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Visuo-Motor Integration in Split-Brain Cats

Abstract. Chiasm- and callosum-sectioned (split-brain) cats and controls were trained to displace the correct one of two different objects, using each forelimb half the time. During this discrimination training, vision was restricted to one eye, thus confining visual input and learning to a single hemisphere in the split-brain animals. It was found that either forelimb could be used about equally well by all the animals.

It has recently been shown that interocular transfer of visual discrimination learning is abolished in both cat and monkey by section of the optic chiasm and corpus callosum (*1*). Apparently, information essential to the learning and recall of visual discriminations fails to reach the contralateral hemisphere when the split-brain cat or monkey is obliged to use one eye.

The experiment described in this report was designed to determine whether there is any impairment in the ability of split-brain cats to respond discriminatively to visual stimuli with the forelimb homolateral to the hemisphere receiving the essential visual information. The major cortical motor centers for this limb lie in the hemisphere contralateral to and surgically separated from that of the visual input. Previous experiments on callosum-sectioned animals and human beings (*2*) have not revealed any deficits in bilateral motor coordination or in bilateral transfer of motor learning. However, systematic study of the motor performance of callosum-sectioned animals in which critical sensory information is restricted to one hemisphere is lacking.

Twelve cats served as the subjects (*3*). In seven of the animals, the chiasm and the callosum were sectioned in the midline, and in two, the chiasm alone was sectioned. The remaining three were normal controls. Beginning at least 4 weeks after the operation, the animals were trained to displace a wood block with a forelimb in order to obtain a piece of food covered by the block. During this preliminary training, the animals were adapted to a rubber mask, which restricted vision to one eye, and then to a forelimb restrainer, which consisted of a leather wristband and chain. This preliminary training usually required 3 to 5 weeks.

Discrimination training was begun immediately after the preliminary training was completed. Two discrimination problems were used, each involving a choice between two wood blocks, located 2 inches apart, one of which—the "correct" one—covered food. For the first problem, the blocks were painted to differ in brightness (black and white), and for the second, a different geometric pattern (circle and cross) was painted on the upper surface of each block. The animals were trained to perform the brightness problem first with one eye (eye 1), then with the other (eye 2). During this training, each animal was given 50 trials a day, one forelimb being restrained during the first 25 trials, the other during the remaining 25. The order in which the limbs were restrained was alternated from day to day. Training with a given eye was considered complete when the percentage of correct responses for either one of the forelimbs was above 90 for four consecutive days. Identical procedures were employed for the pattern problem, which was presented after completion of the brightness-discrimination training.

Table 1 shows the mean percentage of correct responses made by each of the three groups of animals on each problem with the forelimb homolateral to and the one contralateral to eye 1. The data for one of the animals in the split-brain group was excluded from the computations because the sectioning was found to be incomplete (*4*). It is evident that the difference between the means for the two forelimbs is small for each group on both problems. The data for individual subjects within each group reveal no systematic relationship between the eye used and forelimb performance, the homolateral forelimb being the superior in about as many animals as the contralateral. The largest difference between forelimbs, in terms of the percentage of correct responses, was 7, which was obtained for one of the normal animals on the brightness problem. During the course of learning, one forelimb was seldom consistently superior to the other. The results were very similar with respect to forelimb differential for eye 2.

The control animals reached criterion on the pattern problem with eye 2 in at least 82 percent fewer trials than with eye 1, whereas, in the split-brain group, the largest percentage reduction in trials to reach criterion was 19. The results suggest a similar difference between the control and the split-brain animals in degree of transfer of the brightness-discrimination learning but cannot be regarded as conclusive because several complicating factors were operating during this portion of the experiment.

These findings indicate that split-brain cats can respond appropriately with the homolateral forelimb to visual discrimination cues that are communicated only to one hemisphere. There are at least two ways to account for the results. First, there is the possibility of direct control of each limb through the homolateral cortex. Although, for example, most of the

Table 1. Mean percentage of correct responses with the forelimb homolateral to and the one contralateral to eye 1 during brightness- and pattern-discrimination training.

Brightness problem		Pattern problem	
Homolateral forelimb	Contralateral forelimb	Homolateral forelimb	Contralateral forelimb
Normal animals			
76	77	72	75
Chiasm-section animals			
78	75	70	72
Split-brain animals			
74	74	73	69

corticospinal fibers innervating a given limb originate in the contralateral cortex, there is evidence that a small portion originate in the homolateral (*5*). Another possibility is that the animal has a subcortical integrating system, somewhat similar to Penfield's hypothetical "centrencephalic system" (*6*), which receives sensory information from both sides of the body, and in which impulses controlling all the limbs originate. These findings also confirm the loss of interhemispheric transfer of visual pattern-discrimination learning in split-brain cats under a new type of training condition. The question of transfer of brightness-discrimination learning in these cats, which has not been studied before, requires further research.

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3. This research was supported by NSF grant No. G-3880 to R. W. Sperry, and by the Frank P. Hixon Fund of California Institute of Technology.
4. At the end of the experiment, the brains of all the operated animals were fixed by perfusion with 10 percent formalin. In most cases macroscopic examination was sufficient to establish the extent of the sectioning. The posterior quarter of the callosum and, roughly, the posterior eighth of the chiasm were found to be intact in the animal eliminated from the split-brain group. This animal had shown a high degree of transfer on both problems.
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