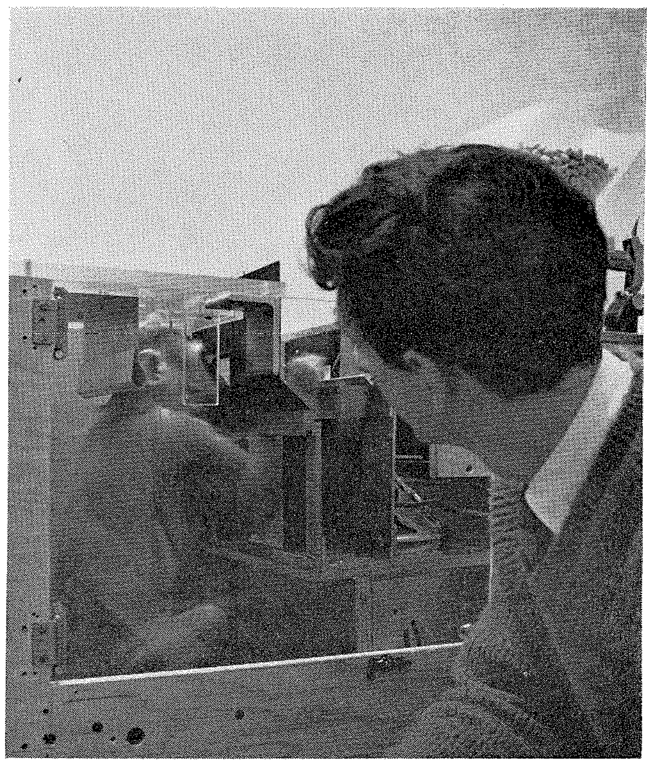
Monkey at work in a training apparatus, under the supervision of Dr. Trevarthen, in Caltech's psychobiology laboratories.



Exploring the Neural Mechanisms of Mind

Psychobiologists look for answers to some of the intriguing questions raised by our present knowledge of the brain

by Colwyn Trevarthen

Medical knowledge of the brain depends upon careful study of the effects of injury or disease on human behavior. Centuries of observation have given us insight into the way different parts of the brain have specific functions. Now it is possible to relate certain intellectual functions with specific areas of the cerebral cortex. Visual, auditory, and touch perception; control of skillful movement; and the ability to understand language or communicate with words may all be located in particular parts of the cortex. Deeper parts in the brain stem seem to be more concerned with the passage of information to and from the cerebral cortex, or with the regulation of attention, posture, and the essential bodily functions.

In the last few decades, however, much that is dramatically new has come to us by way of experimental work where the brain functions are observed or altered precisely and directly. These experiments are rarely made with human subjects, though some startling observations have been made during brain surgery. Neurosurgeons, seeking to remove diseased or damaged parts of the brain, have exposed the active brain while the patient is fully conscious. The brain substance has no feeling of pain so the surgeon can carefully stimulate selected points electrically and ask the patient about the effects. Crude sensations can be produced. Fragmentary memories may appear, or the patient may observe that he is making unintended movements of parts of his body.

These, and much more extensive experiments upon animal subjects, have taught us in recent years that the brain has a pattern of coordination which does not quite fit the classical view. The cerebral cortex is a vastly important element of the working brain, but it collaborates at all times with the brain stem.

Lower parts of the brain have been found to regulate the activity in the cerebral hemispheres and to control the level of consciousness or wakefulness. It has been discovered that the flow of sensory excitations from sense organs into the brain can be modulated, and turned up or down in volume so that the brain can attend to messages of importance. Hearing can be sharpened for a moment, or visual attention can be focused on the fine detail.

An impressive expansion of brain research at the present time is directly attributable to these and other discoveries, and to the invention of powerful new techniques. The many intriguing questions raised by the knowledge we now possess must be answered by further careful experimentation. Now it is more necessary than ever to supplement our medical knowledge of human brain functions by carrying out careful studies of the behavior and brain-physiology of animals.

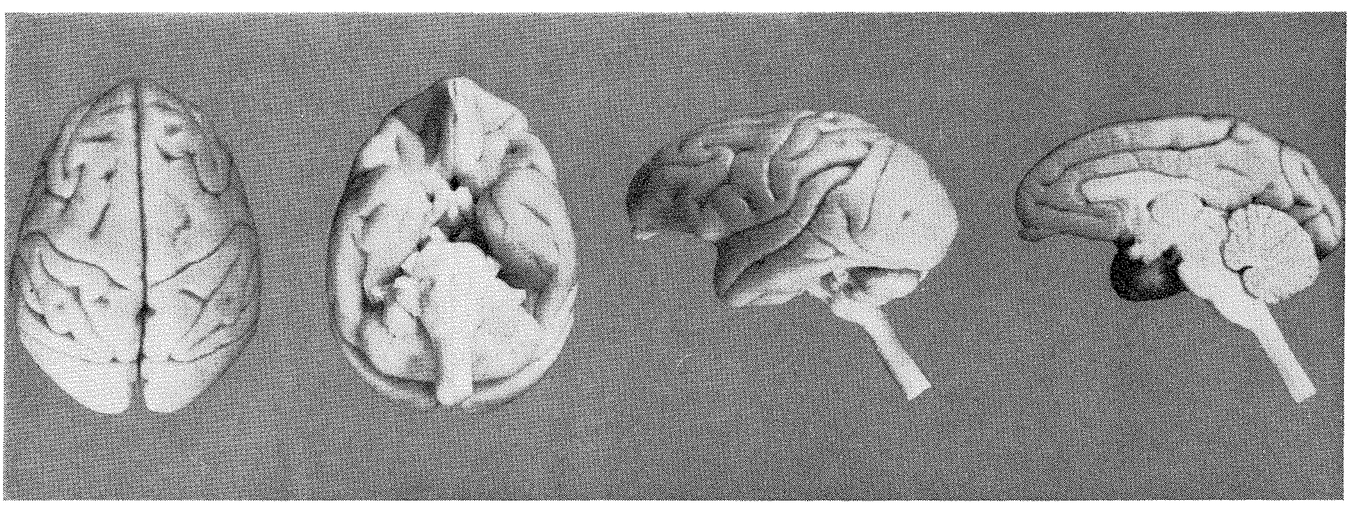
It is quite possible to study intelligence without considering the brain. In fact, it is only in the last two or three hundred years that the brain has been known to be an organ of intelligence. Now scientific knowledge has left us with no alternative but to seek out the mechanism of mind in the brain, and particularly since the methods of investigation are now so wonderfully improved, we may reasonably expect some very significant discoveries to come from a diligent exploration of the workings of the brain.

At Caltech we who call ourselves psychobiologists have been concerned with one particular kind of experimental alteration of the brain. This technique was developed by Dr. Roger Sperry, Hixon professor of psychobiology, and his students about seven years ago. I have been working with him these past five years. In our experiments we do not so much cut out parts of the brain as cut communication cables, and in this way separate selected parts. We modify the brain mechanism by dividing it into parts so that the parts can be studied separately, or at least more separately than was possible before.

Along with the evolution of intelligence in mammals there has been a dramatic relative increase in the topmost part of the brain called the cerebrum, so that one might well expect the cerebrum to be the seat of intelligence – the logical place to begin a search. Furthermore, the brain, like the body as a whole, is bilaterally symmetrical, with most of its centers represented twice – once on each side. At the largest development of all, in man, the cerebrum is a spherical mass filling the domed skull and the two mirror halves are called cerebral hemispheres. The brain of a monkey is very similar to that of man in general appearance, with two large cerebral hemispheres dwarfing the other parts.

Our surgery is called split-brain surgery. Under conditions of an aseptic technique such as is used in hospitals for human brain operations, and with even finer instruments, we carefully cut bundles of nerve fibers which form bridges between the cerebral hemispheres. We work under a binocular microscope and carefully avoid breaking blood vessels or bruising the delicate brain tissue.

After the anesthetic has worn off, the cat or monkey with the split brain wakes up with all direct connections between centers in the cerebral hemispheres cut through. He may feel a little strange, but there is little evidence of this, and the feeling soon wears off along with the weakness due to the anesthetic and the general surgical shock which accompanies any major operation. It is astonishing to see a monkey acting perfectly normal, seeing well, eating well, moving with perfect coordination, and even exhibiting all his old idiosyncracies just one or two days after the major connective fibers between right and left halves of his brain have been cut.

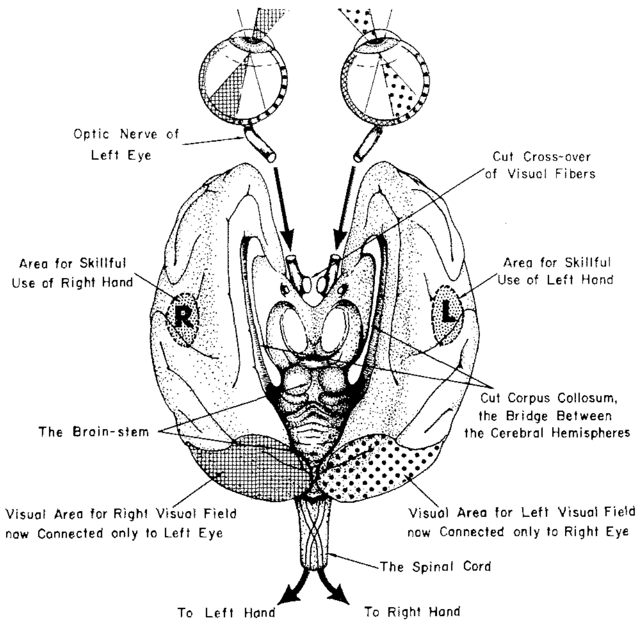


A monkey brain as it looks from above, from below, and from the side. At the right, a half-brain, showing the brain stem sliced through in mid-plane. In split-brain surgery the stem is largely undivided.

The purpose of this surgery is quite simple, really. We want to study the function of the cerebral hemispheres separately and to examine the relationship they have to the brain stem, the generally more primitive part, which remains largely undivided by the surgery. We want to test, for instance, more classical theories of brain function which say that intelligence works in the various parts of the cerebral cortex which have been located by surgical or electrical methods; that skillful voluntary movements are directed by "thought" in the motor area; and that higher functions of reasoning are taking place in the frontal lobes. We already have some new information which gives us opinions on these matters, and yet there are other facts which puzzle us and increase our curiosity in new ways.

In order to test the hemispheres separately we need to have separate access to them through sensory pathways. Luckily, there are anatomical patterns which help us to separate the flow of visual information into the brain. In the case of vision there is a wonderfully orderly projection (like the projection of a slide onto a screen) of the retinal locations into the brain, and finally into the cerebral cortex. Half the retina of each eye projects to one hemisphere and half to the other. There is a crossing over of optic nerve fibers under the brain (the optic chiasm) which takes fibers from the left half of the right eye across to the left hemisphere, and vice versa.

We can cut this crossover of fibers in the midline and then each eye sends fibers from the outer halves of the retinas to the hemisphere of the same side only. The animal after this operation has a narrower visual field because he loses the parts of each retina which receive light from the sides of his view. He also loses the ability to make stereoscopic depth detection. But he learns quickly to overcome these difficulties and the operated cats or monkeys certainly see very well with both eyes. When the chiasm is sectioned, each eye has a private line to one cerebral hemisphere.



A split brain, showing the separated cerebral hemispheres with their centers for vision and for control of skilled hand movements. After the optic crossover is cut, visual impulses from the inner halves of the retinas of both eyes cannot get to the brain.

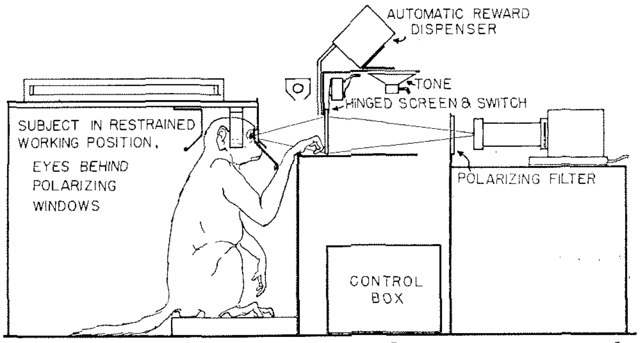
First experiments

The first experiments with split-brain cats showed that the two hemispheres could work independently in seeing, learning, and remembering tasks. When one hemisphere was given a visual task through one eye and it had learned to solve the task without errors, the other hemisphere acted with the other eye as if completely independent and ignorant, and had to start from scratch. If a special part of the main connecting bridge between the cerebral hemispheres (the corpus callosum) was left intact, the learning spread across from one hemisphere to the other and a new memory was imprinted on the other side.

We wondered if these experiments were really final. Perhaps, because the tests were given sequentially, one eye and hemisphere – say the left – would be tuned in and attentive because of receiving the stimuli. It is possible that the right hemisphere could have been deliberately turned off because there was a mask over the right eye. Closely repeated tests seemed to indicate that the two half-brains were separate and independent. It was further shown that contradictory tasks could be learned without confusion. For example, one eye of a cat was taught to pick the pattern II and to avoid = . Then the other eye was taught to pick horizontal lines and to neglect vertical lines. These experiments were done by Dr. Donald Myers, working with Dr. Sperry.

If the half-brains are really independent, they should be able to work side by side without interference, each thinking its own thoughts. In order to test this intriguing possibility of double simultaneous intelligence, double visual perception, understanding, and remembering, we had to find a way of sending visual stimuli separately to the two eyes while the monkey subject was looking at, and responding to, an experimental test situation. We were at a loss to know how to do it until a geologist friend suggested that we use plane-polarized light.

A beam of light may be considered as composed of waves vibrating in all directions perpendicular to the direction of propagation of the light. A plane-polarizer inserted into the light beam absorbs selectively all waves vibrating in one plane, the plane of its absorption axis, and transmits light vibrating in a direction at 90 degrees to this in the transmission axis. Vibrations at angles between these two directions are absorbed in proportion to their orientation with respect to the absorption axis of the polarizer.



Apparatus used for controlling the use of eyes in the guiding of hand movements.

If the polarized beam now passes through a second polarizer whose transmission axis is parallel to the predominant direction of vibration of the beam, little further absorption results. If, however, the second polarizer is rotated to a "crossed" position with its axes at right angles to the axes of the first polarizer, it is almost completely absorbed. For us, the useful point is that polarizing filters (of the linear type) transmit light polarized in one direction best and fail to transmit light polarized in the direction at right angles to this.

One subject is trained to look through polarizing filters in a pair of spectacle-like openings at a screen on which polarized patterns are projected. When he is in position to work, the polarizing filters in front of his eyes are oriented so that they will transmit light polarized in two directions at right angles. Thus, light which the left eye-filter transmits best is not transmitted at all by the right filter, and vice versa. It is easy to see that two patterns of polarized light can be projected onto the screens so that one pattern is seen only by the left eye, and the other pattern is seen only by the right eye.

In order to test the independence of the cerebral hemispheres in the most rigorous manner, we decided to use opposite tasks for the two eyes. In each trial, one of the two screens was correct and a push on it would be rewarded by delivery of a peanut. The other screen would be incorrect and the monkey would go unrewarded. In one trial, for instance, the left screen might be the correct one.

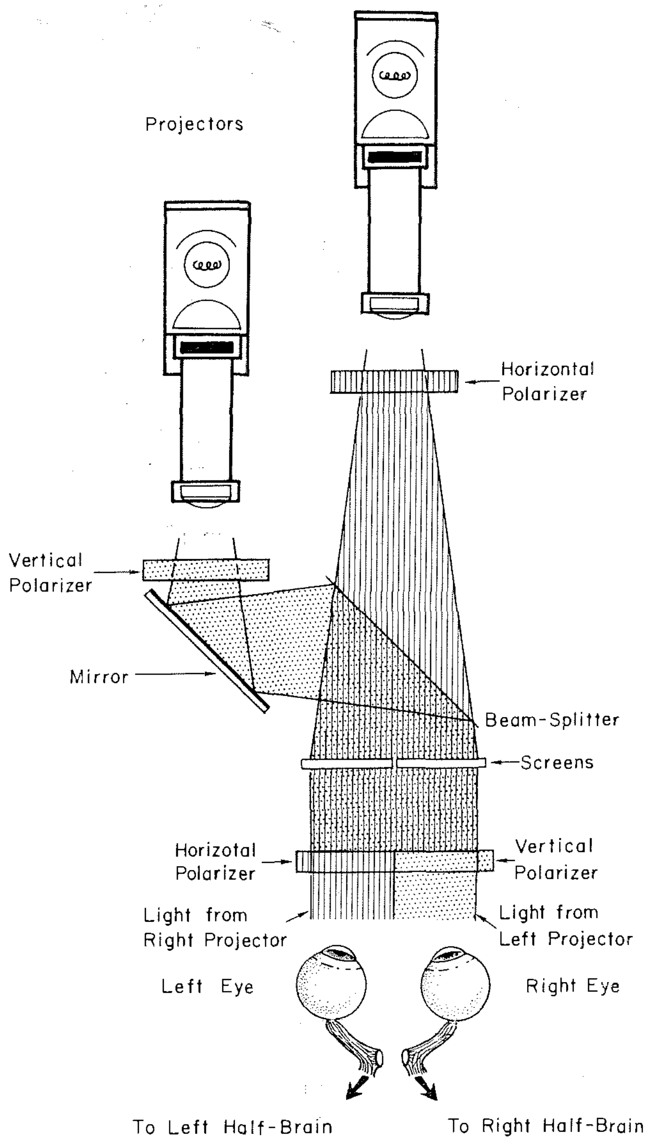
Let us say that in this trial the left eye sees **+** on the left screen and **O** on the right. At the same time we may project opposite patterns to the right eye — **O** on the left and **+** on the right. Over a series of trials in which the stimuli are changing in a random schedule as the reward is shifted from side to side, the left eye always finds the **+** correct and the right always finds the **O** correct. Could a split-brain monkey learn these two tasks in his brain at one time?

The answer is a qualified yes — and the qualifications are most interesting.

There have been a few cases in which the two half-brains seem to have learned side by side, simultaneously. As soon as the subject showed that he knew what to do by making correct choices a significant number of times, we found that both cerebral hemispheres knew their respective tasks.

This learning was well retained. There could be no doubt that both half-brains had learned. We had obtained dramatic indication that the two cerebral hemispheres were functioning separately in the perception and memorizing of the visual tasks. However, we could still not be sure that both halves could work at exactly the same time. We have reason to believe that they might be taking turns, quite quickly, and thus attaining the same average amount of learning.

We hope to know the answer very soon. So far we have proof that the two halves can both be ready to work at a moment's notice. But this is not the same as actually being *in* action simultaneously. The interesting point here is the possibility of a double awareness — two consciousnesses in one head. But



Technique used for projecting overlapping polarized light patterns. Each eye receives a different pattern.

there is a considerable amount of work to be done before we can say what the awareness of a split-brain monkey is really like.

While we were working along these lines, several serious complications arose which diverted our attention to the functions of the unsplit parts of the brain – the parts outside the cerebral hemispheres. There are two kinds of influence which throw the double learning off balance. One is due to the actual transfer or leakage of visual information through regions below the split. The other results from the need to read brain functions only through the response movements of the subject.

In the beginning of this work, about four years ago, we were fairly confident that the two halves of the visual system were separated completely by the split-brain surgery. Then there came definite proof of communication between the two halves of the brain. When split-brain monkeys were presented with a simple brightness discrimination task and its contradiction, the following events were observed:

First, with the two problems presented simultaneously, there was nothing particularly unusual about the learning. But then the monocular tests revealed that only one half knew its task securely; the other half behaved at first as if quite unsure, then suddenly it made a run of completely wrong choices.

Transfer of learning

This could mean only one thing; the learning by one side was being used by the other side, too. During the binocular training, the animal's second side had been inactive and when it was forced into use alone it was able to refer to the only memory in the brain – that of the other side. The wrong choices were not rewarded, and soon the misled half-brain made the necessary reversal of preference. At this stage the brain appeared to have retained the two opposite memories separately. The leakage between the halves had been prevented.

A similar but weaker transfer of learning was observed in the case of a simple discrimination between two colors. At about the same time, two workers at the University of Pennsylvania Medical School showed that split-brain cats could transfer a simple brightness discrimination task (but not a more difficult one, in which the brightness difference was reduced). We are certain now that either brightness differences are perceived and learned in low-level, unsplit parts of the brain, or else the split parts have lines of communication connecting them—loops which pass downwards and across at unsplit levels.

For some time there has been evidence from several studies that brightness discriminations may be made by parts of the brain outside the visual cortex of the cerebrum. In the lower vertebrates, fish for instance, the relatively small cerebrum is not necessary for visual learning. But the indications were that, at least in the more highly evolved mammalian brains, patterns involving more complex brain processes for their recognition were seen only in the cortex. However, we observed that when contradictory tasks were presented simultaneously to the two eyes, some kinds of pattern learning were *not* independent. The two half-brains were somehow still entangling at certain stages of the process of learning. There even seemed to be a hint of gradation from one kind of task to another, as though certain tasks were wholly cerebral, while others were partially dependent upon unsplit, brain-stem processes.

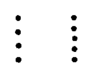
Attacking the question more directly

Lately we have been attacking this question more directly. The experimental method we use is related to the one for presenting two contradictory tasks, but there is one essential difference. Before, we were trying to detect the ability of the two halves to keep contradictory learning processes apart. We were forcing them not to work together. Now we are trying to make the two halves of the split brain join in the solution of one task.

In each trial of these experiments a different pattern is projected to each eye. A correct choice is certain only if the two visual processes are used in conjunction with one another. In one experiment we show two circles, one larger than the other. To be certain of choosing correctly, the monkey must compare the circle seen by one eye with the circle seen by the other, notice the size difference, and pick the larger. We have definite proof now that split-brain monkeys can do this task. In fact, they learn to be almost perfect and to make their choice quickly and confidently. One case has already learned to do all the following comparisons:

Pick the larger of two circles.

Pick the more tilted of two equal area black parallelograms.



Pick the one of two vertical rows of black dots with the smallest number of dots.

Pick the "screw head"-shaped figure which is rotated so that the crosssbar is more vertical.

In each of these sample pairs the pattern on the left is the correct one.

There is another experiment in which one eye sees a sample to which one of two stimuli presented to the other eye must be matched. One eye is told what to choose, the other does the choosing. Color tasks have been successful, and soon we may have data proving that patterns can be compared this way too.

continued on page 22

The second of the two kinds of complications standing in the way of balanced double learning in the split-brain is due to the fact that we have to detect the activity of the brain through the response movements of the subject. If, and only if, the two halves of the split-brain are equally in communication with the mechanisms which control the responses, then can we ask direct questions about the functions of the two halves. In an extreme case, if one half-brain had no connections to the response mechanism, how would we know what was occurring in it?

The first experiments

In the first split-brain experiments cats were used. They were required to respond by pushing a chosen door open with their noses. This response uses symmetrical muscle systems. We have every reason to believe that both halves of the brain would be used equally to control it. Later, cats were required to push aside labelled blocks or to push pedals with one or the other forepaw. The experiments failed to show any preferential linking of either paw with the learning processes of either half-brain, except when the discrimination was based upon the feel of the pedals instead of their appearance.

At first, the experiments with split-brain monkeys seemed to lead to the same conclusion. Monkeys were able to use either hand to perform tasks under visual direction by way of either eye. But then we noted that there was a tendency for the eye and hand of *opposite* sides of the body to be the best combination. I found in the double-learning experiments that whenever only one half-brain had learned, it was the one opposite to the hand which had been chosen by the subject for work. If the monkey chose to be left-handed, as many have done, then it would be the right half-brain which learned while the left half-brain remained naive.

I also noticed that when I forced the sleeping or inattentive half to work, by covering the other eye, there followed a clumsy period lasting several minutes, or even a day or two of training. Then the opposite hand was slowly brought into use. Finally, and usually before 100 trials had been presented, the new cross-combination was working smoothly and the learning of the aroused half-brain began. When there was transfer of learning, it coincided with continued use of the ipsilateral hand.

As an example, suppose that a monkey had been given contradictory stimuli to the two eyes simultaneously, and that he had learned by consistently working with the left hand. When I tested the eyes separately, I found that it was the right eye which knew its task. The left half-brain, when forced to work alone, could not direct movements at first, and they were random. The left hand continued to make the response, and soon negative choices, indicating transfer of learning, were being made. Then, at the same time as correct choices replaced the wrong ones, the right hand became active. The change to the second crossed combination of left eye with right hand seemed to be the signal for correct choices — for learning in the left half-brain.

The crossed combination in half-brain and hand is at first confusing. But neuroanatomists have long known that the so-called motor area of the left hemisphere sends fibers down to the brain stem, where they cross over to the other side of the body en route to the right hand.

Now we have plenty of evidence of the bias towards contralateral coupling. It has caused us to give up hope of obtaining freely balanced double learning unless we do something to control the bias to one side which a naturally-developed or inborn tendency to use one limb imposes. It is like trying to weigh on a balance with a varying force pulling down one side.

Fresh insight

But the complication, as is often the case, has given us some fresh insight into the problems of organization of the processes of intelligence.

With the right half-brain, a monkey may control swift and sure movements of his left hand. With right eye and left hand he seems as good as any monkey. But with the right hand he is much less skillful as long as his right eye is being used alone; that is, presumably, as long as his right half-brain is the one which is most active. Sometimes, perhaps mostly in older monkeys, the right brain-right hand combination is at first almost useless. The hand moves stiffly and seems almost to act blindly. But it is generally not nearly so bad as this. The hand is just vague and wooden. It is forgetful and makes blunders. Occasionally, it will go into a long blank period of quite unintelligent automatic responding. The monkey behaves as if he is a bit puzzled by the incompetence of the hand, but not very distressed. With the other half-brain, the left, the effect is reversed. Now the right hand is the most skillful.

When normally active in his cage or free in the laboratory, a split-brain monkey seems to be able to use both hands normally and he can coordinate them in complicated manipulation with great ease and smoothness. Furthermore, after practice in the experimental box, the superiority of crossed brain-hand combinations becomes less clear. The weaker combinations become quite quickly well-coordinated. A practiced monkey can work very well with any eye-

continued on page 24

hand combination when he is forced to switch attention from one eye to the other rapidly during the testing. These facts have taught us to regard the split-brain monkey as a well-cordinated individual, and we have been impressed with the smooth integration of movement which is possible. Taken alone, this is evidence that skillful responses are controlled by a large, diffusely organized mechanism, much of which remains intact after the surgery.

However, even with highly practiced monkeys we have occasionally seen some strange things. Once, in the course of the experiment in which a split-brain subject is required to compare the sizes of circles seen separately by the two eyes, the two hands of an old pro came up together in a praying position, to push the screens. But this did not occur very many times. Eventually, only one hand was carrying out instructions based upon information sent to both halves of the brain. We might have expected uncoordinated effects like this to be more common after split-brain surgery. But they are merely instructive exceptions to the rule.

A number of questions

There are many questions to find answers for. We want to know in which particular brain centers a hand is readied for a response. Practiced monkeys reach out and push even when the apparatus fails and no stimuli are projected. The stimuli are expected, and the hand goes out automatically, thinking it will get the necessary visual cue at the last moment. We also need to know how an already moving hand is guided to the left or right by visual perception of the cues. Does the hand ask what the eyes have seen, or does the visual process give a push to the movement control centers and so cause a definite shape of response? We do not know. We do know this: When visual attention is restricted to the side of the brain which is on the same side of the body as the preferred hand, this hand becomes clumsy. After a few poor attempts, the other hand seems to wake up and to join in. Eventually the now more skillful partner steals all the trials and the weakened hand stops gesturing and is quiet.

We think that when the split-brain monkey is ready to respond with a particular hand, his brain is set to receive guiding sensations in certain of its parts through specific nervous pathways. For example, when in the habit of working with the left hand, the monkey is more expectant with the right eye and better able to receive visual impressions through it. We have seen (as in the drawing of the split brain on page 17) how the preference for the crossed combinations of eye and hand is definitely related to the way in which the centers for vision and skilled movement are located in the cerebral cortex.

If the right eye is now covered and cannot be used for guiding the responses, we observe that the left-hand movements become weakened. We suppose that this is because the brain has a built-in mechanism for suppressing or inhibiting action patterns which do not receive expected support. Then the other hand gradually assumes the task of responding.

Shift in activity

The shift from one hand to the other is probably caused by a change of the balance of activity within the nervous system which follows automatically from the inhibition of movements of the first hand. Now, with the right eye covered, the visual expectations of our left-handed monkey may be fulfilled if he pays attention more to the left eye. If we could visualize the patterns of impulses in the central nervous system we would probably detect a shift in the activity from the right cerebral hemisphere to the left as the movements of the hands and the direction of visual attention change.

With further study we have found that split-brain monkeys can be trained to attend to one eye even when the hand on the same side of the body is the only one which is allowed to be active. It is as if the brain can develop the art of expecting in two hemispheres rather than one.

The important point of our data at this early stage is that the patterns of nervous activity in the brain of a practiced monkey may be shifted in all the possible ways for the functioning of all possible eye-hand combinations. This integration of movements with sensation occurs in spite of the reduction in communication between brain halves which our surgery imposes. This must mean that the mechanisms for controlling voluntary movement of the hands, together with the mechanisms for directing attention to specific kinds of sensory cues, are still in communication within the split brain.

Intelligence is composed of things which have been the province of philosophers until very recently – the will, consciousness, the building of concepts and judgments in the mind, and the relationship between reality and what we personally experience to be true.

In an experiment, we choose to simplify these mysteries and pay attention only to the movements of the hand of a monkey under the guidance of his eye. Then we are quickly faced with problems which we cannot readily solve. In a small way we have been attempting to identify mind with brain. I think there is no doubt that the attempt is very successful because it brings quickly to light many new things. But as for the complete picture – we are very far away from that.