortical areas, come in matched pairs, right and left mirror mates, with a complete set to each side. Normally, right and left brain halves are in direct communication through a series of commissures, which are defined as fiber systems that cross the midline to form reciprocal cross-connections between corresponding structures on the right and left sides. The largest of these is the great commissure of the cerebral hemispheres, the corpus callosum, the general proportions of which are indicated in Fig. 1, with reference to the rhesus monkey, its relative size in man being somewhat larger.

The corpus callosum is the most massive by far of any single fiber tract in the brain. It was, therefore, cause for some concern that complete surgical section of the corpus callosum in human patients failed to produce any clear-cut functional impairments detectable even with extensive neurological and psychological testing. The discrepancy between the large size, strategic position, and apparent importance of the corpus callosum on the one hand, and the lack of functional disturbance after its section on the other, posed for many years one of the more intriguing and challenging enigmas of brain function.

During the past seven years or so the old "riddle of the corpus callosum" has been largely resolved, in animal studies in which it has been possible at last to demonstrate definite high-level integrating functions for this structure. More important, perhaps, the results have also opened some promising new approaches to the study of cerebral organization, significantly extending the general scope and analytic possibilities of the brain lesion method and related techniques. The following is a generalized survey of some of these developments.

The animal studies from the beginning have confirmed the earlier clinical observations that complete section of the corpus callosum produces surprisingly little disturbance of ordinary behavior. Callosum-sectioned cats and monkeys are virtually indistinguishable from their normal cagemates under most testing and training conditions. This tends to be the case also with further midline sections added, even to the extent of including all the structures labeled in Fig. 1, plus the cerebellum.

Except for causing partial loss of vision, these midline cuts leave nearly all the sensory inflow, motor outflow, and other brain-stem relations intact, and they leave most of the internal organization of each hemisphere undisturbed. Aside from manifesting an initial tremor and unsteadiness when the cerebellum is bisected, monkeys recovered from such midline surgery show no disabling paralysis, ataxia, or spasticity. There is no forced circling, nor are there other asymmetries. The animals are not overly hyperactive or lethargic. Visceral and other homeostatic functions continue as before. The monkeys remain alert and curious and retain fair-to-good muscular coordination. They perceive, learn, and remember much as normal animals do.

However, if one studies such a "split-brain" monkey more carefully, under special training and testing conditions where the inflow of sensory information to the divided hemispheres can be separately restricted and controlled, one finds that each of the divided hemispheres now has its independent mental sphere or cognitive system—that is, its own independent perceptual, learning, memory, and other mental processes. It is as if each of the separated hemispheres is unaware of what is experienced in the other, as if neither has any direct memory of anything that has gone on in the other subsequent to the midline surgery. In these respects it is as if the animals had two separate brains.

## Functions of the Corpus callosum

Although there were indications in the earlier literature on the corpus callosum that this might be the case—indications that now can be picked out, in retrospect—the first convincing demonstration came from the experiments of Ronald Myers on the role of the corpus callosum in interocular transfer in the cat (*1*, *2*). In brief, he found that with both the optic chiasm and the corpus callosum sectioned (see Fig. 2), a cat is unable to perform with one eye visual pattern discriminations learned with the other eye. When obliged to use the second eye such a cat behaved normally except that it appeared to have a complete amnesia for the visual training experienced with the first eye. It learned to respond, with the second eye, to a given stimulus in a manner exactly the reverse of that in which it had been trained to respond with the first eye, and learned the two responses with equal ease.

In controls in which only the chiasm is cut and the callosum is left intact, discriminations learned with the first eye are readily performed with the second. If the corpus callosum is not cut until after training with the first eye is completed, the learning again transfers, and thereafter the learned discrimination can be performed with either eye (*2*). If, after training with the corpus callosum intact, the cortex on the directly trained side is ablated, one still gets transfer of the habit to the second eye (*3*). In other words, the corpus callosum is shown to be instrumental in laying down a second set of memory traces, or engrams, in the contralateral hemisphere—a mirror-image duplicate or weak carbon copy of the engram on the directly trained side, perhaps, to judge from the symmetry of reciprocal cross-connections in the callosal fiber pattern. These ex-

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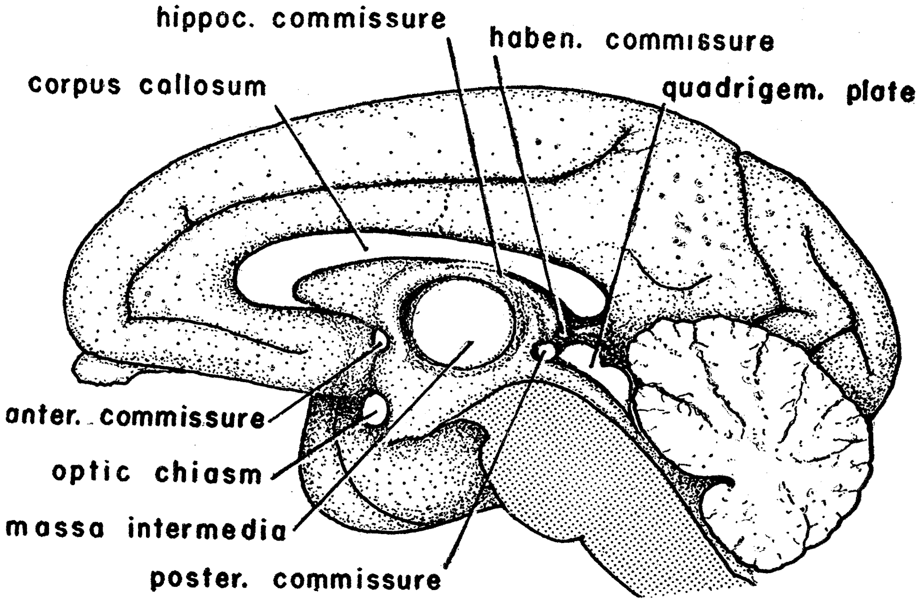
The author is Hixon professor of psychobiology, California Institute of Technology, Pasadena.



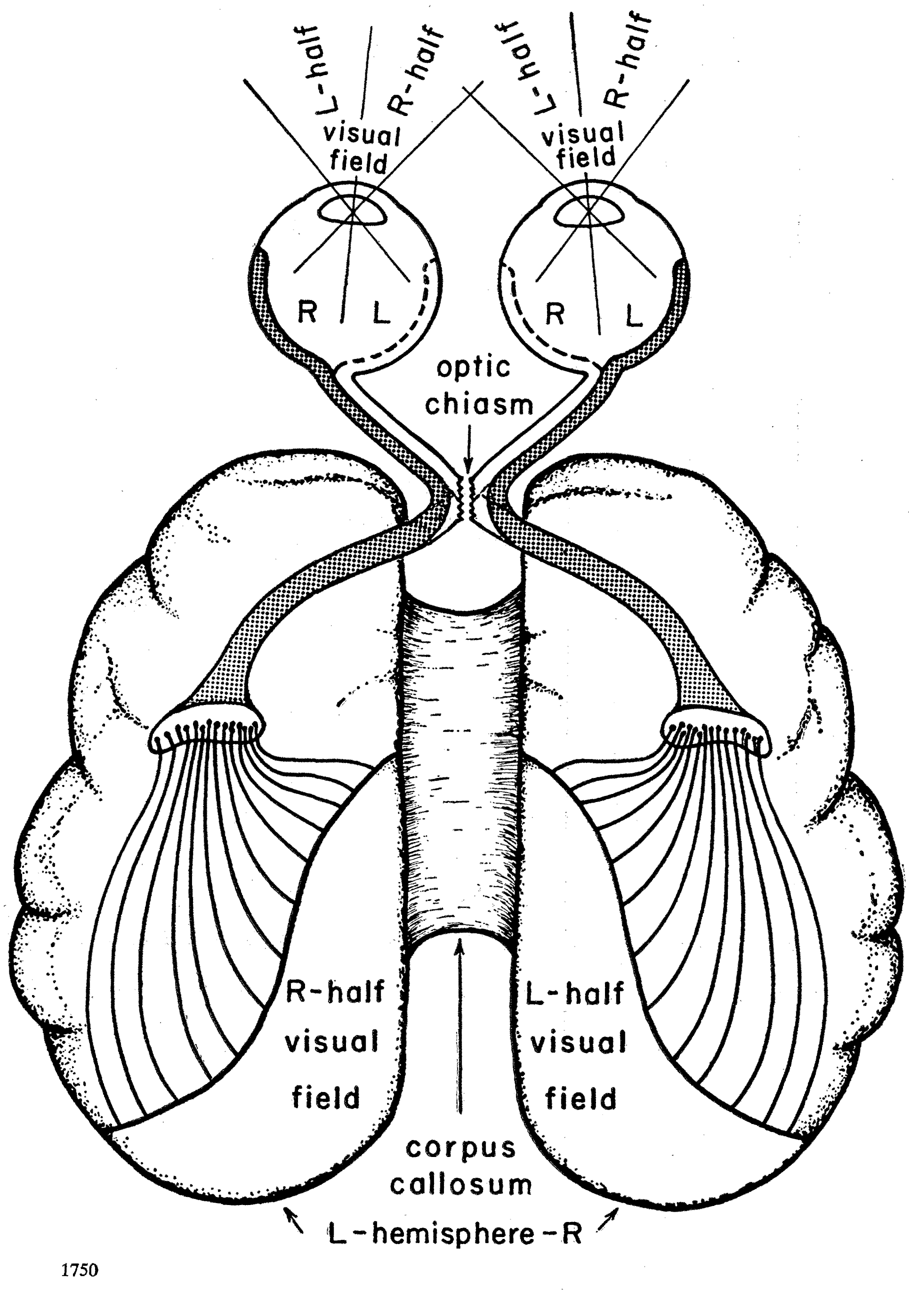


Fig. 1 (top). Midline structures divided in surgical bisection of mammalian brain. Fig. 2 (bottom). Effect of sectioning crossed fibers in optic chiasm. Half-field overlap from contralateral eye is eliminated; this restricts visual inflow to the homolateral hemisphere.

periments were carried out in apparatus of the type shown in Fig. 3, developed earlier for testing and quantifying refined pattern discrimination in the cat.

Because the memory trace or engram has always been extremely elusive and difficult to pin down or localize by the brain-lesion method, this evidence that it could be confined to one hemisphere by cutting the corpus callosum was not to be accepted without question. Might it merely be, for example, that with chiasm and callosum both sectioned, the hemisphere on the seeing side is more dominant than usual and drains the attention and learning processes off to that side? In partial answer, we find that very large cortical ablations, such as that shown in Fig. 4, that markedly depress pattern vision on the same side, still do not force into the contralateral hemisphere the learning and memory of pattern discriminations performed through the homolateral eye (*4, 5*). Also, when we compared the learning curves for the first and second eye on a statistical basis, there was no evidence that learning with the second eye was benefited by the previous experience with the first (*6*).

In a pedal-pressing apparatus, developed largely by Stamm (see Fig. 5), we were able to demonstrate that the same kind of functional independence prevails in the separated hemispheres with respect to somesthetic learning and memory involving touch and pressure on the surface of the forepaw (*7*). Not only sensory discriminations of the kind illustrated in Fig. 5 but also the simple motor patterns acquired in learning to operate the pedals smoothly were transferred to the second paw in normal cats but were not transferred in the callosum-sectioned subjects. Again, statistical comparison of the learning curves for the first and second paws indicated complete absence of any transfer of learning from one to the other hemisphere. Learning a reverse response with the second paw proceeded as easily in these subjects as relearning the original response. Further, the learning of reversed or diametrically opposed discriminations by right and left paws was carried out simultaneously by the split-brain cats when right and left limbs were alternated every few trials during the training, and still with no apparent interference between the conflicting habits (*8*).

The findings with respect to visual learning and memory have been confirmed in the main for the monkey as well, with extension to discrimination of colored and three-dimensional objects (*9–11*). Because the monkey is much less inclined than the cat to be cooperative about wearing an eye patch, a training box was devised like that sketched roughly in Fig. 6, which has one viewing slot accessible only to the left eye and another accessible only to the right eye, each of which can be opened or closed from trial to trial. A sliding arm panel controls the use of the arms and permits the pairing of either eye with either hand from trial to trial.

This has the advantage over the use of an eye patch for monocular testing and training in that one can easily switch from one eye to the other, giving a few trials to the right eye, then a few to the left, and so on. If this is done while the monkey is learning reversed discriminations with the separate eyes, one can show that while one hemisphere is in the process of learning, for example, to avoid crosses and select circles, the other hemisphere can be learning to do exactly the reverse. The learning curves for the two conflicting habits then rise concurrently in parallel in the two hemispheres with no apparent interference. The normal brain does not of course operate in this way—nor does that of controls with only the optic chiasm cut, nor even that of controls with section of chiasm plus anterior commissure plus the anterior half of the corpus callosum.

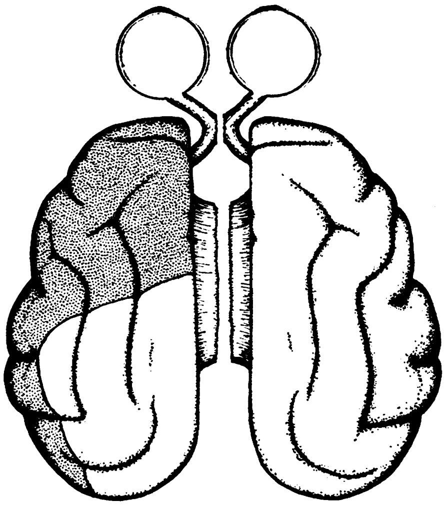


Fig. 4. Extent of the extravisual cortex ablated from the seeing hemisphere of a split-brain cat (*4*).

Without going further into studies dealing with the properties of the callosum, it may be said that several different functions for this structure are now recognized. First, and perhaps most significant, is that of the laying down of duplicate engrams in the contralateral hemisphere, as outlined above. In this the callosum serves to keep each hemisphere up to date on what's new in the other; it tends to equate the two hemispheres for those new organizational properties added through learning. It can also be shown that where learning has been deliberately restricted by experimental procedure to one hemisphere, with the corpus callosum left intact, the callosum can then be utilized by the uneducated hemisphere to tap the engram systems of the trained side (*3*). The callosum also aids in certain types of bilateral sensory-sensory and sensory-motor integration, as for example in visual use of either hand across the vertical midline of the visual field (*8, 12, 13*). A general excitatory tonic effect can also be demonstrated in the unilateral blindness of one or two weeks' duration produced by section of the callosum in animals with a surgically isolated visual cortex (*8*). Qualifications of the above properties and special problems relate to the development of language and its lateralized dominance in the human brain, about which little can be said at present. With further analysis it may prove that some of these diverse functions derive from basically the same mechanism.

Fig. 3. Visual training apparatus. The cat, placed in the darkened box, obtains a food reward by pushing on the correct one of two translucent patterns interchanged in doors at the end of the box. Inset shows enlargement of the cat wearing the eye patch devised by Myers. Made of rubber, it is simply turned inside out to cover the other eye.

## Simultaneous Learning Processes

After it had been found that the split-brain monkey is able to learn reverse discriminations concurrently with the separated hemispheres (*10, 11*), the question arose as to whether the two hemispheres could learn their reverse tasks simultaneously. Instead of alternating between right and left eye during the training, what happens if

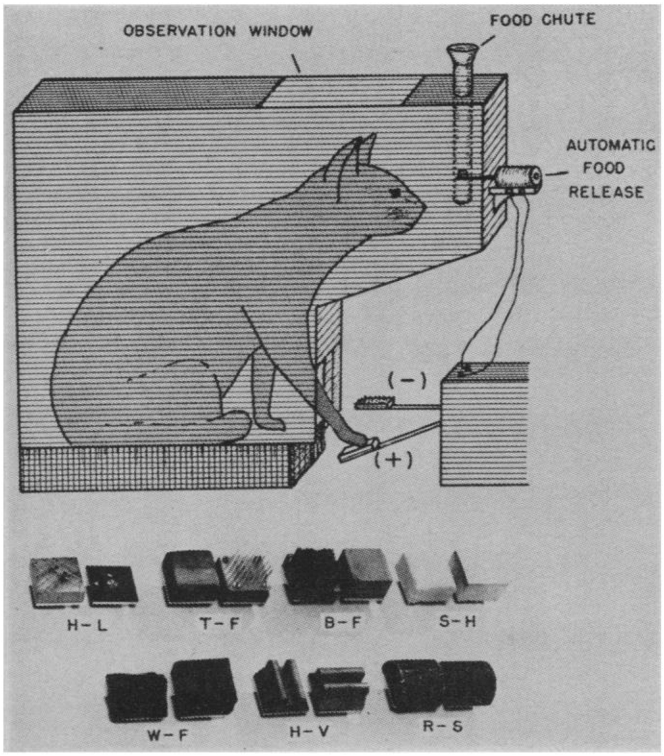


Fig. 5. Simplified diagram of the pedal-pressing apparatus for training in tactile discrimination. Pairs of interchangeable pedal mountings are shown at bottom (*7*, *15*).

both eyes are left open and each trial feeds conflicting information back through the two eyes at the same time? In other words, does the split-brain animal, in order to learn, have to attend to the information entering one hemisphere at a time? Or does it have two separate attention processes, both able to operate simultaneously, handling the diverse sets of information and filing them in two separate memory systems capable of independent recall?

The question has been answered in part by Trevarthen (*13*), with an apparatus incorporating polarized light filters to make the two stimulus objects to be discriminated appear simultaneously different to the two eyes. As explained in Fig. 7, what looks to one hemisphere, for example, to be a circle on the left and a cross on the right is made to look the reverse to the other hemisphere. While one hemisphere observes that the pushing of circles but not crosses is rewarded, the other eye and brain discover, by the same process, the converse—that is, that the pushing of crosses is rewarded and not circles. Any kind of projectable two-dimensional figure, design, or picture may be used, with or without color. Learning is allowed to proceed with both eyes open until the learning curve reaches the 90-percent level. The eyes are then tested individually to find out if the learning has occurred in one or in both hemispheres, and to what degree.

Although the results vary, as expected, Trevarthen finds that during the time required for the dominant hemisphere to learn its problem, the other also, in the majority of cases, has been learning its own reverse problem in part or in full. In some instances, both hemispheres fully learn their separate problems simultaneously. In other words, in approximately the length of time and number of trials required by an ordinary-brained monkey to learn one discrimination problem, these altered, twin-brain monkeys are able to master two such problems. This raises some questions with regard to learning theory and the role in learning of attention, motivation, mental and motor set, and the like. Are all such components of the learning mechanism doubled in these brains, or are some perhaps bifurcate in form, with a common brain-stem element and qualitatively different cerebral prongs? The implications are intriguing and suggest further variations on the initial experiment.

The question of mental conflict is frequently raised in this connection: What happens when one hemisphere has been trained to do one thing and the other trained to do just the opposite, and the animal is given a free choice to perform either or both? With two separate volitional systems inside the same skull, each wanting its own way and each, by training, wanting the opposite of the other, does each of these thinking entities try to decide for itself?

When such a test is run—by rotating one of the eye filters 90° for example—one sees little evidence of internal conflict, apart from, perhaps, a little hesitance (*14*). By and large, the monkey starts selecting circles consistently or crosses consistently, and it may shift from one to a series of the other, thereby telling us which hemisphere is being used at the moment. These shifts are controllable in part by forcing the use of one or the other hand, which then tends to bring into play the contralateral hemisphere, though this latter correlation is not fixed or rigorous. Apparently when a hemisphere once gains the ascendancy, the lower centers tend to throw their full allegiance to this side. Anything coming down from the other hemisphere that is incompatible or out of line with the going activity of the dominant control is automatically inhibited. This is just another example of the general rule that the patterning of excitation in the central nervous system is an either-or kind of thing. Either one unified pattern or another prevails; seldom is there a confused mixture.

The split-brain cat or monkey is thus in many respects an animal with two separate brains that may be used either together or in alternation. With all pairs of major suprasegmental controls bisected, there is no way for the higher-level integration of one hemisphere to reach and influence that of the other except indirectly through the lower brain stem outflow (Fig. 8). By the time the data processing has reached this stage it already is in such form that any recurrent feedback into the opposite hemisphere carries little of the original content.

## Bilateral Hegemony

Each of the twin half brains with its full complement of control centers has much bilateral hegemony over the brain stem and spinal cord and is thus capable, to a large extent, of taking over and governing the total behavior of the body. The cat especially, but also the monkey and even man, with one hemisphere gone manages to get along fairly well, and most central nervous functions are retained. With both hemispheres present, in the split condition, even though one be strongly dominant or in exclusive control of the going higher-level activities, the other presumably continues to contribute much to generalized, background function. Under most ordinary conditions the higher activities also are bound to have much in common. Only in special training and testing circumstances does the double mental control become apparent. The simultaneous use of the two divided hemispheres presents little problem so long as there is unity in the lower centers. Given lower-level harmony, it doesn't matter, as seen above, whether the higher centers function similarly or in direct contradiction.

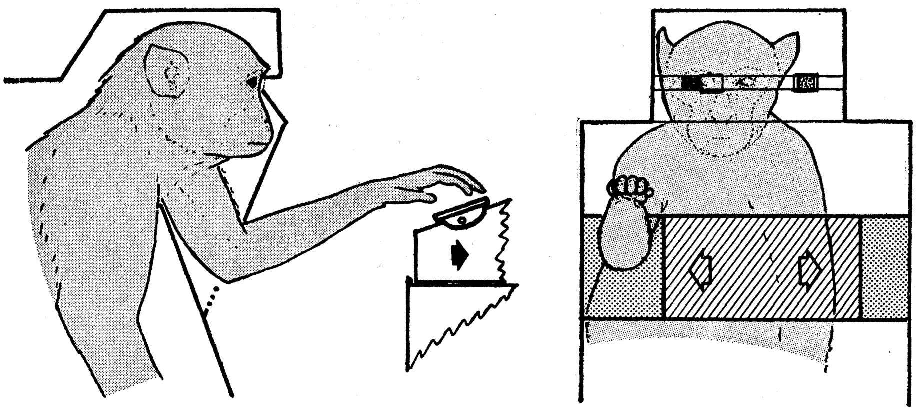


Fig. 6. Profile and front-view outline sketches of a training box for controlling eye-use and eye-hand associations in a monkey.

There is much yet to be learned in following up studies, like the foregoing, that deal directly with the functional properties of the bisected brain, split to different levels and with various incomplete patterns and combinations of commissurotomy. The split brain may also be used to advantage as a basic preparation for attacking other kinds of questions not directly related to problems of commissure function. With the brain bisected, it becomes possible to direct one's ablations, tests, and other analytic procedures to a single one of the hemispheres, leaving the "spare" hemisphere for the use of the animal. In addition to the obvious benefit to the animal over the usual bilateral invasion, there are a number of significant technical advantages in working on the half brain instead of the whole brain. It is important to remember in this connection that the half brain is, in a sense, pretty much a whole brain in that it contains a complete set of cerebral integrating centers and all their interrelations. That is, practically the entire pattern and most of the problems of cerebral organization are there for the unraveling within the half brain.

### Advantages for Experimentation

One obvious advantage of the split-brain preparation lies in the factor of built-in controls within the spare hemisphere, controls for all sorts of experiments ranging from short-term studies on innate organization to studies on the long-term effects of early experience on adult behavior. These controls are not only of the homozygous, identical-twin, type but are equated also for almost all experientially derived organization implanted up to the time of splitting. The control hemisphere is fairly well balanced for additions thereafter, also, except for performances that have been deliberately lateralized. These contralateral cerebral controls

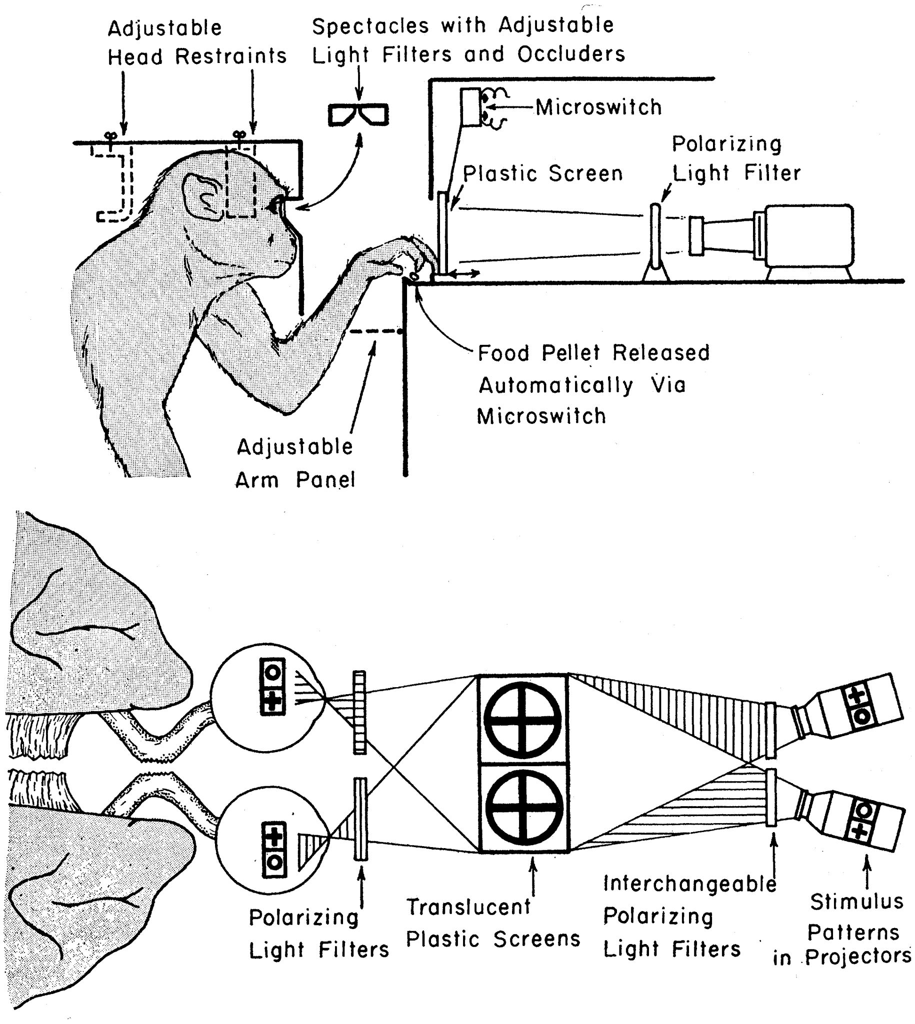
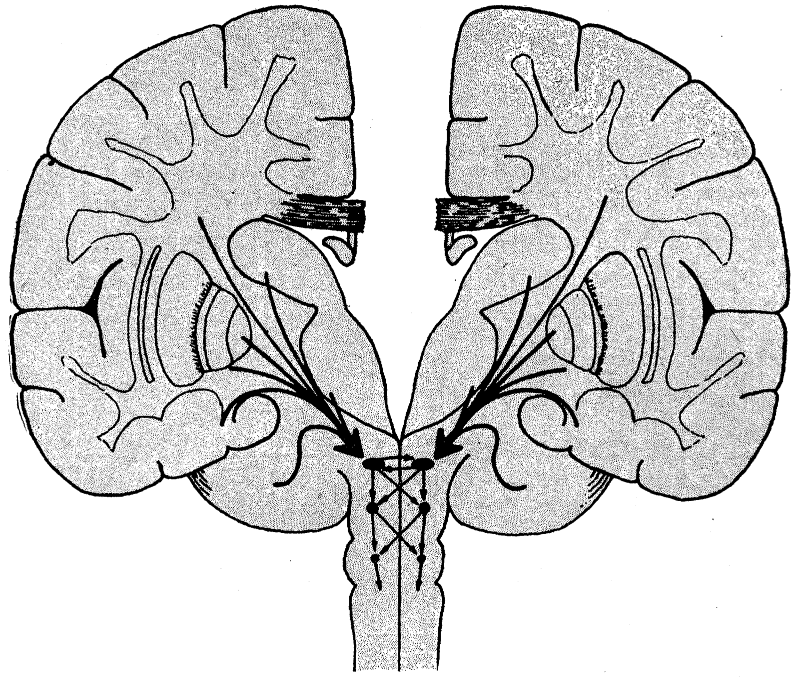


Fig. 7. Profile and schematic diagram of apparatus for testing perceptual conflict in a split-brain monkey (*13*).



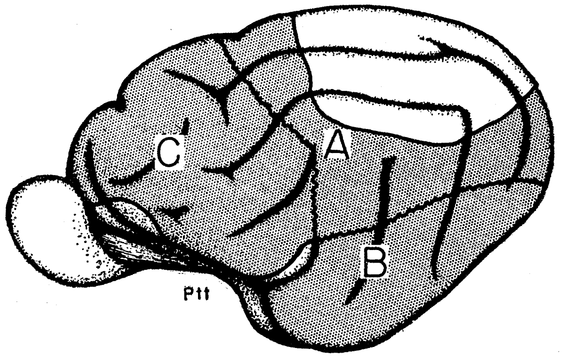


Fig. 8 (left). Schematic diagram to aid in visualizing hegemony of the hemispheres of the split brain over lower centers. Fig. 9 (above). Surgical isolation of central visual cortex in test hemisphere: extravisual cortex removed in three successive operations, *A*, *B*, and *C*, to determine separate functional contributions (*4*).

are thus of a quality almost impossible to obtain by using different animals.

More important is the possibility of extending the surgical analysis within the experimental hemisphere of the split brain far beyond what was possible when the lesions had to be made bilaterally. It has been a long-standing rule in brain-lesion studies of learning and memory that the cortical lesions must be made on both sides to obtain a genuine loss. Unilateral removals are not critical, ordinarily because the functions involved can be handled by the remaining integrating center on the opposite side.

With the split-brain approach it becomes possible to investigate structures like the caudate nucleus, the primary motor cortex, and others, the bilateral ablation of which produces incapacitating or other secondary undesirable effects that act to obscure or confuse possible contributions in other activities. Each brain center tends to be involved in a whole spectrum of different functions. In many cases only the basic impairments can be inferred after bilateral removals, the others being hidden or untestable in the presence of the former.

For the same reasons, with the split-brain approach much larger cortical ablations can be made, even to the extreme of removing most of the cortex and saving only isolated functional remnants—the converse of the usual procedure. We isolated the visual cortex of the cat in this way (see Fig. 9) and found that the primary visual cortex, without aid from other cortical areas, is incapable of sustaining visual functions beyond a bare minimum. A next step is to go back and restore in other animals different portions of the cortex removed in these subjects to determine the respective contributions of each portion to visual learning and memory.

A very different result followed similar surgical isolation of the frontal cortex that includes the somatic sensory and motor areas. In this case the isolated remnant was found to be capable of mediating excellent learning and memory of new somesthetic discrimination habits performed in the pedal-pressing apparatus shown in Fig. 5 (*15*). The ever-elusive engrams or memory traces for these new habits would seem to have been at least cornered within the local cortical area illustrated in Fig. 10. It should be possible to further localize the engram by paring away additional parts of the remaining cortical remnant and also by adding deep electrolytic lesions to test the functional contributions of various subcortical centers that remain undegenerated. This somatic island preparation thus furnishes a promising means of determining the critical minimum cerebral apparatus essential for discrimination learning and memory in the mammalian brain. With one hemisphere preserved intact to maintain background and lower-level activity, it becomes feasible, in the experimental hemisphere, to undertake almost complete surgical dissection and analysis as far as function is concerned. About the only limitations that remain are those imposed by surgical technique, particularly that relating to the preservation of circulation.

To further assure, in these studies of somesthetic discrimination habits, that the habits were not being learned and mediated by the contralateral somatic cortex, a complementary removal of the corresponding area was made on the opposite side. The feasibility of thus adding complementary lesion patterns in the intact hemisphere of the split brain offers further possibilities for the analysis of functional relationships—possibilities not available, of course, where the removals have to be made bilaterally.

There are other promising angles in investigations of this "somatic island preparation." For example, it is possible to test the proven pedal-pressing learning capacity of this cortical area with visual or auditory instead of tactile stimuli—in other words, to answer the questions: Could such a cat learn to press a pedal that activates the correct one of two different tone patterns, or the correct one of two different visual patterns? If not, could it then do so if an isolated patch of auditory or visual cortex were left on the same side as the somatic island? If not, again, what kind of inter- and intrahemispheric bridges and connections are needed to satisfy the learning and memory requirements?

## Visuomotor Coordination

Figure 11 illustrates a type of complementary lesion preparation we have been using, with a number of variations, to determine the neural pathways used in visuomotor coordination. The experimental question here was: Can visual information that is processed in one hemisphere serve as a guide for limb responses for which the cortical centers lie in the opposite hemisphere and are surgically separated from the visual inflow?

Cats, so prepared, and also monkeys that have undergone similar surgery, are able to use vision to direct the homolateral forelimb and to aim it with near-normal accuracy at both stationary and moving objects (*16*). Presumably the speed and accuracy might be shown to be somewhat below that in control animals using the other limb, governed from the same hemisphere, if sufficiently delicate tests were available. However, the performance is still there and not markedly impaired. Where the visuomotor guidance depends on unilaterally learned visual discriminations in split-brain cats and monkeys, either forelimb can still be used without difficulty both during learning and in retention tests (*11*, *17*). The neural pathways for these volitional eye-hand coordinations have yet to be determined.

Somewhat in contradiction to the observations that the split-brain monkey or cat readily pairs either eye with either "hand" is a more recent report (*12*) that visuomotor coordination is markedly disrupted under these conditions, to the extent even that prolonged relearning is required, much like that demanded after unilateral removal of the precentral motor cortex. This observation, though yet unexplained, may be a reflection of particular testing conditions that unduly facilitate the use of the visuomotor system for the contralateral limb.

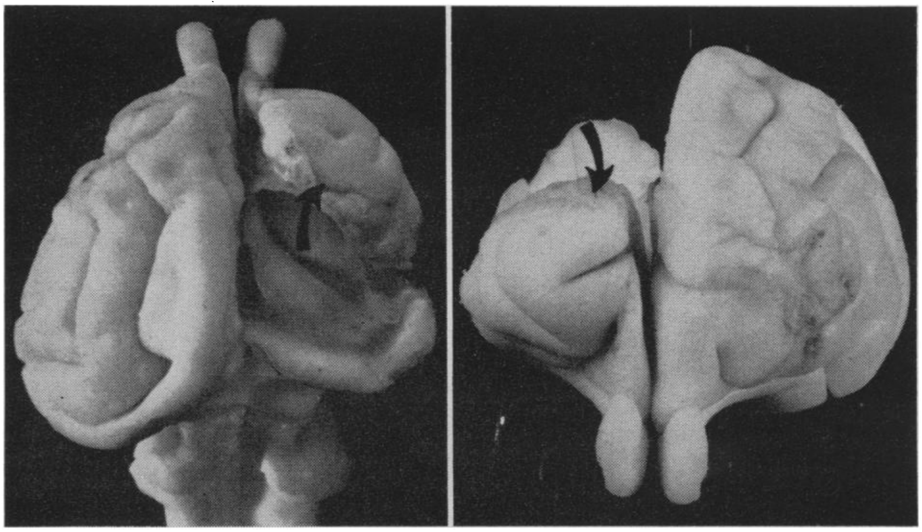


Fig. 10. Top and front views of somatic island preparation with a small complementary ablation in the control hemisphere. Engrams for tactile-discrimination learning appear to be localized within the cortical remnant of the right hemisphere (*15*).

In any case, the expected preference for the favored arm—that is, for the arm governed from the hemisphere that receives the visual inflow—is found and can be demonstrated in more delicate testing conditions such as those obtainable in the training apparatus described above (Figs. 6 and 7), where the monkey is able to use either arm with either eye. This arm preference is easily overcome, however, in a matter of hours in most cases, and may be lacking from the start in animals in which the homolateral arm is strongly dominant, either naturally or as a result of experience in a given testing situation. Trevarthen (*13*) describes distinct differences in the learning curves obtained in pairing the homolateral and contralateral arms with a given eye that indicate basic differences in the neural mechanisms for the two combinations. With the homolateral arm, the reaction time tends to be longer, and the learning slower and more erratic and unstable. The effect is enhanced in monkeys with deeper splits that include the cerebellum.

Surgical preparations similar to that illustrated in Fig. 11 have been used for study of the old and still puzzling problem of the neural pathways involved in the conditioned response. In this case a visual signal is used as the conditioning stimulus to establish a conditioned flexion of the forelimb, the cortical centers for which have been left in the opposite hemisphere. Efforts are now under way to eliminate successively the remaining undegenerated thalamic, midbrain, and other subcortical centers until the critical associations and pathways for the conditioned reflex are delineated (*18*). At the present stage of this program the conditioned forelimb flexion in response to a flashing light signal has been found to survive the following: section of left optic tract; ablation of left occipital (visual) cortex; near-total removal of neocortex from the right hemisphere; midline section of corpus callosum plus the anterior, posterior, hippocampal, and habenular commissures; and midline section of the massa intermedia and the quadrigeminal plate—produced stepwise in the same animal.

Another application of the split-brain approach is indicated in Fig. 12. The behavior under analysis in this case is a kind of sensory-sensory association in which the monkey is trained to perform a discrimination problem that requires in each trial an association of visual plus tactile stimuli. By controlling the hand and the eye used, and thereby the cortical receptor centers involved, it is possible to test intra- and interhemispheric integration with and without different parts of the corpus callosum and then with various types of separating cuts and ablations, to analyze the kind of neural mechanism and associations that mediate this type of perceptual integration.

It was something of a surprise to find that the split-brain monkey was still able to perform the visuotactile integration with the tactile stimuli presumably restricted to the hemisphere opposite that of the visual inflow. In addition to making the animal use the proper hand, the somesthetic cortex was ablated on the side of the visual inflow. We first used color-plus-weight (largely proprioceptive) discriminations (*10*,

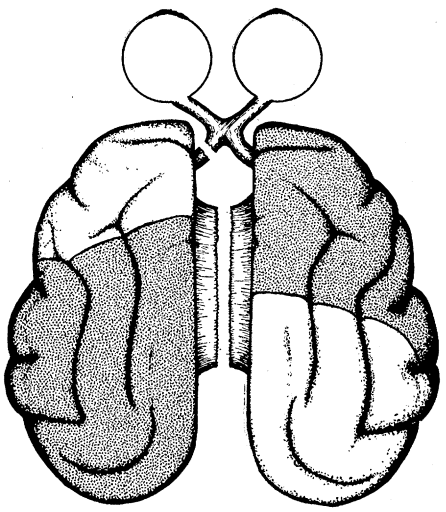


Fig. 11. Basic complementary lesion pattern used with variations for analyzing conditioned response learning and visuomotor coordination.

*11*) and are now repeating the study with black-and-white patterns and cutaneous rough-smooth stimuli. In the latter study the monkey is required to pull the rougher of two levers when they are presented behind one visual pattern, and the smoother of the two when they are similarly presented in back of another visual pattern, the two visual patterns being black and white and equated for brightness. This latter performance ability is retained even after additional midline sections have been made (see Fig. 12) that include the habenular and posterior commissures, the massa intermedia, and the quadrigeminal plate, in addition to the corpus callosum and the anterior and hippocampal commissures. The removal of the arm area of the tactile cortex on the side of the visual input (Fig. 12) abolishes performance with the affected hand for several weeks but fails to disrupt performance with the hand governed from the opposite hemisphere. This puzzling result is under further investigation, along with similar cross-integration effects that have appeared recently in studies of visuo-visual conditional discriminations. The surgical analysis promises to be easier in the latter because the input pathways for vision are less diffuse and more easily confined than are those for touch.

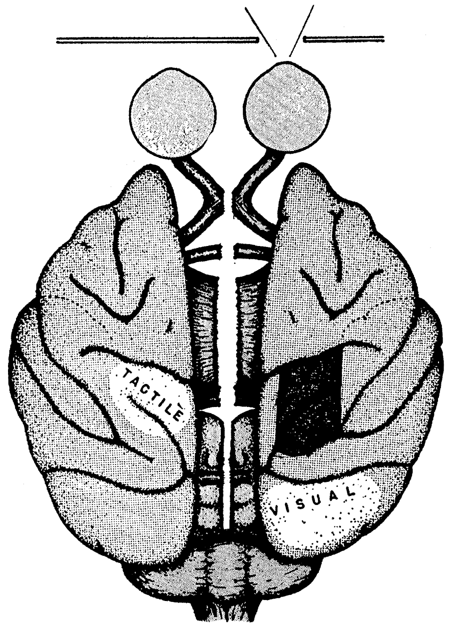


Fig. 12 Stylized representation of monkey-brain hemispheres and underlying midline structures, split through the quadrigeminal plate to the level of the trochlear nerve (*11*), as prepared for a study of visuotactile integration.

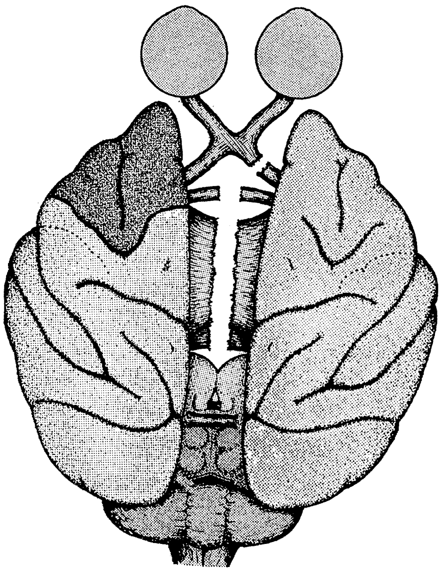


Fig. 13. A split brain, as prepared for a study of prefrontal lobe syndrome (*18*).

## Application to Old Problems

A simple application of the split-brain approach to an old problem is illustrated in Fig. 13. It has been known for many years that bilateral but not unilateral removal of the prefrontal lobes impairs the performance of delayed response in the rhesus monkey. Whether this impairment is indicative of a genuine function of this portion of the brain has been uncertain, in part because the bilateral removals tend to produce also hypermotility and distractibility. It has been found that the impairment, unaccompanied by hyperactivity and distractibility is produced by unilateral lesion in the split-brain animal (*5, 19*). The unilateral approach thus yields new information regarding the nature of the syndrome and its intrahemispheric involvement; also it permits further analysis through partial removals of the corpus callosum in combination with complementary lesion patterns—procedures not feasible with bilateral ablation.

The split-brain approach has been applied also to the classic Klüver-Bucy temporal lobe syndrome and some of its subsequent fractionations (*20*). Bilateral ablation of the temporal lobes in monkeys produces impairments in visual perception, a change in temperament in the direction of tameness, hypersexuality, and certain oral and "stimulus bound" tendencies. Observations to date show that most features of the syndrome are demonstrable after unilateral ablation in split preparations (*21–23*), and the results bring additional insight regarding the underlying neural mechanism. Similarly, a great many of the older brain-lesion studies can be repeated to advantage in the bisected brain, with a gain in information and the possibility of advancing the analysis.

## Transfer across the Midplane

With the growing application of brain bisection to a wide variety of problems, it becomes increasingly important to have background information about the functional properties of the split brain in all its various forms—that is, with the midline sections carried to different levels and with different patterns of commissurotomy and ablation. Particularly critical are questions relating to the leakage or transfer of various functions across the midplane. In this connection, observations bearing on the intermanual transfer of learning (*10, 24*) have not been entirely consistent in primates. In our own experience, section of the cerebral commissures may lead to failure of intermanual transfer, but this is not true in all cases nor under all conditions. We have seen intermanual transfer of tactile discriminations in chiasm-callosum-sectioned monkeys that were already experienced in using either hand with either eye and had been trained with pairs of objects that were left in sight because they were distinguishable only by touch, not by vision, the one being harder or heavier or looser than its mate, and this being discernible only upon palpation. Also, we find that an ablation of the somatosensory arm cortex roughly like that shown in Fig. 12 will induce transfer in split-brain monkeys that had failed to exhibit transfer prior to the cortical ablation (*25*). The interpretation of this latter finding is complicated at present by the fact that when the monkeys are trained to reverse the discrimination response with the second hand, this reversal training consistently fails to transfer back again to the first hand.

Certain types of visual discrimination learning also have been found to be subject to interocular transfer after section of all forebrain commissures plus the optic chiasm. This has been shown for obvious brightness discriminations in cats, whereas the more difficult near-threshold discriminations fail to transfer (*26*). Interocular transfer of easy color and brightness discriminations and possibility of very simple pattern discriminations occurs similarly in the monkey, according to Trevarthen (*14*). All of these transferable aspects of visual learning may be elements of visual inflow or learning that cross at the midbrain level. Extension of the tests for color, brightness, and simple pattern to several monkeys having deeper midline sections that include the posterior commissure and rostral half of the quadrigeminal plate (see Fig. 1), plus the cerebellum in one case, show so far a lack of memory transfer for all except simple intensity discriminations.

Evidence is still sketchy regarding the extent to which the divided hemispheres can function independently with respect to emotion. Incidental observations made in the course of training and testing suggest that milder aspects of emotional attitude and temperament, like stubbornness and sulkiness, can be confined to one side (*10, 11*). By employing deliberate procedures for inducing experimental neurosis, it might thus be possible to make one of the separated hemispheres "neurotic" and leave the other normal. The "taming effect" of unilateral deep temporal lobe ablation is much enhanced and lateralized in the split-brain monkey, according to Downer (*21*) and others (*23*). Such animals act normally fearful, or ferocious when using the eye connected to the intact hemisphere, but promptly become more tame, placid, and generally less "touchy" when the lesion hemisphere is made dominant by switching the visual occluder to the other eye. The placement of complementary lesions in right and left hemispheres that produce opposed emotional effects has yet to be explored.

## Experimental Possibilities

By the use of positive and negative reinforcement through implanted electrodes under remote control, the development of different or opposed preferences in right and left brain could presumably be extended to animate objects and social relationships, with some interesting consequences. The so-called *encephale isolée* and *cerveau isolé* preparations of Bremer and others (*27*) have found considerable use in physiology, and it should not be too difficult to go further and, by adding hemisections of the brain stem to the midline surgery, prepare isolated half brains of different forms and with different kinds and degrees of isolation that would offer significant advantages over the separated whole brain. The isolated half brain could be studied over a long period in the animal in vivo, in the brain's natural habitat, under normal biochemical conditions, and after recovery from the prolonged depression of surgical cerebral shock. To what extent might such long-isolated (or partially isolated) half brains regain wake-sleep states and consciousness and be capable of learning, remembering, feeling emotion, and the like? Where behavioral output is excluded, electrophysiological indications of some of these capabilities could be obtained with implanted electrodes and conditioning techniques.

By combining various ablations and transections like those described above with more localized lesions produced in subcortical nuclei with the stereotaxic apparatus, it is possible today, with methods now available, to attain a fairly extensive surgical dissection of the mammalian brain and to set up a large variety of combinations and permutations of cerebral centers and connecting pathways in animal subjects for long-term functional testing and analysis. Combine with this the analytic potentialities of the chronically implanted electrode for recording, stimulating, and self-stimulating in free-moving, unanesthetized animals, plus the new automated training and programming techniques, along with other technological advances, and those of us working in brain research find ourselves today, as never before, surrounded by seemingly endless possibilities just waiting to be explored (*28*).

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