"Split-Brain Approach to Learning Problems"

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Split-Brain Approach to Learning Problems

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THIS CHAPTER deals with the problems of learning and memory at a level somewhere above that of the brain cell and below that of the whole organism and behavior. The approach might be said to attack learning at the cerebral network level, with an ultimate aim of "breaking the brain code" and understanding the inner "language of the hemispheres." For reasons spelled out elsewhere,[1-3] we have gambled our research efforts largely on the view that the major mysteries in learning and memory, and in the higher functions of the brain in general, lie at this level; i.e., the level of cerebral circuit organization. This view holds that a single brain cell in itself probably does not perceive, think, or emote, nor imagine, decide, reason, nor perform other of the mental functions for which brains are particularly noted, and that a single brain cell probably does not learn or remember anything very elegant. Most or all of these special higher mental or psychic properties of brains are speculatively assumed, in this view,[1-4] to be properties of highly organized circuitry in action, the analysis of which must be tackled accordingly.

To be able to correlate the variables we know in conscious experience with the unknown variables of brain excitation constitutes a primary, though somewhat remote, guiding goal for most of our work in psychobiology. How does the brain code different colors, sounds, flavors, and whole images of the outside world into patterns of cerebral excitation? In brief, it is the problem of the cerebral correlates of subjective experience. As a specific example, take the scene that I can see outside my window. It includes a parked car, a moving taxi, two trees, and a pedestrian. What can we say now about the nature of the inside visual image within the brain? Whether our sample visual image be an initial perception, a particularly vivid visual recall, or exists merely in the form of an illusion, a dream, or a hallucination, there presumably is nothing within the brain that is even remotely similar to the three-dimensional outside scene. The whole scene is somehow re-created, recast, transformed, or coded into the language of the hemispheres. The outside scene, that is, is represented or transformed into a spatio-temporal pattern of cerebral excitation.

The basis of this cerebral representation or brain code still completely eludes us. We assume, of course, that it probably is constructed or constituted of neuronal and perhaps glial activity; that is, of nerve impulses and associated physiological and biochemical events. But this kind of knowledge is somewhat analogous to knowing the chemical constituents of the ink and paper that have been used to print a particular message in an unknown language. When it comes to the meaningful aspects of the brain process, i.e., the symbols, syntax, and logical design of the code used by the brain to build our sample visual scene and other conscious experience, we are still very much in the dark.

Along with various subsidiary codes in the brain, there is also another basic code that is directly and necessarily involved in learning—the memory trace or engram code. The general brain code proper, by which the outside world is brought inside, consists of active, dynamic excitation patterns having a temporal dimension. By contrast, the engrams or memory traces have a static or spatial organization that makes them independent of the dynamic factors and able to survive periods like those of deep anesthesia, electroconvulsive shock, and cerebral anoxia, in which all dynamic organization fades out or is violently disrupted. The memory traces may lie dormant or inactive for years before the particular experience involved is recalled into activity.

Just as the inside brain process for a visual image differs greatly from the actual outside scene represented, so also must memory traces for reactivating that same brain process differ greatly from the active process itself. Especially, there is reason to think that the engram is highly abbreviated. Presumably a few small, critical changes in the cerebral structure are sufficient to steer the over-all dynamic pattern into a specific form, given an appropriate background or context of cerebral activity. In the calling up of a particular memory, the engram and the active process may be thought of as cofunctions that are mutually dependent in most cases.[5] Some behavior patterns are so thoroughly ingrained and completely supported by engrams that they can be activated in nearly any context. Most memories have particular associative contexts that are necessary for recall.

Accordingly, it would seem a logical necessity that, in

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order to analyze the engram code for memory, we must first understand something about the organizational principles or language of those cerebral dynamics in terms of which the engram traces are laid down. It was in this sense that we once described the memory problem as the quest for the secret code of an unknown code for conscious experience, itself a will-o'-the-wisp—a situation with possibilities for confusion, unlimited.[1]

In the problem of learning we must deal, of course, with both of the above two codes, the dynamic and the static. For convenience, we can lump these and related aspects of brain function with which we shall be concerned under the general category of problems in cerebral organization.

Split-brain approach

During the past dozen years or so we have become increasingly convinced that a handy way to approach many aspects of the above problems in cerebral organization is to start by dividing the brain down the middle into its right and left halves.[6,7] From there one may go on to study problems of crossed integration, or integration problems within either of the separated hemispheres, or combinations of these. The vertebrate brain, you recall, is a bilaterally symmetrical organ, and the two hemispheres of the mammalian brain are already fairly separate anatomically in the natural state except for some cross bridges of connecting fibers, the cerebral commissures. It is quite possible to section the commissures surgically either in their entirety or in selected portions, as desired. The complete section of these cross-connecting cables leaves two separate, functional half-brains, each containing for analysis most of the main mental properties of a whole brain. Various experimental advantages are found in working with the two hemispheres separately instead of together as a single organ.[6,8] The bisected preparation provides, for example, superior controls of a quality not obtainable in any other way. There are also a larger variety of circuit combinations for experimental analysis. Further, the possibilities for analysis by surgical elimination of selected centers and cortical areas are greatly extended when the removals can be restricted to a single hemisphere, leaving the corresponding centers intact on the opposite side to maintain background functions.

To help visualize the situation, a schematic view of the bisected monkey brain is shown in Figure 1. Essentially, the commissurotomy leaves two cerebral hemispheres sitting on top of a single brain stem. All direct means of cross communication may be eliminated, or selected parts of the cross-connecting system may be left intact for specific study. Section of the corpus callosum in its entirety plus the anterior commissure eliminates cross communication for the neocortex, which constitutes the great bulk of the cerebral cortex of primates. The optic chiasm is also usually sectioned in experimental studies that involve vision, thus restricting the visual input from each eye to the one hemisphere on the same side of the brain. Each eye thus transmits the contralateral half of the visual field to its respective hemisphere; retinal rivalry and steroscopic vision are eliminated.

It has become fairly routine to carry out these surgical divisions down through the roof of the midbrain, leaving most of the midbrain tegmentum and all structures below intact, and sparing the decussation of the trochlear nerve, which in the monkey is easily seen and avoided. For completeness, the front tip of the tegmentum may also be divided to section the supramammillary commissure. Brain bisection carried to the extent indicated above (Figure 2) is only mildly incapacitating, at least in terms of laboratory existence. Following recovery, monkeys so operated upon are hardly distinguishable from normal animals in their ordinary laboratory behavior.

Marked functional symptoms begin to appear as brain bisection is extended deeper into the tegmentum, pons, and cerebellum. Division of the cerebellum is easily added to the above, but it may leave the monkey shaky and unsteady on its feet for some months afterward, depending on how symmetric and central the section. We have carried out a few deeper sections, extending down through the pons and below, but only on an exploratory basis thus far, and in studies that were aimed at other problems. The minimal symptoms produced by such clean, deep bisections under optimal conditions remain to be determined. It appears feasible, however, to obtain for study apes, monkeys, and lower forms with the brain completely divided down through the pons. Selective preservation of certain structures like the brachium conjunctivum would be highly desirable in many studies. One can foresee endless experimental possibilities that should go far toward an unraveling of cerebral organization, by use of complete or selected partial midline disconnections such as those mentioned above, in combination with lateralized surgical ablations and electrolytic lesions together with lateralized training and testing techniques, electrode implantations, drug injections, and other methods. The disadvantages of this approach fall mainly under the heading of "cumbersomeness." The surgery sometimes involves a long series of successive sections and ablations, and can get into an extended program in itself. Also, the lateralized training and testing techniques may get involved and lengthy, even with automated programing. In general, an average experiment has required months—up to a year or more—rather than weeks or days.

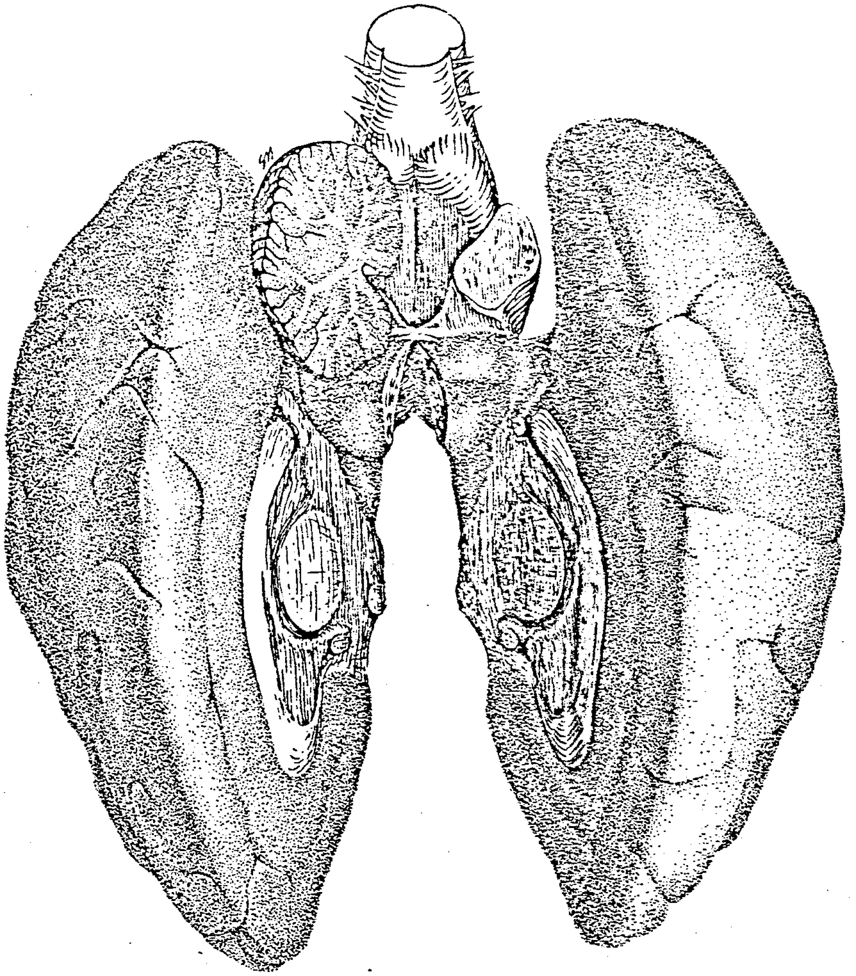

FIGURE 1 View of monkey brain bisected through tectum and cerebellum (schematic).

Complaints about the difficulty of the surgery also continue to be heard, but I don't believe that the surgery in itself need be a major obstacle if one is willing to use proper tools. A good dissecting microscope is essential for cat, monkey, and similar or smaller brains. The microscope should have a light beam set in line with the optics so that it penetrates straight to the bottom of the deep operating field in crevices between the hemispheres. I also use almost continuously the two instruments shown in Figure 3. These are tailormade in different sizes and gauges for specific purposes. The first is a double retractor, Figure 3A, that serves to separate and to hold apart the hemispheres and other deeper structures (Figure 3C). The cutting and other operations are carried out between the blades of these double retractors, using the aspirating needle-knife shown in Figure 3B, which is hollow throughout and connected to a vacuum line. The tips are interchangeable and are made of fine hypodermic needle points in a variety of gauges. Those with tips of gauge No. 26 to No. 30 are used most extensively. In fixed sections of brains that have been divided in this way, one sees very little tissue damage aside from the destruction of the commissures themselves.

BISECTION OF THE LEARNING MECHANISM We turn now to some of the broader features of the findings as they relate in particular to learning and memory. By far the most striking effect of this kind of surgery, speaking very generally, is the establishment of two entirely separate mental domains within the same cranium. Following surgical separation of the hemispheres, things experienced, learned, and remembered by one hemisphere remain quite unknown to the other. The learning experience of the one is inaccessible to, and outside the conscious awareness of, the other hemisphere, almost as much as is the case with two separate brains in separate skulls. As far as we can tell

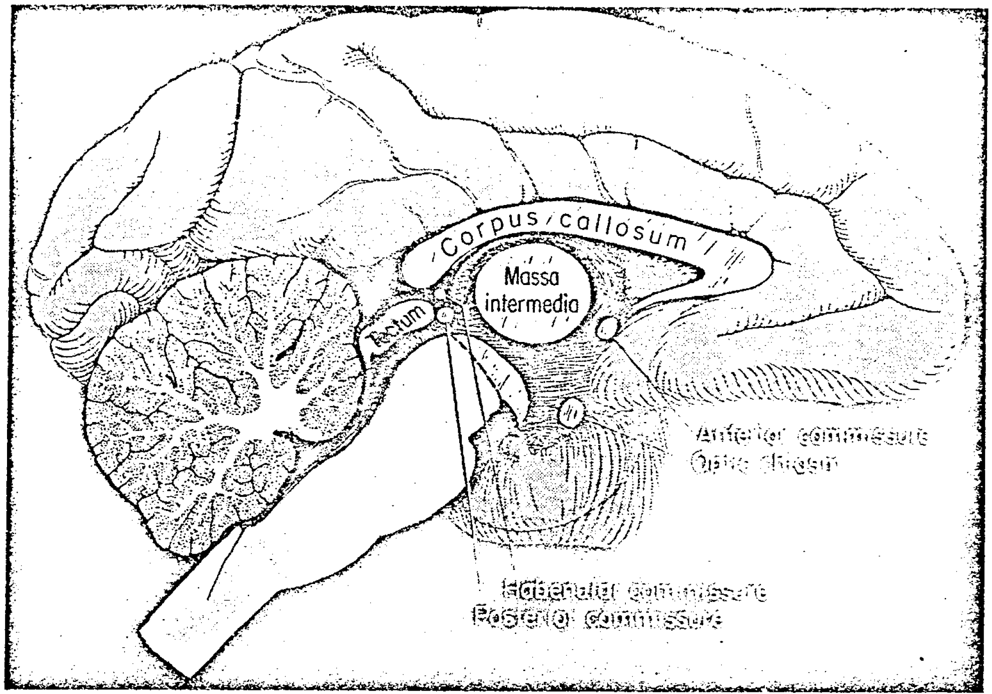

FIGURE 2 The labeled midline structures can be sectioned with only mild effects on ordinary laboratory behavior.

from the evidence to date, it would appear that in the split-brain syndrome, we deal with two separate minds, i.e., two separate realms of conscious awareness, two separate sensing, perceiving, thinking, and remembering systems.

This is shown in many different ways: For example, when the normal individual sees something to the left of his nose and then a little later perceives the same object in the opposite half of the visual field, this same object is, of course, recognized as being the same one seen previously. Not so in the split-brain person, cat, or monkey.[5,9,10] Following disconnection of the hemispheres, things seen in one half-field of vision cannot be recognized in the other half-field. In other words, things seen or remembered through the use of one hemisphere are not recognized when seen through the other hemisphere. Remember that all vision to the left of the vertical midline of the visual field is mediated by the right hemisphere and all vision for the right half of the visual field is mediated by the left hemisphere. Normally, the two half-fields of vision are integrated in the brain into a unified whole, but after section of the commissures each half-field functions separately. Instead of just one inner visual world, therefore, the split-brain animal or man has two inner visual worlds, each quite outside the conscious awareness of the other.

This is demonstrated in human patients who have had cerebral commissurotomy by quick-flash, or tachistoscopic, presentation of visual material to the separate right and left half-fields of vision at 1/10th second or less—too fast, that is, for the subject's eye movements to put the visual stimulus into the wrong or unintended half-field.[10] For example, if a picture of some familiar object such as a pencil, spoon, or cigarette is flashed to the left half-field, the split-brain subject is at a complete loss to try to recognize or identify the same picture when it is flashed to the right half-field. Subsequent memory and recognition are quite normal, on the other hand, when presentation is in the same, or left half-field.

In other words, memory traces laid down in one hemisphere remain confined to that same hemisphere and influence recall within the one hemisphere only. This applies both to short-term and to long-term memory. The only means remaining in the bisected brain for transferring visual memories from one to the other hemisphere are indirect and not unlike those by which one person informs another of something that he has experienced visually.

In commissurotomized animals, hemispheric separation of learning and memory in the visual sphere is demonstrated by cutting the crossed optic fibers in the chiasm so

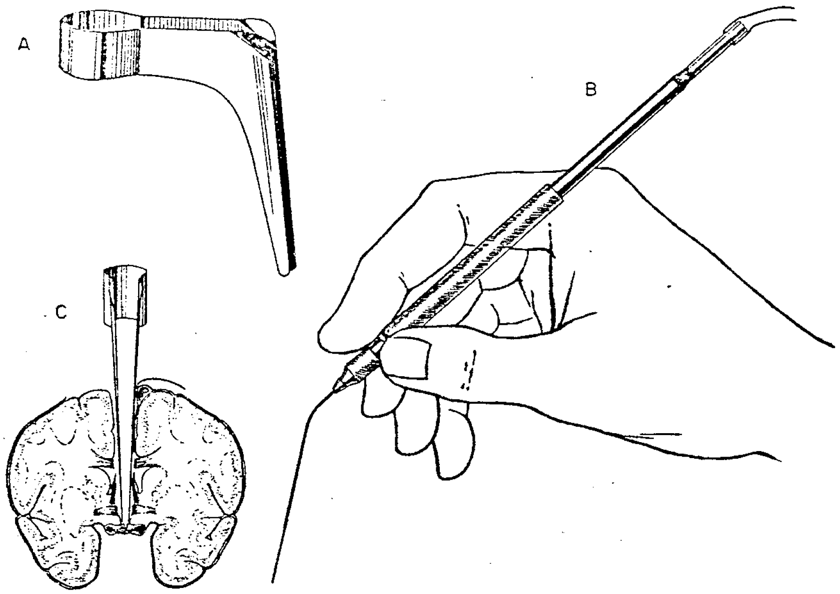

FIGURE 3 Instruments for split-brain surgery. A: Side view of stainless steel cerebral retractor. B: Aspirating needle-knife used between the retractor blades for nearly all the cutting operations carried out between the hemispheres. C: Cerebral retractor in position showing surgical approach to corpus callosum, anterior commissure, and optic chiasm.

that each eye feeds only to the half-field of its own homolateral hemisphere. Independent training and testing of the separate hemisphere can then be carried out by having the animal work through one or the other eye (Figure 4). Monocular vision is obtained by the use of eye covers, contact lenses, peephole arrangements, or differential ocular light filters for polarized or monochromatic light.

Use of special techniques has shown that in animals the separated hemispheres may be trained concurrently and simultaneously to do diametrically opposite tasks. Two mutually contradictory performances may be learned at the same time, something that the normally unified brain, of course, doesn't do. Two sets of polarizing light filters were used by Trevarthen[11] to enable the split-brain monkey to see different things at the same point in space at the same time—again something of which the normal brain is not capable. The filters were arranged so that one hemisphere perceived just the opposite of what the other was perceiving and it was possible to show that with exactly the same set of learning trials, one hemisphere could learn the exact reverse of what the other had been learning with no functional interference evident. Similarly, when different stimuli are flashed simultaneously to left and right half-fields of human patients, separate and conflicting responses are commonly obtained from the two sides, the minor hemisphere expressing itself through the left hand and the major through the right hand speech or writing.[10,12-15]

Two Mental Spheres for Manual Stereognosis

A comparable hemispheric separation has been shown to exist in the somesthetic sphere with reference to things identified by touch with right and left hands or paws.[12,14,16] Recall that the right limbs of a mammal are represented in the left hemisphere and the left limbs in the right hemisphere. In right-handed persons the right hemisphere is usually minor or subordinate to the left. Following surgical disconnection, each hemisphere receives information about the tactual, or stereognostic, activities of its own hand and foot, but has little or no information about the activities of the hand and foot of the opposite side. Deconnection of the hemispheres again seems to create two quite separate realms of inner experience for sensations coming from the right and left extremities. This applies to the right and left halves of the body generally, except that some of the more simple and crude aspects of body sense get bilateral representation in the more axial parts. In the head and neck, bilateral representation is the prevailing rule. In regard to the hands, however, which are the main receptors for stereognosis in man, the cortical representation is more lateralized, and most stereognostic functions of the two hands are effectively separated by commissurotomy in adult patients.

When an object that has been identified by manipulation with one hand only is then placed in a grab bag out of sight among other objects, a normal individual has no trouble identifying and retrieving the given item by blind touch using *either* hand. A commissurotomized subject, however, can retrieve the item only with the *same* hand, i.e., the hand that was used for the initial identification. An object recognized by use of the right hand cannot be identified with the left hand, and vice versa. In the same way, learned performances developed by tactile training in split-brain animals fail to transfer, as a rule, from one to the other forelimb provided all sensory cues have been carefully confined to the one extremity.[17-20]

INTERMODAL TRANSFER A commissurotomy patient holding a familiar object that has been presented out of sight to the left hand can usually identify the same or a matching object, or a picture of the object, when it is subsequently presented visually. This is the case, however, only if the visual presentation is made in the corresponding half-field of vision, in this case the left half-field. The normal person, on the other hand, can use either or both visual fields for recognizing objects identified by either hand. This also works conversely; that is, if a picture of an ob-

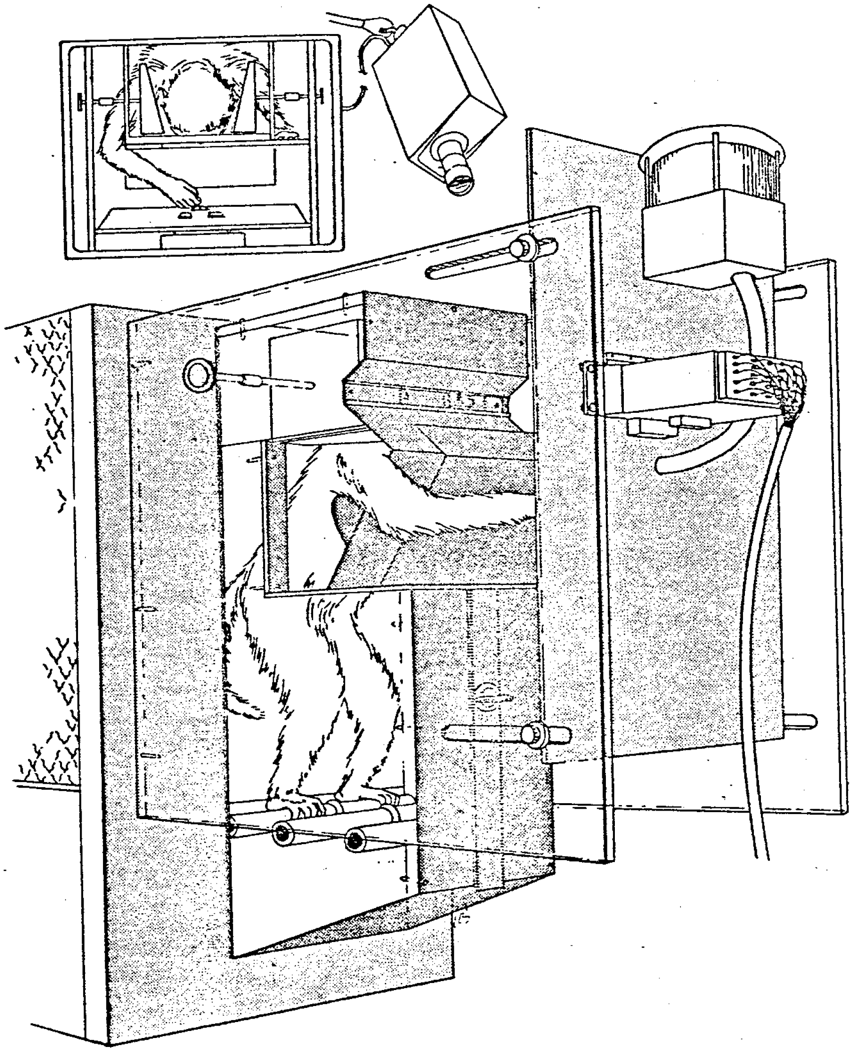

FIGURE 4 Testing unit developed by author for controlling eye and hand use in split-brain monkeys. It may be combined with automated equipment and closed-circuit television as shown, or used with direct manual presentation.

ject is flashed to the left half visual field, a commissurotomy patient can retrieve the corresponding object from a grab bag using blind touch, but only if he uses the hand on the same side. The normal person with commissures intact is able, of course, to use either hand. In summary, cross-modal identification of this sort works readily in these patients within either hemisphere—between the right hand and the right half visual field or between the left hand and the left half visual field—but all contralateral combinations as between the right hand and the left half-field of vision consistently fail. Similar results have been obtained in the monkey.[21] Again we emerge with the conclusion that the conscious experiences and memory of each hemisphere are quite separate and inaccessible one to the other.

LATERALIZATION OF LANGUAGE In performances that involve language, special problems of cerebral organization are encountered that are largely characteristic of the human brain, although they also have some general implications.[14,15] One of the most striking symptoms produced by disconnection of the hemispheres in man is the inability of these patients to describe in speech or writing anything presented to the left hand or the left half visual field. The engrams for speaking and writing seem to be confined almost entirely to the one, the dominant hemisphere, with indications that certain other functions, such as the construction of spatial relations and spatial orientation, are better developed in the right minor hemisphere. Following commissurotomy, the dominant hemisphere talks and writes and communicates generally in a manner hardly distinguishable from normal. Mathematical calculations are also carried out by this hemisphere at approximately the preoperative level.

The minor hemisphere, on the other hand, is rendered almost mute and agraphic. The possibility that a few simple, familiar words can be spoken when they are properly prompted by the examiner cannot be excluded from evidence now at hand, but in general this hemisphere is able to express itself only through simple motor responses like manual pointing, signaling, or drawing. Ordinary tests for perceptual and intellectual capacity that rely on verbal or written expression give an initial impression that the minor hemisphere is generally agnostic, but this clearly is not the case when nonverbal, manual readout is employed. In the two cases most thoroughly tested it seems clear that the minor hemisphere can comprehend both printed and spoken words, but this passive comprehension seems limited to familiar object nouns and perhaps simple adjectives.[13-15] It is uncertain to what extent this language comprehension in the minor hemisphere may have been favored by early brain damage in these epileptic cases or reflects postsurgical learning. In the minor hemisphere, calculations like speech and writing are negligible.

These patients recover the ability to write with the left hand within the first six months after surgery. Tests with lateralized input show that the control, however, comes from the major, not the minor, hemisphere. Writing with the left hand tends to be carried out with the shoulder and upper arm reflecting the greater ipsilateral cortical control over the axial and proximal musculature. The extent to which each hemisphere can control its ipsilateral limbs shows considerable individual variation, correlated largely with the extent of pre-existent brain damage. This suggests that the ipsilateral control mechanisms are delicate and easily disrupted.

We know that the minor, as well as the major, hemisphere is quite capable of learning speech and writing, and does so readily when the dominant hemisphere or the corpus callosum is eliminated in early childhood. In a very small percentage of the population, speech is found to develop bilaterally in the presence of the callosum.[22] Thus, it would seem to follow that an important function of the callosum in the normal human individual is to prevent the bilateralization of learning and memory, especially in the case of language. This seems directly contradictory to the situation in the lower mammals, in which learning and memory tend to be strongly bilateralized in the presence of the callosum and unilateral only after its removal. In split-brain cats a remarkable right–left symmetry has been observed in the learning curves of the two separate hemispheres for both visual and tactual discrimination problems.[16,23] In our split-brain monkeys[24] this kind of right–left similarity was much less evident, and even with the callosum intact, monkeys show some tendency toward unilateral learning.[25] The over-all trend among the higher mammals thus seems to be away from right–left symmetry in hemispheric function.

ROLE OF THE NEOCORTICAL COMMISSURES This brings up the general problem of the basic physiological role of the neocortical commissures. Anatomical and related studies on monkeys and apes have indicated a great predominance of symmetrical cross connections that link mirror foci or homotopic points in the two hemispheres.[26] The anatomical picture has thus appeared to favor a symmetrizing influence of the callosum that would tend to duplicate hemispheric activity and keep the two hemispheres equally advanced in learning and memory. On the other hand, the obvious functional disadvantages that would follow from imposing bilateral symmetry on certain functions suggests that the basic contribution of the callosum may better be conceived as being complemental and supplemental in design rather than symmetrical. Accordingly, it has been inferred that a closer look at the detailed anatomy of the callosum might disclose much more asymmetry, both local and heterotopic, than initially supposed.[27] From electrical studies on the cat it has appeared that the callosum may mediate a rather faithful transfer of the raw sensory input.[28,28a] On the other hand, the sparseness of cross connections between primary sensory and motor projections as contrasted with the richness of connections between associational cortical areas has long been taken to mean that the commissures must be concerned less with raw sensory and motor information than with the deeper stages of data processing.

The latter, along with the recent experimental evidence that the callosum is directly involved in the intercortical transfer of learning and memory, has led us to believe that a detailed study of the connections and functions of the callosum should furnish a rather direct approach to some of the basic principles of cerebral organization. Microelectrodes implanted in specific functional sectors of the callosum, such as that cross-connecting visual areas 18 and 19, should tap high-level inside crosstalk, and provide a sample of the brain code that might be made interpretable in specific experimental situations. Other speculations have implied that the commissures might be largely inhibitory in nature, their function being to prevent interference from the opposite side when a given process that is centered in one hemisphere is in command. Electrical and lesion studies[28-30] indicate a generalized tonic function for the callosum.

That the commissures mediate interhemispheric transfer of learning and memory has been demonstrated repeatedly. We don't know yet, however, in what form information of the directly trained hemisphere is carried across by the commissures. Would the information carried across by the callosum be sufficient, for example, to enable a hemisphere to see visual images via an optic input that had passed through the other hemisphere? The visual island experiment,[30] in which visual responses formerly present were abolished by section of the callosum, was suggestive in this connection, but not conclusive. It remains possible that only an abbreviated and abstracted part of the original visual input crosses in the callosum.

Within each hemisphere there are local fiber systems that link neighboring and distant points of the cortical visual map, particularly in cortical areas 18 and 19. The callosum might be regarded in part as an extension of these fiber systems across the sagittal midplane serving to integrate the two halves of the visual field. Somewhat similar integration between the hands is involved in bimanual stereognosis. In the case of the hands, however, the basic plan would seem to be more complicated than just a zippering together of the projected hand surfaces along the ulnar or thenar edge.

Callosal function is demonstrated in experiments in which part of the sensory information required for performance enters one hemisphere and the rest enters via the other, as in right-left cross-matching and cross-comparison problems.[10,20,31,32] The callosum has also been regarded as essentially a decussation in the descending efferent path for volitional movements, especially in man when a movement conceived and triggered in the dominant hemisphere is carried out by the subordinate hand.

In summary, we have not as yet been able to conceive in any satisfactory detail the basic contribution of the neocommissures to cerebral integration. As the evidence stands, it appears likely that a great many diverse functions: sensory, motor and associational, inhibitory and excitatory, tonic and phasic, are mediated by the callosum, and that these are further subject to considerable individual and species variation. It also seems clear that the basic functional plan of the neocortical commissures in the primates, at least, is plastic and subject to considerable remodeling in the presence of cerebral lesions and in the face of specific learning situations.

ENGRAM LOCALIZATION The aforementioned findings show that learning and memory can be confined to one hemisphere after section of the neocortical commissures, and has been taken to favor a neocortical locus for the memory trace, or engram. Having narrowed the engram locus to the neocortex of one disconnected hemisphere, it then became possible to localize further the engrams for particular kinds of memory and learning by the cortical ablation method. Ablations and other removals for localizing can be carried out on a much more radical scale in the split preparation than is feasible in the usual bilateral approach. With this method it has been possible to localize the engrams for tactile discrimination habits in cats within a moderately small island of somatic neocortex.[33] Attempts to carry the localization further in the monkey were interrupted when it was found that somesthetic learning with one forelimb was not always confined to one hemisphere, depending on a variety of uncertain conditions that only now are sufficiently understood to permit continuation of the localization project.[20] It appears that bilateral projection in the sensory somesthetic system permits ipsilateral as well as contralateral learning in the disconnected hemispheres for some types of manual discrimination in which cues arise from proximal joints in the arm or where extremely simple or crude cues from the hands are sufficient. However, any moderately complex stereognostic discriminations made on the basis of stimuli arising exclusively from the palm and fingers of the hand seem to be safely confined to the one hemisphere in the monkey.

Attempts similarly to localize visual learning to a small island of occipital cortex turned out otherwise. It was found, not unexpectedly, that the visual cortex by itself was not enough for visual learning; nor even enough, apparently, for visual perception. "Visual island" cats behaved as if they were almost blind, despite good preservation of the afferent pathways, unless other nonvisual cortical areas were preserved along with the visual and visual-association cortex.[30] The relation of visual function to the precentral motor cortex and to the cortical representation of the body schema in this experiment remain uncertain along with other unknowns that were left dangling with need for further clarification.

Related experiments have been aimed at determining the minimum critical cerebral apparatus needed for different types of perceptual learning and also at assessing the nature of the contribution of particular brain structures such as the hippocampus, motor cortex, caudate nucleus, etc. It was found, for example,[34] that unilateral removal of the dorsal hippocampus in split-brain cats produced animals that could do reversal learning in one hemisphere but not in the other. Further reduction in the somatic cortical-island preparation mediating somesthetic learning has included the combined removal of hippocampus, anterior thalamus, and most of the caudate and amygdaloid complex on the side of the cortical island. New tactile discrimination learning was still possible in this radically reduced cerebral system. The various functions of the ablated structures are still present in the opposite hemisphere, of course, and could contribute in an indirect way to sustain the learning process. However, the specific mechanism involved in engram formation and directly related processes were presumably confined to the lesioned hemisphere. Another project along the same lines has been pursued by Voneida[35] in an effort to dissect out the various cerebral components most directly involved in establishing a conditioned response, and particularly to find the locus and nature of the "new connections" formed in conditioned-reflex learning.

PATTERN OF THE ENGRAM The problem of the nature of the engram in all its complexity is well illustrated in the case of language. Fairly distinct language centers have been delineated, but nothing in the lesion data encourages the search for a distinct local engram or a distinct molecule for each word. The meaning of words and their recall clearly depend heavily on the context in which they appear. To understand the contextual dynamics of the recall process it is almost necessary to understand the nature of the engram and vice versa. To discover the basic membrane, cytoplasmic, or biochemical change of which all engrams are made, will not help much in understanding these problems of engram patterning and their filing and selective reactivation.[21]

Motor learning and the engram formation involved would seem at first glance to be rather different from perceptual and cognitive learning. The mechanisms would seem to be of a more primitive and structural design in which the basic pattern of the engram might be better illustrated. The problem of motor learning raises the old question of the nature of the representation of movement or motor response at the cortical level, a question for which we still lack a clear answer. There are reasons for suspecting that a motor response may be organized in the cortex, not in terms of patterns of motor unit discharge or in terms of muscular contractions, or even in terms of over-all limb or body movements, per se, nor the end position of the anticipated movement. It is attractive to think of movements being organized at the cortical level in terms of the expected perceptual effect of the given response. The details of the means of achieving the desired response effect on this scheme would then be left to other mechanisms. The cerebellum, the caudate, and other subcortical mechanisms would then have to translate the desired response effect into the details of muscle coordination needed to bring about a successful match with the perceived end result.

There are some advantages in considering motor learning in these latter terms when it comes to questions concerning the relation of movement and the preparation to respond to perception and to the brain code in general. We suggested earlier[36] that each movement, in addition to the efferent outflow of impulses for muscle contraction, must also include corollary central discharges to prepare the sensorium for the perceptual effects of the movement in order to maintain constancy of the perceived world. This may yet be correct, but if the movement itself at the higher cerebral levels is organized largely in terms of the anticipated perceptual effect, this might allow a simplification of the central machinery by obviating the need for separate corollary discharges for preregistration of the perceptual consequences of movement. On this basis, motor responses could conceivably be organized in the visual as well as in other nonmotor cortical areas. There is some evidence for this[37] in that split-brain animals are able to carry out visually triggered and visually guided responses from a hemisphere in which the motor cortex has been entirely removed.