

# Reversal Behavior in Split-Brain Monkeys

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JOHNSON, J. D. AND M. S. GAZZANIGA. *Reversal behavior in split-brain monkeys*. *PHYSIOL. BEHAV.* 6 (6) 707-709, 1971.—Using split-brain monkeys, reversal behavior was observed under two conditions. In the first both hemispheres viewed the discrimination cues. Previous to this one hemisphere had been taught to respond to one cue and the other hemisphere had learned the opposite response. The task was reversed each time after responding to one cue reached criterion. In the second reversal condition, each hemisphere was individually presented the reversal of the task it had initially learned. An analysis of the results indicates that as a function of reinforcement, the response probability of pre-established habits can change without a corresponding change in the strength of these habits.

Split-brain Reinforcement	Reversal learning	Competing responses	Habit strength	Response probability
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THE SPLIT-BRAIN technique allows for the analysis of the dynamics of cortical-subcortical relations. By presenting an experience to one hemisphere, one can get some measure of the general sub-cortical component of the experience by noting its effect on the opposite hemisphere [2]. Another approach has been to lesion unilaterally a subcortical structure in a split-brain to determine the functional relation of this structure with the cortex and the opposite hemisphere. Webster and Voneida [7], for example, lesioned the dorsal hippocampus on one side of a split-brain cat and found that the lesioned hemisphere could not learn a reversal task, while the other hemisphere still could.

The present experiment extended the use of the split-brain technique in the study of cortical-subcortical processes. The probability of responding to one of two visual patterns was seen to change. It was asked whether this reflected simply a cortical change (habit reversal) or if it indicated an alteration of cortical-subcortical (change in hemisphere control) relation. Initially the hemispheres were separately taught the opposite responses in a simple discrimination task. Then with both hemispheres open, the animal was made to reverse its responding from one cue to the other. The results were analysed to determine whether this reversal behavior reflected a change in the habits that were initially learned or a change in performance control between the hemispheres.

## METHOD

Three monkeys (*Macaca mulatta*) were used in this study. All had undergone midline section of the corpus callosum, anterior and hippocampal commissures, and optic chiasm. The results of a post-mortem examination of the brains of two monkeys (BT and BH) appear in an earlier report [3]. The third monkey is still being used in experiments. The

apparatus and general procedure for presenting trials used in the present experiment is also described in this earlier report. But rather than using polarizing filters, the present study controlled presentation of the visual information to each hemisphere by covering either eyehole with an opaque shield. White horizontal or vertical bars served as discriminative stimuli.

Initially, each hemisphere was allowed four hundred trials to learn the visual discrimination. First one hemisphere learned and subsequently the other was taught the reverse discrimination. All animals reached criterion of 20 successive correct trials within 200 trials. At least half of the training trials were spent in overlearning. Subsequently both eyes were exposed to the cues and responding to the horizontal bars was reinforced. When ten correct responses were made in a row the task was reversed so that only responding to the vertical bars was reinforced. When the criterion of 10 out of 10 correct was met the task was again reversed and run to criterion. At this point each hemisphere was tested individually for ten trials on the task which it had initially learned. Each hemisphere alone was then taught the reversal of the task that it had first learned. This training was continued until each hemisphere had reached the criterion of 10 out of ten correct.

## RESULTS

Each animal performed two reversals under two conditions (see Table 1). In the first condition both eyes were open and after 10 successive correct responses had been made to the reinforced cue a reversal was initiated. Trials were run until this criterion was again reached and then a second reversal was run to the same criterion. An average of 93.3 trials were run before criterion was met in the first reversal, and a hundred trials were needed to reach criterion on the second reversal.

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TABLE 1  
NUMBER OF TRIALS TO CRITERION

	Condition I		Condition II	
	Both Eyes Open		Eyes Tested Individually	
	S+ =	S+ = ≡	S+ =	S+ = ≡
BT	70.0	110.0	260.0	180.0
BH	110.0	100.0	130.0	380.0
CP	100.0	90.0	310.0	410.0
Mean	93.3	100.0	233.3	323.3

The table indicates the results of the performance of reversals under two conditions. The values represent the number of trials until 10 successive correct responses were made plus the trials completing the block of 10 during which this criterion was met.

Immediately following the reversal under this first condition, each hemisphere was presented with ten trials of the task that it had initially learned. On these sample trials, the hemispheres that had learned to respond to the vertical bars made an average of eight correct responses (BT = 7, BH = 9, CP = 8). The opposite hemispheres responding to the horizontal bars made an average of 9.3 correct responses (BT = 10, BH = 8, CP = 10).

In the second condition each eye-hemisphere was individually taught the reversal of the task that it had learned in the initial training. An average of 233.3 for one hemisphere and 323.3 trials for the other hemisphere were needed to reach criterion under this condition.

#### DISCUSSION

The results show that reversal behavior was considerably more efficient when both hemispheres were available for the task, each having learned to respond to the opposite cue, than when each hemisphere performed individually. This would suggest that differing processes were involved in the reversal behavior of the first and second conditions. In the second condition in which each hemisphere performed alone reversal behavior was presumably a function of relearning. The performance on trials presented exclusively to each hemisphere following the first condition indicated that each hemisphere had maintained to a degree the habit that it had initially learned. While there may have been some relearning within each hemisphere during the first condition, these results point to the conclusion that reversal occurred in this condition when one hemisphere yielded its control over responding to the opposite hemisphere. Rather than being a relearning process the reversal behavior in the first condition reflected a change in the probability that one or the other hemisphere would control responses.

The results show that a change in the probability that one hemisphere will control responding does not necessarily occur with the weakening or strengthening of the habits stored in this hemisphere. These results distinguish two functions that have been attributed to reinforcement. The traditional notion was that reinforcement strengthened certain S-R bonds, i.e. habits [6]. More recently, reinforcement has been defined as that event which increases the probability of a response [5]. In the present study reinforcement changed the probability of a response without greatly affecting habit strength. Whereas traditionally it was thought that learning occurred with the development of associations across the cortex and that the effect of reinforcement was to strengthen these connections, the present study provides the basis for a model of learning involving cortical-subcortical associations. Since responding appeared to switch from one hemisphere to the other according to which habit was reinforced, it is suggested that in some cases reinforcement shapes behavior not by developing cortical associations, but by altering the associations of pre-existing cortical patterns with subcortical motivating structures.

These results also contribute to the view that competing responses can suppress a behavior without destroying the habit underlying it. In the first reversal condition, a habit in one hemisphere maintained its strength though it was suppressed when the competing responses of the opposite hemisphere were reinforced. This is in line with a recent observation [4] in which extinction rates in an intact animal were enhanced when competing responses were reinforced. The animal returned to the extinguished behavior when this reinforcement was removed.

The conclusion that control over responding can shift from one hemisphere to the other to produce reversal behavior suggests that cerebral dominance in monkeys is quite flexible and is subject to the effects of reinforcement. It suggests that the probability that a hemisphere will control a response is directly related to its history of obtaining reinforcers. The hemisphere which is most successful in earning reinforcement comes to dominate. It would seem from this that what appears to be cerebral dominance in monkeys can be analyzed in terms of learning principles.

Although the reversal behavior occurred under somewhat artificial conditions in the first condition it may give some indication what occurs in the brain after several reversals. Bitterman [1] observed that monkeys and rats became increasingly more efficient in making reversals, whereas fish made about the same number of errors in reaching criterion in each succeeding reversal. This species difference seems to be due to a development of neocortex in rats and monkeys and its absence in fish. In the present study it was found that reversal behavior could be made more efficient when the opposite tasks were stored separately, i.e. in opposite hemispheres. This efficiency was attained by splitting the brain, and teaching each hemisphere separately. Considering this, it may be that the efficiency which Bitterman observed following several reversals occurred when the animals in some natural way began storing the opposite tasks in separate neural systems.

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