

## Hemispherectomy vs Commissurotomy in the Monkey: One Hemisphere Can Be Better than Two

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Split-brain cats using a single hemisphere show impaired performance on a variety of behavioral tasks. This has been attributed to a loss of cortical mass action. To test this proposal in primates, performance on a nested match-to-sample task was compared in split-brain, hemispherectomized, and normal monkeys. As expected, split-brain monkeys using a single hemisphere performed worse than normal monkeys. In contrast, hemispherectomized monkeys were unimpaired, indicating that the deficit in split-brain animals results from interference by the idle hemisphere rather than from a loss of cortical mass. The results also suggest that the processing ability of a single hemisphere is equivalent to that of the normal brain.

### INTRODUCTION

According to Lashley's mass action theory, the critical factor in determining the ability of an animal to process information is the total availability of cortical tissue (3). Localizationist theory, on the other hand, contends that information processing ability is dependent on functional cortical areas and their interactions (2). Lashley's theory has been repeatedly reduced in scope by the identification of functional zones within the cortex which, when damaged, produce behavioral deficits out of proportion to their cortical mass. The theory, however, remains intuitively attractive and is periodically invoked when cortical damage produces an apparently nonspecific deficit.

A seemingly ideal way to differentiate between mass action and localizationist theories involves the "split-brain" preparation in which one cerebral

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hemisphere is isolated from the other using forebrain commissurotomy. In such a preparation, visual information can be restricted to a single hemisphere by cutting the optic chiasm midsagittally and covering one eye (1, 7). The information processing ability of such an isolated hemisphere would be predicted by the mass action theory to be much inferior to the normal brain because 50% of the cortical mass has been made unavailable. On the other hand, the localizationist theory would predict normal processing because cortical systems are bilaterally duplicated. Past studies using this approach seemed to support the notion of mass action when split-brain cats using one hemisphere showed reduced information processing efficiency (4, 6, 8).

We suggested earlier that the split-brain preparation is not appropriate for examining the question of cortical mass action (5). We showed that split-brain monkeys using a single hemisphere are impaired on performance and learning tasks but that such monkeys are unimpaired when using both hemispheres. We rejected mass action theory as an explanation of these findings because the theory does not provide a reasonable mechanism by which a split-brain monkey using both hemispheres should show normal processing. Two hemispheres isolated by commissurotomy cannot be added to produce a normal cortical mass without direct pathways for information sharing.

To better account for the data, we proposed that the single hemisphere in a split-brain animal cannot demonstrate normal processing only because the opposite hemisphere, which was deprived of task information, generated interference through its independent control of the animal's common attentional and motor apparatus. This interference does not exist in the both-hemisphere condition because, sharing the same information and goals, they cooperate. If our interference theory is correct, it predicts that the deficits shown by a single hemisphere will not be present following a hemispherectomy. Mass action theory, in contrast, predicts similar impairments in split-brain and hemispherectomized monkeys. The present experiment thus compares performance of hemispherectomized animals on the nested match-to-sample task with the performance of split-brain and normal monkeys reported earlier (5).

## METHODS

The details of split-brain surgery and experimental methodology have been reported earlier (5) and these will be described here only briefly.

*Subjects.* Two rhesus monkeys (*Macaca mulatta*), WT and TP, were tested in this experiment after surgery intended to remove one hemisphere down to, but not including, the thalamus. TP's left hemisphere and WT's right hemisphere were removed. TP's hemispherectomy was superimposed

on a preexisting commissurotomy. WT had previously been tested as a normal animal (5).

These animals were compared with five monkeys (including WT as a normal) whose results have already been reported and whose training and testing procedures were handled identically. Four of these monkeys (CH, MR, PR, and WT) were normal controls and four (CH, MR, PR, and SC) had the forebrain commissures and optic chiasm divided.

*Procedures of Hemispherectomy.* The monkey was placed under sodium pentobarbital anesthesia and surgery was carried out using aseptic precautions. A bone flap was made over the selected hemisphere and the entire cerebral hemisphere was removed under visual control by aspiration down to the level of the thalamus. No attempt was made to control bleeding and in both cases bleeding spontaneously declined to minimal levels by the end of the operation. The empty cavity was then packed loosely with Gelfoam sponge soaked in thrombin solution and the dura was reapproximated and sutured. The bone flap was replaced and the skin sutured. The animal was injected with procaine penicillin G immediately and again 3 days postoperatively. Both animals regained consciousness by the next day but were unable to right themselves. The side contralateral to the hemispheric removal showed clear flaccid paralysis and visual neglect. The monkeys were handled 3 days during which self-righting returned. With righting came compulsive circling toward the affected side as well as an increasing rigidity of that side. By the fourth or fifth postoperative day, self-feeding returned and was accompanied by an increased rate of circling. Within 1 month the affected side could be used for some locomotion and climbing although it remained clumsy and was never used for feeding or manipulation. Compulsive circling ended gradually and although a clear directional preference for turning remained permanently, turning could be accomplished in both directions. Visual neglect of the hemifield contralateral to the removed hemisphere remained until the animals were killed. Observations of recovery in these animals were consistent with the findings of others (9).

*Procedures of Commissurotomy.* Animals in the commissurotomy group (MR, SC, PR, and CH) had the corpus callosum, anterior commissure, and optic chiasm divided midsagittally using a dorsal approach under visual control.

All animals had a recovery period of at least 2 weeks before being reintroduced to the testing booth. No formal tests were given to the monkeys for at least 3 months after surgery.

*Histology.* In the hemispherectomized monkeys there was complete removal of the cerebral cortex in both animals except for a small area of the medial temporal lobe.

TP showed complete removal of basal ganglia and only degenerated

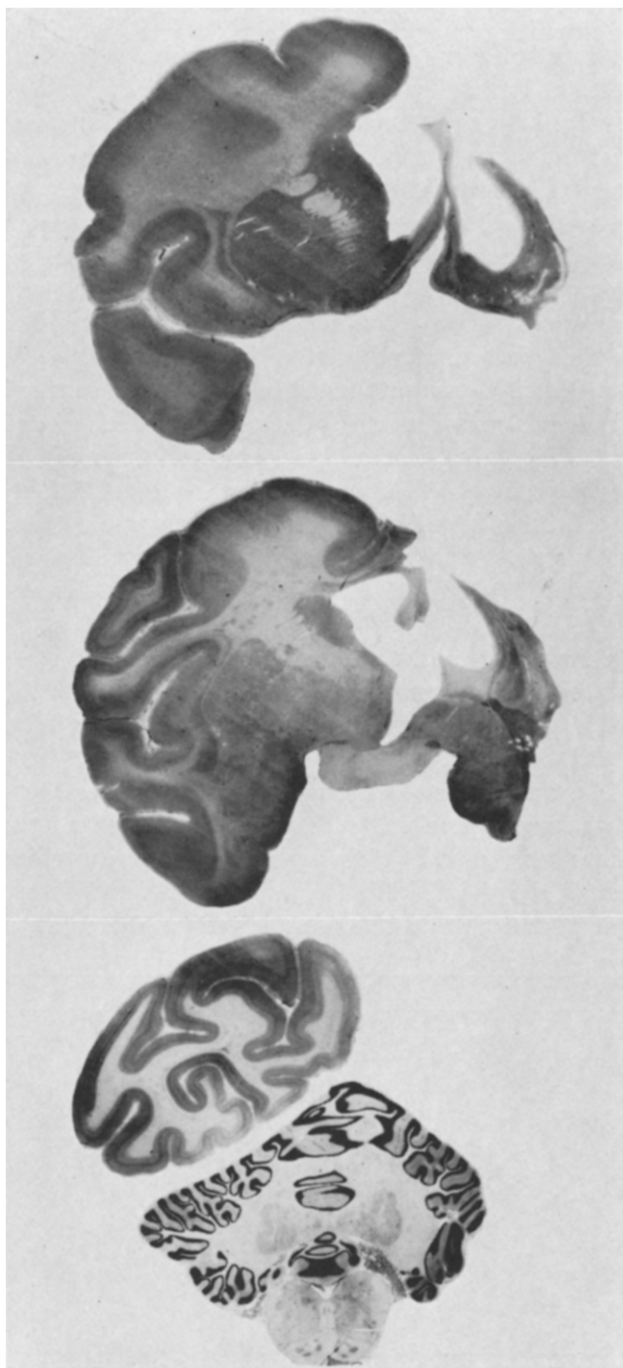


FIG. 1. Frontal section from WT at the levels of the caudate-putamen (top), optic chiasm (middle), and occipital lobe (bottom).

remnants of thalamic structures on the ablated side. Of limbic structures, only a small medial portion of amygdala and hippocampus remained intact. As expected after the earlier optic chiasm division, the intact hemisphere showed loss of cell layers 1, 4, and 6 in the lateral geniculate body.

In WT, the basal ganglia showed nearly complete removal or degeneration. The thalamus was largely intact although severe gliosis was apparent. As in TP, a small medial remnant of amygdala and hippocampus survived on the side of the hemispherectomy. Typical cross sections from the brain of WT are shown in Fig. 1.

Histological details of the split-brain monkeys were described previously (5). Briefly, the bisections were found to be as intended.

*Apparatus.* The monkeys were tested in a sound-resistant isolation booth with their heads in a restrainer that permitted restriction of vision to either eye. They sat facing a black Plexiglas panel with three stimulus-response panels onto which visual information was rear-projected. The reward for a correct response was 0.5 ml of water. All stimulus presentations, response records, and rewards were controlled by computer. Animals were deprived of water 20 h before testing and given supplementary water after testing.

*Pretesting.* Animals were trained on red-green and 8-1 match-to-sample tasks for 200 trials per day until both were at a criterion of 90% for more than 200 trials. Then they were transferred to the nested match-to-sample task.

*Testing.* The nested match-to-sample task intermixes the pattern and color match-to-sample problems such that one (color) starts before and ends after the other (pattern), thus nesting the pattern problem inside the color problem, as shown in Fig. 2. There is a 4-s intertrial interval and each trial is completed as rapidly as the monkey responds after the color sample

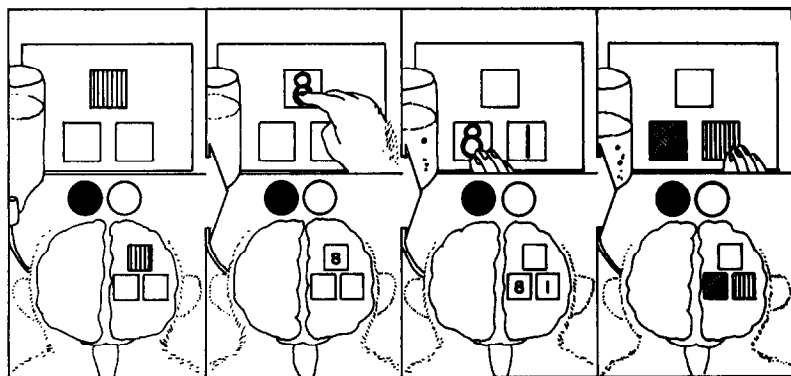


FIG. 2. Diagram illustrating the sequence for one representative trial on the nested match-to-sample task.

is introduced. Correct matches for each problem produce independent water reinforcements of 0.5 ml.

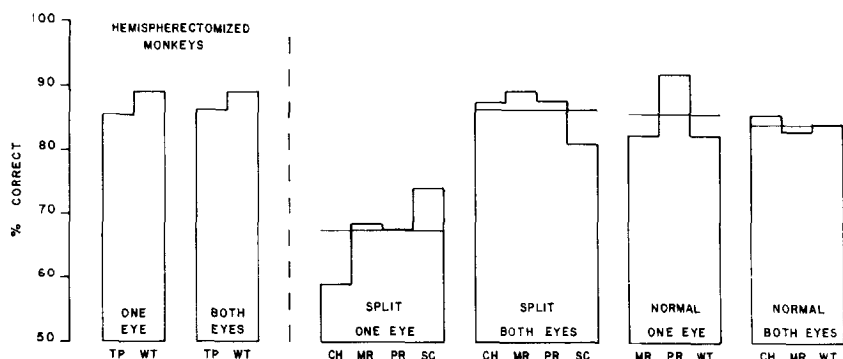
Eighty trials were given each day. The monkeys were run until performance ceased to improve during 10 consecutive days. The one change from Nakamura and Gazzaniga (5) was in the order of eye conditions. In the earlier paper, the monkeys were first tested with one eye open and then with both eyes open. Here, the hemispherectomized animals were tested with both eyes open because only one hemisphere could receive this information. Then they were tested with the eye ipsilateral to the intact hemisphere to see if the additional restriction of the visual fields and loss of depth sensitivity could have affected performance in the split-brain monkeys.

## RESULTS

The best 3-day performances for hemispherectomized animals TP and WT are graphed in comparison to the performances of the split-brain and normal animals tested on the nested match-to-sample task in Fig. 3. TP and WT are clearly in the normal range in their performance of the task under either eye condition. The *t*-test shows that the hemispherectomized monkeys under single- and both-eye conditions do significantly better than the split-brain animals with one eye open ( $t = 4.5$ ,  $df = 4$ ,  $P < 0.02$ ).

## DISCUSSION

This experiment makes it clear that hemispheric isolation accomplished by forebrain commissurotomy is different from isolation accomplished by



NESTED MATCH TO SAMPLE TASK

FIG. 3. The mean of the best 3 consecutive days' performances on the nested match-to-sample task of each monkey grouped by eye and surgical conditions. The hemispherectomized monkeys on the left are compared with previously reported split-brain and normal monkeys on the right. The straight line through each group on the right shows the mean performance of the group.

hemispherectomy. The split-brain monkeys, although showing normal bi-hemispheric performance on the nested match-to-sample task, are impaired when using one hemisphere. In marked contrast, hemispherectomized monkeys perform normally. The normal performance of the hemispherectomized monkeys under all eye conditions argues against the notion that split-brain monkeys with one eye shut are impaired due to surgical diaschisis, sensory reduction, or a loss of cortical mass.

Our results support the hypothesis that the single hemisphere isolated by commissurotomy suffers from interference by the unseeing hemisphere. In addition, the normal performance of the hemispherectomized monkeys suggests that the single hemisphere and its extracortical connections are a complete processing unit, perhaps the basic unit of the brain. The quality of neural connections rather than the quantity apparently determines the information processing ability of an organism. Localizationist theory rather than mass action theory appropriately describes the organization of information processing in the brain.

Although the emphasis has been placed on the completeness, independence, and essential normality of processing in the hemispherectomized animal, it must be stressed that this operation considerably reduces the capabilities of an organism. In the hemispherectomized animal, information can be gathered from a much smaller area of the environment and the ability to act is correspondingly reduced by hemiparesis. However, the sorts of transformations and processing that can be done on the information that is obtained appears to be normal.

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