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Some developments in brain lesion studies of learning[1]

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THE FOLLOWING IS A RAPID SURVEY of some of the things we've been doing in recent years in following up what for present purposes may be called "the split-brain approach to the learning problem." The general idea involved is simple enough: we first split the brain longitudinally down the middle to separate the right and left hemispheres, one of which is then reserved for the use of the animal, while the other is donated to science for application of the ablation and other methods of analysis.

In the surgery, we first sever the large corpus callosum, the main connecting link between the hemispheres. Along with this we generally cut also the smaller hippocampal and anterior commissures (see fig. 1). If vision is to be involved, the optic chiasm is divided in the midline or one of the optic tracts. For other purposes the following may also be sectioned: the massa intermedia, the habenular commissure, the posterior commissure, the quadrigeminal plate containing the commissures of the colliculi, and, in some of our more recent cases, also the cerebellum. The fibers of the small supraoptic commissures are presumed to be cut also.

This is as far as we have carried the midline sections to date, but this does not necessarily represent a limit from the surgical standpoint. It would be quite feasible to continue cutting into the upper end of the tegmentum, but here one soon begins to encounter important decussating fiber systems that connect structures up and down the brain, the cutting of which, of course, is quite a different thing from the cutting of commissural cross connections between homologous pairs of control centers.

It can be seen that these midline sections, except for loss of part of the visual inflow, leave nearly all the sensory, motor and other brain-stem relations intact. Also the great bulk of the internal organization of each hemisphere is preserved. Accordingly, the two separated hemispheres following recovery from the surgery continue to carry on most of their regular functions and the subsequent behavior is remarkably normal in character. In fact, monkeys so operated upon are hardly distinguishable from their normal cage mates under most ordinary circumstances, especially if the cerebellar section is not included. One does not notice any paralyses, spasticity, ataxia, no forced circling or other asymmetries, no hyperactive pacing nor apathy, automatisms nor mutism, nor have we observed to date any autonomic dysfunctions. Some slight changes in eye movements may be noticed in cases with section of the posterior commissure and/or quadrigeminal plate. Those with the cerebellum divided have shown some weakness and unsteadiness especially noticeable during the first months after surgery but it diminishes gradually. For the most part the monkeys appear normal and are quite suitable for behavioral testing.

However, when one studies more carefully the learning and memory of such "split-brain" animals under special training conditions where the inflow of sensory information to each hemisphere can be separately restricted and controlled, it is possible to show that each of the divided hemispheres now has its own separate gnostic or cognitive system: its own separate perceptual, learning, and memory processes. It is as if neither hemisphere any longer has any direct knowledge of what the other is doing, nor any direct memories of what has been going on in the other hemisphere subsequent to the time of section.

Although there were some intimations that this might be the case in the earlier literature on the corpus callosum, they were outweighed by confusing and contradictory observations (1). The first convincing demonstration was obtained by Ronald Myers in a nice series of experiments beginning about 1953 (16) which he carried out on the functions of the corpus callosum and on interocular transfer in the cat. In brief, Myers showed that a cat with midline section of the optic chiasm and forebrain commissures is unable to remember with one eye visual pattern discriminations learned with the other eye (12–14). In fact, with the second eye such a cat easily learns a discrimination habit that conflicts directly with what it had just previously learned with the first eye.

At this point the question immediately arose as to how separate in their function the two hemispheres really are: For example, might it be that the unblinded side in a commissurotomized cat is simply much more dominant than is usual with the corpus callosum intact and tends to drain the attention off to the unblinded side? In partial answer to this we find that extensive cortical removals

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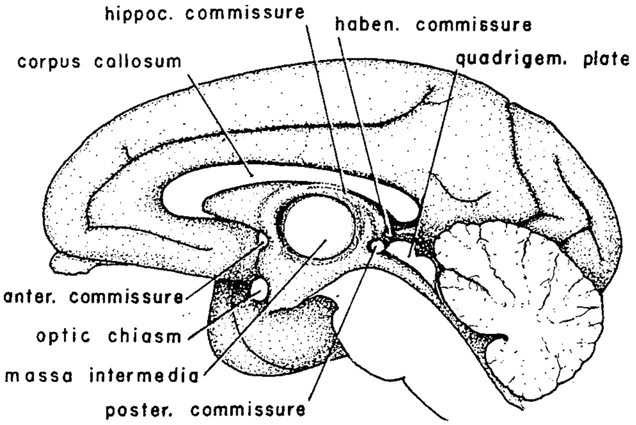

FIG. 1. Midline structures sectioned in surgical splitting of brain into right and left halves. Division of cerebellum has been added to above in some experiments.

on the unblinded side, that would be expected to depress severely any dominance of this hemisphere, still do not force visual learning of pattern discriminations over into the other separated hemisphere (20, 24). Also, when we compared the learning curves of the second eye with those of the first eye on a statistical basis, we found no significant carry-over from the training of the first eye to that of the second (25). Thus the visual learning of the second eye seemed to benefit in no way from that of the first. It was as if in using the second eye, the cat had a selective visual amnesia for the learning experience with the first eye.

The training and testing in these experiments is carried out in a type of discrimination box that I had designed earlier for studies of detailed pattern perception in the cat. The basic principle involves putting the animal inside a darkened box where the only light enters at one end through a pair of translucent stimulus patterns that the animal is being trained to discriminate. The cat walks up to and pushes its head into the stimulus figures, mounted in swinging doors, the correct one of which will open and give access to a bit of food on a tray outside the box. And the final technical point—the stimulus figures are of a size roughly the same or slightly smaller than that which will admit passage of the animal's head. Whatever the critical factors, the apparatus has enabled us to get extremely refined pattern and size discriminations, and to quantify the cat's perceptual performance with test scales based on graded reduction of dissimilarity. Vision of one eye is occluded during the training sessions by having the cat wear a rubber eye patch as devised by Myers.

Let me emphasize at this point that I am serving pretty much as a spokesman here, for work that has been very much a group effort. In addition to Myers who got the project off the ground to a good start, there have since been a dozen or so research fellows, graduate students and assistants who have all made their important contributions.

In another apparatus engineered by John Stamm, we found that the same kind of functional independence prevailed in the separated hemispheres with respect to the learning of somesthetic discriminations that involved touch and pressure on the surface of the forepaw (26). The cats were trained to push the correct one of two pedals which they were unable to see and had to discriminate entirely on the basis of touch. Again, a comparison of the learning curves revealed that the strong transfer of training from the first paw to the second in normal control cases was entirely lacking in those cats in which the corpus callosum had first been sectioned. This lack of transfer applied as well to the motor learning that was involved in gaining proficiency in the operation of the pedals. Hence it was inferred that in the split brain cat "the left forepaw knoweth not what the right forepaw doeth."

With respect again to learning and memory in the visual sphere, the findings in the cat have been confirmed also for the monkey by both Dr. Downer (2) and myself (21) quite independently. Perhaps it should be mentioned here that the attempt to test the effect upon visual learning and memory of combined section of both the optic chiasm and corpus callosum is something that has been tried a number of times in the past and abandoned, largely because of the surgical problems. The present-day success can be attributed in large measure, in our own case at least, to the carry-over to the mammalian brain of the surgical procedures of experimental embryology adapted originally to salamander larvae and frog tadpoles. In the main this involves the use of a high-powered stereoscopic microscope for most of the finer aspects of the surgery along with correspondingly delicate instruments. In our own case it also includes adaptation of the operating table for use in the sitting position, not only because of the fatigue factor, but also for the increased support, steadiness, and prolonged concentration that it favors.

The monkey is much less inclined to be cooperative than is the cat about the wearing of an eye patch, and accordingly I devised a training box by which we can restrict vision to one or the other eye. Essentially it has two eye apertures so positioned with reference to head restraints that one of the peepholes is accessible only to the right eye, and the other only to the left eye (fig. 2). Either or both eye apertures can be opened or closed from trial to trial. In addition, there is a sliding panel that controls the use of the arms and allows the pairing of either eye with either hand from trial to trial. This has the advantage over the use of an eye patch, corneal occluders, or sewing of the eyelids in that it is possible to switch easily back and forth from one eye to the other in a given series of trials.

One can give a few trials to the right eye and then a few trials to the left eye, and so on. If this is done while the monkey is in the process of learning two conflicting pattern discriminations with right and left eyes, it is possible to show that while one brain half is learning to select, say a triangle and avoid a square, the other hemisphere can be learning at the same time to do exactly the reverse. Under these conditions the two learning curves then rise in parallel concurrently in the separated hemispheres, with no particular retardation nor cross interference apparent (23). Needless to say, the normal monkey brain does not operate in this way.

More recently we've been trying to carry this a step farther in an effort to find out if such reversed discrimination learning could proceed in the separated hemispheres, not only concurrently but really simultaneously. Instead of switching alternately from one to the other eye, both eyes are used on all trials and the training conditions are arranged so that each single trial feeds back conflicting data simultaneously into the separate hemispheres. To state the problem another way: does the split-brain monkey, while learning new visual habits under these conditions, have to pay attention to what's coming into only one eye at a time—or, can the monkey attend to what is coming into both eyes simultaneously, deal with both sets of conflicting information, file them in two separate memories, and so on thus learning simultaneously and in parallel the two reversed discriminations?

A method by which this can be tested based on the use of polarized light (27) had already been devised by Colwyn Trevarthen for studies on conflict. In his apparatus diagrammed in figures 3 and 4 the pair of patterns to be discriminated is shown through two projectors, one for each eye. Each of the projectors has a polarizing filter in front of it, the one filter set at right angles to the other. These two filters are interchanged at random, right to left, from trial to trial. Both sets of patterns from each projector are projected on top of each other on two plastic screens, one of which the monkey pushes in order to obtain a reward. Another filter in front of each eye cuts out the patterns from one or the other projector from trial to trial.

With this set-up the two plastic screens appear to one eye as if, for example, there is a circle on the left and a cross on the right, while to the other eye it appears just the reverse, as if the cross were on the left and the circle on the right. Thus, while one eye sees the hand reach out and push the circle on the left, the other eye views the same act as a reaching out and pushing of the cross on the left. Any kind of projectable figure can be used and the pairs of patterns can be simply different as well as reversed. Essentially the apparatus is a monkey automat; a correct choice activating a micro-switch that releases a peanut, dehydrated banana tablet, or other monkey delicacy.

The procedure is to allow learning to progress under these conditions with both eyes open until the learning curve reaches a level of 85 or 90 % correct. At this point each eye is tested individually to find out if the learning has been taking place in one hemisphere only, or in both, and to what degree. In his tests to date involving three split-brain animals, Trevarthen has found that the proportion of learning found in the right and left eye varies: *a*) One eye may learn fully, the other only partly or not

FIG. 2

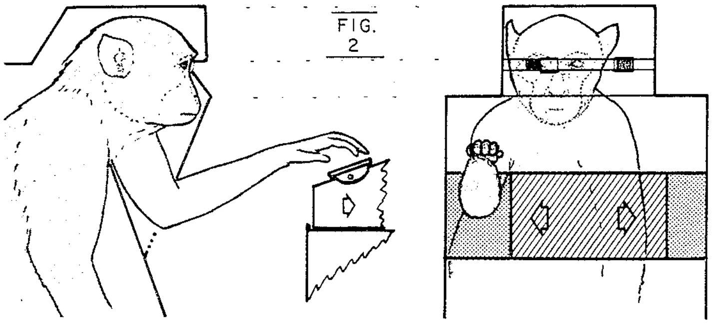

FIG. 4

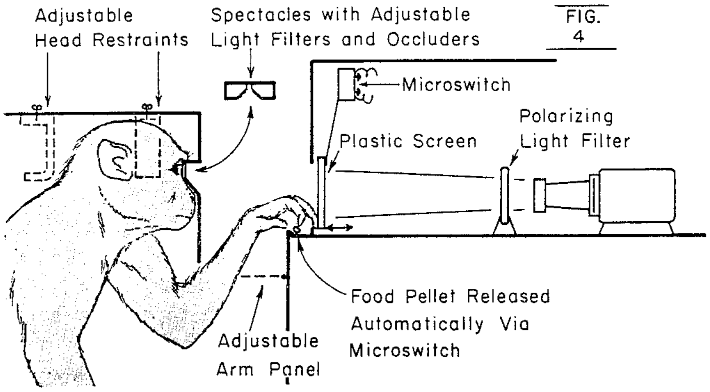

FIG. 3

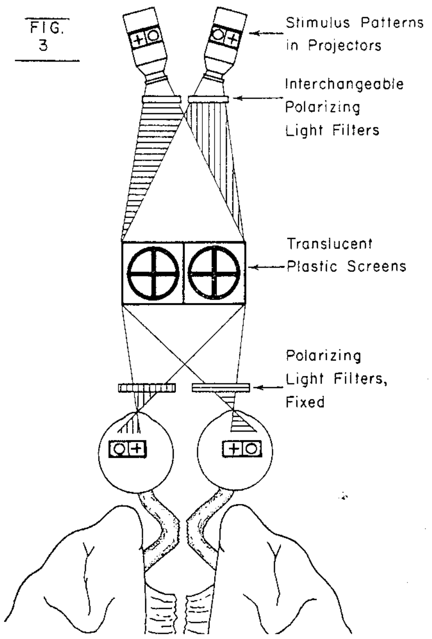

FIG. 2. Profile and front diagrams of visual discrimination training apparatus for controlling use of different eye-hand combinations.

FIG. 3. Diagram illustrating use of polarizing light filters to present different visual problems to right and left eyes simultaneously. Inversions produced by projector and ocular lenses are omitted.

FIG. 4. Profile sketch of same apparatus illustrated in fig. 3.

at all. *b*) In some cases neither eye can perform the discrimination alone, but together they are successful, suggesting that different components of the same habit complex may be learned on right and left sides and that the neural changes of an engram may be complex and divisible. *c*) Each eye may fully learn its own problem. Although chance is largely against such an equal balance of the learning on both sides, occasional instances have emerged in which both eyes have fully learned, simultaneously, their opposed discriminations.

In other words, in these instances, in approximately the same order of time that it takes a plain ordinary-brained monkey to learn one discrimination habit, the altered, double-brained monkey may successfully master two such problems. This result is less favored during the first few problems than it is later after the monkey has become proficient in the use of the box and in the pairing of either hand with either eye.

This evidence of simultaneous reversed learning in the separated hemispheres, gives us some things to think about with respect to learning theory, and the role in learning of the attention process referred to above and of other components of learning, such as the motivational background and mental, perceptual and motor sets. Are all these constituents of learning duplicate, or perhaps bifurcate in structure, with prongs qualitatively different in the two hemispheres? The next step calls for tachistoscopic (quick flash) presentation of the stimulus figures to further reduce the attention span.

When the monkey has been trained through the left eye to select a circle and avoid a cross and through the right eye to do just the reverse, the two hemispheres get along harmoniously enough so long as what looks like a circle to the right eye appears like a cross to the left. But now suppose that we rotate one of the eye-filters 90°, so that each eye sees the same set of patterns from the same projector. With one brain trained to reach for the left plaque containing the circle and the other trained to reach for the right plaque containing the cross, what kind of mental conflict will arise? Will each hemisphere try to decide for itself, or will one follow the decision of the other? Actually, what Trevarthen finds is that the monkey in this situation may exhibit some extra hesitancy and indecision, but no extreme conflict. One or the other brain tends to take over to select consistently either crosses or circles. The dominance shifts from time to time from one hemisphere to the other as a result of factors that only in part can now be predicted or controlled. This would seem to be just another example of the fact that brain organization from the highest to the lowest level tends to be an "either/or" kind of thing. Either one excitation pattern prevails or another; but it is the rare exception that competing patterns produce a confused mixture.

So much for the evidence for independent learning and memory in the two separated hemispheres. Given now these two independent learning and memory systems operating in parallel, let's turn back to our original proposition: that is, to leave one of the learning systems for the use of the animal, while we take the other for experimental analysis.

Briefly, what are some of the kinds of things that have been and can be done with this approach? Especially what are some of the advantages of using the half brain for analysis instead of the whole brain? The advantages to the animal over the usual bilateral invasion are obvious; the gains are also considerable from the experimental standpoint. But first in this connection, it is worth our remembering that the half brain is, after all, nearly a whole brain in the sense that it contains a full complement of all the cerebral integration centers and cortical areas and all their interrelationships excepting only the right-left cross connections. Practically the entire pattern and most of the problems of cerebral organization above the midbrain level are there for the unravelling within the half brain.

One obvious advantage of the split-brain preparation lies in the factor of built-in controls—of many kinds, of the homozygous, identical-twin quality with additional common denominators in experiential factors—not only for the testing of learning and memory, but also for acute physiological studies as well. By restricting the sensory inflow to one side, or by other procedures that cause the animal to attend in, and use, one hemisphere; the effect of unilateral lesions, drugs, shock and anesthetic administrations can be checked and compared with the function of the normal side.

Another advantage lies in the possibility of investigating the role in learning of cerebral structures such as the caudate, the primary motor cortex, and others, the bilateral ablation of which produces incapacitating or other secondary effects that act to obscure or confuse possible contributions to learning. Each control center tends to be involved in a whole spectrum of different functions, and in many cases only the more basic impairments can be inferred after bilateral removals, the others being hidden or untestable in the presence of the former.

The split preparation similarly offers the possibility of using much larger ablations even to the extreme of removing most of the neocortex and working with isolated functional remnants. We have isolated the visual cortex of the cat in this way (see fig. 5) and found that extremely little vision survives such isolation (20, 24). A next step is to go back and to restore in other animals different portions of the removed cortex to determine the respective contributions of each to visual learning and memory. Comparison of the effects of temporal and frontal removals indicates that in the cat the temporal lobes are not as important for visual discrimination as they are in the monkey (11).

A very different result was found to follow similar surgical isolation of the frontal cortex including the somatic 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 a pedal-pressing apparatus (22). The elusive engrams or memory trace for these new habits would seem to have been, if not trapped, at least cornered within the local

FIG. 5

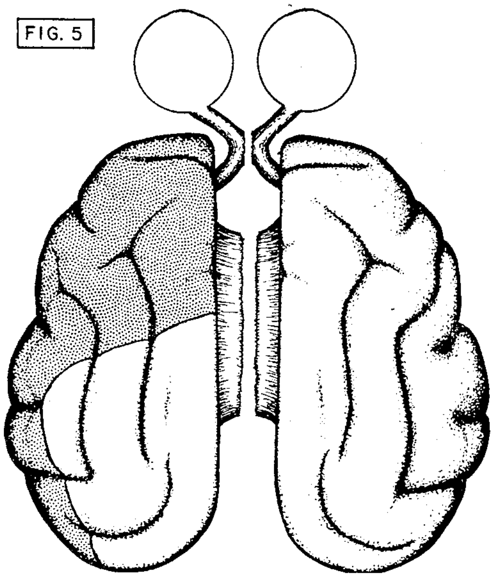

FIG. 5. Central visual cortex is surgically isolated in left hemisphere; right hemisphere serves as control.

FIG. 6

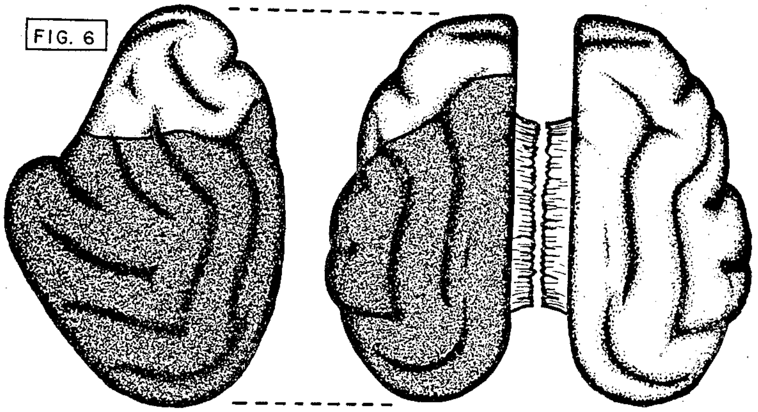

FIG. 6. Capacity for high-level somesthetic discrimination learning and memory survives isolation of the frontal cortex as shown.

cortical area indicated in figure 6. It should be possible to further localize the engram by paring away the anterior, medial, and ventral edges of the area, and also to test the contribution of various subcortical centers that remain undegenerated like the caudate, amygdala, and hippocampus by prior placement of deep stereotaxie lesions. The preparation thus furnishes a promising means for determining the critical minimum cerebral apparatus essential for learning and memory of somesthetic discrimination in the mammalian brain.

To further assure in the foregoing experiment that the habits were not being mediated by the contralateral somatic cortex, a complementary removal of the same area was made on the opposite side. To start making lesions in the hemisphere that was set aside for the use of the animal may not seem exactly fair, but at least a "trade" was made. At any rate, the feasibility of adding complementary lesion patterns in the intact hemisphere of the split brain offers further possibilities for the analysis of functional relationships.

There are other promising angles in the foregoing "somatic island preparation" for the investigation of learning: For example, we could test its proven pedal-pressing learning capacity using visual or auditory instead of tactile stimuli; that is, we could ask, "Could such a cat learn to press a pedal that activates the correct one of two different tone patterns, first, with the auditory cortex in the opposite hemisphere?" If not, could it then do so if an isolated patch of auditory cortex were to be left on the same side as the somatic island? Should the answer still be no, then what kind of intracortical bridges and connections are needed to satisfy the learning requirements?

Figure 7 illustrates a basic type of complementary lesion preparation we've been using with a number of variations to study visuo-motor coordination. The experimental question here was: "Can visual information that is processed in one hemisphere serve as a guide for limb responses, the cortical centers for which lie in the opposite hemisphere and surgically separated from the visual inflow?" And, in another experiment with the same type of preparation, "Could a visual signal be used as the conditioning stimulus for a conditioned flexion response of the forelimb in question?" The evidence so far indicates that the answer will be "yes" to both of these questions (unpublished observations of R. E. Myers, R. W. Sperry and Nancy Miner, and of T. J. Voneida and R. W. Sperry), but there are qualifications and of course each new answer raises four new questions.

The visual guidance of a limb, the main cortical control centers for which lie in the hemisphere opposite that of the visual inflow presents certain problems. The split-brain monkey with unilateral vision shows a tendency to prefer to use the arm governed from the same hemisphere, i.e. the contralateral arm. However, this is only a tendency and it is easily overcome in a matter of hours in most of our training situations (23, 27, and unpublished observations of R E. Myers, R. W. Sperry and Nancy Miner). On the other hand, this tendency can be enhanced in other testing circumstances to the point where use of the ipsilateral arm may appear extremely difficult or impossible for a prolonged period (3). However, preference for the ipsilateral arm may prevail when the given arm is strongly dominant either naturally or as a result of training in a particular apparatus.

It was found that the split-brain cat readily uses either forepaw to carry out visual directives in the learning of visual discriminations with one eye (19). Monkeys also are able to use either hand under similar conditions, but there is a difference between the ipsilateral and contralateral performance, the contralateral arm having the advantage (27).

FIG. 7

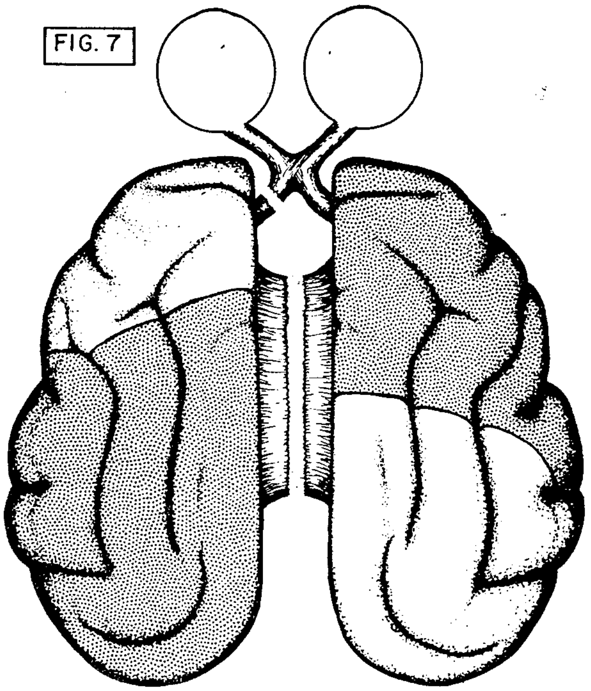

FIG. 8

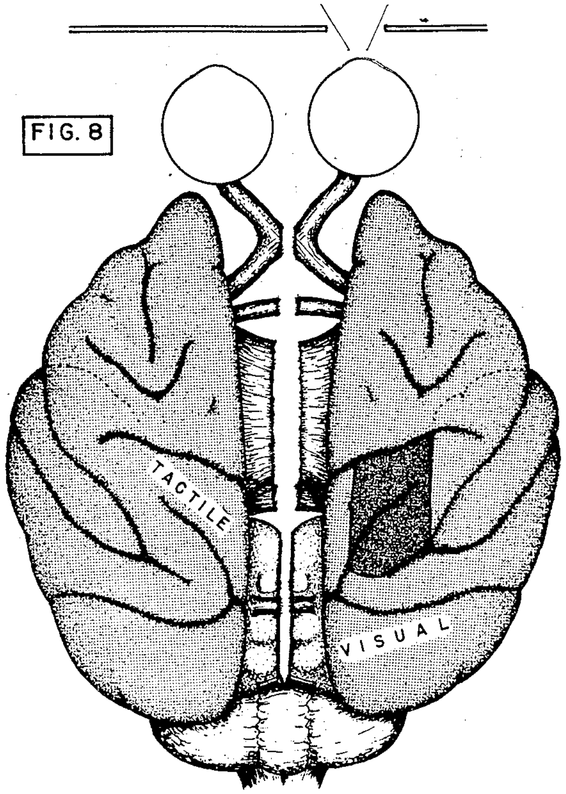

FIG. 9A

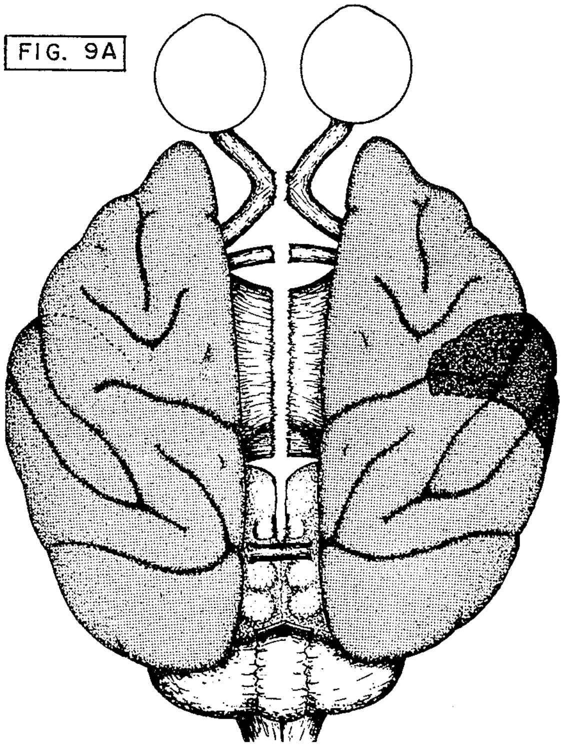

FIG. 9B

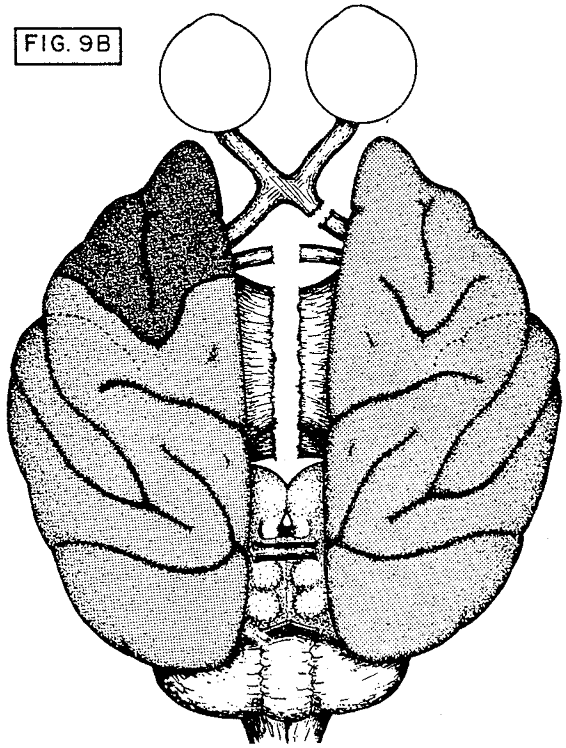

FIG. 7. Visuo-motor coordination and visual conditioning of right foreleg response survive this kind of surgical separation of visual and limb areas of cortex.

FIG. 8. Capacity to integrate visual stimuli with somesthetic stimuli from right hand survives surgical splitting and cortical removal as indicated.

FIG. 9. Two of various possible unilateral approaches to the classical temporal and prefrontal lobe syndromes.

Analagous to the above sensori-motor type of integration, there are various sensori-sensory integrations that can be analyzed to advantage with the split-brain technique. Figure 8 illustrates an approach to a form of visuo-tactile association. The monkey is trained to perform a discrimination problem that requires in each trial an association of both visual plus somesthetic cues. By controlling the hand and the eye used, and thereby the cortical receptor centers involved, we can test intra- and inter-hemispheric 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 association required for such a performance.

It was somewhat of a surprise to find that with somesthetic stimuli entering the hemisphere opposite that of the visual inflow, the monkey was still able to perform the visuo-tactile integration. I first used color and weight (largely proprioceptive) discriminations (23) and have now repeated the results with black and white pattern and cutaneous rough-smooth stimuli. Performance with the latter is retained even after midline section of the habenular and posterior commissures, the massa intermedia, and the quadrigeminal plate in addition to the corpus callosum and anterior and hippocampal commissures. Removal of the bulk of somatosensory arm cortex, on the side of the visual input as indicated in the figure, abolishes the performance with the affected hand for several weeks. Meantime, however, the other hand continues to perform above 95% correct. This puzzling result is under further investigation.

In this connection I am reminded that it is perhaps as important as anything to point out that in working with this twin brain preparation we have often been forced into new patterns of thinking. That is, not only does one see new approaches to old problems, but in many cases one is forced into asking entirely new kinds of questions about brain physiology, questions of a sort that I, at least, would never even have thought of asking with the usual bilateral approach.

When we turn to the evidence regarding intermanual transfer of somesthetic discriminations and of motor learning in the primates, the results have not been entirely consistent (4, 6–8, 10, 15, 21, 23). In our own experience section of the cerebral commissures may lead to failure of intermanual transfer but not in all cases nor under all conditions. We have observed intermanual transfer in chiasm-callosum sectioned monkeys that were sophisticated in using either hand with either eye and were trained with pairs of objects that were left in sight because they were distinguishable only by touch not vision, the one being harder, or heavier, or looser than its mate and this being discernible only upon palpation. Also, removal of the somatosensory arm cortex as shown in figure 8 has been found to evoke transfer on subsequent testing in split-brain monkeys that had formerly failed to exhibit transfer on problems tested prior to the cortical removal (10). The interpretation of this is complicated at present by the fact that a trained reversal of the transferred task consistently fails to transfer back again to the first hand (10).

Some transfer effects also show up in visual learning, according to data obtained by Trevarthen in monkeys with presumably complete section of the callosum, anterior and hippocampal commissures and optic chiasm. So far the transfer influences seem to be confined to brightness, general color and possibly very simple forms of pattern discrimination. All these may be aspects of visual stimulation that cross at the collicular level of the midbrain and hence cases are being tested with more extensive midline sections that include the posterior commissure and quadrigeminal plate.

In figure 9*A* may be recognized a unilateral approach to the classical Klüver-Bucy temporal lobe syndrome and some of its subsequent fractionations (5) and in 9*B* the same for the old prefrontal lobe syndrome and its role in visual delayed response. In the former case the operation may make the monkey "unilaterally tame" for a while, i.e. placid in its response to touch and stroking of its limbs and body parts contralateral to the temporal lesion (John Steiner, unpublished observations). In the latter case (9) the delayed response performance is impaired in the absence of the usual hypermotility and distractibility that have followed bilateral removals and that for years, have tended to confuse the interpretation. In each instance one gains new data and information as to whether certain of the symptoms involve direct intrahemispheric relations or are perhaps more distant secondary effects stemming from hyperactivity, temperament changes, and the like, involved in the bilateral removals.

The so-called *encephale isolée*, and *cerveau isolé* preparations of Bremer and his group (1) have found considerable use in physiology. It should not be out of the question to go further and prepare isolated half-brains of different forms and degrees of isolation that would be used in the chronic condition, i.e. carried around by the animal *in vivo* in the brain's natural habitat under normal biochemical conditions, and recovered from the acute effects of diaschisis for use in implanted electrode conditioning and other physiological studies.

By combining various ablations and sections like those described above with local stereotaxie lesions in subcortical nuclei, 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 in chronic preparations for functional testing and analysis. Combine with this the analytic possibilities brought by the chronically implanted electrode for recording, stimulating, and self-stimulating plus the new automated training and programming techniques, and those of us working in the physiology of behavior find ourselves today surrounded by seemingly endless new possibilities just waiting for the doing.

In the outlook for physiology, particularly that of the younger people, perhaps even those top level secrets of brain function that to Professor Herrick were always primary and which gave a perspective and an added meaning to all his observations, whether he was looking at a synapse or at a hemisphere, need not remain so much longer, "impossibly remote and out of reach."

Our brain surgery on monkeys has been performed during the past 18 months almost exclusively by Dr. Harbans Arora. Lois MacBird has carried the major responsibility for the training, and medication of the animals and for general laboratory assistance. I wish also to thank Colwyn Trevarthen and Drs. Mitchell Glickstein and John Steiner for permission to mention some of their unpublished findings.

REFERENCES

1. Bremer, F., J. Brihaye and G. Andre-Balisaux. *Arch. Swiss. Neurol. Psychiat.* 78: 31, 1956.
2. Downer, J. L. de C. *Fed. Proc.* 17: 37, 1958.
3. Downer, J. L. de C. *Brain* 82: 251, 1959.
4. Ebner, F. and R. E. Myers. *Fed. Proc.* 19: 288, 1960.
5. Ettlinger, George. *Brain* 82: 232, 1959.
6. Glickstein, M. and R. W. Sperry. *Physiologist* 2 (No. 3): 45, 1959.
7. Glickstein, M. and R. W. Sperry. *Amer. Psychol.* 14: 385, 1959.
8. Glickstein, M. and R. W. Sperry. *J. Comp. Physiol. Psychol.* 53: 322, 1960.
9. Glickstein, M. and R. W. Sperry. *Physiologist* 3 (No. 3): 66, 1960.
10. Glickstein, M. and R. W. Sperry. *Amer. Psychol.* 15: 485, 1960.
11. Mishkin, M. *Amer. Psychol.* 13: 414, 1958.
12. Myers, R. E. *Jour. Comp. Physiol. Psychol.* 48: 470, 1955.
13. Myers, R. E. *Brain* 79: 358, 1956.
14. Myers, R. E. In: *Brain Mechanisms and Learning*, edited by J. F. Delafresnaye. Oxford: Blackwell, 1961, pp. 481–505.
15. Myers, R. E. *Fed. Proc.* 19: 289, 1960.
16. Myers, R. E. and R. W. Sperry. *Anat. Rec.* 115: 351, 1953.
17. Myers, R. E. and R. W. Sperry. *Fed. Proc.* 15: 134, 1956.
18. Myers, R E. and R. W. Sperry. *A. M. A. Arch. Neurol. Psychiat.* 80: 298, 1958.
19. Schrier, A. M. and R. W. Sperry. *Science* 129: 1275, 1959.
20. Sperry, R. W. Physiological plasticity and brain circuit theory in *Biological and Biochemical Bases of Behavior*, edited by H. R. Harlow and C. N. Woolsey. Madison: Univ. of Wisconsin Press, 1958.
21. Sperry, R. W. *Anat. Rec.* 131: 297, 1958.
22. Sperry, R. W. *J. Neurophysiol.* 22: 78, 1959.
23. Sperry, R. W. *Transactions of the Macy Conference on Central Nervous System and Behavior*, 1958.
24. Sperry, R. W., R. E. Myers and A. M. Schrier. *Quart. J. exper. Psych.* 12: 65, 1960.
25. Sperry, R. W., J. S. Stamm and Nancy Miner. *J. Comp. Physiol. Psychol.* 49: 529, 1956.
26. Stamm, J. S. and R. W. Sperry. *J. Comp. Physiol. Psychol.* 50: 138, 1957.
27. Trevarthen, C. B. *Amer. Psychol.* 15: 485, 1960.

"In attacking the problem of the origin and biological significance of the cerebral cortex comparative neurologists have hitherto generally directed their attention primarily to the cortex itself and its supposed primordia in the lowest vertebrates. As a result of these studies it is becoming increasingly evident that the key to this difficult question is to be sought in the subcortical centers of the primitive types, that is, in the 'old brain' (palaeencephalon of Edinger, segmental apparatus of Adolf Meyer), which attains its definitive pattern as a mechanism for reflexes and instincts prior in evolutionary history to the emergence of true cortex (neencephalon, or suprasegmental apparatus of the forebrain). It is important, therefore, that the exact pattern of these primitive sensori-motor mechanisms of the forebrain be determined in advance; for here are to be sought the primary physiological factors through whose interaction the functional pattern of the cerebral hemisphere has been elaborated." (C. Judson Herrick. The internal structure of the midbrain and thalamus of Necturus. *J. Comp. Neurol. 28:* 216, 1917.)

"The anatomical configuration and connections of the amygdaloid complex suggest that as a whole it possesses a certain physiological unity and that the component parts of this integrated complex are diversely represented in various vertebrate types, in accordance with their respective modes of life. The amphibian relations suggest, further, that the correlation of olfactory, gustatory, and perhaps other excitations arising from food within the mouth was the original integrating physiological factor. . . .

"The mammalian amygdala, like many other complex correlation centers, is a mechanism in which there converge into final common paths numerous very diverse kinds of peripheral excitation—some of visceral (interoceptive) type and some of somatic (exteroceptive) type." (C. Judson Herrick. The connections of the vomeronasal nerve, accessory olfactory bulb and amygdala in *Amphibia. J. Comp. Neurol. 33:* 274, 1921.)